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EVOLUTION OF HYPSODONTY IN A CRICETID (RODENTIA) LINEAGE: PRELIMINARY RESULTS USING PATCH ANALYSIS

EVOLUCIÓN DE LA HIPSODONCIA EN UN LINAJE DE CRICÉTIDOS (RODENTIA): RESULTADOS PRELIMINARES UTILIZANDO “PATCH ANALYSIS”

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ABSTRACT

The development of hypsodonty in the Cricetulodon hartenbergeri – Cricetulodon sabadellensis- Rotundomys montisrotundi – Rotundomys bressanus lineage is studied using patch analysis. The lower second molar of a sample of each species is scanned using a 3D laser scanner. Then, the scans are processed with GIS software which provides orientation maps of the slopes of the occlusal surface. Contiguous points with the same orientation are grouped into a ‘patch’ that represents a functional structure of the molar crown, so the number of patches relates to dental complexity. This parameter is found to decrease in the lineage coupled with increased crown height. This is interpreted as a result of the evolution of crown planation and loss of cusp interlocking in Rotundomys.

Palabras clave: Morfología funcional, “patch analysis”, Rodentia, Cricetidae, Cricetulodon, Rotundomys, Mioceno, Cuenca del Vallès-Penedès.

RESUMEN

Se estudia el desarrollo de la hipsodoncia en el linaje Cricetulodon hartenbergeri – Cricetulodon sabadellensis – Rotundomys montisrotundi – Rotundomys bressanus mediante “patch analysis”. Para ello se ha escaneado mediante un escáner 3D el segundo molar inferior de una muestra de cada especie. Los escaneos son procesados mediante programas de GIS los cuales permiten obtener un mapa de orientación de los pendientes de la superficie oclusal. Los puntos contiguos con la misma orientación son agrupados en un “patch” que representa una estructura funcional de la corona, de modo que el número de “patches” se relaciona con la complejidad dental. Dicho parámetro decrece en este linaje conforme incrementa la altura de la corona. Esto se interpreta como resultado de la evolución de una superficie de desgaste plana y a la perdida de la oclusión inter-cúspides en Rotundomys.

Keywords: Functional morphology, patch analysis, Rodentia, Cricetidae, Cricetulodon, Rotundomys, Miocene, Vallès-Penedès Basin.

1. INTRODUCTION

1.1. HYPSODONTY IN MAMMALIAN HERBIVORES

The acquisition of a hypsodont dentition is a classic example of evolutionary process among mammals (Janis, 1988; Fortelius, 1985). Hypsodonty refers to the tooth crown height (the higher the crown of the tooth is the more hypsodont the animal) and is considered to be an adaptive response to cope with the excessive rates of dental wear brought about by a new diet (grazing) in more open and dry environments (grasslands).

Although there is an ongoing discussion on the causes behind hypsodonty, silica phytoliths and fiber of grasses (McNaughton et al., 1985), exogenous particles (grit and dust) attached to the vegetation (Williams and Kay, 2001; Mendoza and Palmqvist, 2007), and higher masticatory efforts as a result of low-nutritional foods (Janis, 1976)
Hypsodonty has been acquired independently by several mammalian herbivores, particularly during the last 20 million years. Interestingly, a number of lineages of rodents have also experimented a convergent evolution toward increased crown height (Mödden, 1994). Hence, and since rodents are the more diversified of all mammalian orders and show an equally diverse suite of feeding specializations (seeds, fruits, grass, tubercles and roots, insects or even fish) and morphological modifications, they constitute a relevant group for the study of hypsodonty within the context of morphological, dietary and environmental changes.

Cheek teeth of rodents include an astonishing array of different morphologies from the simple molars of the piscivore species that consist only in shallow basins surrounded by cutting edges to the incredibly complex molars of the hazel dormouse with many parallel ridges, or the lamellar molars of the capybara, just to cite two examples. The same dietary adaptations have appeared independently in different rodent families, and the evolution of increasingly hypsodont molars is not an exception. High-crowned molars have arisen convergently in almost every rodent family, sometimes more than a single time within the same family.

1.2. THE ‘MICROTOID CRICETIDS’

During the Late Miocene several unrelated muroid rodents developed higher crowned molars almost simultaneously. These muroid lineages include murids (rats and mice), gerbillids (gerbils) and a number of cricetids (relatives of hamsters and New World rats and mice) that comprise the genera Microtocricetus, Microtodon, Anatolomys, Microtoscopes, Ischymomys, Celadensia, Blancomys and Rotundomys. The emergence of the arvicolid (voles), perhaps one of the muroid groups where the development of hypsodonty is taken further, by the Late Miocene (Martin, 2008) may be seen as part of this radiation as well. Schaub (1934) coined the nontaxonomic term ‘microtoid cricetids’ to refer to all the Late Miocene and Early Pliocene (e.g. Trilophophymys, Bjornkurtenia, Baranomys) cricetid genera that developed similar hypsodont teeth with a lophodont occlusal pattern. This parallel development of hypsodonty may have been related to the consumption of more fibrous, less nutritive vegetal material, such as grasses, but this hypothesis has not been formally tested. The Late Miocene coincides with the time of major expansion of grass-dominated ecosystems in Eurasia (Quade and Cerling, 1995; Cerling et al., 1997; Jacobs et al., 1999). Grasslands now occupy wide areas of central Asia, defining a wide and continuous belt from the shores of the Yellow Sea to those of the Black Sea. However, major grass-dominated ecosystems never extended across the Mediterranean regions (Jacobs et al., 1999), so the evolution of hypsodonty in certain ‘microtoid cricetids’, such as Rotundomys and Microtocricetus, could be related to other factors.

Rotundomys is one of the first ‘microtoid cricetids’ (only Microtocricetus occurs in older deposits) which is only known from the Late Vallesian (MN 10) of France, Spain and Portugal. It is believed to have evolved from the more widespread brachyodont genus Cricetulodon (Freudenthal, 1967) that ranges from the Late Aragonian (MN7+8) in Turkey (Ünay et al., 2003) to the Middle Turolian (MN12) in Spain (Freudenthal et al., 1998). The genus Rotundomys developed higher crowned molars with a simpler lophodont occlusal pattern as compared to Cricetulodon. The wear surface in Rotundomys is completely plane whereas Cricetulodon shows crested to terraced molars (terminology for dental planation follows Hershkovitz, 1967). The development of flat wear surfaces in the rodent molars has been related to the simplification of the chewing stroke, which originally consisted of two phases (buccal and lingual) with cusp interlocking, to a single oblique or propalinal stroke with no cusp interlocking (Butler, 1980, 1985; Lazzari et al., 2008).

Two different Rotundomys lineages are known. The first one is a small-sized one of rather unknown phylogenetic relationships that includes R. freirenensis and R. mundi from Portugal and Spain, respectively. The second one, is known from France and Catalonia only, and includes the larger-sized species Rotundomys montisrotundi and Rotundomys bressanus. Freudenthal (1967) was the first to establish the phylogenetic lineage Cricetulodon hartenbergeri – Cricetulodon sabadellensis – Rotundomys montisrotundi in which each successive species would show increasingly hypsodont teeth coupled with a progressively simplified lophodont pattern. Later on, Mein (1975), added a last member to this lineage, Rotundomys bressanus, which he wrongly interpreted as a missing link between cricetids and arvicolids. This well-defined lineage has been confirmed by successive reviews of the genus and its phylogenetic relationships (see for example Freudenthal et al., 1998). Nevertheless, there are still many unanswered questions regarding the evolution of hypsodonty in this cricetid lineage: the chewing stroke was oblique or propalinal? when was cusp interlocking lost? did this imply any change in the masticatory muscles? to which dietary changes (grass-, fruit- or leaf-eating) was it related?

In order to answer all these major questions we have designed a multiproxy study of these rodents that will make use of all the techniques that have been successfully applied to the study of feeding specializations in the dentitions of larger mammals (dental microwear, analysis of the stable isotopes in tooth enamel, geometric morphometrics and 3D modelling of teeth). Here we present our preliminary results of the application of 3D modelling and GIS (Geographical Information Software) to study the complexity of the dental pattern of these rodents by the means of the patch analysis technique (Evans et al., 2007).
2. MATERIAL AND METHODS

2.1. STUDIED SPECIES AND PROVENANCE OF THE MATERIAL

The studied material comprises complete molar series as well as isolated molars that belong to four different species C. hartenbergeri, C. sabadellensis, R. montisrotundi and R. bressanus. All the specimens are housed within the collections of the 'Institut Català de Paleontologia' (ICP) and were recovered from different Vallesian sites of the Vallès-Penedès Basin. The Vallès-Penedès Basin is a relatively small and elongated half-graben that is situated between the Catalan Coastal Ranges, thus being parallel to the Catalan coastline. This basin originated as a result of an extension episode that affected much of the Western Mediterranean during the latest Paleogene and the Neogene and was filled mostly during the Miocene by continental sediments (see Cabrera et al., 2004). The Miocene Vallesian successions have been particularly well studied and have delivered an important number of rich sites for which an accurate dating on the basis of bio- and magnetostratigraphy is available (Agustí et al., 1997). The specimens analyzed come from four different sites: Can Ponsic (C. hartenbergeri; Hartenberger and Crusafont, 1979), Can Llobaters 1 (C. sabadellensis; Hartenberger, 1965), Rubi-Terrassa motorway site 11 (R. montisrotundi; listed as sp.nov for Agustí et al., 1997) and Torrent de Febulines 3 (R. bressanus; Agustí and Gibert, 1982). Can Ponsic and Can Llobaters 1 are placed in the Early Vallesian, although Can Llobaters 1 is certainly younger, with an estimated age of 9.5-9.7 Ma (Agustí et al., 1997). The Late Vallesian site of Rubi-Terrassa is somewhat younger than Can Llobaters 1 (9.3-9.5 Ma) whereas Torrent de Febulines 3 belongs to the latest Vallesian (9-8.7 Ma).

2.2. TOPOGRAPHIC MODELS OF MOLAR CROWNS AND MEASUREMENT OF DENTAL COMPLEXITY

In this preliminary study just one lower second molar (m2) of each one of the four species is studied in order to test the validity of the methods. The study focuses on the m2 because these teeth show an intermediate wear stage, and microwear pattern, between the first and the third molar.

The methods for generating the 3D elevation models, to build topographic and orientation maps and to calculate measures of dental complexity are after Evans et al. (2007). First, the teeth were scanned using a 3D laser scanner Hawk Nextec at the Viiki Kampus of the University of Helsinki. The scanning resolution is 10 μm. In order to avoid sparkles and obtaining clearer pictures the teeth were covered with powdered talcum spray. The molars were oriented according to their mesio-distal axis and inclined to maximize crown-base projection. The scans were plotted using Surfer for Windows (Golden Software, Inc.). Image size was standardized by re-gridding the initial scans to a resolution of 150 data rows so all the teeth were scaled to the same length. Then, topographic and orientation maps of the molars were generated using a GIS software written by one of the authors (A.R.E; see also Evans et al., 2007). Using the same software orientation maps were generated after calculating the slope direction for all the points with a minimum slope of 10 degrees in the topographic maps. Then, these slopes were

Figure 1. Molar complexity in the Cricetulodon-Rotundomys lineage. Three-dimensional occlusal reconstructions, patch maps and rose diagram for slopes directions of a second lower molar (m2), the number of patches is also indicated. A) Cricetulodon hartenbergeri. B) Cricetulodon sabadellensis. C) Rotundomys montisrotundi. D) Rotundomys bressanus. The Cricetulodon sabadellensis specimen is a right m2 that has been reversed and the Rotundomys montisrotundi specimen and their respective rose diagrams have been slightly rotated for the sake of comparison.
classified into 8 different categories of orientation, each one covering 45º (see Fig. 1). The maps of the rodent molars were divided into different patches that result from grouping contiguous points with the same orientation as a patch (Fig. 1). This was done using the OPC (Orientation Patch Count) algorithm with a minimum patch size of 15 points. The measurement of OPC can be used as a measure of dental complexity since it can be interpreted as the number of functional areas or ‘tools’ in the molar crown used to process food items. This functional complexity is thought to be related to the dietary habits so the ingestion of foods that require more mechanical processing result in more complex molar morphologies (Evans et al., 2007).

Tooth wear is known to alter crown topography. This is not very important in molars with a flattened crown (Hershkovitz, 1967) but it dramatically alters the topography of cuspidate molars (see Lazzari et al., 2008 and references therein). In our case, Cricetulodon has cuspidate molars and in order to compare the different specimens it is mandatory to take into account the degree of wear since it may have profound effects on the measure of dental complexity. Therefore, and after excluding unworn teeth as well as specimens in very late wear, we have established three very broad categories of tooth wear: 1) nearly unworn teeth displaying wear only on the tips of the main cusps; 2) wear exposes a wide area of dentine in the main cusps and also affects the ridges connecting these tubercles, eventually exposing a narrow dentine band in the ridges; 3) worn molars with wide dentine areas exposed in the main cusps and ridges. In our analyses we have only considered molars in wear stage 2. This wear stage is chosen because of the availability of specimens. A subdivision of the degree of wear into more than three categories may be possible, especially in the case of Cricetulodon. This question as well as the intra-specific variation in the number of patches between the categories of dental wear is going to be approached in forthcoming studies.

3. RESULTS

Fig. 1 shows the number of patches for the m2 of each one of the species considered. The number of coloured patches is indicated below each one of the figures so it can be appreciated that it decreases throughout the members of this lineage. C. hartenbergeri shows 129 patches, C. sabadellensis 128, R. montisrotundi 91 and R. bressanus 87. While the number of patches is almost identical in the two Cricetulodon species it is markedly lower in Rotundomys, especially in R. bressanus. Dental complexity, measured by OPC, seems to decrease with increasing hypsodonty in this cricetid lineage.

4. DISCUSSION

The evolution of the C. hartenbergeri – R. bressanus lineage implies the increase of tooth crown height, the development of a flat wear occlusal surface (implying no cusp interlocking) and a reduction in dental complexity in the m2 of Rotundomys. The evolution of crown planation results from a progressive change in the shape of the cusps and crests so their walls tend to become more vertical (Lazzari et al., 2008). Since dental complexity is measured as the number of orientation patches (OPC) it is expected that this parameter will show lower values in plane (sensu Hershkovitz, 1967) molars as compared to crested or terraced ones because the diversity of orientations is reduced and all the slopes approach 90º. The evolution of simpler dental morphologies is known to have evolved in association with increasing hypsodonty in lineages from several rodent families, including the theridomyids (Hautier et al., 2010), cricetids (Hershkovitz, 1967) or the heteromyids (Wood, 1935) just to cite some examples. In these rodent families increasingly hypsodont teeth are supposed to have evolved in relation to an increased intake of grasses and abrasives, so in the more hypsodont species the proportion of more though and fibrous plant materials and exogenous particles is greater. Evans et al. (2007) found that the complexity of molar morphology was greater in herbivorous Rodentia and Carnivora as compared to carnivorous ones. The OPC values obtained for C. hartenbergeri and C. sabadellensis fit within the range of values for omnivore Rodentia as calculated by Evans et al. (2007, fig. 2), even though they are close to the lower boundary. Quite surprisingly, the OPC values for R. montisrotundi and R. bressanus are below the range of rodents and fall within those of carnivore Carnivora (Evans et al., 2007, fig. 2). This discrepancy with the results of Evans et al. (2007) may be related to the fact that these authors considered the whole molar series whereas we are just considering a single molar. Furthermore, it could also be related to the fact that these authors only included a few relatively hypsodont species in their sample of 49 muroid species. That work just considered three muroid subfamilies, namely the sigmodontids, the otomyids and the murids, discarding markedly hypsodont muroid families such as the arvicolid and the spalacids (blind mole rats). This question cannot be solved for the moment since it requires the collection of new data for both extant and fossil specimens.

As we have already exposed, simplification of the dental morphology can also be related to the loss of cusp interlocking and to a change in the orientation of the chewing stroke from two-phase ectetal movement (see Butler, 1980, 1985) to a more oblique or even propalinal stroke. On the basis of dental microwear analyses and cusp orientation (measured using different methods) Lazzari et al. (2008) have shown that R. montisrotundi had an oblique chewing stroke. The more advanced R. bressanus may have also had an oblique stroke or a propalinal one, but this question will be approached in forthcoming studies.

5. CONCLUSIONS AND FUTURE PROSPECTS

Our results point towards a reduction of dental complexity coupled with the evolution of hypsodonty and planation in the C. hartenbergeri – R. bressanus lineage. This simplification of the tooth pattern may well be related to the development of a flat wear surface (which requires
the slopes of the main cusps and ridges to be vertical according to Lazzari et al., (2008) and to the loss of cusp interlocking as well. Nevertheless, our results are still too preliminary to provide a cogent answer to this question and further analyses in combination with other methods, such as dental microwear analyses, will be required. Furthermore, it will be of the greatest interest to compare the development of hypsodonty in this lineage with the evolution of hypsodont teeth in other muroids to investigate if this reduction in dental complexity is a generalized rule.

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