Artificial neural networks reconstruct missing perikymata in worn teeth

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1 Abstract

Dental evolutionary studies in hominins are key to understanding how our ancestors and close fossil relatives grew from the early stages of embryogenesis into adults. In a sense, teeth are like an airplane's 'black box' as they record important variables for assessing developmental timing, enabling comparisons within and between populations, species, and genera. The ability to discern this type of nuanced information is embedded in the nature of how tooth enamel and dentin form: incrementally and over years. This incremental growth leaves chronological indicators in the histological structure of enamel, visible on the crown surface as perikymata. These structures are used in the process of reconstructing the rate and timing of tooth formation. Unfortunately, the developmentally earliest growth lines in lateral enamel are quickly lost to wear once the tooth crown erupts.

We developed a method to reconstruct these earliest, missing perilymata from worn teeth through knowledge of the later-developed, visible perikymata for all tooth types (incisors, canines, premolars, and molars) using a modern human dataset. Building on our previous

research using polynomial regressions, here we describe an artificial neural networks (ANN) method. This new ANN method mostly predicts within 2 counts the number of perikymata present in each of the first three deciles of the crown height for all tooth types.

Our ANN method for estimating perikymata lost through wear has two immediate benefits: more accurate values can be produced and worn teeth can be included in dental research. This tool is available on the open-source platform R within the package `teethR` released under GPL v3.0 license, enabling other researchers the opportunity to expand their datasets for studies of periodicity in histological growth, dental development, and evolution.

Keywords: neural network, tooth, enamel, perikymata, reconstruction

2 Introduction

Human teeth are an invaluable source of information, not only from a forensic point of view (Sweet et al., 1996; Wang et al., 2010; Higgins & Austin, 2013; García-Campos et al., 2016), but also from an evolutionary perspective (e.g., Dean & Smith, 2009). Ancient human behavior, diet, pathology and development can be inferred from internal enamel structure and composition (Guatelli-Steinberg, 2016; Smith, 2018; Ungar, 2007, 2010, 2018). Furthermore, the microstructure of tooth tissues has also been used, for example, to track environmental changes by analyzing oxygen isotope composition during primate lifespans in the Cenozoic (Green et al., 2022), and to analyze seasonal calving in prehistoric cattle by studying stable oxygen isotopes (Balasse et al., 2021).

When these growth markers are visible as horizontal lines on the tooth crown surface, they are referred to as perikymata, and have formed the basis of a rich field of dental developmental research (Hillson & Bond, 1997; Lacruz et al., 2008; Mahoney, 2008; McGrath et al., 2018; Newell et al, 2006; Skinner, 2014). Because the outer surface of enamel is worn during use, unfortunately, this biomarker is often quickly lost. Consequently, research is typically restricted to unworn or only lightly worn crowns, and many investigators must base their conclusions on relatively small sample sizes (Guatelli-Steinberg et al., 2005, 2007, 2018; Ramírez Rozzi & Bermúdez de Castro, 2004). Here, we address this limitation by developing a method that enables worn teeth to be included in studies of perikymata.

Perikymata result from the nature of tooth development. Teeth are composed of three hard tissues: enamel, dentin and cementum (FitzGerald, 1995). Enamel and dentin form through rhythmic cellular secretion, producing a permanent record of mineralized growth layers (Smith, 2008). There are two types of layers in these two tissues: short-period (daily) and long-period (~weekly) increments. When these long-period lines are visible in the enamel surface, they are referred to as perikymata (Fig. 1). When a tooth first erupts into the oral cavity, enamel is fully formed and at its fullest crown height. The crown is divided into two continuous regions depending on whether long-period incremental lines within the enamel reach the surface (known as lateral enamel) or not (known as cuspal enamel) (FitzGerald & Rose, 2008). Crown formation time can be calculated by summing cuspal enamel formation time with lateral enamel formation time (Smith, 2008).

The time and rate of lateral enamel formation is estimated by counting the number of perikymata visible on the tooth surface. However, another approach to get information of these growth markers is by making histological sections. This approach was not used in this study due to it requires partially destroying the samples. Given that the tooth starts forming from the cusp tip down to the cervix, it has been proposed to divide the crown height into ten equal proportions (e.g. Reid & Dean, 2006; Guatelli-Steinberg et al., 2007, 2005). These segments are known as deciles, and are used to scale for differences in crown height (Fig. 1). Perikymata can be counted in each segment or decile, so that an estimation of how the number varies along the crown height can be evaluated (Cares Henriquez & Oxenham, 2019; Guatelli-Steinberg et al., 2018; Ramírez Rozzi & Bermúdez de Castro, 2004). The numbering of deciles goes from decile 1 (DC1, located in the cusp tip or incisal

edge) to decile 10 (DC10, located in the last part of the enamel, approaching the cemento-enamel junction) (see Fig. 1).

The assessment of developmental timing is based on counts of the incremental growth layers observed within enamel and dentin, providing a relatively accurate method to estimate chronological age (Bromage & Dean, 1985; Dean & Smith, 2009; O'Hara et al., 2023; Reid et al., 1998; Smith et al., 2010). The accuracy of this estimated chronological age of an individual along with the approximate initiation age for the tooth and the variation in the timing of when and how these tissues grew over time are crucial for discerning the paleobiology of living and extinct organisms, including humans and our ancestors. Not only overall crown formation times can be assessed, but also enamel growth trajectories, although perikymata from deciles 3 to 10 were also relevant to detect taxonomic differences (Dean & Reid, 2001; Guatelli-Steinberg et al., 2018). In the paper published by Guatelli-Steinberg et al. (2018), they excluded deciles 1 and 2 because many perikymata were missing due to wear. The first attempt to reconstruct missing perikymata in a particular decile was based on the adjacent perikymata spacings inside that decile (Dean & Reid, 2001). However, these authors excluded a tooth to be used in their analysis if more than 10% of the crown height was affected by wear. Some authors excluded teeth if more than 20% of the crown height was missing (Guatelli-Steinberg, et al. 2008). Regarding perikymata estimation in any decile, other methods were developed to estimate missing perikymata, as the standard perikymata profile (O'Hara, 2017).

Many teeth in the fossil record are naturally worn due to masticatory forces during the life of the individual, and the part of the crown preserving the perikymata lines on the surface of the crown are lost. One key question before predicting perikymata in the first deciles is to know which is the original crown height of the tooth. This situation was already addressed, as we previously employed polynomial regressions to reconstruct the missing crown heights by predicting the cuspal area morphology (Modesto-Mata et al., 2017, 2020). However, there are more methods to reconstruct crown heights with various results and validations (Saunders et al. 2007; Smith et al. 2012; O'Hara & Guatelli-Steinberg, 2022). In Modesto-Mata's cited papers, the percentage of difference between real and estimated crown heights are below 4% in premolars, 3% in molars and below 1% in the remaining tooth types. The impact of these estimated crown heights is minimal when predicting perikymata in the missing enamel, as these percentages represent, on average, only one third in one decile. Here, we present a new method that employs artificial neural networks to accurately predict the perikymata counts in the first deciles of worn teeth.

Artificial neural networks (ANN) define information processing models that are inspired by the nervous system present in living beings. As in biological nervous systems, which have a huge number of interconnected cells called neurons, ANNs are formed by interconnected nodes (Ciaburro & Venkateswaran, 2017; Hastie et al., 2013; Rai, 2019). Neural networks form a complex adaptive system, which means that they can change their structure by adjusting the weights of inputs to solve a wide-range of different problems. The first such mathematical model – known as the McCulloch-Pitts model – described a simple neuron as taking and processing inputs, and returning an output (McCulloch & Pitts, 1943). In the learning process, the network can adjust the weights across an expanded set of these neurons linked together.

There are two main types of ANNs (Ciaburro & Venkateswaran, 2017). The first is feed-forward ANN, in which the analysis is not recursive and means neurons of one layer only connect to neurons of the next layer, so that the signal travels in one direction. The second type of ANN is called feed-backward (also known as recurrent neural network, RNN). In RNN, neurons can travel in both directions, from one layer to the next and vice versa. The intrinsic unidirectional way of transferring information in the feed-forward ANN is strongly limiting. Unlike feed-forward ANNs, RNNs can use internal memory to improve predictions as the information travels back and forth, therefore optimizing the results (Salem, 2022). Based on the advantages of RNNs, we decided to train ANNs models based on feed-backward ANNs. As RNNs are ANNs, we are using the acronym ANN in the manuscript in order to keep consistency.

The application of deep learning techniques and ANNs in dentistry is relatively new (Chen et al., 2019; Hwang et al., 2019; Park & Park, 2018). This technique has been primarily applied to identify caries in the teeth (Devito et al, 2008; Javed et al., 2020; Kositbowornchai et al., 2006; Prados-Privado et al., 2020). The application of these techniques in dental evolutionary anthropology is rare and, to date, mostly focused on taxonomic attribution (Coppa et al., 2007; Monson et al., 2018; Yi et al., 2021). Our ANN models presented here represent, to our knowledge, the first application to dental tissue growth studies.

Our aim in this study was to build ANNs that can predict the number of missing perikymata in the first three deciles of worn teeth. We built the model using perikymata counts from entirely unworn teeth from a geographically diverse sample of *Homo sapiens*. To be sure that teeth were entirely unworn, we checked that they were not displaying any wear facet or diet marks in the cuspal area. This accurate ANN can be used to reconstruct missing perikymata when teeth have lost up to 30% of the enamel in the crown height during life (i.e., through occlusal wear) or to predict perikymata counts when crown height is preserved but perikymata are not seen (i.e., due to taphonomic mild labial wear). In either case, it is a requirement to know/estimate crown heights. In order to facilitate the use of these trained ANNs, we developed a package in R named `teethR` to predict perikymata counts in an user-friendly way.

3 Material

To estimate missing perikymata, we employed 164 unworn modern human teeth from a diverse range of geographic regions (Table 1). All samples belong to the species *H. sapiens*, either coming from archaeological contexts or from recent modern human collections. The archaeological remains were discovered in different Spanish caves (Galls Carboners, Guineu, Maltravieso, Mirador and Santa Ana caves), whereas the modern human collections come from the University College London (the Sudanese sample) and from the Alicante University (the African, American and Asian samples).

Maltravieso and Santa Ana caves are located in Cáceres (Extremadura, Spain). In Maltravieso cave, human remains were part of a collective grave and they were ascribed to belong to the half of the second millennium BC (Callejo Serrano, 1958; Cerrillo Cuenca &

González Cordero, 2007; Muñoz & Canals, 2008). Santa Ana cave presents several stratigraphical units that correspond to the Pleistocene (Carbonell et al., 2005); however, sediments from historical ages have also been found. Galls Carboners cave is located in the Prades Mountains (Tarragona, Spain) and it contains a collective burial dated in 3,310 ± 30BP (Cal BP 3,620–3,460). Guineu cave is located in Font-Rubí (Barcelona, Spain) and the teeth studied come from the 4th and 3rd millineum BC, when the cave was used as a burial place (Morales et al., 2013). El Mirador cave is located in the Sierra de Atapuerca (Burgos, Spain). The human assemblage is a collective burial of the Chalcolithic period (4.760–4.200 years cal. BP) and there are a minimum number of 22 individuals of different sexes and ages (Gómez-Sánchez et al., 2014). The current Sudanese population comes from a sample from the North of Sudan (Jaali, Mahasi, Shaigi, Bedairi, Halfawi and Dongalawi groups) (Elamin & Liversidge, 2013). The collection from Alicante University is composed by high-quality casts of modern human teeth located at different institutions from different modern human populations worldwide distributed.

In order to count the perikymata, we use the environmental scanning electron microscope FEI Quanta 600, housed at the National Center for Research on Human Evolution (CENIEH, Burgos, Spain) with the following settings: low vaccuum (60–80 Pa), voltage 15-16 kV, spot of 3.5–3.6 and intensity of 60 μA. The teeth were positioned obliquely to the electron beam in order to maximize the visibility of their crown heights and perikymata. Several images at maximum resolution (4096 × 3773 px) were collected at 50x–70x on their buccal aspects (lingual aspects in upper molars), attempting to capture as much dental surface as possible in order to be able to resolve the count of continuous perikymata when some part of the surface is worn or they are not clearly visible for any reason. In order to increase the ease of counting the incremental lines, a highpass filter was used in all the pictures taken with the ESEM using software Darktable 2.0.1 and increasing the contrast boost up to 100%.

We divided the data in four groups taking into account the tooth type and regardless their position (upper and lower teeth were combined): 26 incisors, 36 canines, 68 premolars and 34 molars (Table 1). Clustering by tooth type rather than tooth position provided sample sizes large enough to run the statistical models and trainings.

4 Methods

We focus our analysis on predicting perikymata over the first three deciles (DC1, DC2 and DC3), applying ANNs with three different models. The first model uses `DC1` as dependent variable. Only the first decile, or part of it, is missing, so that a prediction of the missing perikymata lines is required in this decil. The second model uses `DC1` and `DC2` as dependent variables. The first decile is missing, and the second decile might be completely or partially missing, so that a prediction of the missing perikymata lines on both deciles are required. The third model uses `DC1`, `DC2` and `DC3` as dependent variables. The first and second deciles are missing, and the third decile might be completely or partially missing, so that a prediction of the missing perikymata lines on those three deciles are required. With “part of the decile missing” we mean that if the decile with wear is incomplete (it can happen in our models either in the first, second or third deciles, respectively), we can predict the

perikymata number in the entire segment and then compensate the perikymata prediction and the underrepresented perikymata count in that decile.

All missing deciles were calculated separately. In this way, when three deciles are missing in a particular tooth, we are training an ANN to predict perikymata in `DC1` based on perikymata from `DC4` to `DC10`, and identically for `DC2` and `DC3`. In total, 24 ANNs were trained to predict the number of perikymata in each decile depending on the number of missing deciles present in the tooth.

We employed R language (R Core Team, 2022) to code the algorithms and to train the ANNs. To run the neural networks, we used the package `neuralnet` (Fritsch et al., 2019). This package allows training artificial neural networks using backpropagation. All the variables have been transformed by using the scaling and centering method. This transformation is achieved by using the `method = c("scale", "center")` within the function `preProcess()` of the `caret` package in R. The `method = "center"` subtracts the mean of the predictor's data from the predictor values while `method = "scale"` divides by the standard deviation.

As there might be a relatively large number of combinations when selecting the number of hidden layers and neurons per layer, a first step was to select the combination of neurons and hidden layers that presented the lowest value of root mean square error (RMSE) per tooth type and formula. In this regard, we iteratively calculated the RMSE taking into account the next values: 3 hidden layers, each of them with various neuron combinations (from 1 to 5 neurons). The resulting combination with the lowest RMSE value per tooth type in each formula was employed to calculate the predictions of missing perikymata.

To set all the possible combinations of neurons in the three hidden layers, the `expand.grid()` function was used. In this function we define the number of possible neurons in each layer. We name it as `tune.grid.neuralnet` (Code S1).

The parameters of every ANN are: the threshold for the partial derivatives of the error function as stopping criteria is 0.01; the maximum steps for the training of the ANN is 100000; the learning rate is 0.01 and the activation function is *softplus*. The *softplus function* is a smooth approximation of the *rectified linear unit function* (ReLU) (Dugas et al., 2001). The use of any of these functions results in a numerical value greater than 0, which is precisely the situation we are dealing with the perikymata counts. Occasionally, the *softplus function* is renamed as *SmoothReLU*. The `softplus` function is calculated as follows: `function(x) log(1+exp(x))`.

To ensure that our results are free of any bias due to the sample selection, and to check the robustness of our models, 10-fold cross validation has been was applied. We repeated the 10-fold cross-validation 5 times in what is known as repeated cross-validation. In the cross-validation, a 0.8 proportion was employed for the train/test split. This full configuration can be set up by using the function `train()` of the `caret` package (Kuhn, 2022).

In order to evaluate the predictions of the missing perikymata models, three performance measures were employed: the mean of percentage difference between the estimated and

real values, the root mean square error (RMSE) and R-squared. The last two parameters were calculated by using the function `resamples()` of the `caret` package.

A function to run the neural network using repeated cross-validation was created (`nn_pk`). The parameters of the repeated cross validation are defined within the function `trainControl()` of the `trControl` argument. The `nn_pk` function is composed by three arguments (Code S2): `formula` (formula of the model), `train` (name of the train subsample) and `pre_mdl` (name of the scaling method). The argument `formula` can admit three models: model DC1 (`formula(DC1 ~ DC2 + DC3 + DC4 + DC5 + DC6 + DC7 + DC8 + DC9 + DC10)`, where the dependent variable is `DC1`), model DC12 (`formula(DC1 ~ DC3 + DC4 + DC5 + DC6 + DC7 + DC8 + DC9 + DC10)`, where the dependent variables can be `DC1` or `DC2`) and model DC123 (`formula(DC1 ~ DC4 + DC5 + DC6 + DC7 + DC8 + DC9 + DC10)`, where the dependent variables can be `DC1`, `DC2` or `DC3`).

To estimate the missing number of perikymata in the first, first-second, first-second-third deciles (Model DC1, Model DC12 and Model DC123, respectively) per tooth type (incisors, canines, premolars and molars), we built 24 ANN predictive models to accommodate all these combinations. The function `nn_pk()` is run for every tooth type considering Model DC1, Model DC12 and Model DC123 as dependent variables. To understand the method and the different models, combination of neurons and calculated RMSEs, see Fig. 2.

The acquisition of the best-fit model in each of the 24 trainings requires a sequential process (Fig. 2). First, the algorithm starts from the simplest combination of neurons (1-1-1, which means one neuron in the first, second and third hidden layers respectively). Second, it automatically and randomly takes 80% of the data to train the ANN and test it with the remaining 20%. Third, a value of RMSE is obtained when the algorithm compares real versus predicted perikymata counts. This random selection of the 80% of the data and ulterior test with the remaining 20% is done 50 times, as the algorithm is configured to run a 5-repeated 10-fold cross validation. Therefore, this cross validation offers 50 values of RMSE. The final RMSE for the combination of neurons 1-1-1 is the average of the 50 RMSE. This full process is repeated for each of the 125 possible combinations of neurons for this training (i.e. 1-1-2, 1-1-3… 5-5-5), which means that the algorithm calculates 125 averaged RMSE coming from 6250 individual train/test split RMSEs. The combination of neurons with the lowest averaged RMSE from the 125 available is the one used to build the final ANN.

The above-mentioned steps are repeated for each of the 24 models (Fig. 2), which means that in total the algorithm calculated 3000 averaged RMSE coming from 150000 individual train/test split RMSEs and ANN trainings. In the end, we will obtain 24 combinations of neurons with the lowest averaged RMSE, each of them to resolve the perikymata prediction in one specific decile and tooth type.

5 Results

The variability of perikymata number in the different deciles per tooth type can be seen in Fig. 3. In all tooth types, the density of perikymata increases from DC1 to DC10. These data

provided the training and cross-validation data used in the development of the ANN to reconstruct missing perikymata described below. The results are presented in three parts: training the ANN and evaluating performance, assessing its accuracy by comparing the actual (real) number of perikymata to the predicted number, and last, presentation of the R package `teethR`.

5.1 ANN training and performance

The best final combination of neurons in each of the three hidden layers in the twenty four ANNs was obtained after running a 5-repeated 10-fold cross validation with a 0.8 train/test split in each of the 24 trainings. The final combination of neurons that predicts most accurately the perikymata number is the one that has the lowest RMSE value. The combination of neurons and hidden layers with the lowest RMSE for each tooth type according to each of the deciles used as dependent variables (Model DC1, Model DC12, Model DC123) is displayed in Table 2. The plots of the neural networks with the weights are in Fig. S1, Fig. S2 and Fig. S3. The combination of neurons that is more repeated in the 24 ANN models is 1-1-1 (one neuron in each layer, found in eight models), followed by 1-1-2 (in three models); all the other combinations are unique. This is expected as all the models were independently run, and more importantly, this fact emphasizes and reinforces the followed method on identifying which is the optimal combination of neurons in each ANN training. In layer 1, only 1, 3 or 5 neurons can be identified in any of the 24 models; in layer 2 and 3, all of the possibilities from 1 to 5 neurons can be found in different ANN models.

The plots representing the variation of RMSE with all the possible combinations of neurons in the three hidden layers considering every tooth type according to each of the deciles used as dependent variables (Model DC1, Model DC12, Model DC123) are displayed in Fig. S4, Fig. S5 and Fig. S6, respectively. All the plots in these figures represent the 3000 averaged RMSEs obtained for all the models (24 ANNs), tooth types (4 types) and combinations of neurons (125 combinations, from 1-1-1 to 5-5-5).

The performance measurements used were the percentage of difference between the real and predicted perikymata counts, the RMSE and R-squared values. RMSE and R-squared performance measures are in Table 3 for 'Model DC1, Table 4 for Model DC12 and Table 5 for Model DC123. The lowest RMSE mean is 0.52 in canines when ANN predicts DC3 based on DC4-DC10 values, whereas the highest value is 1.21 in molars when ANN predicts DC3 based on the same decile interval as in the canines.

5.2 Real vs. predicted perikymata

The real vs. predicted perikymata counts in the different tooth types and models are presented in Fig. 4, Fig. 5 and Fig. 6. These results show a high correlation between the predicted and actual perikymata counts, although the correlation varies depending on the tooth type. R squared values in Table 3, Table 4 and Table 5 show that incisors and canines are the tooth types with more correlation (with R squared measures generally beyond 0.70), whereas premolars have the lowest correlation.

The number of real perikymata counts compared to the predicted values obtained by running ANNs can be seen in Table S1, Table S2 and Table S3, for models DC1, DC12, DC123, respectively. Mean percentages of error and absolute mean percentages or error per tooth type and decile of the predicted values versus original values are displayed in Table S4 for Model DC1, Model DC12 and Model DC123. Mean percentages of error per decile and across tooth types range from 0.19% (in Incisor-DC2, Model DC12) to 6.03% (in Molar-DC1, Model DC12), whereas the absolute mean errors range from 2.41% (in Molar-DC3, Model DC123) to 18.12% (in Molar-DC1, Model DC123). In Table 6 the overall mean difference values (between real and predicted perikymata counts) per model are displayed, combining tooth types and deciles. These percentages of mean differences are in all cases situated between 2.3% and 2.7%. Concerning the absolute mean percentages of difference, the values range from 10.59% to 11.92%. This can also be observed in Fig. S7, where we present the density curves taking into consideration percentages of difference in all the models, discriminating by tooth type and decil. These results demonstrate that no matter which tooth or deciles ANNs are predicting, the error is very similar.

Remarkably, we quantified total perikymata error and total absolute error of the perikymata predictions in the three deciles in the 164 teeth used in the study (Table S5). As can be observed, there's no skewing toward over or under estimating total perikymata and, second of all, 120/164 teeth (73.17%) and 141/164 teeth (85.98%) had perikymata estimates that were accurate within 3 perikymata in absolute and total values when the three deciles are taken together, respectively.A useful way to show how well the ANN's models predict the perikymata in different tooth types and deciles is by assessing the difference between the real values and the predicted values in perikymata count. This difference is presented in Fig. 7, Fig. 8 and Fig. 9, for Model DC1, Model DC12 and Model DC123, respectively. As it is expected, the vast majority of the ANN's models predict accurately the number of perikymata, or with a difference of just 1 perikymata, or less frequently 2 perikymata between the real and the predicted values. It is rare to have more than 2 perikymata of difference, although this happens more often in the `DC1+DC2+DC3` model (Fig. 9).

5.3 Using ANNs with other teeth

After the validation of the ANNs, next step is to apply them to other data sets and studies. In order to enable anyone to use the ANNs obtained in this manuscript, we have created a package in R with the name `teethR`. We developed a function in this package, `predict_perikymata()`, to facilitate the prediction of perikymata in the first three deciles of the teeth. `teethR` is publicly available in GitHub and it has been released under the General Public License v3.0. To learn how to install and use it in detail, with user case examples, we refer the reader to the *Supplementary: teethR package*.

6 Discussion

The application of deep learning techniques and artificial neural networks in dentistry is relatively new (Chen et al., 2019; Hwang et al., 2019; Park & Park, 2018). This technique has been primarily applied to identify caries in the teeth (Devito et al, 2008; Javed et al.,

2020; Kositbowornchai et al., 2006; Prados-Privado et al., 2020). The application of these techniques in dental evolutionary anthropology is rare and, to date, mostly focused on taxonomic attribution (Coppa et al., 2007; Monson et al., 2018; Yi et al., 2021). Our ANN models presented here represent, to our knowledge, the first application to dental tissue growth studies.

Our training datasets show that there is a considerable variation in the perikymata counts of human teeth, and that the covariance structure of how perikymata form over the course of an individual's dental development means that early development can be predicted from later development using an ANN model. In fact, the first 3 deciles might be easy to predict because there is variation, and that the genetic, developmental, and non-genetic influences on perikymata formation makes it possible to predict deciles 1-3 from the variation in deciles 4-10.

In order to test the performance of artificial neural networks when predicting number of perikymata in the first deciles of the crown height, we used the RMSE parameter to obtain the best combination of neurons. Overall, neural networks offered highly accurate estimates of missing perikymata. In vast majority of ANNs, the prediction of the perikymata counts in the first three deciles were perfect or with only 1 or 2 perikymata difference. Bearing in mind that the min-max perikyma counts in the three deciles of the current modern human sample range from 4 to 16 in incisors, from 7 to 21 in canines, from 4 to 13 in premolars, and from 3 to 15 in molars, the predicted perikymata counts is remarkably accurate.

The periodicity of perikymata (or striae of Retzius) remains constant in one individual throughout tooth development (FitzGerald, 1995), although this assumption has recently been challenged (McFarlane et al., 2021). In modern humans the value of periodicity ranges from 6 to 12 days, although values from 7 to 9 are the most frequent (Reid et al., 1998; Reid & Dean, 2006; Smith et al., 2015). Therefore, an error of 1 or 2 perikymata in the prediction of one decile indicates a difference in the estimation of enamel formation of about one or two weeks. For example, if there were 2 perikymata of difference in each of the first three deciles in a tooth with 10-day periodicity, this would mean 6 perikymata and 60 days of difference between predicted and real formation time. Moreover, if this tooth had 100 perikymata in reality across the entire crown height, which is common to be around that value in humans, total formation time would be 1000 days (2.74 years) with a 10-day periodicity. This means that 60 days of error would represent 6% of difference in total formation time of the lateral enamel. However, this percentage of difference can be considered as one of the highest possible because our ANNs predict perikymata per decile in most occasions to be exact or with one perikyma of difference (Fig. 7, 8, 9), and because in a great majority of cases, teeth show periodicity values below 10 days. Furthermore, if we consider the accumulative error prediction in three deciles across the 164 teeth used in the study, more than 85% of the teeth (141 teeth) had perikymata estimates that were accurate within 3 perikymata. This means that crown formation time estimates will rarely be more than 30 days off. As a consequence, for reconstructions of developmental timing, few weeks of error in the estimation would represent most likely less than 5% of overall time difference between real and predicted lateral formation times.

Our results point to neural networks as a reliable, validated, and accurate approach to expanding the study of perikymata. Our teethR package is designed to be easy-to-use. We see two immediate benefits that our ANN model brings to the study of human dental development.

First, comparative samples can now be expanded to include more individuals, as historically, sample sizes have been limited by the number of unworn teeth available for study (Guatelli-Steinberg et al., 2018; Modesto-Mata et al., 2020).

The second benefit is in the expanded range of variation of perikymata counts observed. It has generally been calculated that perikymata counts in the first and second deciles of incisors (Guatelli-Steinberg et al., 2005) and molars (Guatelli-Steinberg & Reid, 2008) have very low standard deviations, ranging from one to two perikymata in each population. Instead of assuming homogeneity in early development, our ANN enables an accurate prediction of missing data based on the variability observed in the later deciles using the R package named `teethR` that was have made publicly available in GitHub with GPL v3.0 license.

The application of these ANNs will enable an expansion of our knowledge of modern human variation, as worn teeth can be included. The next step is to see if our approach is also useful across different species, including extant and extinct taxa. If the ANNs to predict perikymata are found to be useful for fossil material, this will be a key opportunity to expand our understanding of tooth development through time and taxonomic space with unprecedented accuracy. A hurdle though will be that we need teeth (fossil and modern) where all perikymata are visible in order to train the ANN, as it is unlikely that the genetic, developmental, and non-genetic influences reflected in our human model would accurately reflect those of other taxa.

Another future application of artificial neural networks is to estimate the number of perikymata of deciles other than the first three. This normally occurs on fossil teeth where some parts of the external enamel surface have cracks or is polished by preservation issues in the archaeological site, or just through natural wear polishing of non-occlusal surfaces. This is a question we plan to pursue in the future.

7 Conclusion

The artificial neural networks (ANNs) technique is used to predict any type of variables with high accuracy. Here, we apply this approach to perikymata count on human teeth. The crown surfaces of teeth are normally worn soon after eruption, making it difficult to see the histological evidence of enamel formation times (perikymata). In this work we applied ANNs to predict number of perikymata in the first three deciles of the crown height in human teeth. The results indicate that ANNs predicts very accurately the missing perikymata in all the deciles in all tooth types. In most occasions, the perikymata predictions were exact or within, at most, 2 perikymata difference. The applicability to fossils needs to be pursued in further study, but this ANN model provides a new approach

to calculate crown formation times for fossil teeth. The paleobiological inferences that could be made from this expanded knowledge are exciting to contemplate.

In order to facilitate the usage of the ANNs created in this manuscript to predict perikymata by other scientists, a specific R package has been developed (`teethR`) and has been released under GPL v3.0 license.

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9 Conflict of interest

The authors declare that they have no conflicts of interest.

10 Data availability statement

Data regarding perikymata counts used in this manuscript is available in the supplementary information. Full information of the artificial neural networks is available in the GitHub repository where the R package `teethR` is hosted.

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13 Figure legends

Figure 1: Environmental scanning electron microscope image of the buccal aspect of a lower left P3 (GC_2.225_245) discovered in the archaeological site of Galls Carboners. All the perikymata are visible. The vertical white line represents the crown height divided in ten equal segments (deciles), named from DC1 (cusp tip) to DC10 (cervix).

Figure 2: Step-by-step process of the methods. We originally have four tooth types (A): incisors, canines, premolars and molars. There are 6 models per tooth type predicting perikymata in deciles (B), divided in three groups: Model DC1, which predicts DC1 based on DC2 to DC10; Model DC12, which predicts DC1 and DC2 based on DC3 to DC10; Model DC123, which predicts DC1, DC2 and DC3 based on DC4 to DC10. In (C) it is shown that each model is trained 125 times to accomodate each of the neuron combinations in three hidden layers with a 5-repeated 10-fold cross validation, which produces 50 trained ANNs per model and consequently 50 RMSEs. The final RMSE per combination is calculated as the average of the 50 RMSEs. In each model, the selected optimal combination of neurons in three hidden layers is the one with the lowest value of averaged RMSE. This process is iteratively repeated for all the models and tooth types, which produces 24 models (or formulas), 3 000 combination of neurons, 150 000 RMSEs, 3 000 averaged RMSEs and finally 24 trained ANNs.

Figure 3: Boxplots representing the number of perikymata per decile and tooth type. Each box represents a tooth type, and in the x-axis the ten deciles are shown. Horizonal black line in the box represents the median.

Figure 4: Real versus predicted perikymata counts per tooth type after running ANNs when only the first decile is used as dependent variable (model DC1). The diagonal black-dashed line represents the perfect prediction.

Figure 5: Real versus predicted perikymata counts per tooth type after running ANNs when the first and second deciles are used as dependent variables (model DC12). The diagonal black-dashed line represents the perfect prediction.

Figure 6: Real versus predicted perikymata counts per tooth type after running ANNs when the first, second and third deciles are used as dependent variable (model DC123). The diagonal black-dashed line represents the perfect prediction.

Figure 7: Difference between real and predicted values in perikymata count when DC1 is used as dependent variable per tooth type. For example, bars above x axis = 0 indicate the number of times that the predicted perikymata value is exactly the same as the real value; and bars above x axis = 1 indicate the number of times that there is 1 perikyma of difference between real and predicted values.

Figure 8: Difference between real and predicted values in perikymata count when DC1+DC2 are used as dependent variables per tooth type and decil. For example, bars above x axis = 0 indicate the number of times that the predicted perikymata value is exactly the same as the real value; and bars above x axis = 1 indicate the number of times that there is 1 perikyma of difference between real and predicted values.

Figure 9: Difference between real and predicted values in perikymata count when DC1+DC2+DC3 are used as dependent variables per tooth type and decil. For example, bars above x axis = 0 indicate the number of times that the predicted perikymata value is exactly the same as the real value; and bars above x axis = 1 indicate the number of times that there is 1 perikyma of difference between real and predicted values.