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A NUMERICAL ANALYSIS OF THE VARIATION AND CORRELATION OF CROWN ELEMENTS IN THE UPPER CHEEK TEETH OF THE EUROPEAN BEAVER, *CASTOR FIBER* (RODENTIA, CASTORIDAE), BASED ON GEOMETRIC MORPHOMETRICS

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Individual and age variations and correlation of the upper cheek teeth were studied in the European beaver, *Castor fiber*, based on an “elementaristic” description of dental crown elements by means of geometric morphometrics and applying correlation, cluster, and dispersion analyses. The basic algorithm for both within- and between-teeth comparisons was described. The least individual variability is characteristic of the teeth taking middle positions in the cheek tooth row. No clear-cut relation of the levels of individual variation of crown elements is revealed with respect to either their position in the tooth crown or their complexity. The age differences in the shape of crown elements may occasionally be very significant, with the juveniles being the most specific in this respect. The least individually variable dental units (either total teeth or particular elements) appear to generally be the most variable with age, although this result may be purely “statistical” in nature. The correlation between dental crown elements is generally not very high, with within-teeth correlations being slightly stronger than between-teeth ones. The correlations are generally stronger in the adults than in the other age groups. The dental correlations vary with age, with general trends of age differences in correlations being the opposite for within- and between-teeth comparisons. The general levels of correlations and the magnitudes of their age differences are inversely related in the case of between-teeth comparisons. The overall correlation pattern of dental crown elements is more evident in the combined age group of subadults + adults. Further explorations of both the variation and integration patterns of mammalian dentition should be based on an “elementaristic” description of the dental crown.

Keywords: dentition, European beaver, *Castor fiber*, individual variation, age variation, correlation, geometric morphometrics

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Variation and integration patterns of the complex anatomical structures, including their dynamics during the later stages of postnatal ontogenesis, became recently one of the focal points in the evolutionary morphology considered from an evo-devo perspective (Cheverud, 1996; Bolker, 2000; Callebaut, Rasskin-Gutman, 2005). However, specific studies of this type are still very scarce, such as those on the primate skull (Ackermann, 2002; Gkantidis, Halazonetis, 2011; Jung et al., 2021).

Mammalian dentition holds a great potential for its use in this regard (Ruf et al., 2020). Despite the centuries-long studies of its morphology, including age variation of dental crown elements, its detailed variation and integration (correlation) patterns in mammalian dentition still remain largely unknown, and this is true even for the most recent works (e.g., Laffont et al., 2009; Gómez-Robles, Polly, 2012; Labonne et al., 2014; Wolsan et al., 2019; Boivin et al., 2022). The main reason is that in the previous studies of these patterns, the entire teeth were most usually considered the elementary units of the tooth row, so their deeper exploration, involving analysis of both variation of and correlations between particular crown elements, remained beyond their attention. However, the use of an “elementaristic” approach in such studies, which focused on the analysis of particular dental crown elements, has revealed a very interesting dental correlation patterns in two unrelated mammal species, a horse and a rodent (Pavlinov, Spasskaya, 2021; Pavlinov, 2022). With this, the just cited and other similar studies focused primarily on the dental crowns that were fully developed and minimally modified by wear, so any questions of possible age-related effects in the variation and especially integration patterns could not even been raised, and there seemed to be the only published attempt to reveal these effects (Scarano, Vera, 2017).

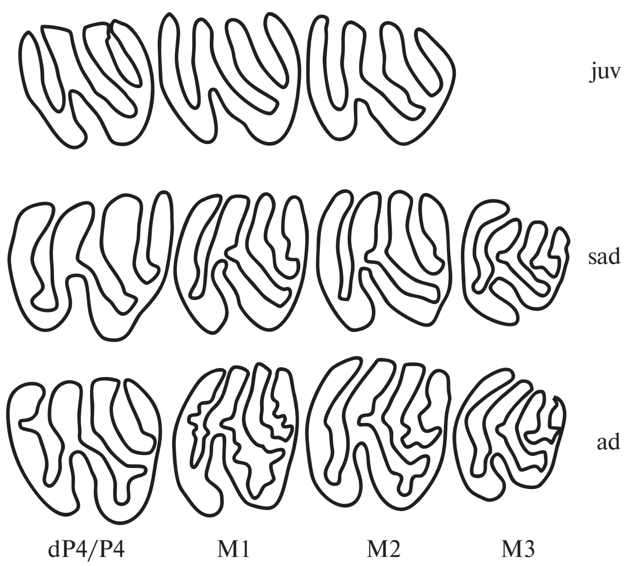

Figure 1. Typical configurations of the upper cheek teeth crown surface in different age groups of *Castor* (schematically). Standard designations: juv, sad, ad – juveniles, subadults, and adults; dP4/P4 and M1–3 – teeth in the tooth row.

Since the 1950s, numerical studies of the variation and correlation of the anatomical structures became very popular. Those dealing with the individual variation used to employ standard coefficient of variation and some other dispersion-based estimates (Van Valen, 1965; Yablokov, 1974; Hayes, Jenkins, 1997), whereas the analyses of the age variation were based on some simple indices (Mina, Klevezal, 1976). In the studies of the morphological integration, the traditional correlation analysis became the most popular due to both its simple procedure and easily interpretable results (Olson, Miller, 1958; Terentiev, 1959; Gould, Garwood, 1969; Rostova, 2002; Pavlinov et al., 2008). In all these works, linear measurements were used to characterize particular anatomical structures. However, the recently developed methods of geometric morphometrics (GM) enable a direct comparison of these structures by their shapes and thus provide the new opportunities in the study of their morphological variation and integration (Zelditch et al., 2004; Vasil'ev et al., 2018; Machado et al., 2019). Of prime importance is that GM provides certain numerical estimates for the shape variation and covariation, with the reservation that many of them are approximate rather than precise because of certain specific calculation techniques (Rohlf, 1996). In the case of mammalian dentition, GM methods made it possible to analyze both the entire tooth crowns (Hallgrímsson et al., 2009; Klingenberg, 2009, 2014; Goswami, Polly, 2010; Lawing, Polly, 2010; Cardini, Loy, 2013; Klingenberg, Marugán-Lobón, 2013) and their particular elements (Pavlinov, Spasskaya, 2021; Pavlinov, 2022).

This article considers variation and correlation of the upper cheek teeth crown elements, described and evaluated by GM and some other numerical techniques, in the rodent species *Castor fiber*. The choice of this object is justified by that (a) the variation and correlation patterns of its dentition, which is classified as lophodont (Fig. 1), were not studied numerically "elementaristically" so far (unlike those of the cranium, see: Puzachenko, Korablev, 2016), (b) the basic crown elements are easily susceptible to an "elementaristic" analysis by means of GM, and (c) this rodent has a rather long lifespan (up to 20 years), with its dental crowns noticeably changing during postnatal ontogenesis.

The basic issues addressed in this report were more methodological rather than proper biological. The author's main task was to consider the principal possibilities of the approach, having been developed in his previous works (cited above), to study various aspects of variation and correlation of the dental crown elements in mammals. As far as the numerical analysis of shape variation of the latter, considered "elementaristically", is in its infancy, only few and still rather simple specific hypotheses could be presently formulated about dentition in *Castor fiber*. Some of them concerned a possible dependence of the variation of dental crown elements on both their position in the tooth row and complexity. Others were about the general pattern of correlation between these elements: was it expressly hierarchical, which particular elements were most correlated, and which correlations were subject especially to certain age-related effects.

MATERIALS AND METHODS

The studied sample included 37 specimens of the European beaver (*Castor fiber*) collected in the 1970s and kept in the Research Zoological Museum at the Lomonosov Moscow State University. The sample was divided into several groups according to the age (Lavrov, 1953): (1) juveniles ($n = 8$) with milk dP4 and not fully erupted M3, (2) subadults ($n = 14$) with completely developed permanent dentition and with minimally worn flexi on dental crowns, (3) adults ($n = 15$) with noticeably worn dental crowns, but with flexi on them not yet divided into isolated facets. Besides, subadults and adults were united in (4) a combined group; juveniles were not included in it because of their P4 and M3 not fully developed. Senile specimens were not studied, as they faced certain problems with the definite GM-description of their fragmented crown elements.

Our sample was strongly limited in its size by the availability of specimens, which were not so numerous in the collections as, say, the voles and mice most usually studied with regard to the dental variation and correlation. So one might reasonably suspect that such a scanty material made it hardly possible to apply standard statistical methods, based on the frequency distribution analyses. However, it is to be taken into account that GM methods do not presume such kind of analyses and normally consider the resultant numerical estimates without their traditional statistical evaluations (Rohlf, 1996). So, even with such limited data in hand, it was proved possible to attain certain interesting results (Scarano, Vera, 2017; Wolsan et al., 2019; Pavlinov, Spasskaya, 2021). With this, given the relatively small sample size used in this study, we opted for the more simple numerical methods to ensure their results more reliable and clearer for biological interpretations. Accordingly, the quantitative estimates were analyzed directly without considering their statistical significance; Shrader-Frechette (2008) and Wasserstein et al. (2019) have provided a general substantiation of the validity of such a "non-orthodoxal" approach.

The dental crown elements in *Castor fiber* were identified taking into consideration (a) the accuracy of both their standard individuation in the specimens of different ages and (b) certain requirements of GM methodology. The nomenclature of these elements was adopted after Korth (2002). The re-entrant flexi were treated as the elementary units to be compared (fig. 2), namely hypoflexus (*Hyf*), metaflexus (*Mef*), paraflexus (*Paf*), and posteroflexus (*Pof*). They were delimited at the tips of the salient angles (lophs) by either the latter's maximal curvature or the points of enamel layer interruption on them.

The left-side upper cheek tooth row of each specimen was digitized by the camera Olympus SP-570 UZ, with tooth orientation being standardized with respect to a plane surface. For GM tools to be applied, the enamel layers of dental crowns were first manually outlined on their images in CorelDRAW program using its Shape tool, with the lines of minimum thickness being drawn along the midlines of the enamel layers. These vector contour lines were converted into high-resolution raster images to be processed by GM tools. Each crown element was initially described by an array of semilandmarks set automatically equidistantly along its contour line between two points fixed at its boundaries (Mitteroecker, Gunz, 2013), with semilandmark number, in our case, varying from 20 to 40 per a contour line depending on its length (see fig. 2). After that, some semilandmarks were appropriately "slided" by hand along the contour lines (in the sense of Bardua et al., 2019) to make them fitting more precisely to the shapes of respective flexi. The semilandmarks were set and their *x*, *y* coordinates were acquired with tpsDig2 program (Rohlf, 2017), and they were converted into the standard landmark data with tpsUtil program (Rohlf, 2019). Each crown element was run twice through tpsDig2, and its consensus configuration was calculated with tpsRelw program (Rohlf, 2019a) to become an actual studied shape. The initial *x*, *y* coordinates were transformed into Procrustes coordinates using generalized least-square Procrustes superimposition, and pairwise Procrustes distances were calculated between specimens in each group using PAST program (Hammer et al., 2001). In the subsequent specific analyses, either landmark *x*, *y* coordinates or pairwise Procrustes distances were used (see below for detail).

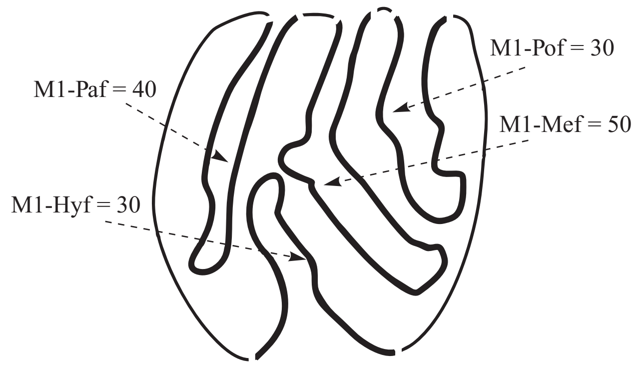

Figure 2. Recognition and nomenclature of the upper dental crown elements in *Castor*. The analyzed crown elements (flexi) are marked with bold contour lines, with the gaps marking their boundaries. Element designations: *Hyf* – hypoflexus, *Mef* – metaflexus, *Paf* – paraflexus, *Pof* – posteroflexus. In each designation, the first part refers to a particular tooth (here M1), figure indicates the number of semilandmarks for respective contour lines.

Two kinds of comparisons of crown elements were undertaken, either within or between teeth, with variation and correlation of these elements being considered in two following combinations. In *within-teeth comparisons*, each tooth was taken for a basic unit of comparison, so all of its crown elements were mutually compared. In *between-teeth comparisons*, each crown element was taken for such a unit, so all elements were mutually compared across all teeth in the tooth row.

Individual variation of the shapes of crown elements was estimated by the averaged Procrustes distances calculated as an arithmetic mean for each element in each age group (Pavlinov, 2011). These distances were then averaged for within- and between-teeth comparisons to estimate general levels of individual variation of the shapes of dental crown elements.

To characterize the age differences in the shapes of these elements, principal component analyses of the latter's *x*, *y* coordinates were run for the pairwise combinations of age groups using the above-mentioned tpsRelw program. The PC (relative warp) scores thus obtained were analyzed by ANOVA using STATISTICA program (StatSoft, 2012). The magnitude of age difference between groups was estimated (Pavlinov, 2011) as a ratio of the sum of squares of the explained variance (EV) to the total variance of the first ten PCs that explain cumulatively (in our case) about 95–99 percent of the total variance. This measure seemed to be similar methodologically to the index CR defined as a ratio of between- to within-covariances (Adams, 2015). For the final comparisons, the average EV estimates were calculated, as in the case of means of Procrustes distances, for both within- and between-teeth comparisons.

Table 1. Individual variation and age differences of the upper cheek teeth crown elements in *Castor fiber*

Age groups	**Within teeth** (over all crown elements)					**Between teeth (**crown elements across all teeth)				
	dP4/P4	M1	M2	M3	Average	Paf	Mef	Pof	Hyf	Average
					Individual variation					
Juv	0.16	0.14	0.18	—	0.16	0.14	0.16	0.14	0.20	0.16
Sad	0.18	0.13	0.12	0.20	0.16	0.13	0.13	0.16	0.19	0.15
Ad	0.19	0.17	0.19	0.22	0.19	0.16	0.18	0.21	0.21	0.19
Average	0.18	0.14	0.16	0.21		0.14	0.16	0.17	0.20	
					Age differences					
Juv–Sad	0.23	0.40	0.52	—	0.38	0.41	0.45	0.37	0.23	0.39
Juv–Ad	0.27	0.33	0.46	—	0.35	0.39	0.44	0.39	0.20	0.35
Sad–Ad	0.20	0.16	0.18	0.20	0.18	0.32	0.29	0.31	0.18	0.27
Average	0.25	0.31	0.41	0.20		0.37	0.38	0.36	0.19	

Notes. See fig. 2 for the designations of crown elements; see text for the explanation of indices.

To reveal correlation patterns in each of the age groups, the Procrustes distance matrices were vectorized, and the pairwise Pearson correlations and Euclidean distances were calculated between these vectors for all crown elements using STATISTICA program. The average correlation values were next calculated, based on the pairwise ones, for within- and between-teeth comparisons. Following N. Rostova (2002), these average correlations were treated as a measure of the overall integration of respective anatomical units, either teeth or crown elements in our case. Being rather simple in its calculation and straight forward in its interpretation, this integral estimate was shown to be fully comparable with a more sophisticated index based on the covariance matrices analysis (Pavlicev et al. 2009; Machado et al., 2019). The age differences between groups in these correlations, both for withtin- and between-teeth comparisons, were numerically estimated by pairwise rank (Spearman) correlation R_M of correlation matrices for particular crown elements. The index AD = $(1 - R_M)$ was actually used for illustrating just the differences instead of similarities.

The hierarchical cluster analysis of the Euclidean distance matrices was applied to reveal the overall correlation patterns of dental crown elements in each of the age groups. The phenograms illustrating these patterns were produced by the Ward algorithm with bootstrap estimations of cluster support (1000 replicates). This support was considered a rough quantitative estimate of the "constancy" of association of respective elements. An average bootstrap support of the cluster hierarchy was calculated for each of the phenograms as a measure of the structuredness of the overall correlation pattern in respective age group. Such measure seemed to be more appropriate for our purposes as compared to the analysis of cluster structure borrowed from standard phenetic techniques (e.g., Young, 2008).

RESULTS

Individual variation of the shapes of dental crown elements was shown to be somewhat higher on average in the adults (Table 1). Among particular teeth, M1 appeared the least and M3 the most variable in general (0.14 and 0.21, respectively), and among the elements, *Paf* appeared the least and *Hyf* the most variable (0.14 and 0.20, respectively). The age differences may be assessed in general as average to rather high, with the ratio of EV varying from 0.16 to 0.52 (the same Table). The differences between subadults and adults appeared the least and those between juveniles and two other groups the most expressed (0.18 and 0.35–0.38, respectively). In average, M3 and P4 were the most stable and M2 was the most variable with age (0.20–0.25 and 0.40, respectively). Of particular crown elements, *Hyf* appeared the least variable in average as compared to others (0.19 and 0.36–0.38, respectively).

Correlations between crown elements, both for within- and between-teeth comparisons, were not especially high on average, with their most frequent values being located between 0.15–0.35, and their upper limits rarely reaching 0.85. Three principal kinds of frequency distributions of correlations were revealed in different pairwise comparisons, namely symmetrical unimodal, asymmetrical unimodal, and slightly bimodal (fig. 3), of which the former appeared the most common.

The average correlation between crown elements within particular teeth was equal to 0.08–0.38 (table 2). The most integrated were P4 and M2 (0.26–0.28 on average) and the least so M1 and M3 (0.16–0.17 on average). Regarding particular homologous elements on different teeth, the lowest estimates were obtained for *Paf* and the highest for the rest (0.13 and 0.19–0.22 on average, respectively). On average, within-teeth correlations were slightly higher than between-teeth ones (0.16–0.28 and 0.13–0.22, respectively), and both particular teeth and homologues were the most integrated in the adults as compared to the juveniles and subadults (0.28 and 0.20 against 0.16–0.17 and 0.12–0.16, respectively). It is to be noted that the combined age group (subadults + adults) demonstrated the highest or nearly so level of dental integration (0.26) in both within- and between-teeth comparisons.

The AD values indicating the age differences in dental correlations (table 2) varied from 0.01 to 0.95 for particular pairwise comparison: the former meant no difference and the latter corresponded to no similarity between age groups. For within-teeth comparisons, the least different with age were the correlations between crown elements of M2 and the most different were those of dP4/P4 and M1 (0.38 and 0.89–0.90, respectively). For between-teeth comparisons, the least different with age were the mutual correlations of *Mef* and the most different were those for *Hyf* and *Paf* (0.22 and 0.59–0.62, respectively). Regarding particular age groups, within-teeth correlations appeared the most different between juveniles and subadults (0.82) and the least different between subadults and adults (0.56); between-teeth correlations revealed an opposite relation, with the former pair being the least and that latter pair the most different (0.29 and 0.69, respectively).

The averaged bootstrap supports of the overall correlation patterns of dental crown elements vary from 37–42 percent in adults and juveniles to 70 percent in subadults and in the combined group. A visual analysis of the structure of phenograms illustrating between-elements correlations in particular age groups (fig. 4) indicated the following. In the juveniles, the most stable were associations between *Mef* and *Hyf* in dP4 and less so between *Pof* in dP4 and *Paf* in M1 (bootstrap support is 90 and 78 percent respectively), whereas all other associations were much weaker. In subadults, most of the branching points had rather strong bootstrap supports exceeding 50 percent. Most strongly supported (90 and higher percent) were the associations between some homologues in different teeth (*Hif* in P4 and M3, *Paf* in M1 and M3) and also strongly to moderately supported (about 70–80 percent or higher) between some elements in the same teeth (*Hyf* and *Pof* in M3, *Mef* and *Pof* in each of P4 and M2). In the adults, there were several noteworthy rather strongly supported associations of homologues in different teeth (*Hif* in P4 and M3, *Paf* in M2 and M3). Regarding the combined group, all branching points had strong bootstrap supports exceeding 50 percent. Among quite strongly supported associations, of interest were those of the elements in the same teeth (*Hyf* and *Pof* in M1, *Mef* and *Pof* in M2), though one seemingly “odd” association (*Paf* in M3 with *Mef* in M1) was also highly supported.

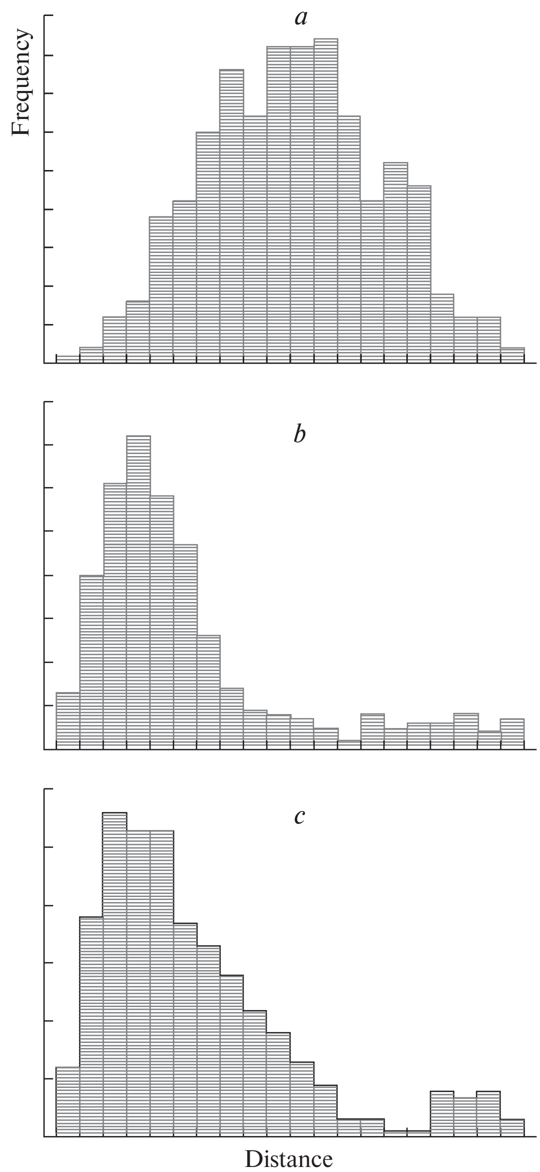

Fig. 3. Three principal kinds of frequency distributions of the correlations between dental crown elements in the combined age group: *a* – symmetrical unimodal (M3-*Pof*), *b* – asymmetrical unimodal (M2-*Paf*), *c* – bimodal (M3-*Hyf*).

DISCUSSION

To begin with, it is to be noted once more that the numerical analysis of the shape variation in mammal dentition, considered “elementaristically”, is in its earliest infancy. So any findings in this new field of odontology may bear new light on the general trends of dental variation and correlation patterns. In particular, it seems very important to have numerical estimates of these patterns, which make them commensurable in some respects. Thus, the following principal results of our study of the European beaver (*Castor fiber*) deserve a closer consideration.

First, it is to be pointed out that a certain correspondence seems to exist between individual variation of particular teeth and their position in the tooth row.

Table 2. Correlations between upper cheek teeth crown elements and their age differences in *Castor fiber*

Age groups	**Within teeth** (over all crown elements)					**Between teeth** (crown elements across all teeth)				
	dP4/P4	M1	M2	M3	Average	*Paf*	*Mef*	*Pof*	*Hyf*	Average
					General levels					
Juv	0.21	0.08	0.18	—	0.16	0.14	0.13	0.09	0.11	0.12
Sad	0.34	0.12	0.13	0.08	0.17	0.17	0.17	0.14	0.18	0.16
Ad	0.27	0.19	0.38	0.29	0.28	0.08	0.21	0.24	0.28	0.20
Sad+Ad	0.30	0.25	0.37	0.14	0.26	0.15	0.38	0.32	0.20	0.26
Average	0.28	0.16	0.26	0.17		0.13	0.22	0.20	0.19	
					Age differences					
Juv–Sad	0.95	0.86	0.63	—	0.82	0.49	0.01	0.12	0.56	0.29
Juv–Ad	0.92	0.98	0.37	—	0.75	0.52	0.09	0.23	0.57	0.35
Sad–Ad	0.79	0.88	0.14	0.64	0.56	0.87	0.58	0.67	0.67	0.69
Average	0.89	0.90	0.38	0.64		0.62	0.22	0.45	0.59	

Notes. Designations of crown elements are the same as in Table 1; see text for the explanation of indices.

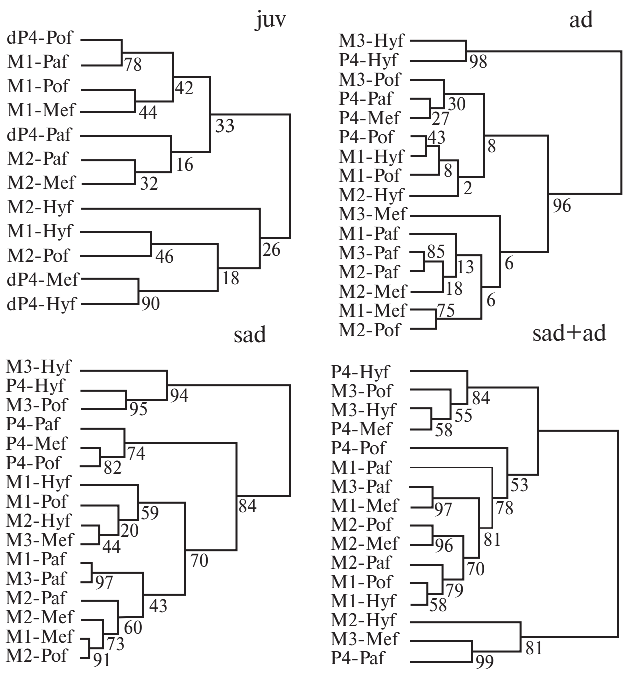

Figure 4. Phenograms illustrating correlation patterns of dental crown elements in different age groups. Designations of the crown elements as in fig. 2.

The least individual variability is characteristic of M1 and M2 taking middle position in the row (0.14–0.16), as compared to anterior P4 and especially posterior M3 (0.18–0.21). This result largely agrees with the previous observations: the teeth in the middle position of the tooth row were usually reported to be the least variable individually in various mammals (e.g., Gingerich, 1974; Gingerich, Schoeninger, 1979; Polly, 1998; Pavlinov, 2022). Regarding particular crown elements, the interior most simple *Hyf* is the most variable, the anterior moderately complex *Paf* is the least variable, whereas the most complexly shaped *Mef* and *Pof* do not tend to be more variable, as one might expect. Thus, no clear-cut relation of individual variation of crown elements is revealed with respect to either their position in the tooth crown or their complexity.

The age differences in the shape of dental crown elements may occasionally be very significant by reaching up to half of the total variance. For both within- and between-teeth comparisons, the juveniles appear the most specific in this respect, and the least differences occur between the subadults and adults, thus indicating that the tooth crowns remain nearly unchanged in them. An overall trend of relations between the levels of individual and age variation seems to be the same for both within- and between-teeth comparisons: the least individually variable dental units (either total teeth or particular elements) appear in general the most variable with age. However, one cannot exclude a possibility that this result, though looking interesting from a biological perspective, may be of a pure “statistical” nature: it is normal for the ANOVA that the higher is the within-group (individual) dispersion, the lower, other things being equal, is the between-group (age) dispersion.

The general level of correlations between dental crown elements is not very high, with within-teeth correlations (0.16–0.28) being slightly stronger than between-teeth ones (0.12–0.26). This ratio between within- and between-teeth correlations differs from those obtained earlier for *Equus* and *Ondatra* (Pavlinov, Spasskaya, 2021; Pavlinov, 2022), which indicate that the crown integration patterns may differ among different types of mammalian dentition. The correlations are somewhat stronger in the adults in both within- and between-teeth comparisons, so one may speculate that a slight wear of the dental crown surface entails a certain strengthening of its "elementary" integration, probably by an elimination (wiping away) of some "random" variations in the elements. It is to be noted also that the correlations in question are the highest or nearly so in the combined group, which indicates that a mixture of subadults and adults better reveals correlation patterns in the lophodont dentition.

The correlations between crown elements vary with age, though at a different magnitude for different dental units. It is of interest that the trends of the differences between age groups appear opposite for within- and between-teeth comparisons. Indeed, juveniles and subadults are the most different with regard to within-teeth correlations and the least different with regard to between-teeth ones. The most intriguing moment in this difference is that the elementary units of comparisons are the same in both cases, which are particular crown elements, so it remains unclear what might be a cause of such an "opposite" effect.

With regard to within-teeth correlations, the most stable with age are those within M2 and the least stable are those within dP4/P4 and M1, whereas of particular crown elements, the most stable is *Mef* and the least so are *Hyf* and *Paf*. With regard to the relation between general levels of correlations and the magnitudes of their age differences, it is nearly absent for within-teeth comparisons and is evidently negative for between-teeth comparisons; the latter means that the less intercorrelated crown homologues generally are, the less stable their intercorrelations tend to be with age.

Our analyses of relations between different aspects of variation and correlation of dental crown elements in *Castor fiber* do not reveal any clear-cut trends in them deserving a more detailed consideration. With this, however, certain findings are to be highlighted that may indicate some possible biologically interesting trends worthy of further exploration. For instance, for both within- and between-teeth comparisons, the least individually variable dental unit (M1 and *Paf*, respectively) appears also the least correlated with others, although other units display no relation of such kind. In this regard, an absence of a clear relation between the magnitudes of age differences in crown elements proper and their correlations may deserve a more close attention, as it concerns an important issue of the ontogenetic regulation of dental crown pattern in general.

The frequency distributions of correlations seems to be quite indicative for a preliminary consideration of the basic properties of the general correlation pattern of cheek teeth (see fig. 4). The nearly symmetrical unimodal distribution indicates an absence of any clear-cut hierarchy in it, and this was the most common correlation pattern in the studied sample. The asymmetrical strongly left-skewed distribution indicates certain elements of the hierarchy in the correlation pattern, though without a clear-cut discreteness. The bimodal distribution clearly indicates the occurrence of two-level basic nearly discrete levels in the pattern in question, with the major peak of the distribution corresponding to the prevailing lower-level correlations and its minor peak corresponding to the higher-level one. Such discrete correlation pattern was revealed in the studied dentition for but a few pairwise comparisons.

Both overall correlation patterns and their age-related differences are clearly illustrated by the distributions of particular dental crown elements over cluster phenograms (see fig. 4). In general, judging by their bootstrap supports, the overall patterns in both the juveniles and adults are evidently more "loose" as compared to the subadults; or in other terms, the hierarchical arrangement of these patterns in the two former is expressed much weaker than in the latter. With interpreting the most supported groupings of crown elements as the so-called "correlation pleiades" (in the sense of Rostova, 2002), it becomes evident that the overall "pleiade" structure of cheek teeth dentition in *Castor fiber* is not well-defined in general and fairly unstable with age in particular. Indeed, (a) not many crown elements are assembled in such "pleiades", and (c) there are but two "pleiades" that coincide in subadults and adults. Only few of these "pleiades" seem to be biologically sound, some uniting within-teeth correlations (those of dP4/P4 in the juveniles and subadults, of M2 in the subadults), while others corresponding to the correlations between homologous elements in different teeth (*Paf* of M1 and M3, *Mef* in M1 and M2 in subadults, *Hif* of P4 and M3 in subadults and adults).

It is to be noted also that the overall correlation pattern of dental crown elements is generally more evident in the combined (subadults + adults) age group. This finding seems to be of a certain relevance to the methodology of the analyses of dental correlations in mammals. It indicates that the correlation patterns in question could be uncovered more definitely and profoundly if the dentitions at several wear stages are jointly studied in this respect – of course, as long as the particular crown elements remain clearly identifiable.

It would be more than premature to consider here in detail any possible causes, either biological or "statistical", of variation and correlation patterns of the "elementaristically" interpreted dental crowns in *Castor fiber*. However, our findings presented in this article, together with the earlier ones (referred to above), allow us to conclude positively that such an "elementaristic" approach provides apparently a more thorough and informative picture of these patterns. Therefore, I would suggest that the further explorations of both the variation and integration patterns of mammalian dentition, including age-related effects in them, should adopt this approach applied to different dental crown types (bunodont, solenodont, lophodont, prismatic, etc.). This would provide a more comprehensive knowledge of both specific and common features in the regularities of the variation and correlation patterns in dentition in various groups of mammals.

CONCLUSIONS

The principal results of this study can be summarized as follows.

1. The least individual variability is characteristic of the teeth taking middle position in the cheek tooth row. No clear-cut relation of the levels of individual variation of crown elements is revealed with respect to either their position in the tooth crown or their complexity.

2. The age differences in the shape of crown elements may occasionally be very significant, with the juveniles being the most specific in this respect. The least individually variable dental units (either total teeth or particular elements) appear in general the most variable with age, though this result may be of a pure "statistical" nature.

3. The correlation between dental crown elements is generally not very high, with within-teeth correlations being slightly stronger than between-teeth ones. The correlations are generally stronger in the adults than in other age groups.

4. The dental correlations vary with age, with crown elements differing significantly in this regard. The general trends of age differences in correlations are shown to be opposite for within- and between-teeth comparisons. The general levels of correlations and the magnitudes of their age differences are inversely related in the case of between-teeth comparisons.

5. The overall correlation pattern of dental crown elements is more evident in the combined (subadults + adults) age group.

6. The further explorations of both the variation and integration patterns of mammalian dentition should be based on an "elementaristic" description of dental crown.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The author of this work declares that he has no conflicts of interest.

REFERENCES

Adams D.C., 2015. Evaluating modularity in morphometric data: challenges with the RV coefficient and a new test measure // Methods in Ecology and Evolution. V. 5. № 5. 3. 565–572.

Ackermann R.R., 2002. Patterns of covariation in the hominoid craniofacial skeleton: implications for paleoanthropological models // Journal of Human Evolution. V. 42. № 1. P. 167–187.

Bardua C., Felice R.N., Watanabe A., et al., 2019. Practical guide to sliding and surface semilandmarks in morphometric analyses // Integrative Organismal Biology. V. 1. № 1. obz016 [An electronic source]. Accessed through: https://academic.oup.com/iob/article/1/1/obz016/5526881?login=false. The last upgrade date: 05.07.2019

Boivin M., Alvarez A., Ercoli M.D., 2022. Integration patterns of cheek teeth and ecomorphological evolution in grinding herbivores: the case of caviine rodents (Caviomorpha: Caviidae) // Zoological Journal of the Linnean Society. V. 196. № 3. zlac005 [An electronic source]. Accessed through: https://doi.org/10.1093/zoolinnean/zlac005. The last upgrade date: 12.03.2022.

Bolker J.A., 2000. Modularity in development and why it matters to evo-devo // American Zoologist. V. 40. № 5. P. 770–776.

Callebaut W., Rasskin-Gutman D. (eds), 2005. Modularity: understanding the development and evolution of complex natural systems. Cambridge: MIT Press 472 p.

Cardini A., Loy A., 2013. On growth and form in the "computer era": from geometric to biological morphometrics // Hystrix, Italian Journal of Mammalogy. V. 24. № 1. P. 1–5.

Cheverud J.M., 1996. Developmental integration and the evolution of pleiotropy // American Zoologist. V. 36. № 1. P. 44–50.

Gingerich P.D., 1974. Size variability of the teeth in living mammals and the diagnosis of closely related sympatric fossil species // Journal of Paleontology. V. 48. № 5. P. 895–903.

Gingerich P.D., Schoeninger M.J., 1979. Patterns of tooth size variability in the dentition of Primates // American Journal of Physical Anthropology. V. 51. № 3. P. 457–465.

Gkantidis N., Halazonetis D.J., 2011. Morphological integration between the cranial base and the face in children and adults // Journal of Anatomy. V. 218. № 4. P. 426–438.

Gómez-Robles A., Polly P.D., 2012. Morphological integration in the hominin dentition: evolutionary, developmental, and functional factors // Evolution. V. 66. № 4. P. 1024–1043.

Goswami A., Polly P.D., 2010. Methods for studying morphological integration, modularity and covariance evolution // The Paleontological Society Papers. V. 16. № 2. P. 213–243.

Gould S.J., Garwood R.A., 1969. Levels of integration in mammalian dentitions: an analysis of correlations in *Nesophontes micrus* (Insectivora) and *Oryzomys couesi* (Rodentia) // Evolution. V. 23. № 2. P. 276–300.

Hallgrímsson B., Jamniczky H., Young N.M., et al., 2009. Deciphering the palimpsest: Studying the relationship between morphological integration and phenotypic correlation // Evolutionary Biology. V. 36. № 4. P. 355–376.

Hammer Ø., Harper D., Ryan P.D., 2001. PAST. PAleontological STatistics software package for education and data analysis // Palaeontologia Electronica. V. 4. № 1. P. 1–9.

Hayes J., P., Jenkins S.H., 1997. Individual variation in mammals // Journal of Mammalogy. V. 78. № 2. P. 274–293.

Jung H., Simons E., von Cramon-Taubadel N., 2021. Ontogenetic changes in magnitudes of integration in the macaque skull // American Journal of Physical Anthropology. V. 174. № 1. P. 76–88.

Klingenberg C.P., 2009. Morphometric integration and modularity in configurations of landmarks: Tools for evaluating a priori hypotheses // Evolution & Development. V. 11. № 4. P. 405–421.

Klingenberg C.P., 2014. Studying morphological integration and modularity at multiple levels: concepts and analysis // Philosophical Transactions of the Royal Society B: Biological Sciences. V. 369. № 1649. P. 20130249. doi: 10.1098/rstb.2013.0249

Klingenberg C.P., Marugán-Lobón J., 2013. Evolutionary correlation in geometric morphometric data: analyzing integration, modularity, and allometry in a phylogenetic context // Systematic Biology. V. 62. № 4. P. 591–610.

Korth W.W., 2002. Comments on the systematics and classification of the beavers (Rodentia, Castoridae) // Journal of Mammalian Evolution. V. 8. № 4. P. 279–296.

Labonne G., Navarro N., Laffont R., et al., 2014. Developmental integration in a functional unit: deciphering processes from adult dental morphology // Evolution & Development. V. 16. № 4. P. 224–232.

Lawing A.M., Polly P.D., 2010. Geometric morphometrics: recent applications to the study of evolution and development // Journal of Zoology. V. 280. № 1. P. 1–7.

Laffont R., Renvoisé E.,, Navarro N., et al., 2009. Morphological modularity and assessment of developmental processes within the vole dental row (*Microtus arvalis*, Arvicolinae, Rodentia) // Evolution & Development. V. 11. № 3. P. 302–311.

Lavrov L.S., 1953. Age determination in the river beavers // Trudy Voronezhskogo Gosudarstvennogo Zapovednika (Proc. State Voronezh Rereve). V. 4. P. 77–84.

Machado F.A., Hubbe A., Melo D., et al., 2019. Measuring the magnitude of morphological integration: The effect of differences in morphometric representations and the inclusion of size // Evolution. V. 73. № 12. P. 2518–2528.

Mina M.V., Klevezal G.A., 1976. Rost zhivotnyh: analiz na urovne organizma (Growth of animals: an analysis at the organismal level). Moscow: Nauka Publ. 292 p.

Mitteroecker P., Gunz P., 2013. Semilandmarks: A method for quantifying curves and surfaces // Hystrix, Italian Journal of Mammalogy. V. 24. № 1. P. 103–109.

Olson E.C., Miller R.L., 1958. Morphological integration. Chicago: Univ. Chicago Press. 376 p.

Pavlicev M., Cheverud J.M., Wagner G.P., 2009. Measuring morphological integration using eigenvalue variance // Evolutionary Biology. V. 36. № 1. P. 157–170.

Pavlinov I.Ya., 2011. Morphological disparity: an attempt to widen and to formalize the concept // Pavlinov I. Ya. (ed.), Research in biodiversity: models and applications. Rijeka: InTech Open Access. P. 341–364.

Pavlinov I.Ya., 2022. Variation and correlation of the molar crown elements in the genus *Ondatra* (Rodentia, Arvicolinae) // Russian Journal of Theriology. V. 21. № 2. P. 139–145.

Pavlinov I.Ya., Nanova O.G., Lissovsky A.A., 2008. Correlation structure of the cheek teeth in the polar fox (*Alopex lagopus*, Canidae) // Zool. Zh. (Moscow). V. 87. № 7. P. 862–875.

Pavlinov I.Ya., Spasskaya N.N., 2021. Correlation structure of the cheek teeth enamel crown patterns in the genus *Equus* (Mammalia: Equidae): an analysis by geometric morphometrics with outline points // Russian Journal of Theriology. V. 20. № 1. P. 70–81.

Polly P.D., 1998. Variability in mammalian dentitions: size-related bias in the coefficient of variation // Biological Journal of the Linnean Society. V. 64. № 1. P. 83–99.

Puzachenko A.Yu., Korablev N.P., 2016. Allometry of the skull in one autochthonous and two reintroduced populations of Eurasian beavers (*Castor fiber*, Castoridae, Rodentia) // Russian Journal of Theriology. V. 15. № 1. P. 28–33.

Rohlf F.J., 1996. Morphometric spaces, shape components and the effect of linear transformations // Marcus L., Corti M., Loy A., Slice D. (eds). Advances in morphometrics. New York: Plenum Press. P. 131–152.

Rohlf F.J., 2017. tpsDig2 ver. 2.31. New York: State University at Stony Brook (software).

Rohlf F.J., 2019. tpsUtil ver. 1.78. New York: State University at Stony Brook (software).

Rohlf F.J., 2019a. TPSrelw32: relative warps, version 1.7. New York: State University at Stony Brook (software).

Rostova N.S., 2002. Korrelyztsyi: struktura i izmenchivost' [Correlations: structure and variability]. St. Petersburg: St. Petersburg University Publ. 307 p.

Ruf I., Schubert A.M., Koenigswald W., 2020. Case studies on functional aspects and constraints in early and late tooth ontogeny // Martin T., Koenigswald W. (eds). Mammalian teeth – form and function. München: Verlag Dr. Friedrich Pfeil. P. 102–124.

Scarano A.C., Vera B., 2017. Geometric morphometric analysis as a proxy to evaluate age-related change in molar shape variation of low-crowned Notoungulata (Mammalia) // Journal of Morphology. V. 279. № 2. P. 216–227.

Shrader-Frechette K., 2008. Statistical significance in biology: neither necessary nor sufficient for hypothesis acceptance // Biological Theory. V. 3. № 1. P. 12–16.

StatSoft Inc., 2012. STATISTICA (Data Analysis Software System), Version 12. Hamburg: StatSoft Europe (software).

Terentiev P.V., 1959. A method of correlation pleiades // Vestnik Leningradskogo Universiteta. № 9. P. 137–141.

Van Valen L., 1965. Morphological variation and width of ecological niche // The American Naturalist. V. 99. № 2. P. 377–390.

Vasil'ev A.G., Vasil'eva I.A., Shkurikhin A.O., 2018. Geometricheskaya morfometriya: ot teorii k praktike [Geometric morphometrics: from theory to practice]. Moscow: KMK Sci. Press. 471 p.

Wasserstein R.L., Schirm A.L., Lazar N.A., 2019. Moving to a world beyond "p < 005" // Journal of the American Statistical Association. V. 73. Supl. 1. P. 1–19.

Wolsan M., Suzuki S., Asahara M., Motokawa M., 2019. Dental integration and modularity in pinnipeds // Scientific Reports. V. 9. № 4184. P. 1–13.

Young N.M., 2008. A comparison of the ontogeny of shape variation in the anthropoid scapula: functional and phylogenetic signal // American Journal of Physical Anthropology. V. 136. № 3. P. 247–264.

Zelditch M., Swiderski D., Sheets D.H., Fink W., 2004. Geometric morphometrics for biologists. Elsevier: Acad. Press. 437 p.

Yablokov A.V., 1974. Variability of mammals. New Dehi: Amerind Publ. 350 p.

КОЛИЧЕСТВЕННЫЙ АНАЛИЗ ИЗМЕНЧИВОСТИ И КОРРЕЛЯЦИИ ЭЛЕМЕНТОВ КОРОНКИ ВЕРХНИХ ЩЁЧНЫХ ЗУБОВ ОБЫКНОВЕННОГО БОБРА (*CASTOR FIBER*, RODENTIA, CASTORIDAE) НА ОСНОВЕ ГЕОМЕТРИЧЕСКОЙ МОРФОМЕТРИИ

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Индивидуальная и возрастная изменчивость элементов коронки верхних щёчных зубов и их корреляции изучены у грызунов рода *Castor* на основе "элементаристского" описания зубной коронки с помощью геометрической морфометрии и с использованием корреляционного, кластерного и дисперсионного анализов. Описан базовый алгоритм сравнения элементов коронки внутри каждого зуба и между зубами по указанным характеристикам. Наименьшая индивидуальная изменчивость характерна для зубов, занимающих среднее положение в щечном зубном ряду. Не выявлено четкой зависимости уровней индивидуальной вариабельности элементов коронки ни от их положения в зубной коронке, ни от их сложности. Возрастные различия в форме этих элементов иногда могут быть очень значительными, причем молодые особи наиболее специфичны в этом отношении. Наименее индивидуально изменяющиеся зубные единицы (либо зубы целиком, либо отдельные элементы), как правило, оказываются наиболее изменчивыми с возрастом, хотя этот результат может носить чисто "статистический" характер. Корреляции между элементами зубной коронки в целом не очень высокие, причем корреляции внутри зубов в среднем несколько сильнее, чем между зубами. Корреляции, как правило, сильнее у взрослых, чем в других возрастных группах. Корреляции между элементами зубной коронки меняются с возрастом и в этом отношении существенно различаются. Показано, что общие тенденции возрастных различий в корреляциях противоположны для внутри- и межзубных сравнений. Общие уровни корреляций и диапазоны их возрастных различий находятся в обратной зависимости. Общая закономерность корреляции элементов зубной коронки более очевидна в комбинированной возрастной группе (полувзрослые + взрослые). Дальнейшие исследования как изменчивости, так и корреляционной структуры зубных рядов млекопитающих следует проводить на основе "элементаристского" описания зубной коронки.

Ключевые слова: зубная система, обыкновенный бобр, *Castor fiber*, индивидуальная изменчивость, возрастная изменчивость, корреляция, геометрическая морфометрия