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GEOMETRIC MORPHOMETRICS OF GLIRID DENTAL CROWN PATTERNS

Igor Ja. PAVLINOV

ABSTRACT. Variation of dental crown patterns among seven glirid genera (*Myomimus, Peridyromys, Microdyromys, Dryomys, Glirudinus, Muscardinus, Glis*) was studied by means of geometric morphometrics. Rationales for description of this pattern by a set of landmarks are provided and some problems of this concern are discussed. The genera *Muscardinus* and *Glis* are most distinct both from each other and other glirids studied, while *Peridyromys, Microdyromys, Dryomys* and *Glirudinus* are most similar to each other.

Key words. Geometric morphometrics, Gliridae, dentition.

GLIRIDLERDE DENTAL TAÇ DESENLERININ GEOMETRIK MORFOMETRIKLERI.

ÖZET. 7 glirid cinsinde (*Myomimus, Peridyromys, Microdyromys Dryomys, Glirudinus, Muscardinus, Glis*) dental taç desenleri geometrik morfometrikleri açısından araştırılmıştır. Bu desenlerin tanımını açıklamak üzere bir seri işaret noktaları yaratılmış ve bu konuyla ilgili sorunlar tartışılmıştır. *Peridyromys, Microdyromys, Dryomys* ve *Glirudinus* birbirlerine en çok benzeyen cinsler iken, *Muscardinus* ve *Glis* cinsleri hem birbirlerinden hem de incelenen diğer cinslerden en farklı olanlarıdır.

Anahtar kelimeler. Geometrik morfometrik, Gliridae, dental taç desenleri

INTRODUCTION

In the rodent family Gliridae, dental crown pattern is a key morphological character used in taxonomy and stratigraphy. This pattern consists of a set of varying numbers of primary and secondary transverse ridges which undergo the following transformations. They differ slightly in their position and in length, they joint or disjoint at their ends, and some secondary ridgelets may eventually disappear. Traditionally, these variations are described by discrete morphotypes, each reflecting a number of states of a particular ridge. The taxa are compared by the frequencies of the total set of morphotypes recognized for a particular dataset. Needless to say that such comparisons, although numerical (at least in part), are quite rough and subjective, depending on how detailed is prior classification of morphotypes.

During several recent decades, a new methodology of strictly numerical multivariate analysis of morphological structures has been actively developing. It is called *geometric morphometrics* [1]. Its most fundamental idea is to make it possible to compare morphological objects by their shapes regardless of their size. For this, it rejects the standard linear measurements between certain points on the object surface and, instead, employs Cartesian coordinates of these points (called *landmarks*). Thus, the specimens are compared by these coordinates, whose values undergo multivariate analysis that produces so called *shape variables* (here termed *warps*). They are strictly numerical and define a unique position of each specimen in so called *shape space*, which in a sense is analogous to familiar "phenetic hyperspace" studied by standard morphometrics. It is of special importance that at least some of these variables can be treated and manipulated as standard linear traits of the specimens. Theoretical considerations, methodology, and applications of geometric morphometrics can be found elsewhere [2, 3, 4, 5, 6]. Few examples of its application to mammalian dentition could be found in the papers [7, 8].

Zoological Museum, Moscow M.V.Lomonosov State University,
ul. Bol. Nikitskaia 6, 103009 Moscow, Russia.
e-mail: igor_pavlinov@zmmu.msu.ru

Glirid dentition has not been studied from this standpoint, although it looks quite attractive as a potential demesne of geometric morphometrics. A set of ridges constituting the glirid dental crown pattern can be considered as a shape, and the above variations in which these ridges are involved can be considered as shape transformations. Placing the landmarks at certain points of the ridges makes it possible to describe the whole tooth by the set of landmark coordinates, and subsequently to compare different teeth by these coordinates. Thus, geometric morphometrics might provide a very good, and strictly quantitative toolkit for comparative investigations of dental crown patterns in the family Gliridae.

It must be pointed out that, due to some limitations, the entire approach is based on analysis of flat (two-dimensional) projections of the glirid dental crown. So, it is only precise under initial assumption of flatness of the glirid dental crown is correct. Thus, it is does not allow incorporation in analysis such an important feature as concavity of the dental crown in some glirids. Due to this restriction, there is little sense in comparing such genera as, say, *Muscardinus* and *Gliravus* that differ drastically in this respect. However, the glirid teeth with more or less flat dental crowns are directly comparable using a geometric morphometrics approach.

In the present paper, under consideration are two aspects of application of geometric morphometrics to analysis of glirid dentition. First, some rules of placing landmarks on the glirid tooth crown are suggested that take into account discontinuous (from a topological viewpoint) transformations of the crown patterns. Based on these rules, a kind of "pilot study" of variation of the glirid tooth crown is conducted to show the potential of this approach.

MATERIALS AND METHODS

The sample studied includes crown patterns of the first upper molar of glirid genera *Myomimus, Peridyromys, Microdyromys, Dryomys, Glirudinus, Muscardinus, Glis*, each represented by 3 to 7 specimens (34 in total, see Fig. 1). Respective dental images have been grabbed by scanner from the figures published elsewhere [9, 10, 11, 12, 13, 14]. These "real" shapes were redrawn quite schematically in order to reflect basic patterns of the ridges only.

In order to evaluate transformations of glirid crown patterns by means of geometric morphometrics, the following provisions are to be taken into consideration. First, the existing methods allow only comparison of the shapes with exactly the same number of the landmarks. That means, second, that both most complex (with fully developed and completely disjoint ridges) and any simpler (with at least partially joint and disappeared ridges) patterns have to be described by the same number of landmarks. So, third, absent ridgelets are to be incorporated in all analyses, as well.

To do so, these absent (or "virtual") ridgelets were defined arbitrarily as points representing "averages" of respective ridgelets occurring on some teeth. Their imaginary positions on particular crowns was determined after manual alignment of all crown images (using *CORELDRAW*! software) so that their longest anterolabial–posterolingual axes were of the same length and would take the same position on the screen.

In total, 28 landmarks were placed on each drawing to describe glirid crown pattern as a shape (Fig. 2). For each primary (long) ridge, 3 landmarks were used, two of them being placed at the tips and the third placed at an intermediate position. For each secondary (short) ridgelet, 2 landmarks were placed at its tips. To make absent ridgelets fully compatible with the existing ones, each of them was also marked by 2 landmarks placed at one point.

The entire procedure of placing the landmarks was the following. First, all the landmarks were placed on a hypothetical crown pattern with fully developed and completely disjoint ridges and ridgelets deduced from the observed real data (Fig. 2A). This pattern served as the basis for defining position of the landmarks on each particular crown with its particular ridge pattern. In order to reflect joining of the ends of any two ridges, the landmarks denoting these joint ends were assumed taking the same position on the crown (Fig. 2B: landmarks 1,6,11; 16,21,26; 3,8,23,28). The landmarks denoting the point corresponding to an absent ridgelet were treated in a similar way (Fig. 2B: landmarks 4,5; 9,10; 14,15; 19,20; 24,25). For any set of landmarks taking the same position on the crown, whether they correspond to either ridge joint ends or absent ridgelet, they were assigned the same *x,y* coordinates.

Fig. 1. Glirid dental crown patterns used in this study

After the landmarks have been set on each crown, their coordinates were taken from the screen images using the program *TPSdig* [15]. Both these original coordinates and their averages (consensus configurations) calculated for each genus using the program *TPSrelw* [16] were undergone the subsequent analyses. First, relative warps were calculated for the both datasets using the same program *TPSrelw*, with the uniform component excluded as irrelevant, and scaling coefficient α given zero value (for definitions, see [17]). The superimposition of consensus configurations was used to calculate transformation grids which illustrate graphically the differences among particular genera, the program *TPSsplin* [18] was employed.

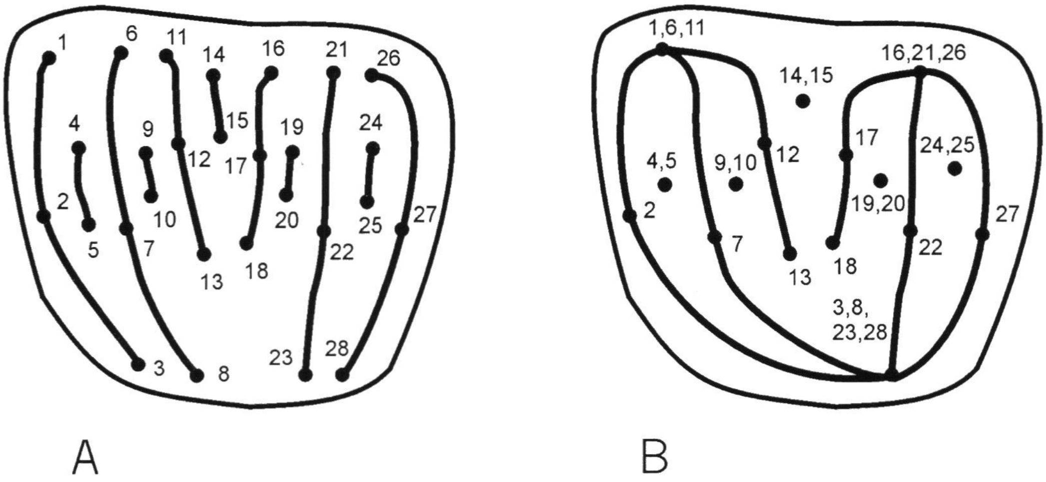

Fig. 2. Position of landmarks on hypothetical dental crowns with fully (A) and minimally (B) developed patterns of ridges and ridgelets

RESULTS AND DISCUSSION

The first two relative warps extracted from individual data explain 42.8 per cent of total variation. Judging by the weight matrix, the first relative warp (24.6 per cent of total variation) is mostly associated with the landmarks 3, 12, and 13, while the second relative warp (18.2 per cent of total variation) is mostly associated with landmarks 16,18, and 24. Thus, the first conclusion is that the main impact on transformations of the first upper molar crown pattern studied here belongs to variations in position of the lingual portion of anteroloph (landmark 3), both anterior (landmarks 12, 13) and posterior (landmarks 16, 18) centrolophs, and most posterior ridgelet (landmark 24). The second conclusion is that changes of anteroloph and anterior centrolophs are just weakly correlated with those of posterior centrolophs and most posterior ridgelet. That is, transformations of the entire crown pattern occur more or less independently in its anterior and posterior parts.

Distribution of individual specimens on the scatter plot of the first and second relative warps (Fig. 3A) indicates that *Muscardinus* and especially *Glis* take the most isolated position among glirids. *Myomimus* is also clearly identifiable, other genera being not distinctly separated from each other. Comparison of respective consensus (average) configurations (Fig. 3B) agrees with this general trend but some details become more explicit. In this case, the first two relative warps explain about 69.8 per cent of the total variation. It is confirmed that *Myomimus* is quite specific by dental crown pattern, although not so much as *Glis* and *Muscardinus* are. On the other hand, the genera *Microdyromys, Glirudinus, Peridyromys,* and *Dryomys* are most similar, especially the last two.

In order to visualize the differences among particular crown patterns, be it individual teeth or their group consensuses, the transformation grid is especially useful (Fig. 4). This grid indicates in which part and to what extent one shape changes relative to another. In the present case, comparison made between consensus dental crowns of glirid genera placed at opposite sides of the 1st relative warp gradient. At the left side of the gradient is *Muscardinus* and at the right side is *Myomimus* (see Fig. 3). The grid in question is orthogonal at the zeroth point of the 1st relative warp axis (Fig. 4A) which corresponds to the overall consensus (average) of all glirid teeth studied. In *Muscardinus* (Fig. 4B), the crown is modified mainly in its lingual portion due to anterior displacement of the landmark 3 and lingual displacement of the landmark 13. In *Myomimus* (Fig. 4C), it is modified mainly in its central portion due to anterior displacement of the landmark 18.

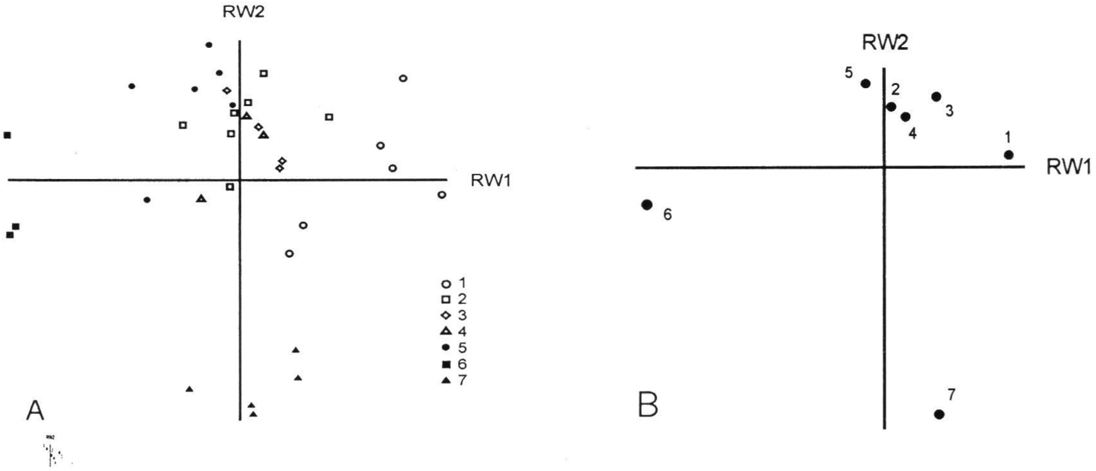

Fig. 3. Scatter plot of distribution of individual specimens (A) and generic consensus configurations (B) in the space of 1st (RW1) and 2d (RW2) relative warps. Genera: 1- *Myomimus*, 2- *Peridyromys*, 3- *Microdyromys*, 4- *Dryomys*, 5- *Glirudinus*, 6- *Muscardinus*, 7- *Glis*

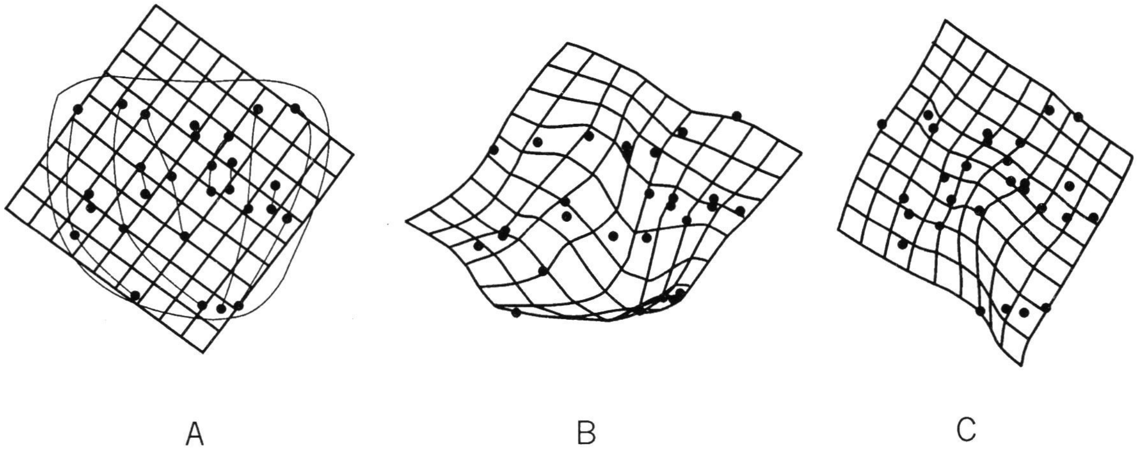

Fig. 4. The transformation grid showing change of dental crown pattern in consensus configuration (A) as it is transformed into *Muscardinus* (B) and *Myomimus* (C) patterns

The similarity relations uncovered by geometric morphometrics do not agree with either of the known glirid classifications. For instance, de Bruijn and Daams [13, 19, 20] placed *Glis* and *Muscardinus* in the same subfamily Glirinae sensu stricto, while the above results indicate they are most dissimilar to each other. On the other hand, the four genera constituting one compact group according to geometric morphometrics of their dentitions (*Peridyromys, Microdyromys, Dryomys* and *Glirudinus*) are placed by these authors into three separate subfamilies. However, it is of interest that within this group of genera, *Glirudinus* shows some similarity to *Muscardinus*, a genus to which it is usually thought to be closely related.

Of course, the results of geometric morphometrics are purely phenetic and do not need to fit completely the "natural" classification burden with phylogenetic information. However, such a drastic contradiction between similarity and taxonomic arrangements deserves special consideration in the future in order to clarify the point. On the one hand, it is evident that geometric morphometrics discards at least some phylogenetically important information, for instance the concave surface of dental crown in some and its plane surface in other glirid genera. On the other hand, it might be that the authors of "natural" subfamilial classifications of Gliridae underestimate at least some differences in the dental crown pattern that become more clear-cut after geometric morphometric analysis.

One very important point of this disagreement is that pure morphometric and phylogenetically sensible descriptions of the dental crown pattern might disagree in establishing homology of at least some elements. For instance, endoloph is considered as one of the key (heavily weighted) characters by phylogeneticists who use it for recognition of some subfamilies [14, 20], while in the above geometric morphometric routine it is treated as just an extension of the anteroloph. So, in future studies special attention is to be drawn to setting up of standards of homology (equivalency) of the landmarks to make geomteric morphometric description of glirid dentition more compatible with phylogenetic one.

CONCLUSIONS

By using geometric morphometrics, it is shown that *Glis* and *Muscardinus* are most unique in respect to their dental crown pattern. Among other genera, *Myomimus* is also characterized by specific dental traits, while other glirids studied are more similar to each other.

Such similarity does not agree with the usually acknowledged subfamilial arrangement of the family Gliridae. One of important sources of this disagreement might be that equivalency of landmarks is not fully compatible to homology of crown elements adopted in glirid phylogenetics.

Thus, geometric morphometrics seems to be most effective in comparison of glirid taxa with not very different ridge patterns in which no problems of equivalency of landmarks occurs.

The problem of fixing disappearing elements on glirid dental crown deserves more detailed analysis. The procedure used above is just intuitive rather than rationally based and requests more formal generalization.

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