



# Fractal dimension and cheek teeth crown complexity in the giant rodent *Eumegamys paranensis*

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In this work, we analyse cheek teeth crown complexity through the calculation of fractal dimension in the giant caviomorph rodent *Eumegamys paranensis* (Late Miocene of Argentina) and evaluate its functional significance. Our results indicate that, in all teeth of *Eumegamys paranensis*, the fractal dimension was around 1.5, similar to the Koch quadratic curve type two. The anterior portions of the molars, with the highest values of fractal dimension, are interpreted as areas that supported greater occlusal pressures. Crown complexity in *E. paranensis* is related to the increased mechanical capacity to process relatively demanding food items and to allow more food to be divided in each masticatory cycle. *Eumegamys paranensis* would have been a mixed feeder, consuming a variable diet obtained close to the ground. This feeding behaviour is compatible with the heterogeneous environment inferred for the Mesopotamic area during the Late Miocene. *E. paranensis* was probably a wide ranging species, being able to eat close to water bodies and in gallery forests that occurred in the surrounding of the pre-Paraná river system. □ *Body mass, enamel crest crenulation, giant caviomorph rodent, Late Miocene, leading and trailing edges, palaeobiology.*

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## Introduction

Derived from the Latin 'fractus', the term *fractal* is used to describe mathematical objects that possess repeating patterns when viewed at increasingly fine magnifications (Hagerhal *et al.* 2004). This self-similarity in invariant scale can be identified and quantified by a parameter called the fractal dimension ( $D$ ), which is fractional, in contrast to the integer dimensions (0, 1, 2, 3) of Euclidean man-made shapes (e.g. squares and cubes). So, fractals occupy a non-topological dimension (i.e. their Hausdorff–Besicovitch dimension is greater than expected in the Euclidean space; Mandelbrot 1982). Thus, for a fractal line,  $D$  will be  $>1$  and  $<2$ . Fractal dimensions have proven useful for analysing complexities of many natural objects (Hastings *et al.* 1992; Corbit & Garbary 1995; Nicolay & Vaders 2006), including the teeth of elephantid species (Proboscidea; Stone & Telford 2005).

In this work, we analyse the complexity of cheek teeth in the Late Miocene giant Caviomorph rodent *Eumegamys paranensis* (Family Dinomyidae),

recorded from eastern Argentina (Mesopotamic area; Kraglievich 1926), through the calculation of fractal dimensions, and analyse it from a functional/adaptive approach. This approach improves the understanding of the palaeobiology of giant caviomorphs and provides information for future studies exploring the relationships between large herbivorous mammals and the biotic and abiotic variables dominant during the Late Miocene in South America.

Dinomyidae are today represented by *Dinomyx branickii*, a poorly known species that inhabits forested areas of eastern Andes of Brazil, Peru, Ecuador, Bolivia, Venezuela and Colombia (White & Alberico 1992). Throughout their long evolutionary history, recorded since the Late Oligocene, dinomyids developed an important taxonomical richness, particularly in the Late Miocene (e.g. Kraglievich 1926; Candela & Nasif 2006; Nasif 2010). As *Eumegamys paranensis*, several species of dinomyids reached an extremely large size during the Late Miocene and Pliocene in South America (e.g. Nasif 2010; Kraglievich 1926; Rinderknecht & Blanco 2008; Rinderknecht *et al.* 2011). Given that body size is a key

variable influencing physiological and ecological aspects of organisms (e.g. Smith *et al.* 2010; Owen-Smith 1988), increased body size in giant dinomyids almost certainly operated on other features, such as metabolic rate, life strategies, locomotor behaviour and feeding habits. However, the influence of large body size on other morphological features and biological aspects in giant dinomyids has not been studied yet (with a few exception; see Blanco *et al.* 2011). Specifically in the case of teeth, it has not been inspected what features of cheek teeth could have evolved in association with the increase in body size or with the type of food items consumed. Adjustments of the dental morphology were required to compensate for the increase in body size and the metabolic requirements of the largest species of dinomyids, which is one aspect inspected in this work.

## Materials and methods

‘Dental complexity’ (*sensu* Evans *et al.* 2007, p. 78) has been considered as any measure of the number of features, tools or breakage sites on a tooth. Following Stone & Telford (2005), we use the fractal dimension ( $D$ ) to evaluate how an object (enamel edges) fills the available space (tooth occlusal surface area), expressing tooth complexity. Calculation of  $D$ , used as a proxy to calculate dental complexity in cheek teeth of *Eumegamys paranensis*, is based on the type specimen of this species, the MLP 15-245, a right mandible, almost complete, within the p4-m3 (fourth pre-molar and molar series; Fig. 1), recorded from the base of Ituzaingó Formation (= ‘Mesopotamiense’, Entre Ríos Province, Mesopotamic area, eastern Argentina; Late Miocene; see Cione *et al.* 2000).

The specimen MLP 15-245 was photographed in occlusal view with a 10 Megapixel digital camera. Using the ImageJ software (Rasband 2007), enamel edges were traced and saved as a TIFF files. Box counting  $D$  was obtained with FracLac 2.5 Release 1d-ImageJ Plugin, using seven pixels as a minor unit, 45% of foreground pixels as a major unit and a mean  $D$  of twelve repetitions calculated in batch mode. The  $D$  for the total occlusal pattern of each tooth crown (p4 to m3) and individual transverse crest of each lophid for each tooth were obtained. In addition, three Tiff images of known fractals of dimensions nearest one, middle range and nearest two (Gosper’s isle edge, Koch curve type 2 and Sierpinski carpet, respectively; Fig. 2) were included in the same batch process to assess the accuracy of the  $D$  calculated. Departures from expected normality of data were analysed by Shapiro–Wilk test. Theoretical and mean values of known fractals were compared

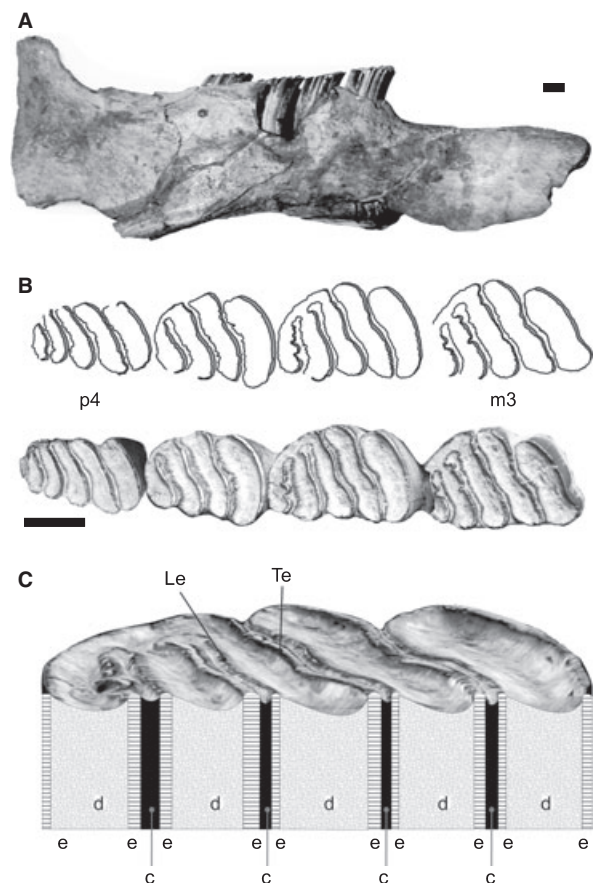


Fig. 1. *Eumegamys paranensis*, MLP 15-245 (type specimen). (A), showing mandible in labial view; (B), showing the complete cheek teeth series (right p4-m3) in occlusal view; (C), detail of m2 showing leading and trailing enamel edges; Le, leading edge; Te, trailing edge; c, cement; e, enamel; d, dentine.

by two-tailed Student’s  $t$ -test. Differences on means of teeth and individual crest  $D$  were analysed by ANOVA procedures and post hoc Tukey’s  $t$ -test.

A body mass (BM) estimate was obtained assuming geometric similarity among different sizes, where overall size was based on the total dentary length. Using a close extant relative (*Dinomys branickii*, of known BM of 15 kg; White & Alberico 1992), BM was calculated as  $M_f = (L_f/L_a)^3 \times M_a$ , where  $M_f$  is fossil BM;  $M_a$  is the BM of extant dinomyid;  $L_f$ , length measured on fossil specimen (total dentary length, this work), and  $L_a$ , the same length measured on the extant specimen. Body mass was also estimated based upon the equations published in Hopkins (2008), using the lower tooth row length (LTRL) and the RTRA (rectangular lower tooth row area) of the type specimen of *Eumegamys paranensis* (MLP 15-245; Fig. 1).

The reconstruction of *Eumegamys paranensis* is based on the proportions of the dentary of the type specimen for this species (MLP 15-245; Fig. 1) and on a pair of preserved skulls MACN 4006 (figured in

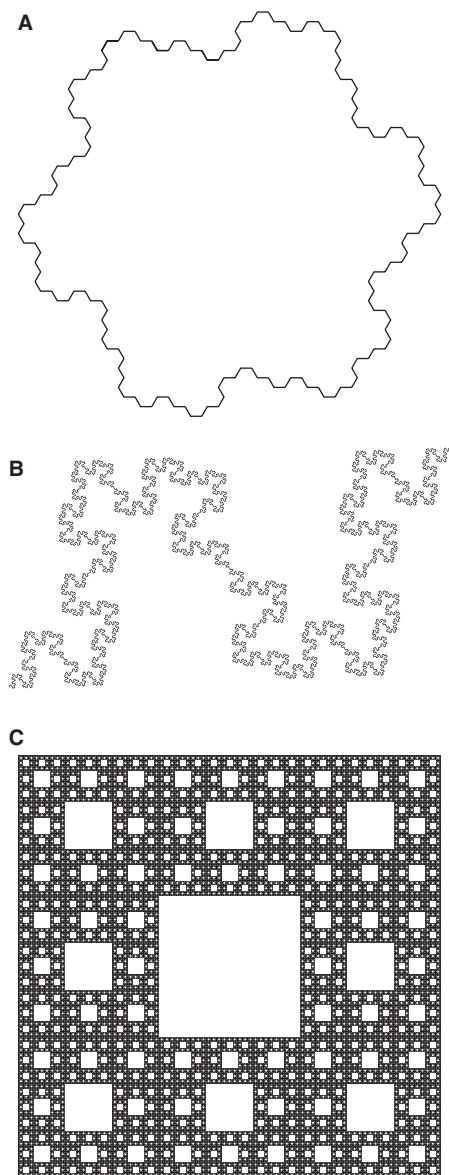


Fig. 2. Theoretical known fractals; (A) Gosper's isle edge; (B) Koch curve type two and (C) Sierpinski.

Kraglievich 1926; fig. 6) and MLP 41-XII-13-237, originally assigned to *Eumegamysops praependens* (Ameghino) Kraglievich but recently assigned to *Eumegamys paranensis* (Nasif 2010). For the reconstruction of post-cranial features of *E. paranensis*, we used information provided by Krapovickas & Nasif (2011) for fossil and living dinomyids in the context of post-cranial anatomy of caviomorphs (Candela & Picasso 2008).

#### *Institutional abbreviations*

MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina.

## Results

### *Body size and occlusal molar patterns*

The Dinomyidae includes relatively medium-size species (i.e. between 10 and 100 kg; *sensu* Cassini *et al.* 2012), such as the living *Dinomys branickii*, to giant species (i.e. over 1000 kg, a megamammal; *sensu* Owen-Smith 1988), such as *Josephoartigasia monesi*, which supposedly reached nearly one tonne in weight (Rinderknecht & Blanco 2008; but see Millien 2008). The dentary of *E. paranensis* is over twice the length of *Dinomys branickii* (125 mm) (see Nasif 2010) and shows the largest dentary length (263 mm; see Fig. 1A) among extinct species of dinomyids known from mandibular remains. It is slightly longer than that of the large extinct dinomyid *Telicomys gigantissimus* Kraglievich 1926 (dentary length approximately 260 mm; Nasif 2010).

Under a model of geometric similarity, based on dentary (=mandible) length of *Dinomys branickii* and known BM of 15 kg (White & Alberico 1992), the dinomyid *Eumegamys paranensis* would have had a BM of 139.7 kg. Therefore, *Eumegamys paranensis* represents a large-size dinomyid (i.e. between 100 and 1000 kg; *sensu* Cassini *et al.* 2012). Applying the equation of Hopkins (2008) based on LTRL, the BM of *Eumegamys paranensis* would be 121.03 kg 95% CI: 109.37–133.93 kg; and using the equation based on RTRA (rectangular lower tooth row area), the BM would be of 120.67 kg. 95% CI: 103.31–140.94 kg.

Hopkins (2008) suggested that their regressions may underestimate body masses of large animals, especially if this taxon violates the fundamental requirement of a BM proxy [i.e. 'the fossil taxon for which a value is predicted must be a member of the population from which the taxa used to generate the prediction equation are a sample' (Smith 2002, p. 276)]. Therefore, as the BM calculated under geometric similarity (139.7 kg) lies on the superior confidence limits, we can assert that the values obtained by the two methods give a reasonable range estimation.

The cheek teeth of *Eumegamys paranensis* are euhypsodont (*sensu* Mones 1982) and pentalophodont (see Fig. 1B). The number of lophids can decrease as a consequence of wear, a generalized tendency in Dinomyidae (Nasif 2010). In the m1 of the type specimen of this species, the two more anterior lophids are joined as consequence of tooth wear. As in extant and extinct dinomyids, cheek teeth of *Eumegamys paranensis* have laminar lophids, each comprising a layer of enamel surrounding dentine. The three most

anterior lophids are joined labially in the protoconid region, a pattern exhibited since the earliest worn stages of the tooth. Lophids are connected between them by cementum. As teeth are worn, lophids are revealed as parallel enamel crests: one anterior and posterior for each lophid. The anterior crest of enamel (recognized here as ‘leading edge’, *sensu* Greaves 1973) is thinner (fine) than the posterior crest of each lophid (the ‘trailing edge’ *sensu* Greaves 1973; Fig. 1C). Both crests of enamel are crenulated, a condition similar to that of *Potamarchus murinus* (a protohypsodont and medium-size dinomyid from the Late Miocene of Mesopotamic area; Argentina; see Candela & Nasif 2006; Nasif 2010).

*Fractal dimension*

The fractal dimension (*D*) obtained for known fractals does not differ significantly from their theoretical values, with a very good accuracy to the second decimal place (Table 1). The *D* of all teeth was around 1.5, similar to the Koch curve type two (Table 1). Although departures from 1.5 seem to be slight (differences on second decimal), such differences were significant among teeth values as found in ANOVA ( $F_{[3; 44]} = 131.75; P < 0.0001$ ). Tukey’s post hoc multi-comparison test revealed significant differences between all values of cheek teeth (all *P*-values < 0.00273), with m1 having the greater fractal dimension. Nevertheless, it must be noticed that the m3 has the first leading edge broken, so the 1.47 value could be underestimated. When individual leading and trailing edges are considered for each lophid in each tooth, ANOVA results show significant differences among them (Table 2). Post hoc Tukey’s test indicates differences between leading edges for each tooth (also trailing edges) (Fig. 3). Among leading edges, the highest *D* values were concentrated in one lophid by tooth (Fig. 3). Whereas in p4 and m3, they correspond to the third lophid (topographically situated on the posterior end on the first half of the tooth), in m1 and the m2, highest

Table 2. ANOVA results of both enamel crests. All *F*-tests with degree of freedom (d.f.) were significant at 0.05 level.

Tooth	Leading edge			Trailing edge		
	<i>F</i>	d.f.	<i>P</i> -value	<i>F</i>	d.f.	<i>P</i> -value
p4	4.91	3, 55	0.0019	4.90	3, 55	0.0019
m1	7.88	3, 44	0.0003	5.13	3, 44	0.0040
m2	38.60	3, 55	<0.0001	27.95	3, 55	<0.0001
m3	21.2	3, 44	<0.0001	24.50	3, 55	<0.0001

*D* values are concentrated on the fourth and second lophids, respectively (i.e. topographically in the middle and anterior parts of the tooth, respectively). The second and third molars have the lowest *D* in fourth and fifth lophids, sharing the same pattern in the posterior part of the tooth. However, for each tooth, there are different patterns between homologues lophids.

Among the trailing edges, those of the first and second lophids have significantly highest *D*, emerging as a common pattern shared between all teeth, especially by molars (Fig. 3). Whereas the differences between the anterior and posterior trailing edges of the lophids are slighter in p4 and m1, they are more accentuated on m2 and m3. Both leading and trailing edges of the second lophid of m2 have the largest fractal dimension.

Discussion

Tooth complexity in our sense (see materials and methods) is indicative of how the enamel edges of cheek teeth fill up the available occlusal surface area. As the enamel edges of the lophids become more crenulated, they become more complex, and fractal dimension (*D*) is expected to be between one and two. Fractal dimension, calculated for three known fractals of dimension nearest one, intermediate and nearest two, demonstrated that *D* can be accurate to two decimal places (Table 1).

Table 1. Descriptive statistic (mean; sd, standard deviation; and Std, standard error) for fractal dimensions calculated. Twelve observations were obtained for each object. The Student’s *t*-test with (*n* – 2) degree of freedom between theoretical and mean obtained values were non-significant at *P* = 0.05.

Fractal/teeth	Mean	Sd	Std. Error	Theoretical value	<i>t</i> ( <i>n</i> – 2)
Sierpinski carpet	1.89467	0.01173	0.00339	1.8928	0.551
Koch curve	1.50038	0.00789	0.00228	1.5	0.168
Gosper island	1.06580	0.02619	0.00756	1.0689	–0.410
p4	1.50903	0.00787	0.00227		
m1	1.53296	0.00554	0.00160		
m2	1.48762	0.01059	0.00306		
m3	1.47203	0.00711	0.00205		

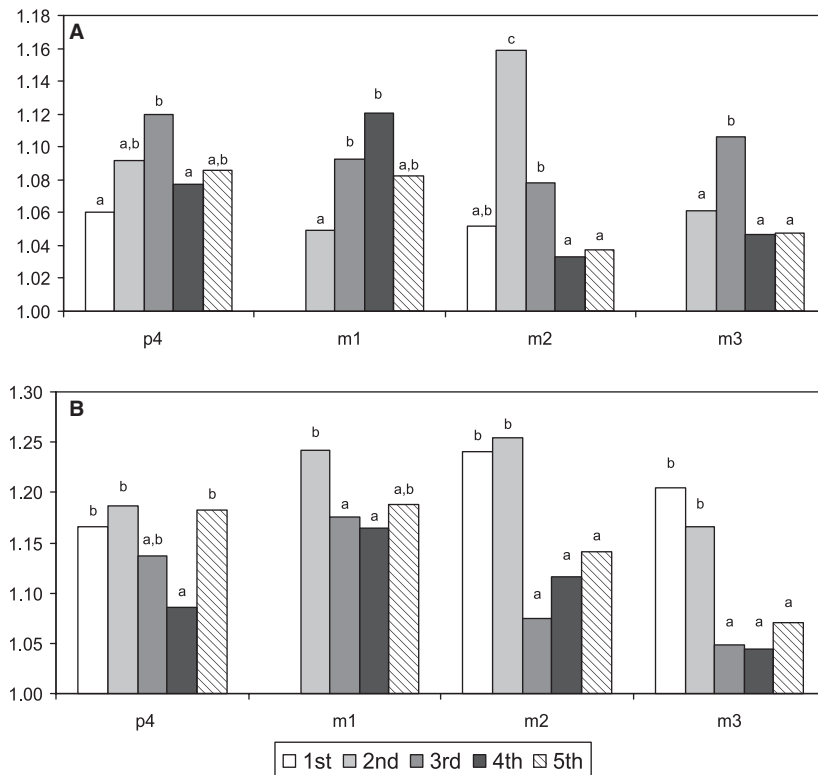


Fig. 3. Bar plot of *post hoc* Tukey's test. Mean fractal dimension ( $D$ ) values from (A) leading edges and (B) trailing edges. Abbreviations: a, lowest mean  $D$  significant value; b, highest significant  $D$  value; a, b, no significant differences with a and b values; 1st to 5th correspond to the first to fifth lophids.

### Complexity of the cheek teeth in *Eumegamys paranensis*

The  $D$  of the teeth of the type specimen of *Eumegamys paranensis* were about 1.5, similar to the Koch curve type two. Among the cheek teeth, the m1 has the highest value of  $D$ , despite having the fewest lophids. The lower number of lophids of m1 is probably compensated by their more complex infolding of enamel ridges. The highest value of  $D$  in the m1 might also be linked to the fact that this tooth is initiated first during ontogeny and must support the most prolonged wear of the molar series (the m2-3 emerge when the m1 already it is in use; Nasif 2010).

Results indicate that the leading edges of the second lophid in the m1 and of the first and second lophids in the m2 exhibit the highest values of  $D$ . Therefore, the highest values of complexity are in the anterior portions of the most anterior molars, with the highest complexity concentrated in the second lophid (considering both leading and trailing edges). This indicates highest crenulation, suggesting that the most anterior portions of the molars support the higher occlusal pressures during masticatory cycles. The connection of the most anterior lophids would also be associated with increased

resistance at the anterior portions of the teeth. From a functional point of view, it is interpreted that these features (increasing crenulation anteriorly) involve an increment of contact area between the teeth, related to a decrease in occlusal pressures, resulting in a high efficiency in the shear of the foods with the consequent application of few masticator movements (Rensberger 1973, 1975; Nasif 2010). The dissimilar degree of complexity along cheek teeth in *E. paranensis* probably reflects their different capacities for breaking food in each masticatory cycle. Values of  $D$  for the cheek teeth in *Eumegamys paranensis* (ranging from ~1.47 to ~1.53; Table 1) indicate that these teeth are more convoluted than are the cheek teeth of Proboscidea, even more so than those with superficially more complex teeth like *Elephas maximus* ( $D = 1.21$ ) and *Mammuthus columbi* ( $D = 1.36$ ) (Stone & Telford 2005).

### Dental complexity: functional/adaptive significance

'Dental complexity' (following Evans *et al.* 2007) indicates the extra tools of the teeth acting in food breakage. As dental morphology is correlated to diet and to individual fitness in processing the food

(Rensberger 1973; Evans *et al.* 2007), the complex crowns of *Eumegamys paranensis* reflect the amount of mechanical processing that food ingested requires. Presence of marked crenulations on the teeth of *E. paranensis* can be interpreted as a way of increasing the mechanical capacity to process relatively demanding foods.

In carnivorans and rodents, it was demonstrated that the complexity of tooth crown directly reflects the foods they consume, and that the larger dental complexity differentiates species according to diet irrespective of body size (Evans *et al.* 2007). In that work, Evans *et al.* (2007) demonstrated that complexity in molars of mammals is strongly indicative of scale-independent and phylogeny-independent effects of diet on general aspects of dental shape. Similarly, it is highly probable that the type of diet has determined the dental complexity in *Eumegamys paranensis*. Other giant extinct dinomyids, such as *Telicomys gigantissimus* and *Josephoartigasia monesi*, do not have marked enamel crenulations, that is, less complex cheek teeth. It is possible that their lower complexity is compensated with greater surface area, such as it occurs in pampatherids and glyptodontids (see Vizcaíno *et al.* 2006 and Samuels 2009 for other examples). Compared with *Telicomys gigantissimus* and *Josephoartigasia monesi*, greater complexity in the teeth of *Eumegamys paranensis* would be indicative of a diet based on tougher or more abrasive food, beyond the functional demand of larger body size. However, the possibility that high complexity is also a consequence, at least partially, of increasing body size cannot completely be excluded. Considering the large body size of this species, relatively large amounts of food had to be processed daily by this large rodent, with their dental complexity a feature that facilitating this task. As in bigger animals, *E. paranensis* would have lived more time than other rodents. As indicated by Evans *et al.* (2007, p. 78): 'The direct functional demands on tooth design depend on the required degree of mechanical processing. In turn, the degree of mechanical processing that is required depends, first, on metabolic requirements of the animal and, second, on the difficulty with which mechanical and chemical breakdown of different kinds of foods can be achieved'. In line with this idea, the increase in tooth crenulations in *E. paranensis* can be interpreted as a way of increasing the mechanical capacity both to process relatively demanding foods and to allow more food to be divided (i.e. reduction in particle size or comminution) in each masticatory cycle (minimizing the processing time of the swallowed food and increasing chewing efficiency (see Pérez-Barbería & Gordon 1998), to satisfy its relatively high metabolic requirements).

### Feeding behaviour

The complex cheek teeth of *Eumegamys paranensis* were probably efficient to cut and grind foods with fibrous components, such as leaves, stems, scrubs, twigs and roots.

On the other hand, the euhippodont teeth of *Eumegamys paranensis* indicate high rates of tooth wear (Fortelius 1985) (see below). In ungulates, crown height has been most frequently considered as indicative of feeding behaviour (i.e. grass consumption) and the spread of grassland habitats (Janis 1988; MacFadden 2000; Strömberg 2005; Fraser & Theodor 2011). However, other authors (Williams & Kay 2001; Mendoza & Palmqvist 2008; Damuth & Janis 2011) indicated that there is no direct relationship between the degree of hypsodonty and the amount of grass consumed and found a correlation between hypsodonty and exogenous grit incorporation, when feeding close to the ground in open habitats.

In a recent contribution, Billet *et al.* (2009) summarized the factors that favoured increasing hypsodonty as two alternative hypotheses: these were 'an increase of abrasives consumed' and 'an increasing chewing effort'. Concerning the first hypothesis, as noted for ungulates, it is possible that hypsodonty in *E. paranensis* was associated with soil ingestion, which acts as an important abrasive agent, rather than with the capacity of food processing (Stirton 1947; see Damuth & Janis 2011 for review).

Therefore, soil consumption could explain, at least partially, the high degree of hypsodonty in *E. paranensis*, which is interpreted here as a feature not associated necessarily with a grazing behaviour (Nasif 2010; Damuth & Janis 2011). The second hypothesis (chewing effort), in particular, concerns the toughness of the plant (i.e. 'a given particle size of food can be obtained by investing less chewing energy when eating fragile plants as compared to tougher species'; Pérez-Barbería & Gordon 1998, p. 246). However, in our context, the association of hypsodonty and chewing effort seems a sub-product of the relation between the fractal nature of enamel edges and the chewing efficiency. In other words, chewing efficiency is functionally more related to teeth complexity than is hypsodonty. Although the relationship between tooth complexity and hypsodonty could be linked to teeth effectiveness, food type and physical form in addition to soil particles ingestion, the relationships remain elusive.

On the available evidence, the occlusal complexity and hypsodonty in the large-size *Eumegamys paranensis* could have been adaptations towards durability of teeth and increased functional efficiency of the

dentition to process relatively large amounts of demanding food on a daily basis, over a relatively long lifespan (i.e. advantageous to eat a variety of diets, like those of the mixed feeders, consumed close of ground).

The idea of hypsodonty in *Eumegamys paranensis* reflecting increased chewing effort and durability is also supported by the example of beavers (Castoridae), which includes hypsodont and euhypsodont species that primarily feed on fibrous parts of trees (Stirton 1947; Samuels 2009).

### *The palaeoenvironment of Eumegamys paranensis*

At austral latitudes of South America, after retraction of the Miocene ‘Paranense Sea’, one of the most significant Atlantic marine transgressions (Pascual *et al.* 1996; Aceñolaza 2000), the development of widespread plains characterized a period recognized as ‘the Age of the Southern Plains’ (Pascual *et al.* 1996). Plains developed under a cooler climate, with more marked seasonality than in the Middle Miocene, and expanded from northern Patagonia, reaching central and northern Argentina (Pascual *et al.* 1996). Particularly, the Mesopotamic area appears to have had its own regional conditions during the Late Miocene due to the interrelationships between various geographical and environmental factors, which seem to have been superimposed on the general cooling trend. During this time, Mesopotamia was a heterogeneous and diverse landscape, composed of forested areas, a ‘deltaic system’, and gallery forests that developed in the surroundings of pre-Parana River, under a warm and humid climate (Cione *et al.* 2000; see Fig. 4). Final regressive stages of the ‘Paranense Sea’ were linked to the formation of the pre-Paraná river system, at the time a wide drainage basin (Aceñolaza 2000), with the consequent physi-



Fig. 4. Palaeoenvironmental reconstruction of the Mesopotamic area (eastern Argentina) during the Late Miocene, showing specimens of *Eumegamys paranensis*. Information used for palaeoenvironmental and specimen reconstructions is included in the text.

cal changes and altered flow regimes. In addition, during the development of this fluvial system, northern ecosystem advanced southwards and eventually reached the Mesopotamic area through a continuous aquatic connection during the Late Miocene (see Cozzuol 2006).

Such environmental changes and migration events had surely a noticeable effect on terrestrial communities close to the fluvial system. The variability of habitats would have been favourable for the coexistence of species with different life styles: forest adapted species, such as porcupines; climate-sensitive and stenotopic species, such as aquatic turtles and booids; species indicative of presence of water bodies and swamps along river banks and warm conditions, such as aquatic birds and hydrochoerids; and wide ranging species, which probably lived in both rainforest and more open forests, such as *Rhea* and glyptodontids (Cione *et al.* 2000).

As discussed above, *Eumegamys paranensis* would not have been a high grazer but rather a mixed feeder, consuming a variable diet obtained close to the ground (see Fig. 4). *E. paranensis* was probably a wide ranging species that probably lived in dense forests and relatively more open but forested areas, being able to eat close to water bodies and in gallery forest that occurred in the surrounding of the pre-Paraná river system (see Fig. 4).

Environmental heterogeneity of the Mesopotamic area during the Late Miocene would have allowed an important ecological diversification of dinomyids, that is consistent with the marked differences in body sizes, degree of hypsodonty and molar complexity of ‘Mesopotamian’ dinomyid species, such as exhibited by *Eumegamys paranensis* and *Potamarchus murinus*.

Interrelationships among various environmental factors associated with the development of the river system could result in new food resources and new opportunities for ‘Mesopotamian’ mammals. It was recently indicated that changes in body size in mammals depend on the availability and characteristics of resources consumed (‘resource rule’; *sensu* McNab 2010). ‘Gigantism’ of *Eumegamys paranensis* could be associated with the abundance of resources available in varied and newly generated habitats. *Eumegamys paranensis* and other Late Miocene ‘Mesopotamian’ dinomyids could have adapted to varied habitats and food resources, factors that can be recognized as key predictors, responsible for changes in body sizes and feeding behaviours.

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