

The hexagonal lattice marks in the muroids rodent explain molar-cusp enamel line

La morfología de la línea de esmalte en los molares de los roedores muroideos es explicada mediante una red hexagonal

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ABSTRACT

The crown enamel line of muroids rodent has geometric traces that coincide exactly with an equilateral triangular lattice. This finding helps to explain the muroids dental pattern from a novel perspective in molar morphology that it is based on hexagonal structures. The adult traces imply that the morphology of the teeth mammals is consequence of a morphogenetic process. This is the study of the hexagonal lattice marks observed in the enamel line, and therefore called odontohehexasymmetry.

The particular dental pattern, which it is passed down from parents to offspring, it start with a genetic algorithm coded in DNA. This includes a system of intelligent self-control, which during the morphogenesis coordinates the morphology of the all teeth of a specimen to get the best occlusion.

The hypothesis of mitosis area loop-development (Ruiz Bustos, 2004a, 2005, 2006 and 2007) explains that in early morphogenesis stage, the initial mass-cell (basal mitosis area), it is repeated in a loop, thereby forming all other mitosis areas of the tooth. At the end of the morphogenesis, the biomineralization processes transform the mitosis areas in the cusps crown.

Key words: Muroids, mammals, tooth, enamel, systematic, phylogeny.

RESUMEN

La línea de esmalte observada en la corona de los roedores muroideos tiene formas geométricas que coinciden exactamente con una red plana triangular equilátera. Esta conclusión ayuda a explicar el modelo dental de los muroideos con una nueva perspectiva denominada odontohehexasimetría, fundamentada en las formas hexagonales observadas en la línea de esmalte.

La morfología de la corona del diente de los mamíferos es heredada de padres a hijos. Esto infiere la existencia en cada espécimen de un autocontrol inteligente codificado en el genoma, que coordina la morfología de los dientes durante el desarrollo embriológico y su oclusión.

La hipótesis del desarrollo el bucle de las áreas de mitosis (Ruiz Bustos, 2004a, 2005, 2006 y 2007) propone, que en los momentos iniciales de la morfogénesis, es observada una masa de células en mitosis (área de mitosis de basal). Esta es repetida en un bucle, hasta constituir todas las restantes áreas de mitosis del diente. Al final de la morfogénesis, el proceso de biomineralización transforma las áreas de mitosis en los tubérculos de la corona del diente.

Palabras clave: Muroideos, mamíferos, diente, esmalte, sistemática, filogenia.

Introduction

The mammal tooth is a morphological and ecological function system made up of mineralized tissues that is not modified once it is fully formed,

because the teeth have to be functional in the adult, they cannot be deformed by mechanical pressures, and they must be wear resistant.

The mammal dental pattern is a relevant topic in studies of taxonomy and in consequence, in phy-

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logeny, because it is specific to each specimen, it has a genetic component that we can observe in the morphological continuity from parents to offspring, and on the geologic time scale, it is a morphology frequently retained by sediments.

The ecological function role of molars is indispensable for transforming food into the energy required for biological activity. Mammals use the mechanical contact of teeth to capture and grind food. This function depends on the biomineralization of embryonic cell masses in order to exert and tolerate mechanical pressure.

The literature on the comparative morphology of the molars of the mammals has the objective of clarifying their origin and evolution, but the analysis of the mammal phylogenetic hypotheses, even in the phylogenies documented with the best fossil and living collections, that they have been expressed over the past century; it shows a constant presence of uncertainties, confusions and conflicting taxonomic views, that they are summarized as taxonomic anomalies.

The criterion used to support the validity of a phylogenetic hypothesis is that: the best phylogenetic hypothesis is the least possible number of taxonomic anomalies. This criterion calls for continuous revision of hypotheses in light of another with a lesser number of anomalies, or for the researcher to infer that the anomalies are of minor significance.

The rodents of the great Muroidea superfamily Miller and Gidley, 1918, is a typical example of the difficulties involved in the establishment of phylogenetic relationships in terms of diversifying dental models, which stands as the factor most probably responsible for their evolutionary success. Despite advances regarding the muroids phylogenetic relationships propose by Simpson, (1945), Hooper and Musser (1964), Chaline *et al.* (1977), Carleton and Musser (1984), Flynn *et al.* (1985), Musser and Carleton (1993), Michaux *et al.* (2001), Jansa and Weksler (2004), Steppan *et al.* (2004), and Musser and Carleton (2005), uncertainties remain.

Given such circumstances, the objective in this note is: how is possible for us go out of criterion of the lesser number of taxonomic anomalies, and we look for other perspectives? We start with the marks in the enamel line the tooth crown shows in the muroids (fig. 1, 2 and 3), that they are understood as concrete examples of hexagonal lattice marks. In this context, the hexagonal morphologies crown are

linked with the data of embryo teeth morphogenesis, with the aim to infer the exactly process that endows the adult molar the capacity to acquire the specific morphology in its enamel line. The consequences are to expound the underlying study method, to be able to identify genetic characteristics in an adult molar, besides in light of the morphologic data of the adult crown, to explain how these characteristics are inherited by the offspring. This allows a biological hierarchy to be established for the tooth enamel line features used in taxonomy. This break with the traditional opinion, which believes that: the best taxonomic criteria are the most frequent and specific characteristics in our fossil collections.

Material and Methods

The teeth studied are identified through a key integrated by the following items: 1) Collection n°. 2) Type of molar. 3) Linnaean taxonomy name. 4) Traditional literary name of the site. 5) Coded (symbol) name site, including the geological age expressed in Biozone-Mark (Ruiz Bustos, 2004b). 6) The institution to which the tooth belongs.

The keys of the teeth studied in this note and methods, they are the following.

1. The arviculids: *Ca.128*; m1 left; *Microtus brecciensis*; Cueva del Agua site; 20-1, Cag; Instituto Andaluz de Ciencias de la Tierra, or I.A.C.T. (fig 1).

2. The cricetids: *Y.033*; M1 left, and *Y.043*; m1 right; *Alloricetus bursae*; Yedras site; 20-2,Y; I.A.C.T. (fig. 2).

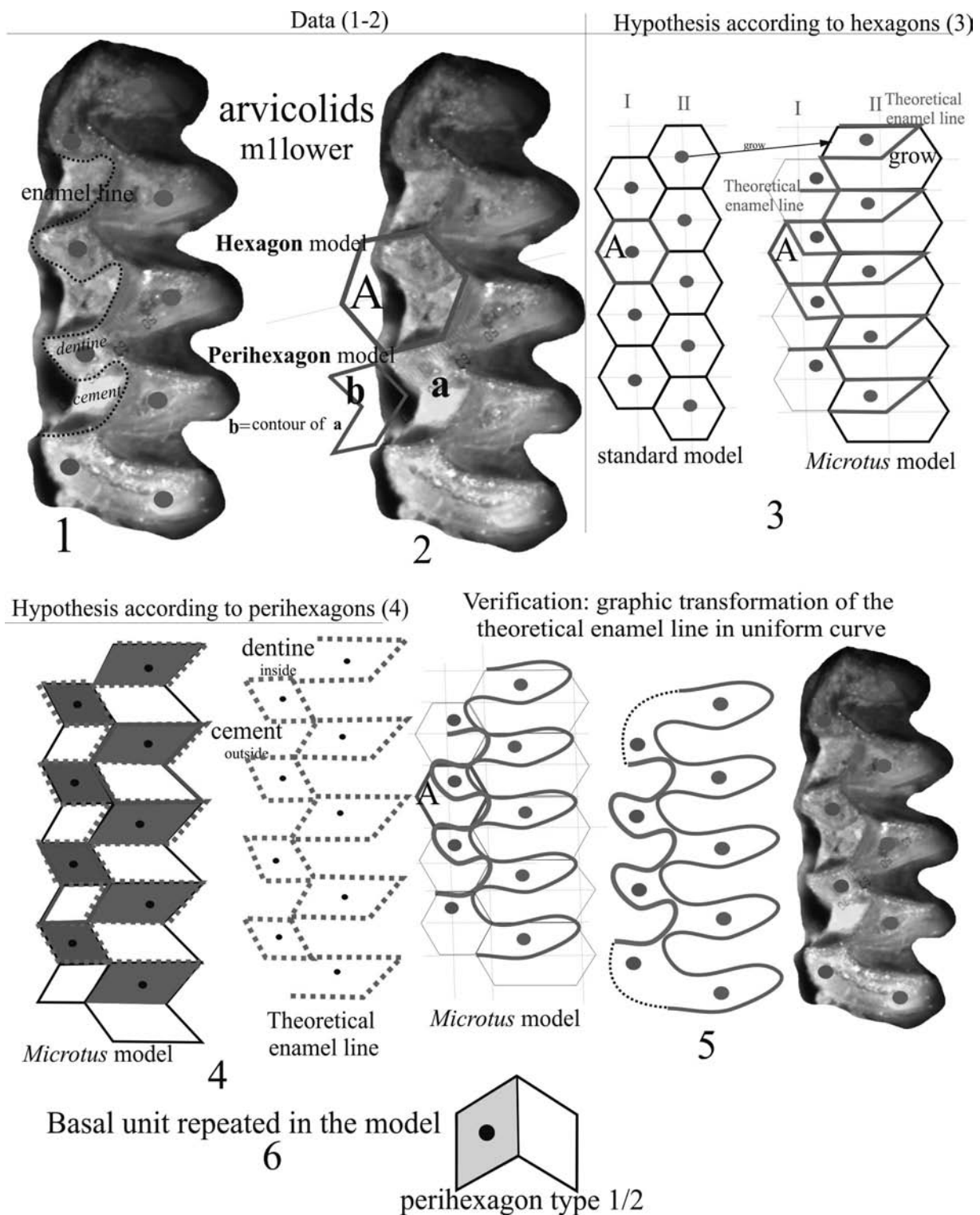
3. The murids: *G-8*; M1 left (holotype), and *G-10*; m1 left (paratype); *Apodemus gorafensis*; Gorafe-A site; 14-2 GoA; I.A.C.T. (fig 3). This species lived during the Pliocene, and its molars have been picked up frequently in over a hundred sites, distributed anywhere from the Iberian Peninsula to central Asia and the Indian subcontinent.

Methods

Superimposition technique

It consists of a digital picture of the molar crown, upon which a hexagonal lattice or equilateral triangular lattice is overprinted, to make evident hexagonal marks in the molar enamel line (Ruiz Bustos 2005, 2006). In any molar, even those undergoing major anomalies during embryonic development, the use of superimposition techniques will reveal marks of hexagonal symmetry in the crown enamel line.

Empirical estimates of the superimposition technique based on dermoskeletal structures from the most primitive fossil dermal scales of fish to the molar cusps of living mammals, applied over geometrical networks of points, indicate that the structures of the dermoskeleton seem to reflect a geometrical hexanet model or hexagonal lattice ($a=b$; $g=60^\circ$), and if we



from data (1, 2) are inferred the hypotheses (3, 4)

Fig. 1.—Data and hypothesis on the lattice hexagonal marks in crown molar (m1) of the *Microtus brecciensis*. The enamel line shows the repetition of perihexagon elemental unit. This has six sides like a hexagon, but one of the vertexes of a hexagon moves up to occupy the centre of the hexagon.

learn to look in mammal teeth, frequently we will discover to cusps with regular faces, that they are identical as crystals of the hexagonal system.

Retrogermination technique

The mechanical sections of molars from top to base, they allow us to describe the geometry of the enamel line in wear-sections of individual cusps. This shows circles of dentine and its geometrical centres, radii, etc. delimited by the circumference sections formed by each cusp of the enamel line. Geometrical analysis shows all these morphological elements of each cusp enamel line to obey euclidian geometrical principles. In the case of ringed enamel line, formed by the fusion of two or more cusps, the arc enamel line corresponding to each of the fused cusps is conserved, and so, this can appropriately be called the principle of cuspidal enamel-line continuity.

The role of the retrogermination technique is born of the fact that we should not forget: the wear-sections is the permanent effect of the embryo morphogenesis in the adult crown.

The retrogermination technique from the crown can be corroborated by findings from embryonic studies. They was formulated by Osman and Ruch (1976), Vaahtokari, *et al.* (1996), Keränen *et al.* (1998), Jernvall and Thesleff (2000), Jernvall *et al.* (2000) and Frade González *et al.* (2001).

The hexagonal lattice enamel line marks observed in muroids

The morphology of specimen *Ca.128*, belonging to *Microtus* (arvicolid), is the starting point for a description of the hexagonal marks of the enamel line revealed by the superimposition technique, because it provides geometric evidence of the contour of a specific polygon, which is repeated, as the elemental unit in the crown of molar m1 *Ca.128* (fig.1). It has six sides like a hexagon, but one of the hexagon vertices moves up to occupy the centre of the hexagon. This polygon may be called a perihexagon (Ruiz Bustos, 2006).

The enamel line in the *Microtus* crown divides the perihexagon in half, into two rhombuses; one of them has dentine inside the enamel line, the other cement outside. The perihexagon model observed in molar *Ca.128* is therefore called: perihexagon-type 1/2.

If we do not first see the perihexagon in the m1 of *Microtus*, then it is more difficult to see the perihexagon as an elemental unit in the *Allocricetus* (cricetids), teeth: *Y.033* and *Y.043* (fig. 2), because the hexagonal marks observed in the *Allocricetus* crown are the result of a process of adapting six perihexagon to alveolar territory of the molar. This process consists of including six perihexagons that are partially overlapped. Consequently, each perihexagon is divided into four equilateral triangles, one of them always surrounded by the enamel line. The specific model of perihexagon observed in *Allocricetus* tooth is thus denoted perihexagon-type 1/4 (fig. 2).

The superimposition technique used in M1 of *Apodemus gorafensis* (G-8) (fig. 3) shows a (α 1) enamel line. This is an enamel line fragment that distributes cusps T4, T5, and T6 inside an equilateral triangular lattice. The T5 cusp verifies the equilateral triangular lattice, as the enamel line in the distal part of T5 is a straight line, while on the contrary, the T5 enamel line in its proximal extreme bends to shape a (U), although the enamel line is much thicker. It would therefore appear to be an indirect mark, indicating the push of the proliferation-cell vector to obtain complete occupation of its hexagonal hole during morphogenesis. The existence of an equilateral triangular lattice is evidenced when the (α 1) enamel line is repeated twice, in the proximal and distal lophes. The α 2 is shown to have the opposite orientation in the crown.

The *Apodemus gorafensis* (G-10) is a lower molar (m1) (fig. 3), which shows a couple of cusps in each transverse loph. Through superimposition, the contour of each couple of cusps consistently shows ten reference points in relationship with two crossed rhombuses of the equilateral triangular lattice. They are referred to as the (β) enamel line. It is significant that the rhombuses overlap when the jaw cannot increase its width, yet not in any other circumstance. This leads one to infer that the β enamel line is an indirect mark, demanded by the narrowness of the jaw.

In the maxillary space, the cusps molar of the muroids and cricetids are limited into a hexagon as a barrier, but in arvicolid, the hexagon barrier breaks, and the cusps molar numbers can be much bigger than six, in theoretical meaning can be limitless. This is interpreted as a progress in the phylogeny of herbivore, and this is a premise to favour that arvicolid are descending of a group with hexagon as a barrier. For example, cricetids.

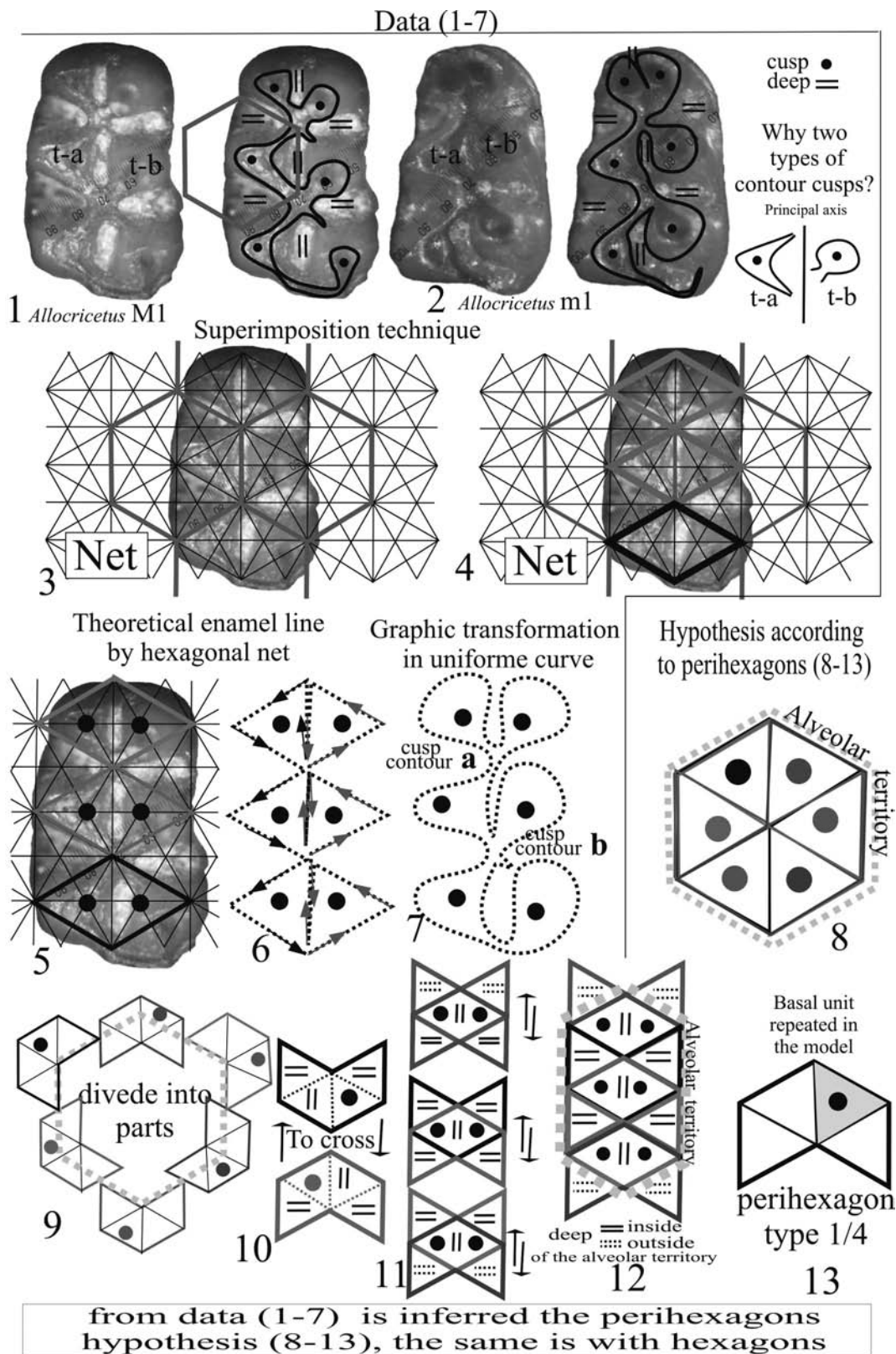


Fig. 2.—Data and hypothesis on the lattice hexagonal marks in crown molars (M1 and m1) of the *Allocricetus bursae*. The crown morphology results from the overlapping of six perihexagons in adaptation to the alveolar space.

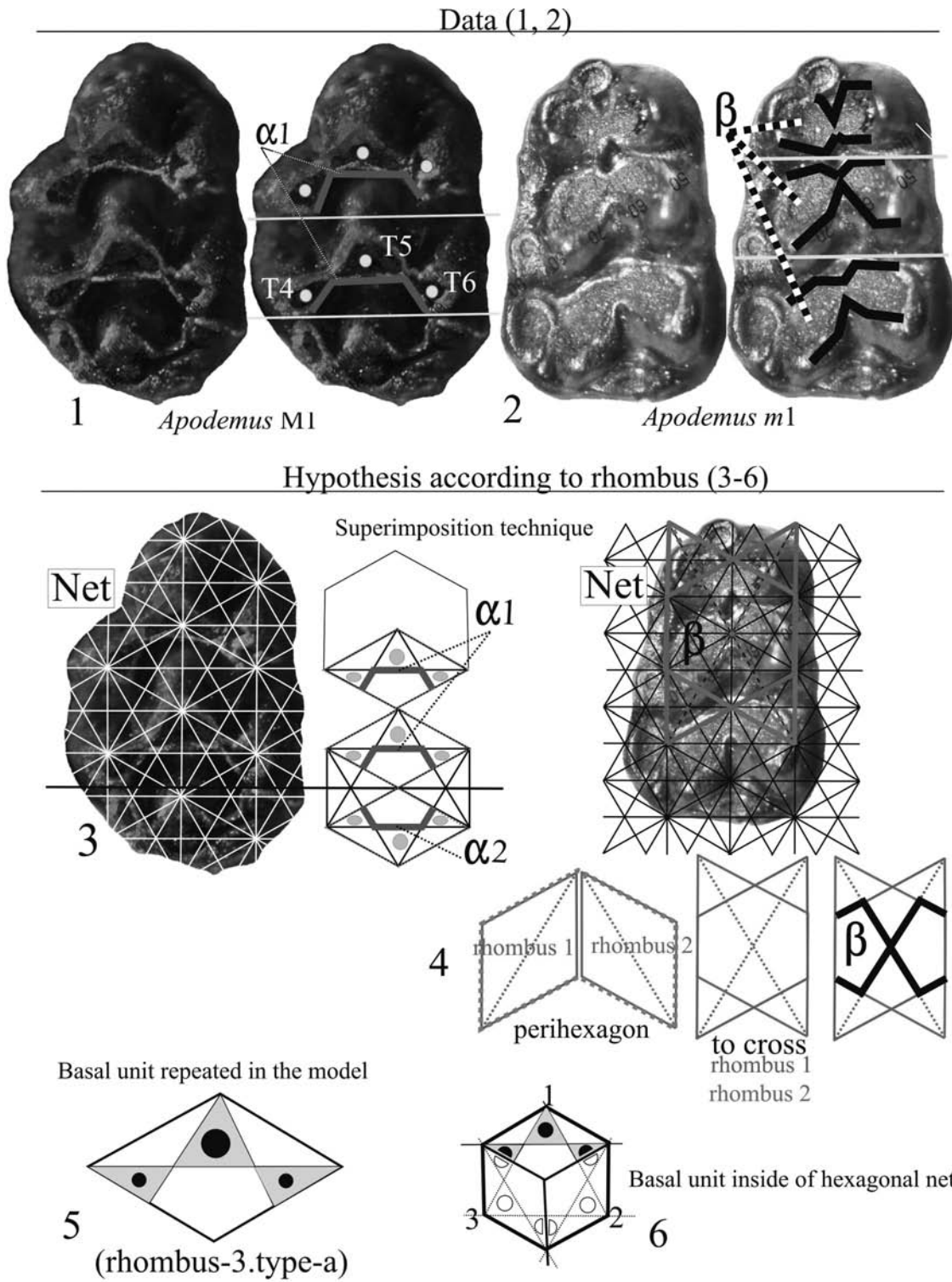


Fig. 3.—Data and hypothesis on the lattice hexagonal marks in crown molars (M1 and m1) of the *Apodemus gorafensis*. The morphology ($\alpha 1$) in the enamel line is the eminent witness of the hexagonal mark in the tooth crown.

Hypothesis of mitosis area loop-development

Mitosis area concept

When I observe in the teeth collection, that perihexagon-type 1/2, perihexagon-type 1/4, (α) and (β), both as morphologies of the rhombus-3 type-a (fig. 1, 2 and 3), they are passed down from parents to offspring and in successive fossil populations, I have two options: one, this is a biological question and is not a paleontological problem, other, if the science of palaeontology increases more and more biological data on the fossils morphologies, why not a cusp of a fossil tooth can be biologically interpreted using the principles of Comparative Morphology? I am follower of the second opinion.

In relationship with de second option, and in living mammals in order to more clearly understand the cell-proliferation processes occurring during cusp genesis, I stain sections of lab mice embryos, with basic colorants and easy color techniques to distinguish mitotic cells. The results of author experience are: in the mesenchyme of the dental lamina, during the early embryo, more or less in the Bud stage, the first stain is drawn by numerous cells in mitosis, and it is associated with the primary enamel knot from the epithelium. Further dermal stains with intense mitotic cells become visible in succession during morphogenesis, and each one are associated with a secondary enamel knot (Vaahokari *et al.*, 1996; Keränen *et al.*, 1998; Jernvall *et al.*, 2000; Jernvall and Thesleff, 2000, Ruiz Bustos, 2007 in the Plate, 1) and (fig. 4.3).

More data is obtained on dental embryos cultured in vitro, they indicate that if these are not supported on a solid substrate, or at least a semi-solid one, their dental embryo mesenchyme becomes disorganized, because in a liquid culture-medium proliferating cells in mitosis encounter no obstacles to growth in all directions (Osman and Ruch, 1976).

And to understand better dental stains with intense mitotic cells, it is helpful to compare the dental stains through basic staining of salivary gland tumours (Frade González *et al.*, 2001). Both show spatial continuity within their perimeter. Furthermore, stains of mitotic cells and tumours succeed in occupying the maximum space available in the embryo, adapting their theoretically circular contours to the available shape of the embryo. This adaptation is determined by the fact that, upon encountering obstacles, the contours undergo elastic

deformation without breaking. Finally, in these cell masses, a model of growth by means of mitotic proliferation can be discerned, where pressure is exerted by outer cells needing space to divide, and they thereby limit the space of inner cells, which in turn reduce their mitotic rhythm for lack of space.

If the contours of the mitosis areas undergo elastic deformation without breaking, this is a fact to infer the starting point of the polarity hypothesis of the mitosis area. They are the following: a) the embryonic masses push against the contour of the mitosis area without breaking the contours or penetrating them, because the cells of the contour are joined with polarity, b) the order shows that the enamel prisms during secretion and maturation phases need a polarity reference in the mitosis area contour; and c) all dermoskeletal elements of the vertebrates have orientation, indicating polarity.

When in living rodents, I understand that molar cusps must need to grow in some moment during morphogenesis, because they have to be formed of something, and then, I see stains of the mass-cells in continuous expansion due to cell proliferation, I infer the mitosis area concept, and I understand the fact that the mass-cells stains are ultimately responsible for the tooth phenotype (fig. 4). An indirect argument regarding the relationship of the dermal stains with the cusps crown, it is that the final number of main stains observed in a tooth is always equal than the number of principal cusps present in the crown (Ruiz Bustos 1987, 1988, 2004, 2005, 2006, 2007).

I need a name to identify each cell mass stained that they are the origin of cusps. The first stain is named: the basal mitosis area. The next dermal stains with intense mitotic cells that they appear during morphogenesis on the position of basal mitosis area, each one is named as: mitosis area.

The conclusion arrives from the addition of the next three data: 1. The observation in the teeth collection the data: Perihexagon-type 1/2, perihexagon-type 1/4, (α) and (β) morphologies of the rhombus-3 type-a. 2. The fact that the mineralized tissues are not modified once they have completely formed in the embryo; that is, the enamel line preserves the morphology of the embryologic cellular masses that it covers. 3. The observation about that each cell mass stained in the embryo, it occupies the place corresponding to a cusp in the tooth crown. These three data, allow me infer that the enamel line is a witness of tooth morphogenesis. Therefore, in wear-sections of individual cusps, the

Hypotesis of mitosis area loop-development

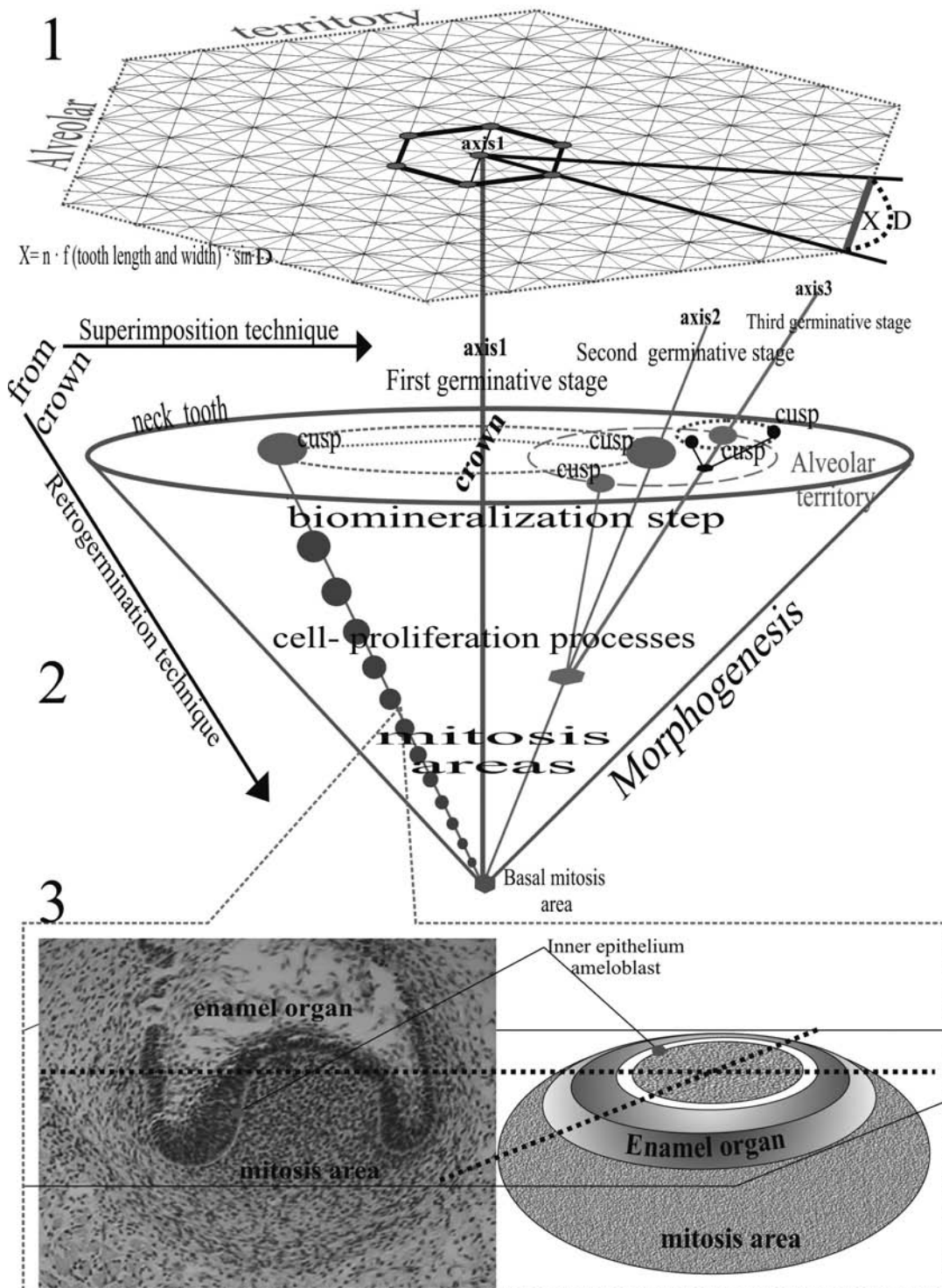


Fig. 4.—The framework of mammalian dental morphology is interpreted by means of a loop-development mitosis area hypothesis. 1) The standard tooth model involves a periodic function (a wave), which spreads the germinative point of every tooth-group genesis by the hexanet model. 2) The basal mitosis area has specific germinative points, each one replicating a mitosis area identical to the basal mitosis area; they comprise the first germinative stage. The following stages -second, third, and so on- take place by development in loop. 3. Histological section of embryo tooth with basic colorants. The mitosis area is a dermal stain with intense mitotic cells.

geometrical centre and radii of cups enamel line must be understood in relationship with vectors of expansion due to cell proliferation.

The mitosis area concept imply to understand that the mitosis area acts as a powerful translator, connecting and making the embryonic morphology data compatible with the adult crown data, and vice versa.

In these circumstances, the phylogenetic origin of a specific basal mitosis area must necessarily be another mitosis area, with reproduction of the same structure or a variation there of, that it taking place through mutation. Therefore, the characteristics of any specimen's molar crown will always reflect one particular and unique model of the basal mitosis area.

The palaeontologist needs the mitosis area concept as an intellectual instrument, in the meaning defined by Bacon (1620). Palaeontologists might simply examine adult molar crowns, with no need to use embryos, to confirm the data provided by biochemical and morphological analysis of dental embryos. The mitosis area concept is a copernican overturn in the explication of crown morphology, because the enamel line indirectly serve to specify the dynamic processes of morphogenesis.

The mitosis area loop-development concept

The start point of the hypothesis on the cause-and-effect relationships among the factors that interfere in the genesis of the adult molar morphology, they are the geometric evidence of the hexagonal net marks (fig. 1, 2 y 3). They form a contour of a specific polygon which is repeated, as the elemental unit in the tooth crown. This hypothesis is known as loop-development of the mitosis areas (Ruiz Bustos 1987, 1988, 2002, 2004a, 2005, 2006, 2007).

The loop-development of the mitosis areas proposes the next items:

1. The origin of adult molar cusps is a genetic algorithm inherited from the parents, which is codified in the DNA.

2. The basal mitosis area is a stain with numerous cells in mitosis that it is observed in early morphogenesis stage. The loop development repeats the basal mitosis area until to form all other mitosis areas of the embryo tooth.

3. The germinative points are specific places inside of the basal mitosis area where emergent new

smaller stains during the morphogenesis. The germinative points of the basal mitosis area are repeated in all mitosis area of the embryo tooth.

4. The first germination stage consists in each germinative point of the basal mitosis area, it is the origin of a new mitosis area identical to the basal mitosis area.

5. The second germination stage consist in the loop where each germinative point of the mitosis areas, belonging to the first germination stage, it gives rise to a second-generation mitosis area.

6. With the third germination stage there is no space in the embryo, and the loop-development is stopped (fig. 4).

7. The adaptation of the mitosis areas to alveolar territory is a process to occupy each mitosis area the maximum alveolar territory available. The earlier mitosis area appears in the morphogenesis, the bigger is the alveolar territory available.

8. The biomineralization process. After of the adaptation process to alveolar territory, at the end of the morphogenesis, all mitosis areas present in the embryo crown are covering up with an enamel layer to form the cusps. This is verified for us with the concrete examples of hexagonal lattice marks showed in this note (fig. 1, 2 y 3).

9. The main factors that interfere in the genesis of the adult molar morphology, by loop-development of the mitosis areas are: models of distribution of germinative points inside of basal mitosis area, numbers of germinative points inside of basal mitosis area, polarity of the basal mitosis area, and adaptation of the molar's genesis group to alveolar territory (Ruiz Bustos, 2005, 2006, 2007).

10. The rule of the loop-development of the mitosis areas in any tooth is each germinative point from any mitosis area of the tooth will produce a new stain, equal to the basal mitosis area as long as there is enough embryonic space. In the adult crown, each cusp tries to reproduce the contour of the basal mitosis area, if they have enough space to grow in the embryo. Therefore, during the morphogenesis, the basal mitosis area gives rise to the remaining mitosis area of the tooth. Within each molar, during the morphogenesis the mitosis areas form the molar's genesis group, and in the adult crown, the cusps constitute the molar group cusps.

11. Types of mitosis area loop-development. Thinking from the embryo during the morphogenesis, there are two important questions. First, how many mitosis areas could be materialized in a tooth

embryo? And second, how many basal mitosis areas could be positioned in the embryo maxillas. And thinking from the phenotype in the adult: first, how many cusps there are in the tooth? And second, how many teeth are positioned in the mouth of a specimen?

The answer to the first question is: the loop-intradevelopment. It consists of the repetition of a basal mitosis area during tooth morphogenesis, until to form the mitosis areas genesis group. The result of the loop-intradevelopment in the adult crown is the molar cusps group, it is formed by the mains cusp, its corresponding adjoining cusps: first, second, and successively until forming the molar cusps group. An example is the morphology of any tooth (Ruiz Bustos, 2005, 2006, 2007).

The answer to the second question is: the loop-epidevelopment. It consists in the spatial replications of the basal mitosis area, until covering a surface of the embryo maxillas, which is delimited by particular somatic conditions. The loop-epidevelopment explains the repetitions of the morphological pattern of the first molar, in the places occupied by the second and third molar.

The design of successive basal mitosis areas by loop repetitions (loop-intradevelopment and loop-epidevelopment) during the morphogenesis, this implies a germinations process of the cell-mass proliferation (mitosis areas), that finally they are covered by an enamel layer.

12. The most important argument for the validity of hypothesis of mitosis area loop-development is: the embryo data formulated by Osman and Ruch (1976), Vaahtokari, *et al.* (1996), Keränen *et al.* (1998), Jernvall and Thesleff (2000), Jernvall *et al.* (2000) and Frade González *et al.* (2001) do not contradict the hypothesis of the loop development of the mitosis areas. The primary enamel knot develops from the epithelium observed in the embryo, always associated with the stain of the basal mitosis area in this author's experience, and each of the remaining mitosis area of the tooth are associated with a secondary enamel knot.

The mutations occurring in the basal mitosis area during the phylogeny, they are observed for us when it appears as elemental polygon unit in the crown molar (rhombus, perihexagon, and hexagon). The Nature Selection is extremely demanding with the perfect functionality of the self-controlled system, because if the adult teeth of a specimen are not functional, this dies without reaching the age of reproduction.

Biological nature of the enamel line tooth

In the coronal plane, at different crown heights of the molars with moderate coronal wear, or in the mechanical sections of molars, they show the molar framework. It is a great hollow in the tooth neck, filled partially or wholly with pulp, and this is connected directly to the main cusps or largest cusps, and around each main cusp is connected to successively adjunct cusps forming a series, and we observe ringed enamel lines belonging to the cusp and groups of fused cusps. In the histological inspection of individual cusps sections, we may see circles of dentine delimited by enamel line curves. The radii from the geometrical centre of the dentine areas to its enamel line points represent continuous vectors of expansion due to cell proliferation.

All these morphological elements that are drawn by enamel line, they obey Euclidian geometric principles. In the case of a ringed enamel line, formed by the fusion of two or more cusps, each arc of enamel corresponds with each of the fused cusps.

Given that the hexagonal marks in the crown are the loop repetitions of an elemental unit during morphogenesis. The molar cusps correspond to final moments of morphogenesis, when the mitosis areas are being covered by an enamel layer; that is, each cusp of the adult molar (fig. 4). The crown morphology provides clues as to the cell proliferation process during the morphogenesis of each cusp, with no need to use embryos.

From the molar framework, we may infer that:

1) The appearance priority of the mitosis areas in the phylogeny implies appearance priority in embryogenesis (Haeckel's law). The consequence is that the sooner a mitosis area appears in the phylogeny, the sooner a mitosis area appears in the embryo. This implies that the embryo is more mesenchymatic (undifferentiated) and there are fewer obstacles (tissues and organs) which could slow down the expansion of the mitosis area, and in these circumstances the cusps reaches the largest size possible. The embryological role of cups, from its morphology in the crown, can be infer by the size and frequency of the cusp features, presence in successive broods and populations of zoological groups conserved in museums.

2) The base of the molar crown corresponds to the site of basal mitosis at the beginning of morphogenesis. All germinative points were born inside of the basal mitosis area and its daughters during embryonic development (one after the other, during

stages of morphogenesis). Therefore, the contours of basal mitosis area correspond in the adult tooth with the base of the crown and it occupies the alveolar territory (fig. 4).

3) Each one of the mitosis areas by adaptation to alveolar territory available, and they covering with an enamel layer form the cusps group of the tooth.

4) The dental genome (DNA), as fraction of the genome of a mammal specimen, it has a self-controlled system, which by loop-intradevelopment and loop-epidevelopment, it controls the location and building of each mitosis area of the embryo, equal of the basal mitosis area, until cover the maxillas space. The dental self-controlled system guarantees the best occlusion of the teeth in the adult mammal.

The hierarchy of the enamel line character in the crown must be based: on the one hand, on the genetic role of each feature. This is quantified with the morphology percentages observed in successive broods and populations. Yet on the other hand, the functional role is crucial, expressed in terms of the size of the enamel line, as a greater size means greater participation in chewing. The adult size in the crown implies and evidences a hierarchy among molar cusps.

The traditional opinion, which believes that: the best taxonomic teeth criteria are the most frequent, clear and specific characteristics in our collections of mammals, it breaks after we know that the mitosis area loop-development is the reason of the biological hierarchy established among the enamel line features in the molar crown.

The murids morphology explained by the mitosis area loop-development

The murids molar architecture and the hypothesis of the mitosis area loop-development, they allow us to infer that a large cavity in a tooth neck; it represents a basal mitosis area, which during embryological development delimits the alveolar territory of the molar. The basal mitosis area has a specific number of germinative points with precise and constant localizations (fig. 5.1). Afterwards, in the first germinative stage, and at precise germinative points inside of the basal mitosis area, each germinative point gives a new mitosis area, and then, in the embryo three new mitosis areas become visible. I referred to as a new name: hexatrirhomb (three

rhombuses inside a hexagon). These mitosis areas (listed type m-tn) correspond to the main cusps or greater-sized cusps of the molar (fig. 5.2).

The hexatrirhomb undergoes a process of adaptation to the alveolar territory conditioned by the available place. It is important that the rhombuses overlap when the jaw cannot increase its width, yet not in any other circumstance, and the rhombus that cannot adapt to the jaw width, it is blocked (fig. 5.3b).

In the second germinative stage, around the principal mitosis areas appear the mitosis areas corresponding to smaller cusps (adjunct cusps), occupying empty spaces in the remaining alveolar territory, until the alveolar territory available becomes too small to trigger cell proliferation, and the loop process stops (fig. 5.4 a and b).

The murids getting with its basal mitosis area, called: rhombus-3.type-a (Ruiz Bustos, 2007), the greatest possible packaging of cusps in the two dimensions of the alveolar plane. The second loop gives rise to the adult molar morphology (fig. 5.5a and b).

By Butler (1985) the murids are anomalous in chewing movements because they combine cuspidate molars with propalinal chewing, but the figure 5.6 shows the packaging of cusps in longitudinal row, explaining why the murids do not need transversal chewing movements.

The reference series (RS)

The crown traits are clearly expressed in terms of their biological nature with a numerical value in relation to, firstly, the capacity of a cusp to be inherited, which depends on its location in the structure of the loop-genesis group (genetic role); and secondly, its functional capacity, quantified in proportion to its adult size in the crown (functional role), because the bigger the cusp size, the more it participated in chewing.

The Reference Series (RS) (Ruiz Bustos 1999, 2004a, 2005, 2006, 2007) is made up of a group of molar crown traits, each one must be recognized on the enamel line with precision, and its objective is to express the hierarchy among the cusps of each molar by means of a numerical series of parameters.

The distances on the enamel line between distinct enamel line points are the parameters, each having an explicit numerical value in view of its biological nature; afford a good synthesis of the biological

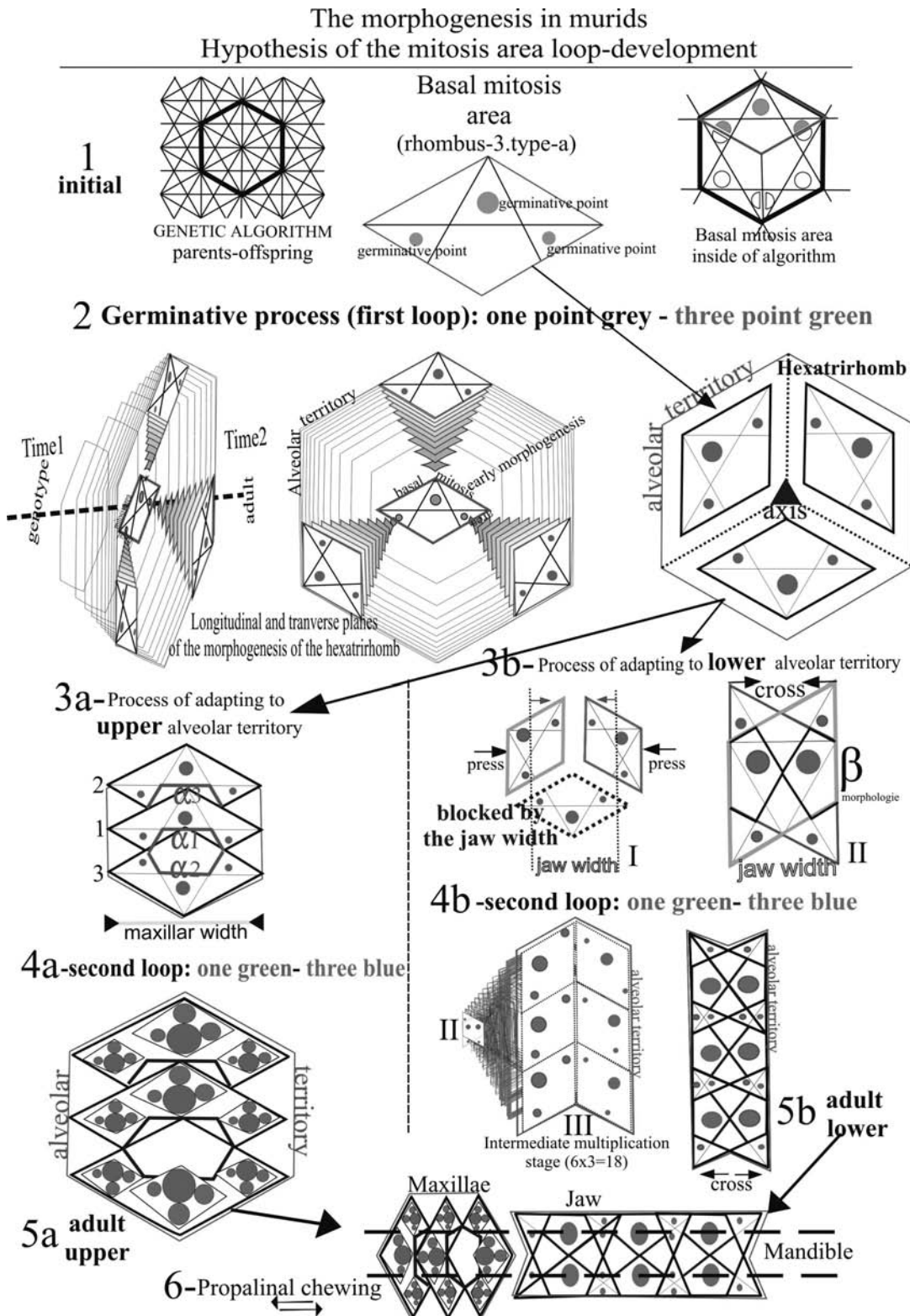


Fig. 5.—The loop-development of the mitosis areas hypothesis in murine dental pattern *Apodemus*. The initial rhombus basal mitosis area is referred to as: rhombus-3.type-a; the first loop gives rise to a new element with three mitosis areas of the type: m-tn, referred to as a new name: hexatrirhomb (three rhombuses inside a hexagon), the hexatrirhomb undergoes a process of adaptation to the alveolar territory conditioned by the available place; the second loop gives rise to the adult molar morphology.

nature of traits that integrate the Reference Series as numerical values. This allows us to mathematically identify each molar by its adult morphology and distinguish it from any other molar. Each Reference Series (RS) signifies the mathematical expression of the cusps hierarchy.

The biological plasticity concept

The reference series of adult molars has an objective meaning with counterparts in fields of biology other than comparative morphology.

1. In the field of genetics, the DNA sequence as a function of the chemical nature and location of each nitrogen base can be converted into a numerical sequence to provide a Gene Reference Series (GRS) (Ruiz Bustos, 2006). Also the Reference Series (RS) is numerical sequence that could be stored in a reference-series bank, taking as its model banks of DNA gene sequences (GeneBank, EMBL, DDBJ). Therefore, the molar reference series (RS) and gene reference series (GRS), they are two numerical sequences, which could be mathematic compared.

2. In the ecology field, the soma obtains the energy resources necessary for its reproduction in the ecosystem, and the germ source of the energy of the soma. This gives rise to a possible path leading from the reference series (RS) to the very conditions of its ecological setting. This is drawing on the concept of biological plasticity (BP), which can be numerically expressed in relationship among: gene reference series (GRS), reference series (RS), and the environmental conditions, in turn quantified by the Biocenogram in Mammal Climatic Units (MCU) (Ruiz Bustos 1993, 1995, 2002, 2004b).

Phylogenetic relationships among muroids hexagonal lattice marks

During the mammals' phylogeny, the possible habitats in an ecosystem and its crises are determined by the climatic conditions.

The summary of the mammals phylogeny is: the mammals need, at least a habitat that it offers minimum conditions of survival, and from these habitat, they start processes of adaptation by positive mutation to the remaining habitats of the ecosystem, until obtaining the possible biggest food with the functional smallest effort.

The probability that a morphology carries out a ecological function, it can be calculated starting from the relationship among: energy expended by morphology, and energy benefits that the morphology obtains, and also another condition is necessary, that the Natural Selection obtains immediate adaptive advantages or immediate beneficial consequences, at place and time circumstances where morphology and its ecological function are located in the ecosystem.

Mutations in biological nature of the teeth are changes in the genetic code, which leads to change in the population. The mutations that improve the energetic saving, they materialize the best possible morphologies and their ecological respective function from among those that they can be possible in the ecosystem.

Once a link has been already established, it will try to reach the possible biggest functionality with the lost minor possible of energy by acquired characters until the mutation appears. The mammal species to get survival long time, they evolve from a strategist (r) until to be a strategist (K). The cost paid is bigger specificity and loss of evolutionary potential. Therefore, each new model of the basal mitosis area in the phylogeny, it becomes again the starting point for the new mutation tendencies, this happen again and again, throughout phylogeny. For example the mutations: 1, 2, 3, 4, 5 and 6 (fig. 6).

The morphology and its ecological function in the ecosystem is explained by the Plastic Evolution theory (Ruiz Bustos 1994), as interaction among the principles of Evolutionary Indetermination, Morphological Determination and Natural Selection.

The relationship among morphology (genetic algorithm) analyzed using geometric postulates (fig. 1,2, 3, 4 and 5), ecological function and Natural Selection, are sufficient to explain muroid phylogeny.

We observe that the morphologies of the muroid basal mitosis areas are petrified in the molar crown by the enamel line. Then the characteristics of any individual's molar crown will always reflect a particular model, and no other, of the basal mitosis area. In this context, the origin of a specific muroid basal mitosis area can only have been another such area, with reproduction of the same structure or a variation thereof having occurred through mutation during phylogeny.

The database for inferring the genetic role of molar crown morphology is drawn from observations of mammalian molar collections comprising

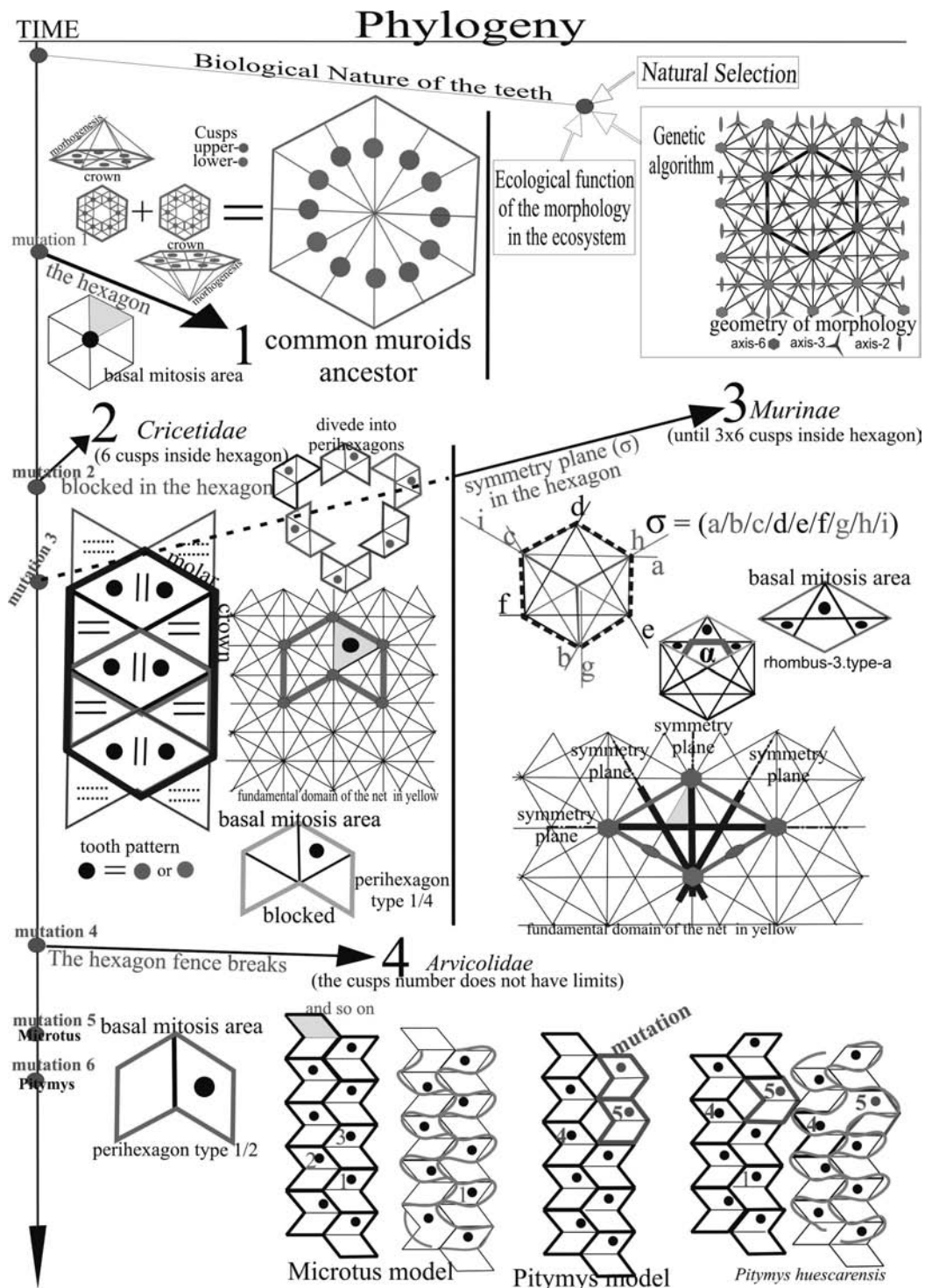


Fig. 6.—The biological nature of the mammal teeth in the muroids phylogeny. 1) The hypothesis of the common ancestor is inferred from the enamel line crown of muroids. 2) Basal mitosis area present in cricetids as result of the germinative point and polarity blocked, and its adaptation to alveolar territory. 3) Basal mitosis area present in murids. This morphology would not directly derive from cricetid morphology, because a new symmetry plane appears in the murid rhombus. This allows to the murids getting the greatest possible packaging of cusps in the two dimensions of the alveolar plane. In these constraining geometric circumstances (blocked cricetids and symmetry plane murids) is unlikely to change the geometrical fundamental domain between cricetids and murids or the contrary. 4) Basal mitosis area present in arvicolids and its adaptation to alveolar territory. The arvicolids bear relation with cricetids. *Pitymys* genus is mutation of the *Microtus* model.

successive broods and populations of zoological groups conserved in museums.

The inheritance of molar morphology implies genetic algorithms, which have codified in the DNA, that direct the cell-proliferation process during embryonic development, thereby determining the cusps, which each one is a mass-cell of the adult tooth, which we can observe as a sketch of the enamel line in the crown.

The phylogenetic evolves of the cricetids shows a basal mutation of blocked the hexagon to form the perihexagon (fig. 6), and the murids show a basal mutation in the basal mitosis area to obtain a repetitive group trends to find the best possible packaging spheres (cusps), within two dimensions (fig. 6).

The morphology of both basal mitosis area, let us to infer, that murid morphology has no direct derivation from cricetid morphology, and that they probably share a common ancestry (fig. 6).

Ecological affinity would indicate that cricetids prefer a more open habitat than murids. This follows from the functional viewpoint, in that the cricetids in open habitats are equipped with better dental scissors for grass than the murids; while contrariwise, the murids residing around shrubbery are more effective grinders of dry fruits.

The arvicolid origin with basal mitosis area: perihexagon type 1/2, it is very probable from the cricetids with basal mitosis area: perihexagon type 1/4, it would explain the cricetid facility for cutting grass, which reaches its maximum development and efficiency of the arvicolids in the cold steppe (fig. 6.4).

Conclusions

To sum up, the key data communicated in this note reside in the identification of the rhombus, perihexagon, (α) and (β) morphologies pertaining to muroids enamel line, which coincide within an equilateral triangular lattice, as shown in figures 1, 2 and 3.

The most noteworthy inference using data from the morphology of the adult crown is the morphology of the basal mitosis area inside the hereditary algorithm and its loop-development (fig. 4). The data regarding crown morphology, the hexagonal lattice and cell proliferation, and biomineralization processes, are all interrelated under the hypothesis of loop-development of mitosis areas. This provides a framework for Holistic Taxonomy, arising from a

cause-and-effect relationship between mitosis areas and cusps.

The enamel line bend is not a random factor. Thus, if the enamel line in the crown bends some factor has to push (cells, polarity or a lack of space).

Using the molar Reference Series (RS) to formulate and to compare mathematic indices may explain the phylogenetic identity of the molars and eliminate taxonomic uncertainties.

For the dental crown morphologist, the significance of the mitosis area is that in the embryo, each mitosis area occupies the place corresponding to a cusp inside the tooth crown, and the shapes of the enamel line serve to indirectly specify the dynamic processes of morphogenesis.

According to the hypothesis of the loop-development of the mitosis areas, the hexagonal lattice marks are the result of the genetic algorithm codified in the genome, whose morphogenetic appearance is petrified by the enamel crown layer. Observation of elemental unit in the tooth crown morphologies that are identical to the basal mitosis area shows, which the morphology that is codified in the genetic algorithm of the genome. Therefore, we can use these crown morphologies to detect and specify the dental genetic algorithm inherited by offspring from their parents, meaning it is a self-controlled system. Information, rules and processes are coordinated so as to adjust the basal mitosis area pattern to the specific physical and chemical conditions prevailing in each embryo maxillary territory.

The dental algorithm stands as a success of organic evolution, assuring the best possible occlusion and resistance in the molars for executing chewing movements. The specimen that has anomalies in its genetic dental algorithm cannot feed and will die without having descendants. In other words, only the specimen whose dental self-control system works will manage to survive. Mutations may also take place, however, allowing mammals to survive unexpected environmental changes, and avoid extinction.

A Systematic Mammal Teeth table (Ruiz Bustos, 2007) is a project to be formulated in the coming years, presenting basal mitosis areas corresponding to fossil and living mammalian species in logical order, and providing the foundation for a means of establishing mammalian phylogeny. In the context of descriptive and comparative mammalian studies, such a table could mark a new stage of synthesis in molar morphology based on hexagonal structures.

At the moments of this note, the genetic code of teeth undetectable for palaeontologists, it is translated to enamel line tooth morphology. The mitosis area in the embryo and cusp in the crown, both in coordination open the study field of the lattice marks in teeth, which is called odontohexasymmetry.

The concepts and data about the marks of enamel line are a turning point in crown morphology analysis.

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References

- Bacon, F. (1620). *Novum Organum*, Lib.I aphorism II.
- Butler, P.M. (1985). Homology of cups and crest, and their bearing on assessments of rodent phylogeny. In: *Evolutionary relationships among rodents* (Luckett, W.P. & Hartenberger, J.-L., eds). Plenum, New York, 381-401
- Carleton, M.D. & Musser, G.G. (1984). Muroid rodents. In: *Orders and Families of Recent Mammals of the World* (Anderson, S. & Jones J.K., eds.). John Wiley and Sons, New York, 289-379.
- Chaline, J.; Mein, P. & Petter, F. (1977). Les grandes lignes d'une classification évolutive des Muroidea. *Mammalia*, 41: 245-252. doi:10.1515/mamm.1977.41.3.245
- Cope, E.D. (1883). On the trituberculate type of molar teeth in the Mammalia. *Proceedings of the American Philosophical Society*, 21: 324-326.
- Cordy, J.M. (1976). *Essai sur la microevolution du genre Stephanomys (Rodentia, Muridae)*. PhD Thesis Univ. Liege, 351 pp.
- Flynn, L.J.; Jacobs, L.L. & Lindsay, E.H. (1985). Problems in muroid phylogeny: relationships to other rodents and origin of major groups. In *Evolutionary Relationships among Rodents* (Luckett, W.P. & Hartenberger, J.-L., eds). Plenum Press, New York, 589-616.
- Frade González, C.; García-Caballero, A.; Lozano Ramirez, A. & Labella Caballero, T. (2001). Proliferación celular en tumores de glándulas salivales. *Acta Otorrinolaringológica Española*, 52: 456-460.
- Hooper, E.T. & Musser, M.D. (1964). The glans penis in Neotropical cricetines (family Muridae) with comments on classification of muroid rodents. *Miscellaneous Publication of the University of Michigan*, 123: 1-57.
- Jansa, S.A. & Weksler, M. (2004). Phylogeny of muroid rodents: relationships within and among major lineages as determined by IRBP gene sequences. *Molecular Phylogenetics and Evolution*, 31: 256-276. doi:10.1016/j.ympev.2003.07.002
- Jernvall, J. & Thesleff, I. (2000). Reiterative signaling and patterning mammalian tooth morphogenesis. *Mechanisms of Development*, 92: 19-29. doi:10.1016/S0925-4773(99)00322-6
- Jernvall, J.; Keränen, S.V.E. & Thesleff, I. (2000). Evolutionary modification of development in mammalian teeth: Quantifying gene expression patterns and topography. *Proceedings of the National Academy of Sciences of the United States of America*, 97: 14444-14448. doi:10.1073/pnas.97.26.14444
- Keränen, S.; Åberg, T.; Kettunen, P. Thesleff, I. & Jernvall, J. (1998). Association of developmental regulatory genes with the development of different molar shapes in two species of rodents. *Development Genes and Evolution*, 208: 477-486. doi:10.1007/s004270050206
- Michaux, J.; Reyes, A. & Catzeflis, F. (2001). Evolutionary History of the Most Speciose Mammals: Molecular Phylogeny of Muroid Rodents. *Molecular Biology and Evolution*, 18 (11): 2017-2031.
- Musser, G.G. & Carleton, M.D. (1993). Family Muridae. In *Mammal Species of the World a Taxonomic and Geographic Reference* (Wilson D.E. & Reeder D.M. eds.). Smithsonian Institution Press, Washington D.C. 501-755.
- Musser, G.G. & Carleton, M.D. (2005). Superfamily Muroidea. In *Mammal Species of the World a Taxonomic and Geographic Reference* (Wilson D.E. & Reeder D.M. eds.). Johns Hopkins University Press, Baltimore. 894-1531.
- Osman A. & Ruch, J.V. (1976). Topographical distribution of mitoses in lower incisor and 1st molar of mice embryos. *Journal de Biologie Buccale*, 4: 331-348.
- Ruiz Bustos, A. (1987). Consideraciones sobre la sistemática y evolución de la familia arvcolidae. El genero *Mimomys*. *Paleomammalia*, 1(2):1-54.
- Ruiz Bustos, A. (1988). Estudio sobre los arvicolidos cuaternarios. *Paleomammalia*, 2(1):1-89.
- Ruiz Bustos, A. (1993). The relation between mammal fauna and climatic conditions using biocenogram. *Premier Congrès Européen de Paléontologie (Lyon)*. Abstract, 13.
- Ruiz Bustos, A. 1995. Quantification of the climatic conditions of Quaternary sites by means of mammals. *Monografías del Centro de Ciencias Medioambientales CSIC* 3: 69-77.
- Ruiz Bustos, A. (1999). Secuencias de referencia en arvicolidos. *Temas Geológico-Mineros ITGE*, 26: 331-334.
- Ruiz Bustos, A. (2002). Enamel line molar analysis in arvicolid rodents: its potential use in biostratigraphy and palaeoecology. *Micromamíferos y Bioestratigrafía*, 1: 1-24.
- Ruiz Bustos, A. (2004a). Características paleoecológicas y bioestratigráficas del Cuaternario aportadas por el estudio de los mamíferos fósiles en la Cordillera Bética. El Valle del Guadalquivir como ámbito de las primitivas poblaciones humanas. In *Zona Arqueológica, Miscelánea en homenaje a Emiliano Aguirre 4 (II)*

- (*paleontología*) (Baquedano, E. & Rubio Jara, S., eds.). Museo Regional. Madrid. 488-504.
- Ruiz Bustos, A. (2004b). Numerical coding of the molar morphology of the family Muridae Gray, 1821, (Rodentia) for its lineage knowledge and implications in: biostratigraphy, paleoecology and composition of a correlation language from the phenotype to the genotype. *Micromamíferos y Bioestratigrafía*, 2: 1-141.
- Ruiz Bustos, A. (2005). The framework of mammal dental morphology in ontogeny and phylogeny. *Micromamíferos y Bioestratigrafía*, 3: 1-47.
- Ruiz Bustos, A. (2006). The hidden geometry in the enamel line of horse molars. *Micromamíferos y Bioestratigrafía*, 4: 1-112.
- Ruiz Bustos, A. (2007). The framework of the systematic table of the mammal teeth by means of the mitosis areas. *Micromamíferos y Bioestratigrafía*, 5: 1-31.
- Ruiz Bustos, A.; Sesé, C.; Dabrio, C.; Peña, J.A. & Padial, J. (1984). Geología y Fauna de micromamíferos del nuevo yacimiento del Plioceno inferior de Gorafe-A (Depresión de Guadix-Baza, Granada). *Estudios Geológicos*, 40: 231-241. doi:10.3989/egeol.84403-4664
- Simpson, G.G. (1945). The principles of classifications and a classification of mammals. *Bulletin of the American Museum of Natural History*, 85: 1-350.
- Steppan, S.J.; Adkins, R.M. & Anderson, J. (2004). Phylogeny and Divergence-Date Estimates of Rapid Radiations in Muroid Rodents Based on Multiple Nuclear Genes. *Syst. Biol.*, 53(4): 533-553. doi:10.1080/10635150490468701
- Vahtokari, A.; Åberg, T.; Jernvall, J.; Keränen, S. & Thesleff, I. (1996). The enamel knot as a signaling center in the developing mouse tooth. *Mechanisms of Development*, 54: 39-43. doi:10.1016/0925-4773(95)00459-9

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