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# EVOLUTIONARY TRENDS AND STASIS IN MOLAR MORPHOLOGY OF *RHAGAPODEMUS-RHAGAMYS* LINEAGE IN THE PLEISTOCENE OF SARDINIA

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*Abstract*. Stasis, random walk and directional evolutionary patterns have been tested on the lower and upper first molars of the *Rhagapodemus-Rhagamys* lineage (Rodentia, Muridae) from Middle and Late Pleistocene fissure fillings of Monte Tuttavista, Orosei, Sardinia, Italy.

We recorded the maximum length/maximum width ratio and size on 252 lower first molars and 208 upper first molars belonging to different fossil samples of *Rhagapodemus minor* and *Rhagamys orthodon* in order to explore evolutionary dynamics underlying molar morphology evolution. Akaike Information Criterion (AICc) was used for selection of the best model of evolution, in order to distinguish different evolutionary patterns.

Our results clearly show that *Rhagapodemus-Rhagamys* lineage undergoes stasis during the middle and late Pleistocene of Sardinia, while size shows a random walk pattern between populations, characterized by an increase in size at the *Rhagapodemus minor-Rhagamys orthodon* transition.

*Riassunto*. La stasi in senso stretto, l'evoluzione non direzionale e l'evoluzione direzionale sono state testate sui primi molari inferiori e superiori della linea filetica *Rhagapodemus-Rhagamys* (Rodentia, Muridae) del Pleistocene medio e superiore provenienti dalle fessure del Monte Tuttavista (Orosei, Sardegna, Italia). È stato misurato il rapporto tra massima larghezza e massima lunghezza su 252 primi molari inferiori e 208 primi molari superiori attribuiti a *Rhagapodemus minor* e *Rhagamys orthodon* allo scopo di stabilire il corretto modello di evoluzione fenotipica. L'Akaike Information Criterion (AICc) è stato utilizzato per scegliere, tra i diversi modelli, il miglior modello evolutivo. I risultati suggeriscono che la linea *Rhagapodemus-Rhagamys* mostra una stasi fenotipica in senso stretto nei primi molari superiori durante il Pleistocene medio e superiore, mentre la taglia e i primi molari inferiori mostrano un'evoluzione non direzionale. La transizione *Rhagapodemus minor – Rhagamys orthodon* è caratterizzata da un significativo incremento di taglia.

## Introduction

Evolutionary patterns of paleontological time series have been thoroughly investigated in recent years by modern statistical strategies (Freudenthal 1976; Mayhew 1977; Eldredge et al. 2005; Wood et al. 2007; Piras et al. 2009; Hunt 2007, 2010; Hunt & Carrano 2010; Hunt et al. 2010).

Ordered sequences of fossil populations constitute, in fact, the basis for exploring evolutionary transformations of measurable phenotypes in geological time. Since the first formulation of Punctuated Equilibria theory (Eldredge & Gould 1972), the main focus of time series-oriented paleontological studies has been to discern between "stasis" and directional trends by using current statistical tools for time-ordered fossil samples (Gingerich 1993; Wood et al. 2007; Piras et al. 2009; Hunt & Carrano 2010).

The causes of stasis have been deeply discussed from both paleontological (Eldredge & Gould 1972; Gould & Eldredge 1977; Gould 2002; Eldredge et al. 2005) and molecular point of view (Cooper & Lenski 2000; Gavriets 2004, among others). Eldredge et al. (2005) pointed out that stasis is the reflection of natural

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structure of species: a species being structured in semi-isolated metapopulations (Wright 1932), different isolated populations experience different selective pressures thus returning a no neat phenotypic change in time. Extinction and habitat tracking are invoked to explain stasis when a rapid environmental change occurs, while an adaptive shift is regarded as the less probable outcome (Eldredge et al. 2005). In this last case, directional evolution, instead, could be the consequence of directional selection toward a new phenotypic optimum adapted to new environmental conditions.

Taking in account these arguments, most paleontological studies distinguish between random walk, directional evolution and stasis patterns.

Random walk pattern can be defined as a no neat change in successive steps of population means across a discrete ordered time sequence (Hunt & Carrano 2010).

Stasis *sensu strictu* can be interpreted as a special case of random walk where the variance of the total time series sample is not significantly larger than that of a single population in any time lapse (Wood et al. 2007; Piras et al. 2009). Conceptually both random walk and stasis *s.s.* could be considered as evidences of stasis *sensu latu*, a pattern similar to that originally exposed by Eldredge & Gould (1972).

The directional evolution pattern implies a significant trend across population means over the time intervals. It can be achieved by both a directional random walk, i.e. when different steps between successive time intervals follow opposite trajectories but show globally a directional change and by a genuine shift in the same direction for each step of the temporal series (Wood et al. 2007; Piras et al. 2009). The Ornstein-Uhlenbeck (OU) model is a particular case of directional evolution for an evolutionary process with selection. As one varies its parameters, one obtains a variety of distributions that are collectively consistent with phenotypic evolution under both drift and selection (Butler & King 2004).

## Biochronological settings

The Monte Tuttavista (East Sardinia, Italy) fissure fillings time sequence represents a good source of time-ordered paleontological data having different fissure fillings ordered in relative biochronological time during the Pleistocene. The rich fauna coming from these fissure fillings has been extensively studied in recent years (Abbazzi et al. 2004, 2005; Angelone et al. 2008; Delfino et al. 2008; Gallai et al. 2005; Marcolini et al. 2005, 2006a, 2006b; Novelli et al. 2009; Palombo et al. 2006, 2012; Rook et al. 2003, 2004)

This order has been recently updated by using both macro and micro vertebrates appearances and disappearances (Palombo 2006, 2009) and on evolutionary states of *Thyrrenicola*, *Prolagus* and *Praemegaceros*.

A well represented chronospecific evolutionary lineage is the *Rhagapodemus-Rhagamys* lineage (Rodentia, Muridae). Nine different populations corresponding to nine biochronological horizons have been studied here. These populations include the more primitive *Rhagapodemus minor* and its descendant *Rhagamys orthodon* (Angelone & Kotsakis 2001; Kotsakis et al. 2008).

The mainland ancestor of the endemic murids of this lineage, *Rhagapodemus ballesioi* Mein & Michaux 1970, colonized Corsica and Sardinia during the Zanclean/Piacentian transition, i.e. the boundary between Early and Late Pliocene. The first endemic species of the lineage, *Rhagapodemus azzarolii* Angelone & Kotsakis, 2001, is present in Mandriola (W Sardinia), in a vertebrate assemblage of latest Ruscinian age (earliest Late Pliocene) (Angelone & Kotsakis 2001). A second species, *Rhagapodemus minor* (Brandy 1978) is reported from Capo Figari and Orosei and was also present in Corsica. The age of these sites spans along the early Pleistocene (Brandy 1978; Abbazzi et al. 2004; Pereira et al. 2005). In the middle Pleistocene a new species, *Rhagamys orthodon* (Hensel, 1855) evolved anagenetically from *Rhagamys minor*. The last members of this species have been collected in Holocene sites, associated with non endemic mammals introduced by the first human settlers (Sondaar et al. 1984; Vigne 1992).

The change of generic name in an anagenetic lineage (*Rhagapodemus-Rhagamys*) is unorthodox but if one wants homogenize this lineage by attributing all species to the genus *Rhagapodemus*, violates the priority law of the International Code for the Zoological Nomenclature that obliges using the generic name *Rhagamys* (erected by Major, 1905). But in this way all species must be assigned to the genus *Rhagamys* (and not to the genus *Rhagapodemus* originally proposed by Kretzoi (1959)).

In this case *Rhagamys orthodon* must be considered as a type species of the genus.

This species is a very large and extremely hypsodont endemic insular species, highly different from the Neogene and Quaternary other "*Rhagamys*" (now assigned to *Rhagapodemus*) species of Europe and Asia. These continental species are too different to be assigned to the same genus of *Rhagamys orthodon*.

We studied here both the first upper molar (M1) and the first lower molar (m1) by means of traditional morphometrics taking in account length/width ratio, a common morphometric indicator for murid molar shape and the relative tooth size. We evaluated the specific hypotheses about character evolution explained above, regarding both non directional (random walk, stasis) and directional evolution. We then propose a model for evolutionary dynamic of molar shape for

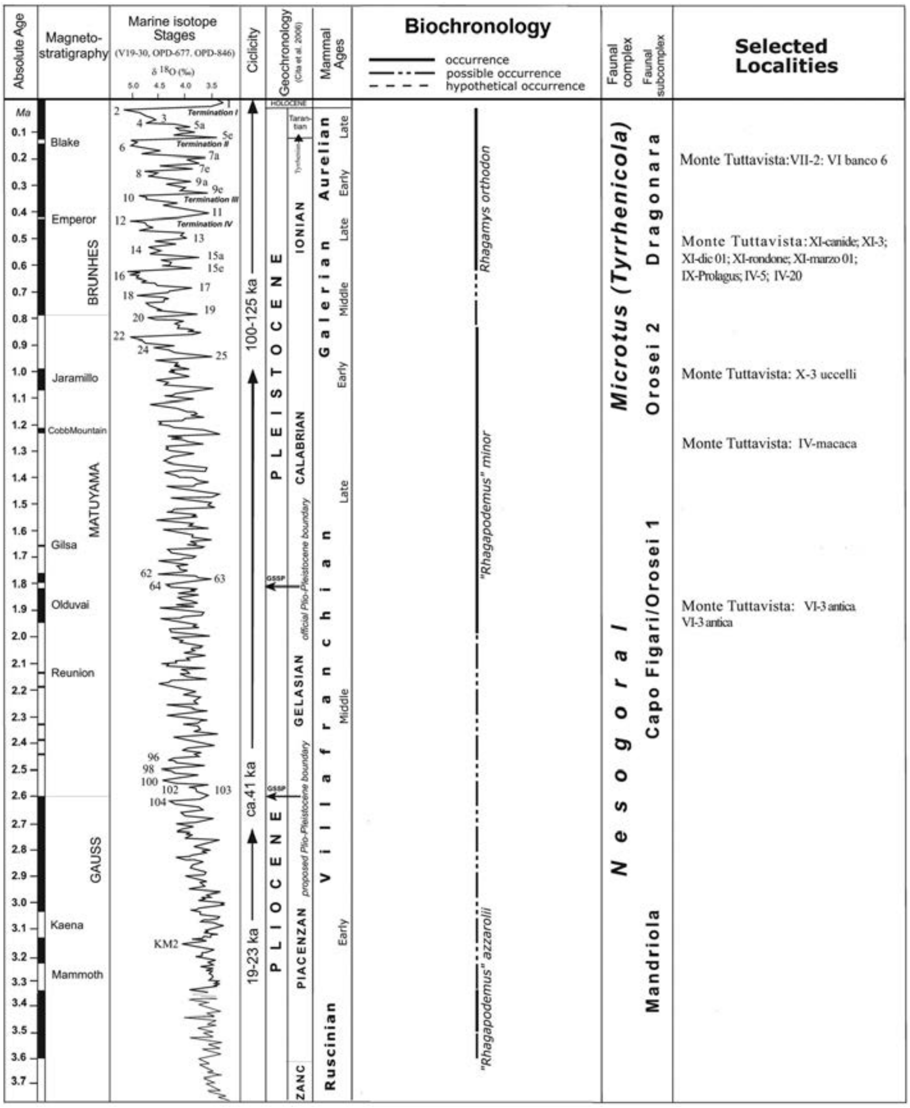


Fig. 1 - Biochronological scheme of Monte Tuttavista fissure fillings analyzed in this study. Modified from Palombo (2006, 2009).

the *Rhagapodemus-Rhagamys* lineage during the Pleistocene of Sardinia.

## Material and Methods

### Biochronology

Fossil-bearing outcrops extend for about 3 km$^2$, to the South-West of Orosei, on the Eastern side of Monte Tuttavista, along the area of Canale Longu, Oroe and Santa Rughe.

The relative ordering of the different fissure fillings is based on biochronological correlations using both macro- and microvertebrates (Rook et al. 2003; Abbazzi et al. 2004; Marcolini et al. 2006a; Angelone et al. 2008; Palombo 2009). Each fissure filling has been calibrated by analyzing the global faunal compositions but their absolute age has not been estimated due to the lack of radiometrically datable beds. For this reason we ordered our sequence from 1 to 9 thus giving to each interval the same step length. We acknowledge that this arrangement does not take in consideration actual time intervals between populations because they remain unknown. Our approach aims modelling phenotypic data by means of recent probabilistic methods developed for ordered time series (Wood et al. 2007; Piras et al. 2009; Hunt 2007, 2010; Hunt & Carrano 2010; Hunt et al. 2010). Precise ages of populations could improve, of course, the assessment of morphological change course trough time, but in the absence of such data we believe that the modelling of phenotypic evolution still deserves particular attention by hypothesis-based quantitative approaches.

On the basis of the most primitive and the most advanced faunas, the nine horizons span from early Pleistocene to the late Pleistocene (Fig. 1). The first three populations (in biochronological order) belong to the species *Rhagapodemus minor* while the remaining ones belong to *Rhagamys orthodon*.

### Material

252 m1 and 208 M1 have been photographed using a Nikon 995 digital camera mounted on a Leica

| Biochronological order | Fissure Fillings name | n° m1 | n° M1 | Systematics |
|---|---|---|---|---|
| 1 | VI3 antica | 20 | 20 | *Rhagapodemus minor* |
| 2 | IV Macaca | 20 | 20 | *Rhagapodemus minor* |
| 3 | X3 Uccelli | 93 | 52 | *Rhagapodemus minor* |
| 4 | Cava IV g.20 | 21 | 20 | *Rhagamys orthodon* |
| 5 | IX *Prolagus* | 21 | 20 | *Rhagamys orthodon* |
| 6 | XI rondone | 20 | 19 | *Rhagamys orthodon* |
| 7 | XI canide; XI Dic. 2001 | 6; 24 | 8; 21 | *Rhagamys orthodon* |
| 8 | Cava VI banco 6 | 21 | 20 | *Rhagamys orthodon* |
| 9 | VII 2 | 5 | 4 | *Rhagamys orthodon* |

Tab. 1 - Material used in this study.

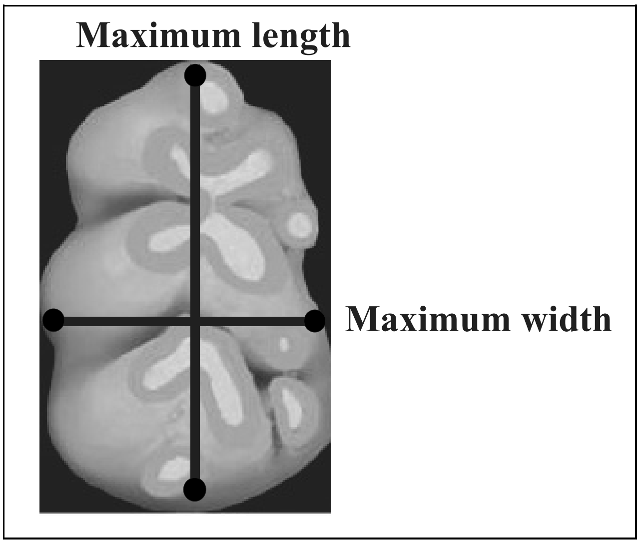


Fig. 2 - Morphometric measures used for this study.

Microscope. Table 1 reports the number of individuals for each horizon as well as the relative biochronological order for each fissure filling bearing the fossil material used for this study. The entire material sample is housed at the offices of the Soprintendenza per i Beni Archeologici delle Province di Sassari e Nuoro, Sardinia, Italy.

Morphometrics

We measured length/width ratio (l-w ratio) on populations coming from different biochronological horizons by digitizing four landmarks representing tooth maximum length and width (Fig. 2) using tpsDig 2.0 software (Rohlf 2006). We computed l-w ratio on all teeth and we quantified their size as the square root of sum of squared differences between landmarks and centroid coordinates, a metric usually called "centroid size" in Geometric Morphometrics studies (Adams et al. 2004). We compared morphology and size between *Rhagapodemus minor* and *Rhagamys orthodon* by performing ANOVA analysis using l-w ratio and size as continuous dependent variables (separately) and species as a factor.

We then used l-w ratio and centroid size as measured phenotypes to look for evolutionary dynamics underlying molar morphology evolution.

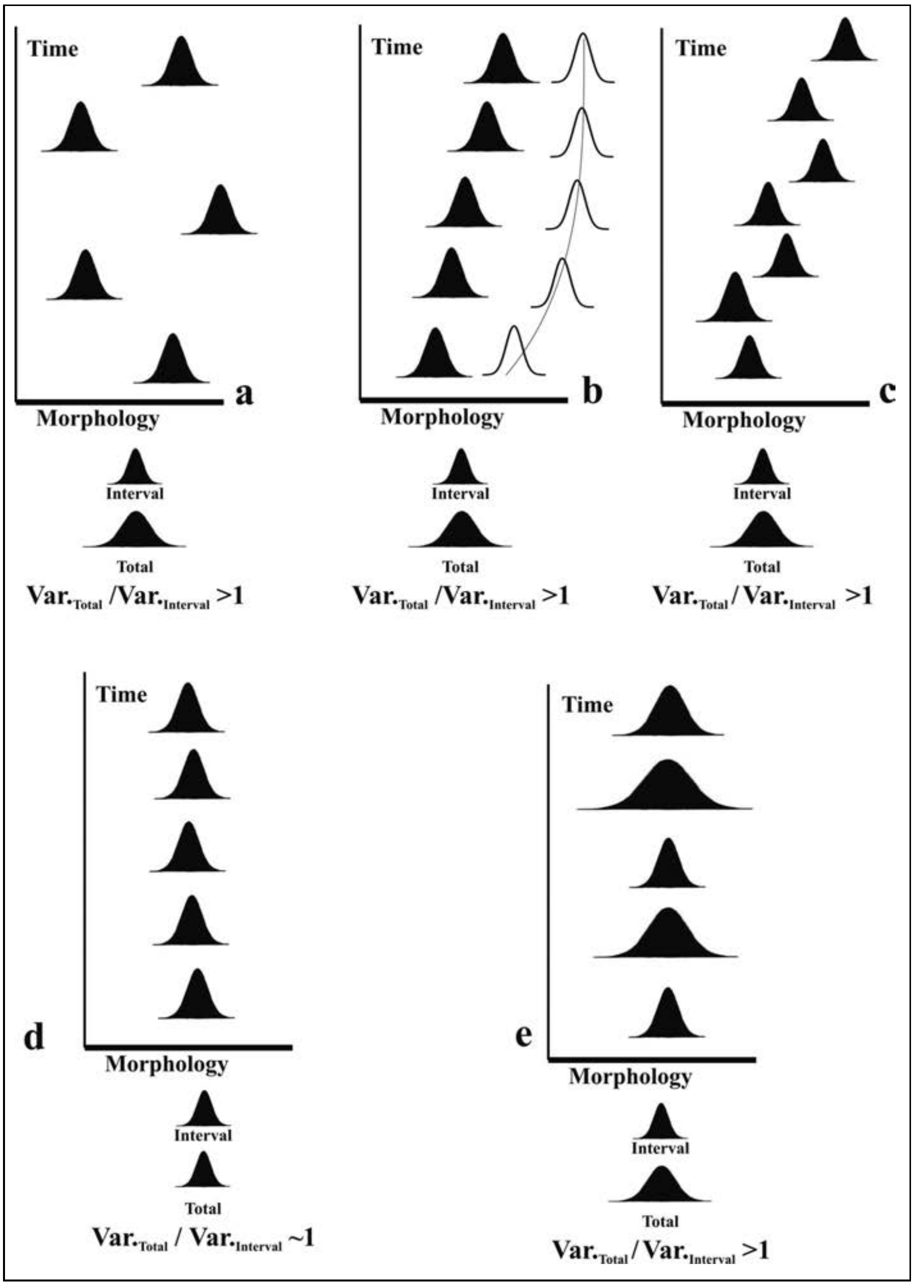
Modes of character evolution

In order to distinguish between patterns depicted in Fig. 3, we used the model based functions available in "paleoTS" R package (Hunt 2011). These functions look for the best maximum likelihood optimization of the data by fitting four main models of character evolution: i) Unbiased Random Walk: there is no tendency between phenotype means in time and the variance of the entire sample is larger than individual populations variances (Fig. 3a); ii) directional evolution: there is a significant trend across population means: this trend can be genuinely directional (Fig. 3b) or due to a directional random walk (Fig. 3c); iii) stasis: there is no trend in time and the variance of the entire sample is not larger than that of individual populations (Fig. 3d); iv) the Ornstein-Ulhenbeck process: is a special case of directional random walk where the course of the phenotype tends toward an adaptive optimum (Fig. 3b, white bells; Hansen 1997; Butler & King 2004). A fifth case is still possible, however, when the total sample variance is larger than single-interval variances, but without showing any kind of directionality (Fig. 4e).

The selection of the best model is made on the basis of corrected Akaike Information Criterion (AICc: Akaike 1974; Hurvich & Tsai 1989; Anderson et al. 2000) as a measure of model fit. It represents a compromise between goodness of fit, measured as log-likelihood, and model complexity, measured as the number of free model parameters. The AICc measures the amount of information lost in approximating reality with a model.

In practice we compare likelihoods of different models to assess which model has the higher probability to explain observed data. In the case of a time series analysis we assess the number of positive and negative deviations from previous interval. In presence of alternating deviations, one single shift, even if large, could be not sufficient to make directional evolution as the best model. Hunt (2008) extensively discussed this pattern (especially fig.1 in Hunt 2008). Hunt (2008) discussed also the punctuated models characterized by a single shift in a temporal series. Punctuated models are more complex (they have more parameters) and their gain in log-likelihood over uniform models is not always large

Fig. 3 - Evolutionary models for different populations in time. Bell distributions represent the distribution of a character around the mean; Var. Total, pooled variance; Var. Interval, variance of a single population. a) Unbiased Random walk; b) Directionality; c) Directional random walk; d) Stasis *s.s.* e) Stasis with changing variances, i.e. when single interval variances are different but the distributions are centred on a statistically equal mean. Modified from Piras et al. (2009).



enough to favor them by AICc, especially in relatively short sequences.

## Results

As for teeth morphology *Rhagapodemus minor* and *Rhagamys orthodon* do not differ (m1: $F_{1,250}$=1.01; *p*-value= 0.32; M1: $F_{1,206}$= 0.91; *p*-value= 0.34), while they are extremely different for size being *R. minor* significantly smaller (m1: $F_{1,250}$= 1103.1; *p*-value= 2.2e-16; M1: $F_{1,206}$= 225.63; *p*-value= 2.2e-16).

For m1 l-w ratio we found that unbiased random walk (Fig. 4a) is the best model for character evolution on the basis of Akaike Information Criterion (AICc random walk: -22.18; AICc directional: -18.33; AICc stasis: -21.55). For M1, instead, stasis returned the smaller AICc (AICc stasis: -23.4; AICc directional: -16.9; AICc random walk: -21.46); this evidence is consistent with patterns of stasis *s.s.* (Fig. 4d).

For m1 size, we found a pattern better explained by unbiased random walk (AICc random walk: 12.05; AICc directional: 16.69; AICc stasis: 14.77); we found similar results for M1 size (AICc random walk: 14.81; AICc directional: 19.43; AICc stasis: 16.47). We then found a still non directional trend but characterized by a significant larger pooled variance relatively to individual population variances.

## Discussion

Our results clearly show that *Rhagapodemus-Rhagamys* lineage undergoes stasis for M1 l-w ratio

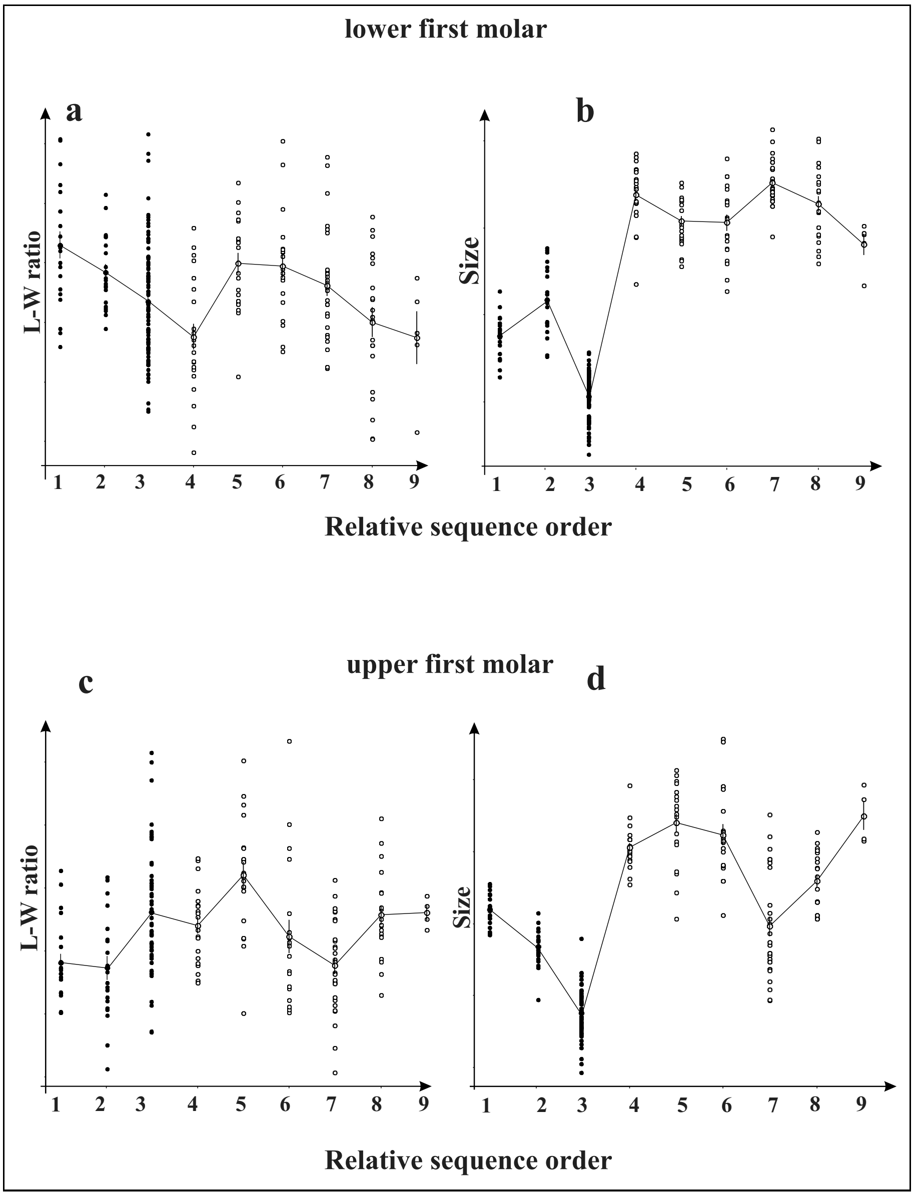


Fig. 4 - Patterns underlying phenotypic evolution in *Rhagapodemus-Rhagamys* lineage. a) m1 l/w ratio evolution in time indicating unbiased random walk. b) m1 size evolution in time indicating unbiased random walk. c) M1 l/w ratio evolution in time indicating unbiased random walk. d) M1 size evolution in time indicating stasis *s.s.* Black circles: *Rhagapodemus minor*; white circles: *Rhagamys orthodon*. Lines connect mean values.

and unbiased random walk for m1 l-w ratio and both M1 and m1 sizes during the Pleistocene of Sardinia. According to Eldredge et al. (2005), Wood et al. (2007), Piras et al. (2009) and Marcolini et al. (2009), a directional trend is more frequent in those samples represented by a few geographically restricted populations (Eldredge et al. 2005) not experiencing very different environmental conditions, while stasis is a consolidated phenomenon when considering a widespread set (in space and time) of different populations experiencing different selective pressures (Cooper & Lenski 2000; Gavrilets 2004). In our study we analyzed a single lineage in a single locality (Monte Tuttavista). Marcolini et al. (2009) found directional trends in the teeth of the arvicolid *Ogmodontomys* in a similar scenario, i.e. a unique fossiliferous site (from the Pliocene of Meade basin of South Western Kansas-USA) bearing populations of different ages. *Rhagapodemus-Rhagamys* lineage, however, does not show any significant directional trend during its evolution in l/w ratio. Renaud et al. (2005) found similar results for the genus *Apodemus*, albeit for a geographically widespread set of populations, for which they found no correlation with climatic change in time. They found, instead, a significant relationship between climate and tooth morphology of *Stephanomys*. Renaud et al. (2005) related the modification in morphology of *Stephanomys* to change in vegetation composition and to its higher dietary specialization in comparison to *Apodemus*. Piras et al. (2010) found similar results for extant populations of the arvicolid *Terricola savii*. Following Renaud et al. (2005), the murid *Apodemus*, due to its dietary generalism, does not show morphological directional trends in time. It is possible that *Rhagapodemus-Rhagamys* lineage had the same ecologic plasticity, showing an oscillating (no neat) phenotypic change during the intense climatic oscillations affecting the middle and late Pleistocene. Unfortunately, a precise correlation between climate (using Isotopes Oxygen values as in Piras et al. 2009) and morphology has not been possible here because no precise population ages were available, thus precluding any correlation test.

Size shows a random walk pattern between populations. This holds even in the presence of significant ANOVA between the two species being *Rhagamys orthodon* larger.

Despite the shift recorded at the transition between *Rhagapodemus minor* and *Rhagamys orthodon*, however, the pattern underlying size evolution both within and between species, does not suggest a significant directional trend. This must be acknowledged on the basis of smaller AICc of random walk model. As stated in Material and Methods, when only one ancestor-descendant transition shows a large shift, a model of a uniform trends like directional evolution is usually not well supported as suggested by Hunt (2008). Together with the primitive *Rhagapodemus azzarolii*, *Rhagapodemus minor* and *Rhagamys orthodon*, *Rhagaodemus-Rhagamys* lineage is considered an anagenetic lineage with two shift in size pattern (between species), a common phenomenon in insular evolution (Sondaar 1977; Lomolino 1985; but see Raia et al. 2010), but without evidences of l-w ratio change in time. The inclusion of *Rhagapodemus azzarolii* in our analysis could be desirable but, the extremely scarce sample size known for complete m1 and M1 (n= 3, as reported by Angelone & Kotsakis 2001) make this inclusion statistically inconsistent. Moreover, *Rhagapodemus azzarolii* was found in an outcrop (Mandriola) that has a precise age, i.e. earliest Late Pliocene, and it is problematic mixing samples coming from some deposits with no precise ages with some others more finely dated.

As a matter of fact we can state that there is a single size shift toward larger size in the whole *Rhagapodemus-Rhagamys* lineage analyzed in this study, but it is not sufficient to make the directional model of evolution the better statistically supported pattern in comparison to random walk.

The precise mode of evolution of the entire lineage cannot be investigated with the specific models used here because the scarce sample size of *Rhagapodemus azzarolii* and the inhomogeneous dating of different deposits.

Our results may be refined if a greater dating accuracy for the main sites is achieved. Additionally, murid molar morphology could be described using more landmarks that capture the main crown features and by taking in consideration molar hypsodonty. However, it is hard to digitize homologous landmarks face also to the dramatic morphological changes caused by wear increasing with individual age.

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