



New data on the taxonomy of the endemic Myomiminae (Gliridae, Rodentia) from the Late Miocene-Early Pliocene of Gargano (southern Italy) with the description of the new species *Stertomys degiulii*

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THIS WORK IS DEDICATED TO THE MEMORY OF CLAUDIO DE GIULI, 21 YEARS AFTER HIS PREMATURE DEATH. HE WAS A FRIEND AND A SCIENTIST FUELLED BY THE INTEREST IN MANY ASPECTS OF PALAEOONTOLOGICAL SCIENCE, BUT NOT LIMITED TO THIS SPECIALIZATION. A MASTER OF GREAT HUMANITY AND A COMPANION DURING WORK AND FIELD EXCAVATIONS.

KEY WORDS - *Stertomys*, *Gliridae*, *Gargano*, *Endemism*, *Insularity*, *New species*.

ABSTRACT - The Late Miocene-Early Pliocene “Terre Rosse” vertebrate assemblages, found in the palaeokarst fissure fillings of the Apricena-Poggio Imperiale limestone quarries (North-Western side of the Gargano promontory, southern Italy), document a very long and complex history of endemic populations of a palaeoarchipelago. That history developed in at least four populating phases, which are characterised by changes in faunal diversity and include taxa with different degree of endemism. They have been subject of several studies since the beginning of the 1970s and deserve a particular attention for their evolutionary and palaeogeographical implications. The sampling of the “Terre Rosse” fissure fillings was carried on during successive field surveys from the Leiden Museum (1969-74) and from the Florence University (1980s). Until now, however, the two resulting collections have always been studied separately by different authors: this work is the first partial attempt to integrate the information derived from the two collections. A biochronological framework is proposed integrating the chronological succession of samples by Freudenthal in the scheme elaborated by De Giuli et al. However, some uncertainty remains in the details of the position of some fissure, in particular Rinascita 1.

After the pioneering description of the gigantic dormouse *Stertomys laticrestatus* Daams & Freudenthal 1985, the interest in the systematic of the Neogene Gargano glirids renewed just in the very last years. Four species have been recently described: *Stertomys daunius* Freudenthal & Martín-Suárez 2006, *Stertomys daamsi* Freudenthal & Martín-Suárez 2006, *Stertomys lyrifer* Martín-Suárez & Freudenthal 2007, and *Stertomys simplex* Martín-Suárez & Freudenthal 2007.

In the present work the description of *Stertomys* from eleven further fissure fillings, documenting most of the whole succession of endemic population phases, is presented and discussed. The samples, for a total amount of 1696 dental elements, have been described by basic statistical parameter of measurements and frequency distribution of Daams’ and Rinaldi’s morphotypes. Where necessary, the differences among samples have been statistically tested (t-test and chi-square test).

Seven taxa have been identified: *S. daunius*, *S. laticrestatus*, *S. aff. laticrestatus*, *S. ex gr. daamsi*, *Stertomys degiulii* nov. sp., *S. cf. degiulii* and *S. aff. degiulii*. In the fissure F15 *S. ex gr. daamsi* has the same size as *S. daamsi* from its type-locality Biancone 1, but a slightly more complex morphology in the upper molars. In Trefossi 1, F21b, Cantatore 3A and Fina D, *S. ex gr. daamsi* shows a rather similar morphology as in F15, but it is clearly smaller in size. *S. degiulii*, from F1, F9 (type-locality) and San Giovannino is distinctly smaller than *S. ex gr. daamsi* and presents a higher frequency of the connection of the trigon crests with the metaloph in the upper molars. *S. aff. degiulii* from F32 is slightly larger in size and shows a higher frequency of connection of the anterolophid with the protoconid in the lower molars. *S. cf. degiulii* from Pirro 11A is intermediate in morphology between *S. degiulii* and *S. aff. degiulii*.

The results of the analysis of the *Stertomys* species occurring in each fissure filling confirm the outline of the proposed biochronological framework and permit some improvement of the definition of the populating phases of the Gargano palaeoisland. Besides, they confirm the presence of some problems in arranging the details of the fissure succession of the oldest phase. Such uncertainties are possibly due to the frequent faunal exchanges among the islands of the palaeoarchipelago and with the mainland during the time documented by this early phase.

The results of the present contribution also suggest that an early radiation occurred in the palaeoarchipelago, producing at least five lineages. These lineages can be arranged in two main branches characterised by different size and morphology. Large-sized *Stertomys* species, although closely related, cannot be considered as belonging to the same phyletic lineage. Among the small-sized taxa, *S. daamsi* and *S. degiulii* might be arranged in a single phyletic lineage where a trend in reduction in size and an increase of the complexity of the pattern of connection among crests occur. *S. simplex* may be considered as a species with primitive morphology, very close to the ancestor of *S. daamsi*. Most of the evolutionary divergence is observed among the different lineages, while phyletic gradualistic changes are documented to a lesser extent.

RIASSUNTO - [Nuovi dati sulla tassonomia delle Myomiminae (Gliridae, Rodentia) endemiche del Miocene superiore-Pliocene inferiore del Gargano (Italia meridionale) con la descrizione della nuova specie *Stertomys degiulii*] - Le faune endemiche delle “Terre Rosse” del Gargano (Miocene superiore-Pliocene inferiore), che si trovano nei riempimenti delle fessure carsiche esposte nelle cave di pietra calcarea dell’area di Apricena-Poggio Imperiale, sono note fin dall’inizio degli anni ‘70 e rivestono un particolare interesse paleogeografico ed evolutivo. Il popolamento garganico è caratterizzato da un’elevata diversità di micromammiferi che, con un massimo di 12 taxa coesistenti, supera abbondantemente quella delle altre isole mediterranee. I numerosi depositi di riempimento documentano la storia del popolamento di un ambiente insulare all’interno di un arcipelago in almeno quattro fasi successive, con cambiamenti nella diversità delle associazioni e con differenti gradi di endemismo. L’intervallo di tempo documentato e la grande quantità di materiale disponibile ben si prestano a ricostruire i processi evolutivi dei taxa endemici. Il campionamento dei vertebrati dei riempimenti a “Terre Rosse” è stato condotto in successive campagne di scavo dal Museo di Leiden (1969-74) e quindi dall’Università di Firenze (anni ‘80). Fino ad ora, tuttavia, le due collezioni sono state quasi sempre studiate separatamente da autori diversi. Il presente lavoro rappresenta il primo tentativo di integrare l’informazione contenuta nelle due collezioni. Il quadro biocronologico proposto nasce dall’integrazione della successione cronologica di fessure proposta da Freudenthal nel 1976 all’interno dello schema

in fasi proposto da De Giuli et al. nel 1987. Tuttavia, rimangono alcune difficoltà nella sistemazione di dettaglio di alcune fessure, in particolare di Rinascita 1.

Nel 1985 Daams & Freudenthal descrivono dalla fessura San Giovannino la specie di ghiro gigante *Stertomys laticrestatus*, attribuendola erroneamente alla sottofamiglia Glirinae. Sono passati oltre vent'anni prima che l'interesse per la tassonomia dei gliridi delle "Terre Rosse" si risvegliasse con la descrizione di quattro nuove specie provenienti da riempimenti che documentano la più antica fase di popolamento della paleoisola. Nel 2006 Freudenthal & Martín-Suárez descrivono *Stertomys daunius* e *Stertomys daamsi* in Biancone 1, ritenuta la fessura più antica dell'intera successione. Nei depositi della fessura Rinascita 1, considerata da Freudenthal quella immediatamente più recente, Martín-Suárez & Freudenthal nel 2007 descrivono *Stertomys lyrifer*, *Stertomys simplex* ed una forma affine a *S. daamsi*, ma di taglia più piccola. Le diverse specie di *Stertomys* sono state suddivise in due gruppi: uno con forme di grande taglia e con morfologie dentarie da complesse a molto complesse, e uno con forme di taglia minore e con morfologie da semplici a moderatamente complesse. Le forme meno derivate di *Stertomys* mostrano chiaramente la connessione fra il metalofo e il protofo sui molari superiori; questo carattere permette di attribuire il genere alla sottofamiglia Myomiminae.

Vengono qui presentati e discussi i risultati dell'analisi su reperti di *Stertomys* provenienti da undici fessure carsiche selezionate in modo da essere rappresentative dell'intera successione delle fasi di popolamento endemico. L'analisi, di tipo morfo-dimensionale, è stata condotta sugli elementi dentari. Sono stati esaminati e misurati 1696 denti che sono stati classificati morfologicamente in base ai morfotipi standard di Daams e ad alcuni morfotipi recentemente proposti da Rinaldi. I campioni sono stati descritti con i parametri statistici delle misure e con le distribuzioni di frequenza dei morfotipi. Ove necessario, le differenze fra i campioni sono state confrontate tramite test statistici (t di Student e chi quadro).

Sono stati identificati i seguenti sette taxa: *S. daunius*, *S. laticrestatus*, *S. aff. laticrestatus*, *S. ex gr. daamsi*, *Stertomys degiulii* nov. sp., *S. cf. degiulii* e *S. aff. degiulii*. Per quanto riguarda gli esemplari di grande taglia, *S. daunius* è stato ritrovato nei depositi delle fessure F15 e F21a, mentre *S. laticrestatus* in quello di F9. In F1 è stato descritto un unico esemplare identificato come *S. aff. laticrestatus*. Per quanto riguarda invece le forme di piccola taglia, in F15 è stata identificata una forma della stessa taglia di *S. daamsi* di Biancone 1, ma con una morfologia leggermente più complessa dei molari superiori. In Trefossi 1, F21b, Cantatore 3A e Fina D è presente una forma confrontabile morfologicamente con quella di F15, ma con una taglia nettamente minore. Tutti questi esemplari sono stati descritti come *S. ex gr. daamsi*. Nelle fessure più recenti, F1, F9 e San Giovannino, è stata descritta la nuova specie *Stertomys degiulii*, che si differenzia da *S. daamsi* per la taglia marcatamente minore e per la maggior frequenza di connessione delle creste interne al trigono con il metalofo nei molari superiori. La fessura F9 è stata scelta come località tipo di questa nuova specie. Nella fessura F32 è stata identificata una forma affine a *S. degiulii*, di taglia leggermente maggiore e con una maggiore frequenza di connessioni nei molari inferiori fra l'anterolofide e il protoconide. In Pirro 11A è presente una forma riferibile a *S. degiulii* ma che tende, per alcuni caratteri, ad avvicinarsi al taxon di F32; per lo scarso materiale disponibile tale forma è stata identificata come *S. cf. degiulii*.

La definizione dell'associazione a Myomiminae permette di definire meglio la successione cronologica delle fessure. Nella fase di popolamento più antica sono presenti *S. gr. daamsi* e *S. daunius*, e limitatamente alla sola Rinascita 1 *S. lyrifer* e *S. simplex*. Se si vuole definire una cronologia di dettaglio, quest'ultima fessura presenta però dei problemi, poiché per le caratteristiche dei ghiri potrebbe essere considerata più antica di Biancone 1. Queste difficoltà sono probabilmente dovute al fatto che nel tempo documentato dai riempimenti più antichi si sono verificati frequenti scambi fra le isole e col continente, come mostra anche la presenza di forme non endemizzate. La seconda fase, comprendente le fessure Fina D e F1, conferma il suo carattere transizionale, evidenziato dal turn over nell'associazione delle specie di *Stertomys*. La terza fase, rappresentata da F9, San Giovannino e Pirro 11A, è caratterizzata dalla presenza di *S. degiulii* e *S. laticrestatus*. L'affinità del ghiro di Pirro 11A con quello di F32, suggerisce che la prima possa essere considerata più recente di San Giovannino. F32 rimane ad oggi l'unica fessura rappresentativa della quarta fase di popolamento. In questa fase si assiste ad una riduzione della diversità (la scomparsa di *S. laticrestatus*) e ad un leggero aumento di taglia di *S. aff. degiulii*.

Da un punto di vista evolutivo le tre specie di taglia grande, benché correlate tra loro, non sembrano avere rapporti diretti di discendenza. Fra le specie di taglia piccola lo stesso si può dire di *S. daamsi* e *S. simplex*. Per quanto riguarda *S. daamsi* e *S. degiulii*, invece, si può ipotizzare una discendenza diretta. Lungo questa linea si nota un trend di diminuzione di taglia e una leggera complicazione del pattern dentale, soprattutto per quel che riguarda le connessioni fra le creste. Come riscontrato anche in altri taxa, le specie disperdono sull'isola già diversificate e i cambiamenti riconducibili ad evoluzione filetica sono di minore entità. Tale ricostruzione evidenzia quindi l'esistenza di minori cambiamenti gradualistici riconducibili ad evoluzione filetica, ma più che altro è in accordo con le attese di un modello ad equilibri punteggiati, in cui la massima differenziazione avviene durante gli eventi cladogenetici.

INTRODUCTION

The "Terre Rosse" endemic fauna

The Gargano "Terre Rosse" faunal assemblages are found in sediments derived from soils (Oxisols), which filled an extensive palaeokarst system, developed within Mesozoic carbonates (Abbazzi et al., 1996). Most of the fissure fillings are located in a rather small area between Apricena and Poggio Imperiale (Fig. 1) where very extensive and intensive limestone quarrying activities occur. The sediments were exposed and sampled thanks to those activities.

Fissure fillings were first intensively sampled by a team of the Rijksmuseum van Geologie en Mineralogie (now Naturalis, Nationaal Natuurhistorisch Museum) of Leiden, the Netherlands, led by Matthijs Freudenthal from 1969 to 1974. In the '80s, Claudio De Giuli and Danilo Torre led a team of the Dipartimento di Scienze della Terra of the University of Florence, Italy, and took over the sampling, collecting a wealthy amount of specimens.

Many fissures yielded a very rich and diversified fauna composed by taxa showing different degrees of endemism. This is the "*Microtia* fauna", named after its most outstanding taxon, the murid *Microtia*, which was first described by Freudenthal (1976) and renamed as *Mikrotia* (Freudenthal, 2006). The Gargano Late Miocene-Early Pliocene faunal assemblages include Amphibia, Reptilia (Delfino, 2002; Delfino et al., 2007), Aves (Ballmann, 1973, 1976; Göhlich & Pavia, 2008), and Mammalia. The latter include Chiroptera, Carnivora (Willemsen, 1983), Insectivora (Freudenthal, 1972; Butler, 1980; Fanfani, 1999), Rodentia (Freudenthal, 1976, 1985; Daams & Freudenthal, 1985; Freudenthal & Martín-Suárez, 2006; Martín-Suárez & Freudenthal, 2007), Lagomorpha (Mazza, 1987a, b, c; Mazza & Zafonte, 1987), and Artiodactyla (Leinders, 1984; van der Geer, 2008). The faunal composition is highly unbalanced: the bulk of the assemblages consists of endemic small mammals, some of which had achieved a "gigantic" size.

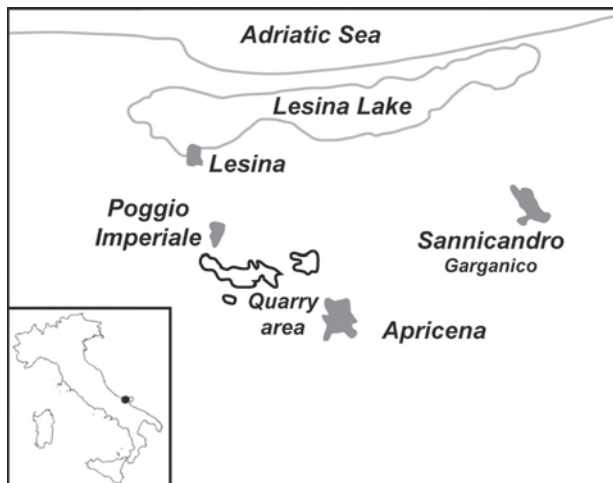


Fig. 1 - Location map of the Apricena-Poggio Imperiale quarrying area.

A number of studies are devoted to the evolutionary and adaptive aspects of the endemic murids *Mikrotia* (Freudenthal, 1976; Torre, 1986; Zafonte & Masini, 1992; Abbazzi et al., 1993; Parra et al., 1999; Millien & Jaeger, 2001) while others give contributions to the local biochronology (Freudenthal, 1976; De Giuli et al., 1987a), to the palaeogeography (De Giuli et al., 1986b, 1987b, c; Abbazzi et al., 1996) and to the evolution of the Gargano fauna (De Giuli & Torre, 1984; De Giuli et al., 1986a).

The numerous fissure fillings document a populating history in an island environment situated in an archipelago (Freudenthal, 1976; De Giuli et al., 1986a, 1990). That history develops into at least four different phases (De Giuli et al., 1987a, 1990; Masini et al., 2008) showing changes in the assemblage diversity that also testify different degrees of endemism. The diversity of small mammal fauna exceeds that of other assemblages in the Mediterranean islands. The Gargano assemblages are often cited as an example of utmost interest in papers involved in the endemism in the Mediterranean Islands (Torre, 1986; De Giuli et al., 1990; Moyá-Solá et al., 1999; Masini et al., 2002a, b, 2008; de Vos et al., 2007). The interest in the systematics of this fauna, however, declined over the past fifteen years even though some taxa still need to be described.

The glirids

The Gargano dormice belong to two subfamilies whose occurrence is very uneven. The Dryomyinae are represented by a limited number of specimens belonging to *Dryomys apulus* (Freudenthal & Martín-Suárez, 2006; *Eliomys* in De Giuli et al., 1987a), which is characterised by “normal size” with respect to its mainland congeners and does not display endemic features. The occurrence of this taxon is apparently limited to the older fissure fillings (De Giuli et al., 1990). On the other hand, the Myomiminae are very diversified and represent the vast majority of the glirid material. They are found in all fissure fillings studied so far, displaying moderate to very high endemic features, both morphological and

dimensional, and a wide evolutionary variation (Freudenthal & Martín-Suárez, 2006; Rinaldi, 2006).

The first taxonomic report on the Gargano Myomiminae was that of Daams & Freudenthal (1985) who described the very large-sized *Stertomys laticrestatus* from a fissure called San Giovannino. The authors reported a rather uncertain taxonomic affinity for this endemic, and they considered it as a possible member of subfamily Glirinae. The correct inclusion of *Stertomys* in the Myomiminae is due to Freudenthal & Martín-Suárez (2006) and Rinaldi (2006). Freudenthal (1971) reported the occurrence of another endemic “normal-sized” glirid in Gargano. It was later quoted as *Peridyromys* by De Giuli et al. (1987a, c; 1990) and as *Myomimus* by Kotsakis (2003). Freudenthal & Martín-Suárez (2006) described two new species from the fissure Biancone 1: the small-sized *Stertomys daamsi* (= *Peridyromys pro parte* of Authors) and the large-sized *Stertomys daunius*. Martín-Suárez & Freudenthal (2007) described two further new species: *Stertomys simplex* and *Stertomys lyrifer* from the fissure Rinascita 1. *Stertomys simplex* is closely related to *S. daamsi*, but it has a simpler morphology, while *S. lyrifer* is considered to be more related to *S. daunius* even though it is much smaller. Martín-Suárez & Freudenthal (2007) described also from Rinascita 1 *S. aff. daamsi* as a taxon close to *S. daamsi* from Biancone 1 but of smaller size. Finally, the same authors reported in Rinascita 1 the occurrence of three more new species of *Stertomys*, which are represented by extremely scant material. Up to date, therefore, five well defined species of *Stertomys* have been described, three of which may be referred to a supra-specific cluster characterised by large to very large size and very complex dental morphology, while the others represent a group of smaller species with simpler morphology. The material examined by Freudenthal & Martín-Suárez (2006) and Martín-Suárez & Freudenthal (2007) comes from two fissures which are considered the oldest of the whole biochronological sequence (Freudenthal, 1976; De Giuli et al., 1987a). The detailed systematic descriptions provided by the former authors serve as a basis for the present contribution. In the present work, based on results by Rinaldi (2006), the systematic study is extended to eleven further selected fissure fillings distributed throughout the whole biochronological range of the “Terre Rosse” endemic phases of population. Some of the Leiden material is directly compared for the first time with samples previously studied by De Giuli et al. (1987a).

BIOCHRONOLOGICAL FRAMEWORK

Remarks on biochronological methods

The lack of stratigraphic superposition renders inferential the reconstruction of the chronological succession of the fissure fillings. One of the methods to unravel such a complex problem relies on the detection of morpho-evolutionary variation among the fossil taxa contained in the different fissure deposits and on the assumption that the variation can be arranged in evolutionary trends. The resulting succession can be

properly defined as a “biochronology”, following the definition of Lindsay (1990). Freudenthal (1976) is the pioneering paper on the “Terre Rosse” biochronology. In this paper, both *Mikrotia* and cricetids are taken into consideration, but most of the issues are based on *Mikrotia*. The basic principle (see Freudenthal, 1976, pp. 7-9 “Principles of *Mikrotia* evolution”) is the recognition of primitive and derived morphological features and the assumption of the ordering criterion “primitive is old”. Small size and simple morphology (close to the basic murid pattern in the case of *Mikrotia*) are considered as “primitive”, while large size and complex morphology are considered “modern”. The second step is the recognition of a phyletic lineage, “medium sized lineage of evolution” in Freudenthal (1976), which is assumed to be present in all samples and to show variation in size and morphological complexity. The assumption that this resident lineage underwent a continuous increase in size is the basis for a finer chronological ordering of samples. In particular, the author assumes a *constant rate (linear) of size increase* and arranges the position of each sample within a “relative virtual time scale” based on the mean values of M_1 length of the samples considered to belong to the resident lineage (Freudenthal, 1976, Fig. 4). Since the plain application of the outlined biochronological method produced some uncertainties and contradictions, particularly for what regards the detailed chronological order of the oldest samples, the author introduces further criteria and assumptions. The relative abundance of different species of the same genus occurring in the same sample is considered as a kind of “fitness” parameter that guarantees the survivorship of the species represented by a greater number of individuals. Therefore, when two species at a close evolutionary level, but with different relative abundance, occur in the same fissure, the most abundant one is considered as belonging to the resident lineage. Finally, to arrange the oldest samples (Biancone 1, Rinascita 1, and Trefossi 1) in a relative chronological order, the author invokes repeated migration events from neighbouring islands or from the mainland and the occurrence of extinction events.

Freudenthal selected about twenty samples among the 75 fissure fillings available, and considered a maximum number of 20 specimens for each sample. A noticeable exception was *Mikrotia parva* from Biancone 1 for which a sample of 118 M_1 was considered. Freudenthal was aware that the sample dimension of 20 specimens was indeed rather small and he declared explicitly the “preliminary nature” of his report. Indeed, twenty specimens are acceptable for the estimate of the mean length of the molars, but this number is too small for a reliable estimate of morphological complexity of the teeth computed by averaging the counts of morphotypes. The chronology proposed by Freudenthal (1976) has been adopted in other papers dealing with cricetids (Freudenthal, 1985), *Deinogalerix* (Butler, 1980) and birds (Ballmann, 1973, 1976), or with particular aspects of *Mikrotia* evolution (Parra et al., 1999; Millien & Jaeger, 2001). However, in none of these papers the problematical aspects of the chronological methodology have been critically discussed.

Freudenthal’s (1976) chronology served as a starting point to the work of De Giuli et al. (1987a). These

authors based their reconstruction on eight selected samples that, for their extremely rich fossiliferous content, could be confidently assumed as appropriate to reconstruct the succession of the phases of population of the palaeoisland. Following Freudenthal’s methodology, the authors carried out a detailed morphological analysis (size and morphotype analysis) on *Mikrotia* and on *Prolagus* (for the latter see Mazza, 1987a, b, c). These data were integrated with preliminary observations relative to the size variation of *Galerix* (*Parasorex*), *Myomiminae* and *Apodemus*. The general criteria adopted were similar to those of Freudenthal (1976), based on the appearance of derived characters in the considered taxa and following the principle that “a sample can be assumed younger than another when at least one population is characterised by the occurrence of a significant frequency of new apomorphies or, at a lesser degree of confidence, when it contains a population with a greater frequency of derived morphotypes” (see De Giuli et al., 1987a, p. 270). The authors considered size variation as useful for chronological purposes when it is related to a trend of morphological variation. Finally, the contradictory chronological sequences that are expected to arise in adopting the above-described principles to the different taxonomical groups, were resolved by applying a “parsimony” constraint to the different hypothetical sequences. According to this methodological choice, it is considered more reliable, and therefore accepted, the solution that implies the minimal number of events occurred, i.e. the least number of hypothesized phyletic lineages and the less number of migration and extinction events (De Giuli et al., 1987a, Fig. 4). As admitted by the authors, in some cases (particularly for those fissures which contain the most primitive populations and are considered the oldest of the sequence) the application of the aforementioned criteria did not give fully satisfactory results and therefore, following Freudenthal (1976), De Giuli et al. (1987a) also considered additional information, such as the abundance of specimens of the various populations, in order to constrain the relative chronology of some samples. De Giuli et al. (1987a) declared explicitly that they were aware of the complexity underlying the problem and considered the proposed solution as a *model*, open to improvement. The biochronological succession of De Giuli et al. (1987a) was tested by the analysis of the variation of enamel microstructure of the teeth of *Mikrotia* and *Prolagus* (Zafonte & Masini, 1992 and Mazza & Zafonte, 1987 respectively), which yielded consistent results (Abbazzi et al., 1993).

While trying to integrate the samples of the Leiden and the Florence collections in a unified chronological scheme, we found many consistent aspects, but we also faced several problems. Firstly, the quality of the sampling published by De Giuli et al. (1987a) and Freudenthal (1976) is not homogenous: few large extensive samples versus many small sub-samples. Secondly, although the general principles adopted in the two papers are roughly the same, the details of the chronology proposed by the Leiden researcher are actually derived from an assumption - the occurrence of progressive linear size increase - that is considered weak by the other authors.

The actual occurrence of such a progressive gigantism, or dwarfing, has been recently criticised on biological and ecological basis by several authors (e.g. Lomolino, 2005). As a matter of facts, size variation should be considered as a result of the selective pressure of many contrasting factors, and the tendencies are expected to be easily reversed by perturbations, internal to the biologic insular system or driven by external factors, such as weakening or reinforcing of the isolating barriers, shrinking or increase of island area, changes in vegetation and environmental parameters due to climatic changes, and so on. Another more practical problem concerns the incomplete knowledge of the faunal composition of some fissures and the taxonomic evolutionary information, which is not homogenous for the two collections. For instance, De Giuli et al. (1987a) did not consider the taxonomy and evolution of cricetids, while Freudenthal (1976) ignored *Prolagus*. A still more practical problem is the fact that, except for San Giovannino, it is impossible to establish a direct correspondence between the single fissures of the two collections, even though several of them might actually be different samples, with different names, of the same deposit.

The adopted biochronological framework

The framework reported in Tab. 1 is an attempt to correlate the biochronological succession proposed by De Giuli et al. (1987a) with the one published by Freudenthal (1976). The succession of De Giuli et al. is here considered as the referent biochronological arrangement to which the samples from the Freudenthal collection have been correlated. Most of the correlations rely on *Mikrotia* data for the reason that this is the only taxon studied in the detail for the two collections. Some other available information has been employed in order to reach a reasonable solution. The taxonomic results relevant to the studied glirids, exposed for the first time in this paper, are not considered here to avoid possible circular argumentation. This scheme serves therefore as an *a priori* reconstruction for the discussion of the biochronological implication of the study of Myomiminae.

The scheme is arranged into four phases (Masini et al., 2008), which are characterised as follows.

Phases*	De Giuli et al., 1987a	Freudenthal, 1976
4	F32	
3	San Giovannino	San Giovannino Pirro 11A
	F9	
2	F1	Fina D
		Cantatore 3A
1	F21a, F21b	Trefossi 1
	F15	Rinascita 1 Biancone 1

Tab. 1 - Tentative correlation of the biochronological successions by De Giuli et al. (1987a) and by Freudenthal (1976). *: *sensu* Masini et al. (2008).

Phase 1 - The samples considered as the oldest are characterised by the occurrence of several, not-endemic taxa such as *Dryomys apulus* (Biancone 1, Rinascita 1, F15), *Cricetulodon*, *Cricetus* sp. (Rinascita 1), *Lartetium* cf. *dehmi* (so far recorded in F15, F21a and F21b; Fanfani, 1999), that foreshadow the occurrence of faunal exchanges from the mainland and possibly with the neighbouring islands. These taxa are limited to this phase or to the oldest samples of this phase. The occurrence of the not-endemic *Megacricetodon* sp. at Biancone 1 is considered doubtful by Freudenthal (1985). *Prolagus*, *Mikrotia*, and *Hattomys* are represented by primitive species; in particular the occurrence of the smallest and less derived *Mikrotia* (Rinascita 1, F15, Trefossi 1 and F21b) so far described is noteworthy. *Stertomys* is present with one large and one small-sized species, although in Rinascita 1 three species occur. Echinossoricinae are represented by the most primitive *Deinogalerix* species (Biancone 1, Rinascita 1, Trefossi 1, F15, F21a and F21b) and by a dwarf *Parasorex* (*Galerix* (*Apulogalerix*) *pusillus* in Fanfani, 1999). A not-endemic, normal-sized *Apodemus* and some *Hoplitomeryx* species occur in this phase.

The relative chronological position of samples F15 and F21b is affected by some uncertainties and is discussed in De Giuli et al. (1987a). In the proposed scheme, Biancone 1 and Rinascita 1 are considered older than F15, since they contain a couple of less derived *Mikrotia* populations. The older position of Biancone 1 compared with Rinascita 1 is according to Freudenthal (see the discussion reported in Freudenthal, 1976, on the difficulties of arranging the chronological position of Rinascita 1 and Biancone 1).

In Trefossi 1, a very small and simple *Mikrotia* species, comparable to those of samples F15 and F21b, together with a larger one belonging to the main evolutionary lineage, comparable in size and morphology to the medium species of F15, occur. Trefossi 1 is considered as possibly slightly younger than sample F15. The position of Cantatore 3A is less uncertain. According to Freudenthal's data, it lacks the very small and simple *Mikrotia* species, and contains two species, very close in size. The size and the morphology of the larger species are comparable to the medium species of F21b. This sample can be therefore placed in a younger position than F21b but definitely older than F1, which contains a larger-sized and more complex representative of the medium lineage of *Mikrotia* (see below). As observed by Freudenthal (1976, 1985), these groups of samples are only some incomplete documents of the most complex phase of the Gargano vertebrate population history.

Phase 2 - This phase is characterised by the occurrence of a single species of *Mikrotia* belonging to the "main lineage of evolution", larger and with more complex M_1 than the most complex *Mikrotia* species of the previous phase. "Continental" species are absent from this assemblage. According to De Giuli et al. (1987a), this phase includes fissure F1. Fina D is tentatively included in this phase because of the occurrence of a single population of *Mikrotia*, recognised by Freudenthal as belonging to the "main lineage of evolution", which displays a much smaller size than F1 *Mikrotia* but a comparable morphological

complexity. Taking into account the smaller size, comparable with that of Cantatore 3A, the sample Fina D seems to be older than F1. In this phase *Stertomys* is represented by a large and a small-sized species. *Deinogalerix*, *Galerix* (*Apulogalerix*), *Hoplitomeryx* and *Apodemus* are all present in these samples and in all the subsequent phases.

Phase 3 - Samples belonging to this phase are by far the most common in the “Terre Rosse” deposits. These assemblages are characterised by the occurrence of three derived species of *Mikrotia*, different in size. The middle-sized species has a more complex morphology and is considered as belonging to the resident lineage. The larger (*Mikrotia magna* Freudenthal 1976) and the smaller (unnamed) species have no apparently direct phylogenetic link to the middle-sized *Mikrotia* of the previous phase and are considered as resulting by dispersals from neighbouring islands. *Prolagus* and *Hattomys* are represented by derived species. *Stertomys* is represented by two species, a large and a small one. According to De Giuli et al. (1987a), fissure F9 is a typical representative of this phase. San Giovannino is considered the youngest sample of this phase (the youngest in the whole Leiden collection) because of the occurrence of the most derived representative of the resident middle-sized species of *Mikrotia*. *Prolagus* is present in San Giovannino with two species. Pirro 11A is referred to this phase because of the occurrence of three species of *Mikrotia*, which have a fairly comparable size to those of San Giovannino, although the middle-sized species (resident) is somewhat less derived in morphology. For this reason, it is placed between F9 and San Giovannino. Freudenthal (1976), however, suggested that Pirro 11A could be very close to San Giovannino, considering that the main evolutionary lineage of *Mikrotia* is underrepresented and that *Mikrotia magna* is larger than that of San Giovannino.

Phase 4 - This phase is apparently documented only by fissure F32 and is not identifiable in Freudenthal (1976) reconstruction. It is characterised by the disappearance of the medium and large-sized species of *Mikrotia*, of *Hattomys* and of the large-sized *Stertomys*. *Mikrotia* occurs with a derived small-sized species larger than that of San Giovannino. Two *Prolagus* species

occur, one of which is the largest present in the whole succession. *Apodemus* and *Galerix* (*Apulogalerix*) are larger than those from San Giovannino and the former species show some derived features not found in the other populations (De Giuli et al. 1987a). In spite of the lack of the medium-sized *Mikrotia* species, the uppermost position of F32 is based on the similarities with San Giovannino (these are the only two fissures in which two evolved *Prolagus* species occur), on the occurrence of the larger and derived *Apodemus* and on the absence of “giant” micromammals such as *Stertomys*, *Hattomys* and two *Mikrotia* species. Placing the F32 assemblage prior to San Giovannino, or even prior to F9, would imply the disappearance of several species and a successive reimmigration from other islands of species quite identical to those which become extinct (a sort of Lazarus effect *sensu* Jablonsky, 1986). We assume that the occurrence of such a complex event is actually not very probable.

MATERIAL AND METHODS

Material

The examined material consists of Myomiminae teeth from eleven fissure fillings, whose biochronology is reported in Tab. 1. The material includes 1696 specimens belonging to fourteen samples and seven different taxa. The material is stored in the collections of Florence and Leiden. The synopsis of the specimens and their repository are reported in Tab. 2. Since the samples were collected by the personnel of two scientific institutions during field surveys that took places in different time spans (seventies and eighties), and since the quarrying activities destroyed most of the locations, it has been impossible to check if some of the samples are replicas from the same deposit, with the exception of fissure San Giovannino. Small-sized specimens from this fissure are those of the Florentine collection. *Stertomys laticrestatus* from San Giovannino and the samples from the fissures Biancone 1 and Rinascita 1 of the Leiden collection, kindly provided by Matthijs Freudenthal, have also been considered.

Species	Fissure	R	Specimens				Dental elements										
			Is	Mx	Md	tot	D ⁴	P ⁴	M ¹	M ²	M ³	D ₄	P ₄	M ₁	M ₂	M ₃	tot
<i>S. ex gr. daamsi</i>	F15	F	124	14	3	141	3	18	24	22	18	1	12	30	18	19	165
	TF1	L	57		1	58		5	7	17	6		4	11	8	4	62
	F21b	F	52	7	3	62		13	14	15	8	1	5	11	12	3	82
	C3A	L	90	1	1	92		3	11	19	12		13	14	12	14	98
	FND	L	125	8	5	138	1	21	17	18	8	3	17	14	31	18	148
<i>S. degiulii</i>	F1	F	76	2	2	80	1	7	13	11	6		6	15	21	11	91
	F9	F	557	7	4	568		54	26	50	58		89	96	113	90	576
	SG	F	151	9	9	169		17	34	32	15		16	27	33	15	189
<i>S. cf. degiulii</i>	P11A	L		10	29	39		9	9	6	1		4	25	20	15	89
<i>S. aff. degiulii</i>	F32	F	112	2		114		14	14	12	11		8	18	20	19	116
<i>S. daunius</i>	F15	F	25	2	6	33		4	4	6	6		2	5	9	7	43
	F21a	F	1			1					1						1
<i>S. laticrestatus</i>	F9	F	28	1	2	31		3	4	7	1		1	5	8	6	35
<i>S. aff. laticrestatus</i>	F1	F	1			1					1						1
Total			1399	63	65	1527	5	168	177	215	152	5	177	271	305	221	1696

Tab. 2 - Synoptic scheme of the examined material. R: Repository of the material (F: Dipartimento di Scienze della Terra, Florence; L: Naturalis, Leiden). Is: isolated tooth; Mx: maxilla; Md: mandible.

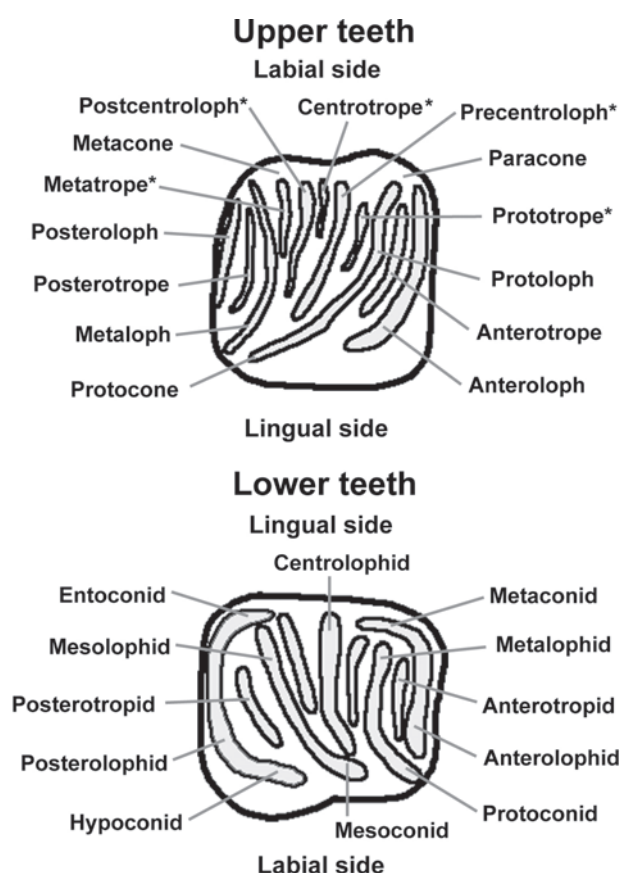


Fig. 2 - Nomenclature of occlusal surface of the glirid cheek teeth. The figures are drawn as right-hand specimens with the anterior side facing to the right. Trigon crests, i.e. crests within the central valley, are indicated by the asterisk (*). See text for the relevant literature sources.

Methods

The length and the width of the dental crown have been measured in millimetres. The material stored in Florence has been measured with a Wild Heerbrugg MMS 235 system positioned on a Wild Heerbrugg Typ 308700 microscope; morphological analysis are based on images captured with a Leica DC150 system mounted on the same microscope. The material stored in Leiden has been measured with a Sony LH20-C system placed on a Leitz Ortholux microscope; images have been captured with a Nikon Digital Sight DS-5M system on a Zeiss Stemi SV 11 microscope. The measurements of Biancone 1 and Rinascita 1 are those published by Freudenthal & Martín-Suárez (2006) and Martín-Suárez & Freudenthal (2007). Matthijs Freudenthal kindly provided the analytic data of *S. laticrestatus* from the type-locality San Giovannino. Those data have been used to compute standard deviation, a parameter not reported by Daams & Freudenthal (1985).

The morphological nomenclature of the occlusal surface follows de Bruijn (1966) emended and extended according to Daams (1981), Freudenthal (2004), and Rinaldi (2006) (Fig. 2). The crests, which occur within the central valley, i.e. the crests comprehended between the protoloph and metaloph, are defined as “trigon

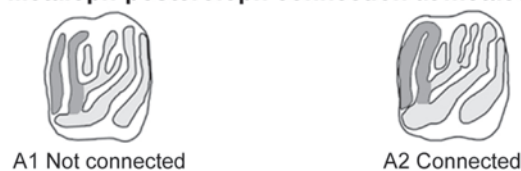
crests”, considering that the central valley is enclosed within the trigon.

The very complex dental pattern of large-sized species is characterized by the occurrence of other crests beside the primary, secondary and accessory crests. Those crests are called additional crests or “surplus of crests” (Freudenthal & Martín-Suárez, 2006). Because of the high variability of these crests in size, shape and relative position, it is useless to give them specific names: they might be identified by their accessory nearby crests and by their relative position (pre-, post-, anterior, etc.).

The morphology of the first and second upper molars of many not-endemic species of Myomiminae is very similar. Many authors do not separate those elements in their description and analysis, treating them as “M^{1,2}” (e.g. de Bruijn, 1966; Daams, 1981). However, in the description of the small-sized Myomiminae from Biancone 1 (*S. daamsi*), Freudenthal & Martín-Suárez (2006) reported six morphological characters that could be used to classify those elements. In the present paper, the two molars are identified following the indications of the latter authors. Indeed, the distinction between the first and second molars is easy for the large-sized species, while for the small-sized ones a certain amount of error cannot be discarded, as also noticed by the previous authors.

The material is subdivided into two groups based on size and morphology. The large-sized, morphologically-complex *Stertomy*s samples are represented by a relatively low number of specimens, while the small-sized *Stertomy*s teeth represent most of the examined material (Tab. 2). The morphological analysis of the latter group has at first been carried out using the “standard” morphotypes introduced by Daams (1981) which roughly account for the complexity of the occlusal surface of the teeth, considering the total

M^{1,2} - Metaloph-posteroloph connection at metacone



M^{1,2} - Trigon crests-metaloph connection



M_{1,2} - Anterolophid-protoconid connection

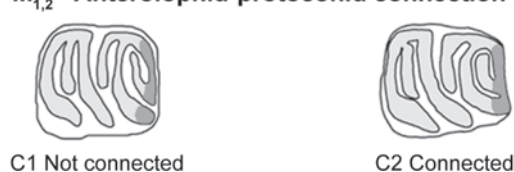


Fig. 3 - Morphological sketches of the most useful patterns of connection between crests in small-sized *Stertomy*s cheek teeth (see Rinaldi, 2006).

number of crests (main, secondary and accessory) in the dental crown. The Daams' method is useful for describing synthetically glirid tooth variability, but it ignores some subtle morphological features, such as the patterns of connections among crests. In order to achieve a more complete description of the morphological variation, the analysis of small *Stertomys* species has therefore been carried out using also some additional morphotypes derived from the detailed analytic study of Rinaldi (2006). The latter work accounts for the connection of crests and provides further morphological characters, which proved to be useful for describing among-sample variability. The distribution of some of these features proved to be effective in the distinction of the samples and they are therefore used for description and diagnosis. These features, illustrated in Fig. 3, are: the labial connection between the metaloph and posteroloph in $M^{1,2}$; the connection between the trigon crests (centrolophs, prototrope, centrotrope, and metatrope) and the metaloph lingually in $M^{1,2}$; the connection between the anterolophid and the protoconid in the $M_{1,2}$, which determines a complete closure of the anterior valley.

In the large-sized species, the low number of specimens and their extremely complex dental pattern rendered the morphotype analysis impractical. Therefore, these taxa are described qualitatively.

Statistical analysis

Basic statistic parameters (minimum and maximum value, mean and standard deviation) and 95% confidence interval of the mean have been computed for the size measurements of each sample. In some cases, differences between means of small samples have been tested with a bilateral t-test. The morphotype frequencies have been analysed with a chi-square test. The significance level in all the tests has been chosen as $\alpha = 0.05$. References for the statistical analysis are Sokal & Rohlf (1995), Garetto (2002), and Soliani (2005).

SYSTEMATIC PALAEONTOLOGY

Preliminary analysis and remarks

The taxonomic identification has been preceded by the analytical examination of the whole Myomiminae collection from each fissure (Rinaldi, 2006). This preliminary investigation has been carried out with the aid of basic statistics applied to the size parameters as well as morphological analysis. Since the large-sized taxa are represented by a very small number of specimens, the quantitative investigation of morphotypes is limited to the small-sized taxa. The analysis permitted to identify, among small-sized teeth from a number of localities, some specimens characterised by outlying values of size and/or by a different morphology with respect to the bulk of the specimens in each sample. The occurrence of these outliers in each fissure as well as their size and morphotype classification are summarized in Tab. 3. They are described and discussed in the paragraph "Description of the outliers of the small-sized *Stertomys* species" and figured in Pl. 4 (figs. 28-44). It should be noted that outliers are present in a limited number (18 specimens) and most of them occur within samples from fissures F21b (8 specimens), Cantatore 3A (3) and Trefossi 1 (2), considered as belonging to the older phases of population of the local palaeoisland of Apricena-Poggio Imperiale. Outliers are absent in samples from fissures F9, San Giovannino and F32.

Some samples apparently display a wider range of variation than the others. Probably some minor time-averaging, reworking or redeposition affect these samples. Such taphonomic noise is normal, given the nature of the considered deposits and the complexity of the history of the "Terre Rosse" populations (Abbazzi et al., 1996).

Descriptions of the small-sized *Stertomys* species

GENERAL DESCRIPTION

The small-sized *Stertomys* populations show a fairly uniform morphological pattern, particularly in the lower

Fissure	Outliers						Statistics			
	R	S	T	L	W	M	Sample size	Freq.	95% C.I.	
F15	S	F15-58	M ₂	1,58	1,38	3	165	1 (0,6%)	0%*	1,8%
TF1	L	RGM436051	P ⁴	1,69	1,98	c	62	2 (3,2%)	0%*	7,6%
	S	RGM436025	M ₁	1,58	1,31	3				
F21b	L	F21b-58	P ⁴	1,66	1,94	c	82	8 (9,8%)	3,3%	16,3%
	L	F21b-45a	M ¹	1,92	2,19	D				
	L	F21b-51	M ¹	1,92	2,17	C				
	L	F21b-53	M ¹	1,96	2,22	C				
	L	F21b-2	M ³	1,60	2,09	S				
	L	F21b-61	M ³	1,58	1,99	S				
	L	F21b-34	M ₁	2,37	2,02	3				
	S	F21b-73	M ₂	1,43	1,49	3				
C3A	S	RGM435912	M ¹	1,43	1,59	E	98	3 (3,1%)	0%*	6,5%
	S	RGM435929	M ²	1,38	1,58	D				
	L	RGM435895	M ₃	1,97	1,84	4				
FND	L	RGM436221b	M ¹	1,90	2,28	E	148	1 (0,7%)	0%*	2%
F1	L	F1-2.20	M ₁	2,03	1,64	4	91	1 (1,1%)	0%*	3,3%
P11A	S	RGM436016a	P ⁴	1,01	1,13	c	89	2 (2,2%)	0%*	5,3%
	S	RGM436016b	M ¹	1,29	1,41	C				

Tab. 3 - Synoptic scheme of the occurrence of the outliers. R: Relative size (L: Larger than the bulk; S: Smaller); S: Specimen ID number; T: Tooth element; L: Length; W: Width; M: Morphotype *sensu* Daams (1981). Freq: Frequency; 95% C.I.: 95% Confidence Interval for proportions. *: When the lower bound of the C.I. is negative, it has been conventionally substituted with 0%. It means that the lower frequency of the population could assume a positive value very close to 0.

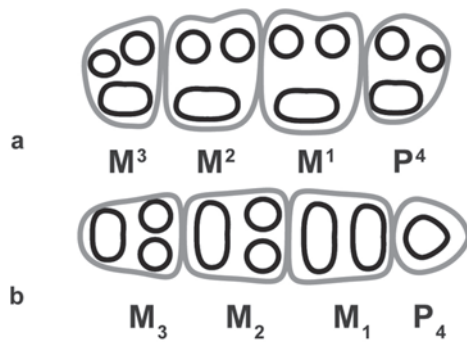


Fig. 4 - Pattern of tooth outline (grey line) and alveoli (black line) in small-sized *Stertomys* teeth. The figures are drawn as right-hand specimens with the anterior side facing to the right. a) upper teeth; b) lower teeth.

teeth. The following section reports the general description of the dentition and of the characters that are shared by all small-sized *Stertomys* species. In the next section, the description is focused on the characters that distinguish the single populations and taxa.

Upper dentition: The teeth are labio-lingually expanded. D^4 and P^4 have an oval outline, M^1 and M^2 are rectangular while M^3 has a trapezoidal, posteriorly narrowed shape. All the teeth have a slightly concave occlusal surface. They have three roots, an expanded one on the lingual side and two roots on the labial side (Fig. 4a). In P^4 the lingual root is smaller and the antero-labial one is shifted towards the central part of the crown; the D^4 has a similar pattern. In P^4 and M^3 the labial roots may fuse; in a few specimens they are fused with the lingual root, anteriorly in P^4 and posteriorly in M^3 .

The occlusal pattern is typical of “complex” Myomiminae. Main crests (anteroloph, protoloph, metaloph and posteroloph) are well-developed (Fig. 5a). In the molars, the anteroloph extends all along the anterior edge of the tooth. The protoloph and the metaloph converge and connect to the protocone closing the central valley lingually, as is typical in the Myomiminae. The posteroloph forms the posterior edge of the tooth. In the central valley, the centrolophs are generally present and well-developed. They tend to connect to each other lingually. Within the same valley, a varying number of accessory crests (up to three) occur. Daams’ morphotype D is usually characterised by the presence of the prototrope. This crest may join the precentroloph lingually, while connections on the labial or on both sides less commonly occur. The trigon crests tend to converge towards the central part of the metaloph. This connection is weak or absent in molars from the oldest fissures, while in the younger ones it is usually fully developed (Fig. 7b, d). There are no accessory crests in the anterior and posterior valleys. Usually, the M^2 and M^3 are progressively more complex than the M^1 . In the older fissures, the labial end of the protoloph in P^4 frequently displays a hook-shaped outline due to the labial fusion of the protoloph with a short labial-placed precentroloph.

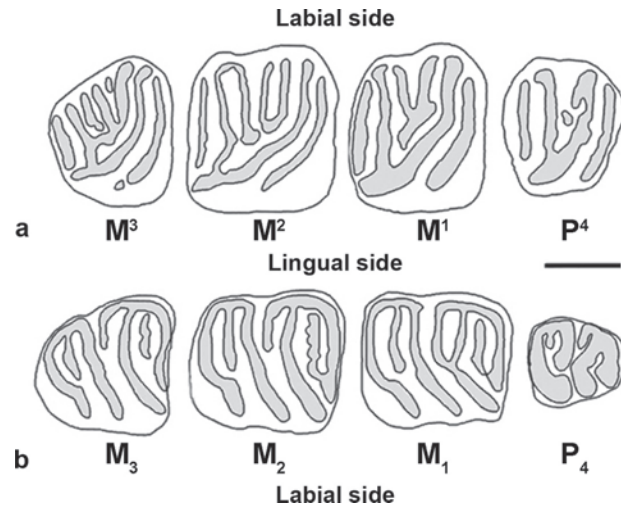


Fig. 5 - Upper (a) and lower (b) teeth row of small-sized *Stertomys*. All specimens are right-hand drawn with the anterior side facing to the right. Scale bar = 1 mm.

The M^3 has generally three crests in the central valley: the prototrope, the precentroloph and the postcentroloph. Because of the posterior narrowing of the M^3 , the postcentroloph is usually shorter than the other two crests in the trigon.

The variation occurring within and among samples in the number of accessory crests, and in the pattern of connection and confluence of some of the crests are reported in Figs. 6 and 7 respectively.

Lower dentition: The teeth are antero-posteriorly elongated. D_4 and P_4 have an oval outline, while molars have a rectangular outline; M_1 is anteriorly narrowed, M_2 tends to narrow posteriorly (posterior wall has frequently a slightly rounded profile) and M_3 is distinctly shorter and posteriorly rounded. All the teeth have a slightly concave occlusal surface. D_4 has two diverging roots, an anterior and a posterior one. P_4 has a single big root. M_1 has an anterior and a posterior root. The first one is variable: it is usually undivided or split distally into two branches or, in a few specimens, it is divided into two individualised roots. M_2 and M_3 have two anterior roots and a wide posterior one (Fig. 4b).

Main crests (anterolophid, metalophid, mesolophid and posterolophid) are well-developed in all dental elements (Fig. 5b). The occlusal surface of the D_4 does not show clear and stable morphological elements. In many specimens a set of small tubercles joining each other in several manners occurs. A detailed description of the variability of D_4 is in Freudenthal & Martín-Suárez (2006). The anterior part of P_4 presents well-developed anterolophid and metalophid; the other two anterior crests, anterotrope and centrolophid, vary in length and in their connections with the main crests. The posterior part of P_4 has well-developed mesolophid, posterotrope and posterolophid.

The morphology of the molars is rather stable. A continuous endolophid occurs rarely as it is typical of Myomiminae. An anterotrope is always present, and it is usually connected to the anterolophid on the labial

side. The frequency of connection of the anterolophid to the protoconid, forming a continuous anterior wall, increases from the oldest to the most recent fissures

P^4				
		b	c	d
<i>S. daamsi</i>	BIA1	2	57	10
<i>S. aff daamsi</i>	RIN1	2	22	6
	F15		14	3
	TF1		4	1
<i>S. ex gr daamsi</i>	F21b		10	3
	C3A	1	2	
	FND		17	4
	F1		4	2
<i>S. degiulii</i>	F9	1	37	14
	SG	1	13	3
<i>S. cf degiulii</i>	P11A		8	2
<i>S. aff degiulii</i>	F32		9	5

M^1						
		B	C	D	E	F
<i>S. daamsi</i>	BIA1	46	55	30	4	
<i>S. aff daamsi</i>	RIN1	9	12	9		
	F15	2	12	8	1	1
	TF1	1	1	4	1	
<i>S. ex gr daamsi</i>	F21b	2	9	3		
	C3A		4	6	1	
	FND	1	10	5	1	
	F1		5	7		
<i>S. degiulii</i>	F9	1	10	14		
	SG	3	13	18		
<i>S. cf degiulii</i>	P11A		5	4		
<i>S. aff degiulii</i>	F32		9	5		

M^2						
		B	C	D	E	F
<i>S. daamsi</i>	BIA1	3	24	108	14	1
<i>S. aff daamsi</i>	RIN1	2	4	23	1	
	F15		3	17	2	
	TF1			14	3	
<i>S. ex gr daamsi</i>	F21b	1	3	8	2	1
	C3A		2	16	1	
	FND			15	2	1
	F1			10	1	1
<i>S. degiulii</i>	F9		4	44	1	
	SG		4	27	1	
<i>S. cf degiulii</i>	P11A			7		
<i>S. aff degiulii</i>	F32		1	10	1	

M^3					
		R	S	T	T1
<i>S. daamsi</i>	BIA1	8	35	8	1
<i>S. aff daamsi</i>	RIN1	13	14	3	
	F15	4	12	2	
	TF1		6		
<i>S. ex gr daamsi</i>	F21b	1	5	2	
	C3A		9	2	1
	FND		6	1	
	F1	1	4		
<i>S. degiulii</i>	F9	4	48	6	
	SG		15		
<i>S. cf degiulii</i>	P11A		1		
<i>S. aff degiulii</i>	F32	2	9		

(Fig. 9). On the labial side of the M_1 , the metalophid and the mesolophid curve markedly anteriorly while in the other molars these crests bend more gently. The

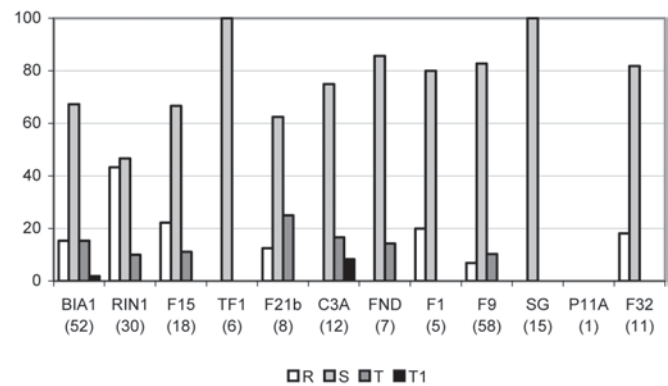
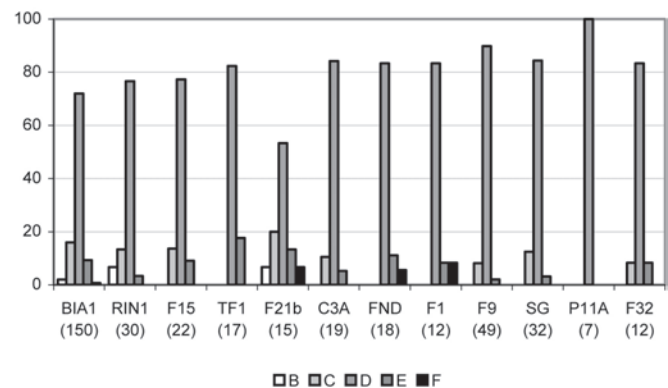
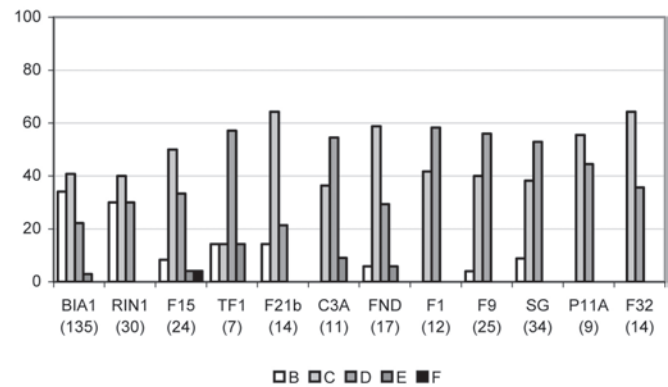
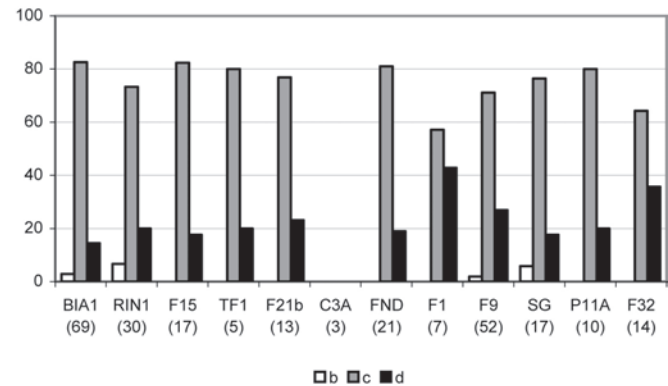


Fig. 6 - Distribution of the Daams' standard morphotypes for the upper teeth (Daams, 1981) within small-sized *Stertomys* samples. The number of analysed specimens is reported between brackets. Samples with less than five specimens are not reported in the graphs.

secondary and accessory crests are distinctly shorter than the main ones, and they usually extend lingually not more than half the tooth width. The length of these

crests is progressively shorter from M_1 to M_3 . The posterolophid tends to assume, with wear, a sinusoidal shape due to the slightly lingual shifted position of the

M^1				
		A1	A2	
<i>S. daamsi</i>	BIA1	104	25	
<i>S. aff daamsi</i>	RIN1	22	8	
	F15	21	2	
	TF1	7		
<i>S. ex gr daamsi</i>	F21b	12	2	
	C3A	7	3	
	FND	14	2	
	F1	8	4	
<i>S. degiulii</i>	F9	19	5	
	SG	24	9	
<i>S. cf degiulii</i>	P11A	8	1	
<i>S. aff degiulii</i>	F32	10	3	

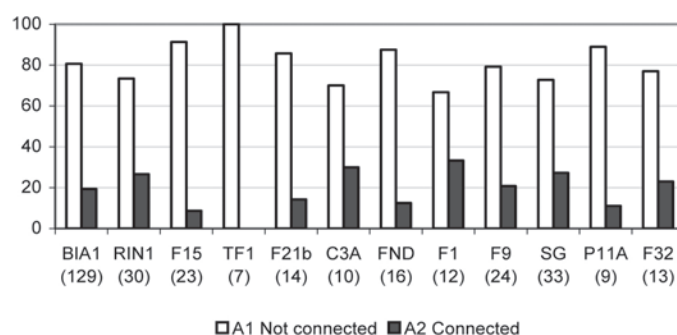
M^1				
		B1	B2	B3
<i>S. daamsi</i>	BIA1	109	12	13
<i>S. aff daamsi</i>	RIN1	23	2	5
	F15	21	2	
	TF1	6	1	
<i>S. ex gr daamsi</i>	F21b	10	3	1
	C3A	8	1	2
	FND	13	3	1
	F1	6	2	4
<i>S. degiulii</i>	F9	10	5	9
	SG	13	7	13
<i>S. cf degiulii</i>	P11A		4	5
<i>S. aff degiulii</i>	F32	5	5	2

M^2				
		A1	A2	
<i>S. daamsi</i>	BIA1	135	12	
<i>S. aff daamsi</i>	RIN1	26	4	
	F15	20	2	
	TF1	16	1	
<i>S. ex gr daamsi</i>	F21b	15		
	C3A	15	4	
	FND	18		
	F1	8	3	
<i>S. degiulii</i>	F9	35	14	
	SG	21	10	
<i>S. cf degiulii</i>	P11A	5	2	
<i>S. aff degiulii</i>	F32	8	3	

M^2				
		B1	B2	B3
<i>S. daamsi</i>	BIA1	112	22	16
<i>S. aff daamsi</i>	RIN1	22	5	3
	F15	18	2	1
	TF1	11	3	3
<i>S. ex gr daamsi</i>	F21b	14	1	
	C3A	14	4	1
	FND	11	2	4
	F1	6	2	4
<i>S. degiulii</i>	F9	17	8	24
	SG	10	7	15
<i>S. cf degiulii</i>	P11A	2		4
<i>S. aff degiulii</i>	F32	2	3	7

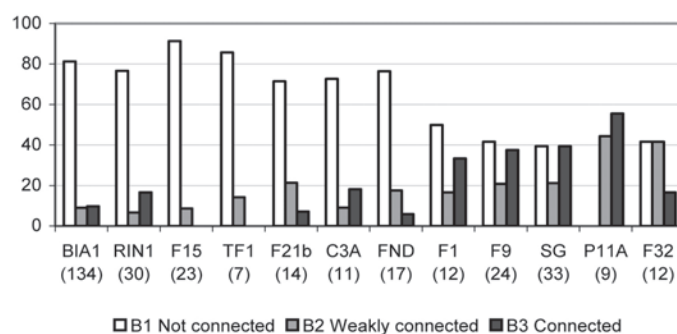
M^1 - Metaloph-posteroloph connection at metacone

a



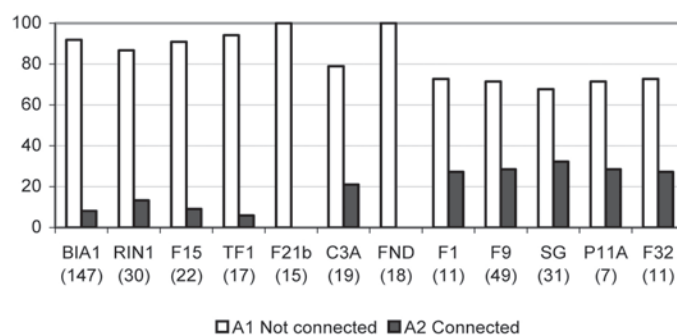
M^1 - Trigon crests-metaloph connection

b



M^2 - Metaloph-posteroloph connection at metacone

c



M^2 - Trigon crests-metaloph connection

d

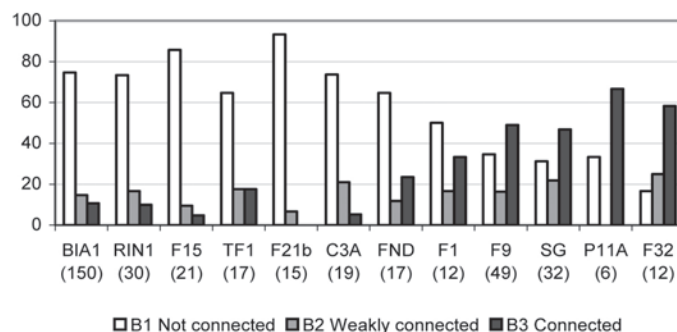


Fig. 7 - Distribution of Rinaldi's morphotypes for the upper teeth (Rinaldi, 2006). The character states are reported in Fig. 3. The number of analysed specimens is reported between brackets.

hypoconid. The centrolophid joins the metaconid lingually, while it usually ends free labially; in some

specimens, it bends anteriorly connecting the central part of the metalophid, while in a few specimens it

P ₄				
<i>S. daamsi</i>	BIA1	2	39	7
<i>S. aff daamsi</i>	RIN1		24	6
	F15		9	2
	TF1		4	
<i>S. ex gr daamsi</i>	F21b	1	4	
	C3A	1	8	4
	FND		9	4
	F1		4	1
<i>S. degiulii</i>	F9	2	51	34
	SG		11	4
<i>S. cf degiulii</i>	P11A		1	2
<i>S. aff degiulii</i>	F32	1	5	1

M ₁					
<i>S. daamsi</i>	BIA1		48	6	
<i>S. aff daamsi</i>	RIN1		29	1	
	F15		27	2	1
	TF1		6	3	2
<i>S. ex gr daamsi</i>	F21b		9	1	1
	C3A		9	5	
	FND		11	2	
	F1		11	3	1
<i>S. degiulii</i>	F9		88	6	2
	SG	1	24		
<i>S. cf degiulii</i>	P11A		23	1	
<i>S. aff degiulii</i>	F32		18		

M ₂					
<i>S. daamsi</i>	BIA1		48	8	
<i>S. aff daamsi</i>	RIN1		30		
	F15		17	1	
	TF1		5	3	
<i>S. ex gr daamsi</i>	F21b		12		
	C3A		10	2	
	FND		28	2	1
	F1		18	1	1
<i>S. degiulii</i>	F9		108	5	
	SG		32		
<i>S. cf degiulii</i>	P11A		20		
<i>S. aff degiulii</i>	F32		19	1	

M ₃					
<i>S. daamsi</i>	BIA1		51	6	
<i>S. aff daamsi</i>	RIN1		30		
	F15		19		
	TF1		5		
<i>S. ex gr daamsi</i>	F21b		3		
	C3A		14		
	FND		17		
	F1		10		
<i>S. degiulii</i>	F9		88	1	
	SG		15		
<i>S. cf degiulii</i>	P11A		15		
<i>S. aff degiulii</i>	F32		19		

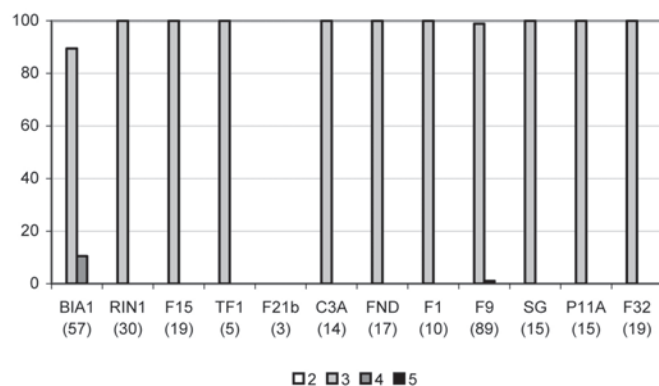
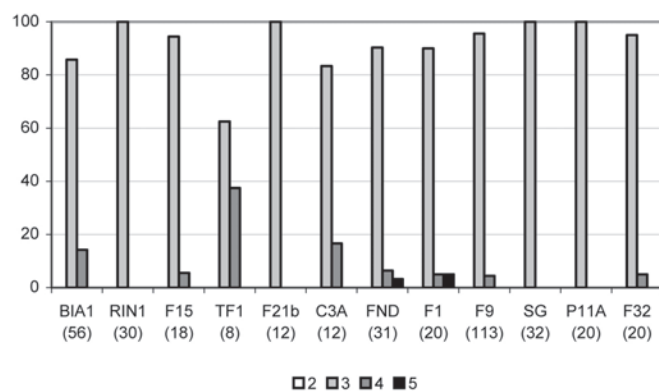
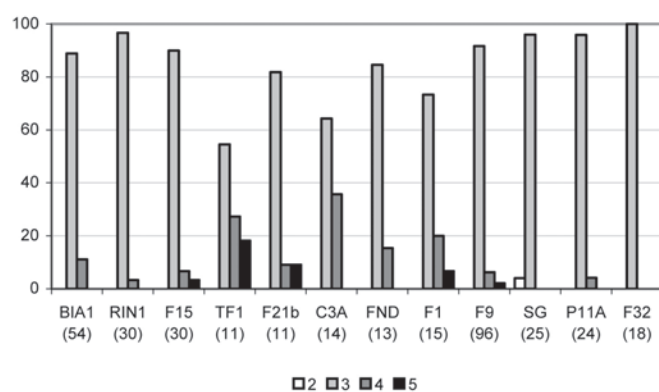
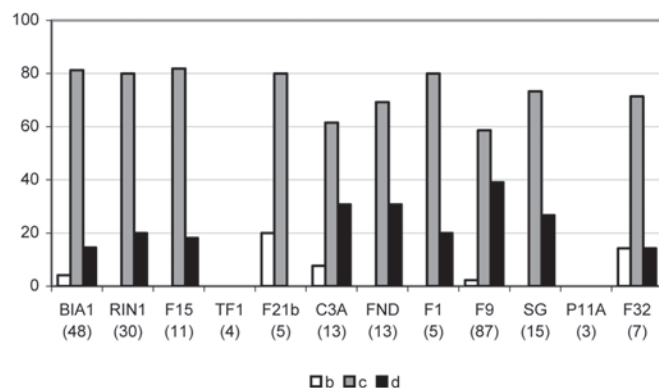


Fig. 8 - Distribution of the Daams' standard morphotypes of the lower teeth (Daams, 1981) within small-sized *Stertomys* samples. The number of analysed specimens is reported between brackets. Samples with less than five specimens are not reported in graphs.

bends backwards, connecting the mesolophid. The last character is more frequent in M_3 . The posterotropid is always present and it may join the entoconid.

The variation occurring within and among samples in the number of accessory crests, and in the pattern of connection and confluence of some of the crests are reported in Figs. 8 and 9 respectively.

The size of teeth shows important variations among subgroups of samples (Tabs. 4-5, Fig. 10). The considerable differences in size, along with the minor morphological differences observed among samples, are used for the taxonomic descriptions and definitions.

TAXONOMIC DESCRIPTIONS

The material is described in systematic order, listing the samples pertinent to the various taxa and discussing them shortly.

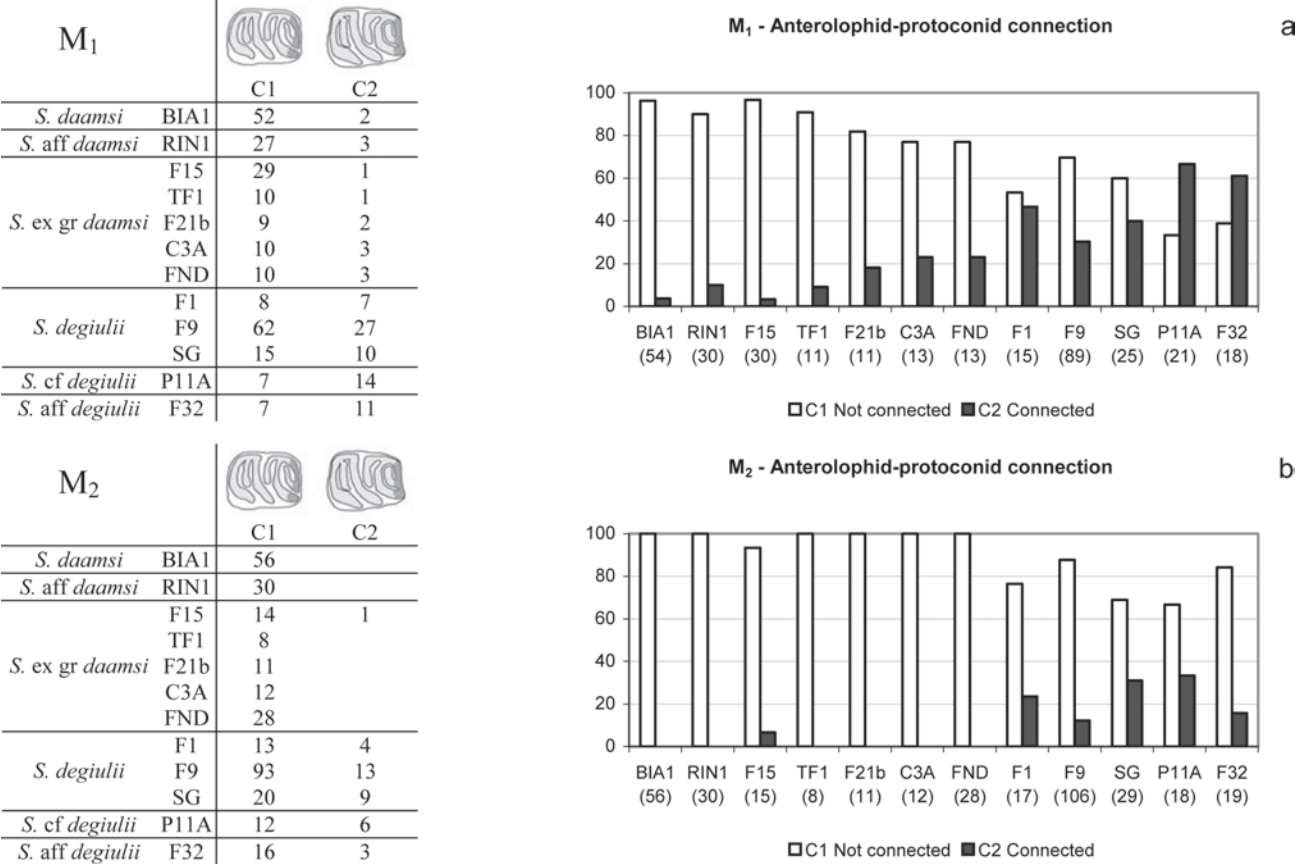
Family GLIRIDAE Thomas, 1897
Subfamily MYOMIMINAE Daams, 1981

Genus *Stertomys* Daams & Freudenthal, 1985

Stertomys ex gr. *daamsi* Freudenthal & Martín-Suárez, 2006

			Length						Width					
			n	min	mean	max	sd	95% ci	n	min	mean	max	sd	95% ci
D ⁴	<i>S. daamsi</i>	Biancone 1	25	0,82	0,97	1,11	0,07	0,94 1,00	26	0,83	1,11	1,3	0,11	1,07 1,15
	<i>S. aff. daamsi</i>	Rinascita 1	3	0,92	0,97	1,02	-		3	1,00	1,05	1,11	-	
	<i>S. ex gr. daamsi</i>	F15	3	0,85	0,90	0,93	0,05	0,84 0,96	3	1,01	1,07	1,12	0,06	1,00 1,14
		Fina D	1		0,98				1		0,82			
P ⁴	<i>S. daamsi</i>	Biancone 1	50	1,44	1,63	1,82	0,09	1,61 1,65	50	1,78	1,92	2,01	0,09	1,90 1,94
	<i>S. aff. daamsi</i>	Rinascita 1	30	1,33	1,47	1,60	0,07	1,44 1,50	30	1,57	1,72	1,92	0,09	1,69 1,75
		F15	17	1,49	1,67	1,82	0,08	1,63 1,71	17	1,72	1,93	2,09	0,09	1,89 1,97
		Trefossi 1	5	1,39	1,45	1,55	0,06	1,40 1,50	5	1,58	1,67	1,73	0,06	1,62 1,72
	<i>S. ex gr. daamsi</i>	F21b	11	1,31	1,41	1,53	0,07	1,37 1,45	12	1,47	1,63	1,78	0,08	1,58 1,68
		Cantatore 3A	3	1,31	1,42	1,48	0,09	1,32 1,52	3	1,67	1,69	1,71	0,02	1,67 1,71
		Fina D	21	1,24	1,37	1,47	0,07	1,34 1,40	21	1,52	1,63	1,77	0,07	1,60 1,66
	<i>S. degiulii</i>	F1	7	1,07	1,15	1,28	0,07	1,10 1,20	7	1,21	1,32	1,49	0,10	1,25 1,39
		F9	53	1,09	1,21	1,34	0,05	1,20 1,22	53	1,22	1,37	1,59	0,07	1,35 1,39
		San Giovannino	17	1,09	1,15	1,26	0,05	1,13 1,17	17	1,2	1,31	1,38	0,04	1,29 1,33
	<i>S. cf. degiulii</i>	Pirro 11A	10	1,21	1,27	1,47	0,07	1,23 1,31	10	1,22	1,36	1,52	0,08	1,31 1,41
	<i>S. aff. degiulii</i>	F32	14	1,18	1,28	1,41	0,06	1,25 1,31	14	1,22	1,43	1,54	0,09	1,38 1,48
M ¹	<i>S. simplex</i>	Rinascita 1	22	1,58	1,67	1,86	0,07	1,64 1,70	22	1,86	1,95	2,11	0,07	1,92 1,98
	<i>S. daamsi</i>	Biancone 1	114	1,79	1,96	2,18	0,08	1,95 1,97	109	1,97	2,25	2,50	0,09	2,23 2,27
	<i>S. aff. daamsi</i>	Rinascita 1	30	1,63	1,79	1,94	0,08	1,76 1,82	30	1,84	2,05	2,23	0,10	2,01 2,09
		F15	24	1,67	1,93	2,20	0,12	1,88 1,98	22	2,01	2,21	2,40	0,11	2,16 2,26
		Trefossi 1	7	1,54	1,68	1,84	0,12	1,59 1,77	7	1,87	1,93	2,04	0,06	1,89 1,97
	<i>S. ex gr. daamsi</i>	F21b	14	1,55	1,68	1,79	0,08	1,64 1,72	14	1,80	1,97	2,10	0,08	1,93 2,01
		Cantatore 3A	11	1,57	1,74	1,94	0,12	1,67 1,81	11	1,81	1,98	2,17	0,12	1,91 2,05
		Fina D	16	1,50	1,65	1,81	0,07	1,62 1,68	16	1,79	1,97	2,11	0,08	1,93 2,01
	<i>S. degiulii</i>	F1	12	1,32	1,45	1,62	0,09	1,40 1,50	12	1,53	1,72	2,00	0,15	1,64 1,80
		F9	26	1,29	1,45	1,58	0,06	1,43 1,47	26	1,55	1,68	1,80	0,06	1,66 1,70
		San Giovannino	33	1,34	1,43	1,57	0,06	1,41 1,45	34	1,50	1,64	1,80	0,07	1,62 1,66
	<i>S. cf. degiulii</i>	Pirro 11A	9	1,43	1,51	1,67	0,09	1,45 1,57	9	1,57	1,70	1,93	0,11	1,63 1,77
M ²	<i>S. aff. degiulii</i>	F32	14	1,42	1,53	1,65	0,07	1,49 1,57	14	1,62	1,75	1,84	0,07	1,71 1,79
	<i>S. simplex</i>	Rinascita 1	23	1,84	1,93	2,04	0,05	1,91 1,95	22	2,04	2,23	2,37	0,09	2,19 2,27
	<i>S. daamsi</i>	Biancone 1	139	1,67	1,88	2,20	0,09	1,87 1,89	134	1,94	2,21	2,50	0,09	2,19 2,23
	<i>S. aff. daamsi</i>	Rinascita 1	30	1,59	1,72	1,90	0,09	1,69 1,75	30	1,83	2,04	2,20	0,11	2,00 2,08
		F15	22	1,71	1,86	2,02	0,10	1,82 1,90	22	1,93	2,17	2,47	0,12	2,12 2,22
		Trefossi 1	17	1,52	1,66	1,80	0,07	1,63 1,69	17	1,80	1,95	2,12	0,08	1,91 1,99
	<i>S. ex gr. daamsi</i>	F21b	15	1,56	1,65	1,79	0,07	1,61 1,69	15	1,74	1,97	2,08	0,09	1,92 2,02
		Cantatore 3A	18	1,49	1,65	1,78	0,08	1,61 1,69	18	1,69	1,95	2,16	0,13	1,89 2,01
		Fina D	18	1,53	1,61	1,73	0,07	1,58 1,64	18	1,79	1,95	2,04	0,07	1,92 1,98
	<i>S. degiulii</i>	F1	12	1,30	1,42	1,62	0,10	1,36 1,48	11	1,57	1,71	1,91	0,09	1,66 1,76
		F9	49	1,31	1,41	1,56	0,06	1,39 1,43	48	1,50	1,70	1,86	0,08	1,68 1,72
		San Giovannino	31	1,29	1,39	1,59	0,07	1,37 1,41	30	1,54	1,65	1,76	0,06	1,63 1,67
M ³	<i>S. cf. degiulii</i>	Pirro 11A	7	1,32	1,43	1,57	0,07	1,38 1,48	7	1,52	1,68	1,81	0,10	1,61 1,75
	<i>S. aff. degiulii</i>	F32	12	1,34	1,47	1,63	0,08	1,42 1,52	12	1,64	1,74	1,83	0,06	1,71 1,77
	<i>S. simplex</i>	Rinascita 1	24	1,69	1,86	1,99	0,08	1,83 1,89	24	1,92	2,18	2,40	0,12	2,13 2,23
	<i>S. daamsi</i>	Biancone 1	50	1,37	1,53	1,74	0,07	1,51 1,55	50	1,77	1,97	2,23	0,09	1,95 1,99
	<i>S. aff. daamsi</i>	Rinascita 1	30	1,23	1,38	1,48	0,06	1,36 1,40	30	1,68	1,81	1,98	0,08	1,78 1,84
		F15	15	1,42	1,51	1,61	0,06	1,48 1,54	16	1,71	1,89	2,19	0,13	1,83 1,95
		Trefossi 1	6	1,25	1,39	1,51	0,09	1,32 1,46	6	1,60	1,73	1,86	0,09	1,66 1,80
	<i>S. ex gr. daamsi</i>	F21b	8	1,24	1,35	1,45	0,07	1,30 1,40	8	1,68	1,75	1,83	0,06	1,71 1,79
		Cantatore 3A	12	1,20	1,34	1,44	0,08	1,29 1,39	11	1,55	1,75	1,86	0,09	1,70 1,80
		Fina D	8	1,21	1,30	1,40	0,07	1,25 1,35	8	1,67	1,72	1,78	0,04	1,69 1,75
	<i>S. degiulii</i>	F1	5	1,05	1,12	1,20	0,06	1,07 1,17	6	1,40	1,46	1,51	0,05	1,42 1,50
		F9	57	1,03	1,13	1,28	0,05	1,12 1,14	58	1,32	1,49	1,64	0,07	1,47 1,51
		San Giovannino	15	0,95	1,07	1,16	0,07	1,03 1,11	15	1,31	1,44	1,53	0,06	1,41 1,47
	<i>S. cf. degiulii</i>	Pirro 11A	1		1,27				1		1,57			
	<i>S. aff. degiulii</i>	F32	11	1,12	1,22	1,28	0,05	1,19 1,25	11	1,42	1,54	1,62	0,06	1,50 1,58
	<i>S. simplex</i>	Rinascita 1	16	1,44	1,55	1,71	0,07	1,52 1,58	16	1,89	2,02	2,17	0,10	1,97 2,07

Tab. 4 - Measurements and descriptive statistical parameters of the small-sized *Stertomys* upper teeth. Data from Biancone 1 and Rinascita 1, according to Freudenthal & Martín-Suárez (2006) and Martín-Suárez & Freudenthal (2007) respectively, are also reported in order to facilitate comparisons. Abbreviations: n: number of specimens; min: minimum value; max: maximum value; sd: standard deviation, 95% ci: 95% confidence interval. Measurements are in millimetres.



			Length						Width					
			n	min	mean	max	sd	95% ci	n	min	mean	max	sd	95% ci
D ₄	<i>S. daamsi</i>	Biancone 1	32	0,80	0,98	1,17	0,11	0,94 1,02	32	0,76	0,91	1,07	0,08	0,88 0,94
		F15	1		0,95				1		0,86			
	<i>S. ex gr. daamsi</i>	F21b	1		0,98				1		0,86			
		Fina D	3	0,70	0,80	0,88	0,09	0,70 0,90	3	0,75	0,76	0,78	0,02	0,74 0,78
P ₄	<i>S. daamsi</i>	Biancone 1	50	1,49	1,61	1,78	0,07	1,59 1,63	50	1,31	1,48	1,66	0,08	1,46 1,50
	<i>S. aff. daamsi</i>	Rinascita 1	30	1,29	1,41	1,56	0,07	1,38 1,44	30	1,19	1,32	1,44	0,07	1,29 1,35
		F15	11	1,22	1,48	1,80	0,16	1,39 1,57	11	1,16	1,38	1,55	0,13	1,30 1,46
		Trefossi 1	4	1,38	1,42	1,45	0,03	1,39 1,45	4	1,29	1,32	1,37	0,04	1,28 1,36
	<i>S. ex gr. daamsi</i>	F21b	5	1,23	1,31	1,36	0,06	1,26 1,36	5	1,17	1,27	1,34	0,07	1,21 1,33
		Cantatore 3A	13	1,27	1,34	1,45	0,06	1,31 1,37	13	1,18	1,25	1,37	0,07	1,21 1,29
		Fina D	17	1,12	1,26	1,39	0,07	1,23 1,29	17	1,12	1,24	1,34	0,07	1,21 1,27
	<i>S. degiulii</i>	F1	6	1,10	1,15	1,21	0,04	1,12 1,18	6	1,10	1,15	1,19	0,03	1,13 1,17
		F9	89	1,04	1,15	1,27	0,05	1,14 1,16	89	0,97	1,11	1,24	0,06	1,10 1,12
		San Giovannino	16	1,03	1,14	1,26	0,06	1,11 1,17	16	1,02	1,12	1,20	0,07	1,09 1,15
	<i>S. cf. degiulii</i>	Pirro 11A	4	1,04	1,12	1,18	0,06	1,06 1,18	4	1,01	1,08	1,12	0,05	1,03 1,13
	<i>S. aff. degiulii</i>	F32	8	1,11	1,19	1,32	0,07	1,14 1,24	8	1,12	1,16	1,25	0,05	1,13 1,19
	<i>S. simplex</i>	Rinascita 1	30	1,48	1,58	1,68	0,05	1,56 1,60	30	1,36	1,48	1,64	0,07	1,45 1,51
	<i>S. daamsi</i>	Biancone 1	50	1,96	2,18	2,43	0,10	2,15 2,21	50	1,69	1,83	2,01	0,07	1,81 1,85
M ₁	<i>S. aff. daamsi</i>	Rinascita 1	30	1,79	1,95	2,09	0,08	1,92 1,98	30	1,51	1,66	1,79	0,08	1,63 1,69
		F15	29	1,93	2,13	2,38	0,11	2,09 2,17	28	1,62	1,82	2,13	0,11	1,78 1,86
		Trefossi 1	12	1,78	1,92	2,06	0,10	1,86 1,98	11	1,52	1,64	1,86	0,09	1,59 1,69
	<i>S. ex gr. daamsi</i>	F21b	11	1,74	1,87	2,00	0,08	1,82 1,92	11	1,55	1,68	1,76	0,06	1,64 1,72
		Cantatore 3A	14	1,74	1,88	2,01	0,07	1,84 1,92	14	1,52	1,59	1,71	0,05	1,56 1,62
		Fina D	13	1,62	1,79	1,91	0,07	1,75 1,83	13	1,43	1,53	1,61	0,06	1,50 1,56
	<i>S. degiulii</i>	F1	15	1,47	1,55	1,63	0,06	1,52 1,58	15	1,29	1,39	1,50	0,07	1,35 1,43
		F9	94	1,41	1,56	1,77	0,07	1,55 1,57	96	1,21	1,41	1,53	0,06	1,40 1,42
		San Giovannino	27	1,41	1,52	1,67	0,07	1,49 1,55	26	1,28	1,39	1,52	0,06	1,37 1,41
	<i>S. cf. degiulii</i>	Pirro 11A	25	1,46	1,57	1,7	0,05	1,55 1,59	25	1,32	1,43	1,55	0,05	1,41 1,45
	<i>S. aff. degiulii</i>	F32	18	1,54	1,65	1,78	0,07	1,62 1,68	18	1,45	1,53	1,64	0,06	1,50 1,56
	<i>S. simplex</i>	Rinascita 1	25	2,02	2,19	2,31	0,08	2,16 2,22	25	1,69	1,85	2,02	0,09	1,81 1,89
	<i>S. daamsi</i>	Biancone 1	50	1,89	2,08	2,36	0,09	2,06 2,10	50	1,80	1,96	2,16	0,08	1,94 1,98
	<i>S. aff. daamsi</i>	Rinascita 1	30	1,79	1,90	2,02	0,07	1,87 1,93	30	1,73	1,83	1,93	0,06	1,81 1,85
M ₂		F15	17	1,85	2,05	2,30	0,12	1,99 2,11	17	1,77	1,96	2,18	0,11	1,91 2,01
		Trefossi 1	8	1,72	1,82	1,93	0,07	1,77 1,87	8	1,53	1,73	1,90	0,12	1,65 1,81
	<i>S. ex gr. daamsi</i>	F21b	11	1,66	1,81	1,88	0,07	1,77 1,85	12	1,69	1,80	1,93	0,08	1,75 1,85
		Cantatore 3A	11	1,62	1,81	1,95	0,11	1,74 1,88	11	1,61	1,71	1,84	0,08	1,66 1,76
		Fina D	28	1,62	1,77	1,89	0,08	1,74 1,80	28	1,55	1,71	1,90	0,08	1,68 1,74
	<i>S. degiulii</i>	F1	21	1,44	1,53	1,66	0,06	1,50 1,56	19	1,36	1,48	1,63	0,07	1,45 1,51
		F9	113	1,42	1,55	1,71	0,06	1,54 1,56	113	1,34	1,51	1,67	0,07	1,50 1,52
		San Giovannino	33	1,37	1,50	1,58	0,06	1,48 1,52	32	1,36	1,47	1,62	0,06	1,45 1,49
	<i>S. cf. degiulii</i>	Pirro 11A	19	1,49	1,58	1,70	0,05	1,56 1,60	19	1,44	1,55	1,64	0,05	1,53 1,57
	<i>S. aff. degiulii</i>	F32	20	1,48	1,60	1,81	0,08	1,56 1,64	20	1,40	1,53	1,70	0,07	1,50 1,56
	<i>S. simplex</i>	Rinascita 1	17	1,98	2,12	2,30	0,08	2,08 2,16	17	1,83	1,99	2,20	0,10	1,94 2,04
	<i>S. daamsi</i>	Biancone 1	50	1,71	1,94	2,13	0,10	1,91 1,97	50	1,52	1,72	1,93	0,09	1,70 1,74
	<i>S. aff. daamsi</i>	Rinascita 1	30	1,64	1,79	1,94	0,08	1,76 1,82	30	1,49	1,63	1,77	0,08	1,60 1,66
		F15	18	1,74	1,94	2,10	0,10	1,89 1,99	19	1,53	1,73	1,90	0,10	1,69 1,77
M ₃		Trefossi 1	5	1,58	1,70	1,84	0,09	1,62 1,78	5	1,45	1,57	1,64	0,07	1,51 1,63
	<i>S. ex gr. daamsi</i>	F21b	3	1,62	1,65	1,68	0,03	1,62 1,68	3	1,42	1,60	1,70	0,16	1,42 1,78
		Cantatore 3A	13	1,56	1,67	1,78	0,07	1,63 1,71	12	1,47	1,55	1,71	0,07	1,51 1,59
		Fina D	18	1,48	1,66	1,81	0,09	1,62 1,70	17	1,42	1,54	1,72	0,07	1,51 1,57
	<i>S. degiulii</i>	F1	11	1,27	1,41	1,59	0,10	1,35 1,47	11	1,10	1,28	1,38	0,09	1,23 1,33
		F9	90	1,32	1,48	1,63	0,07	1,47 1,49	90	1,18	1,35	1,51	0,07	1,34 1,36
		San Giovannino	13	1,28	1,41	1,56	0,08	1,37 1,45	14	1,13	1,31	1,42	0,08	1,27 1,35
	<i>S. cf. degiulii</i>	Pirro 11A	14	1,35	1,47	1,63	0,08	1,43 1,51	14	1,27	1,39	1,50	0,06	1,36 1,42
	<i>S. aff. degiulii</i>	F32	19	1,46	1,55	1,65	0,05	1,53 1,57	19	1,31	1,39	1,54	0,06	1,36 1,42
	<i>S. simplex</i>	Rinascita 1	15	1,86	2,00	2,23	0,10	1,95 2,05	15	1,70	1,86	2,06	0,11	1,80 1,92

Tab. 5 - Measurements and descriptive statistical parameters of the small-sized *Stertomys* lower teeth. Data from Biancone 1 and Rinascita 1, according to Freudenthal & Martín-Suárez (2006) and Martín-Suárez & Freudenthal (2007) respectively, are also reported in order to facilitate comparisons. Abbreviations: n: number of specimens; min: minimum value; max: maximum value, sd: standard deviation, 95% ci: 95% confidence interval. Measurements are in millimetres.

teeth fit the above reported general description. M₁ has two roots, the anterior one is undivided.

Locality - F21b.

Age - Late Miocene-Early Pliocene.

Material - 82 teeth (see Tab. 2, for details) (Pl. 2, figs. 1-17).

Measurements - See Tabs. 4-5.

Description - The specimens are morphologically comparable with the F15 sample, but of smaller size, as those from Trefossi 1. As observed in F15, the Daams' morphotype C is the most frequent in M¹. In M² the Daams' morphotype D is less frequent, owing to the higher frequency of the other morphotypes (Figs. 6, 13). The trigon crests connect to the metaloph in four M¹, and one M², but, except for a single M¹, this connection is weak (Figs. 7, 12). Seven of thirteen P⁴ have a small precentroloph that fuses with the proto-loph in a hook-shaped protocone. The morphology of the

lower teeth fits the description of small-sized *Stertomys* (see "General description" above in this paragraph). In M_1 , one specimen has three roots, and eight specimens have two roots, the anterior of which is divided in two

branches. In two of eleven M_1 , the anterolophid converges to the protoconid, leading to the closure of the anterior valley (Figs. 9, 14).

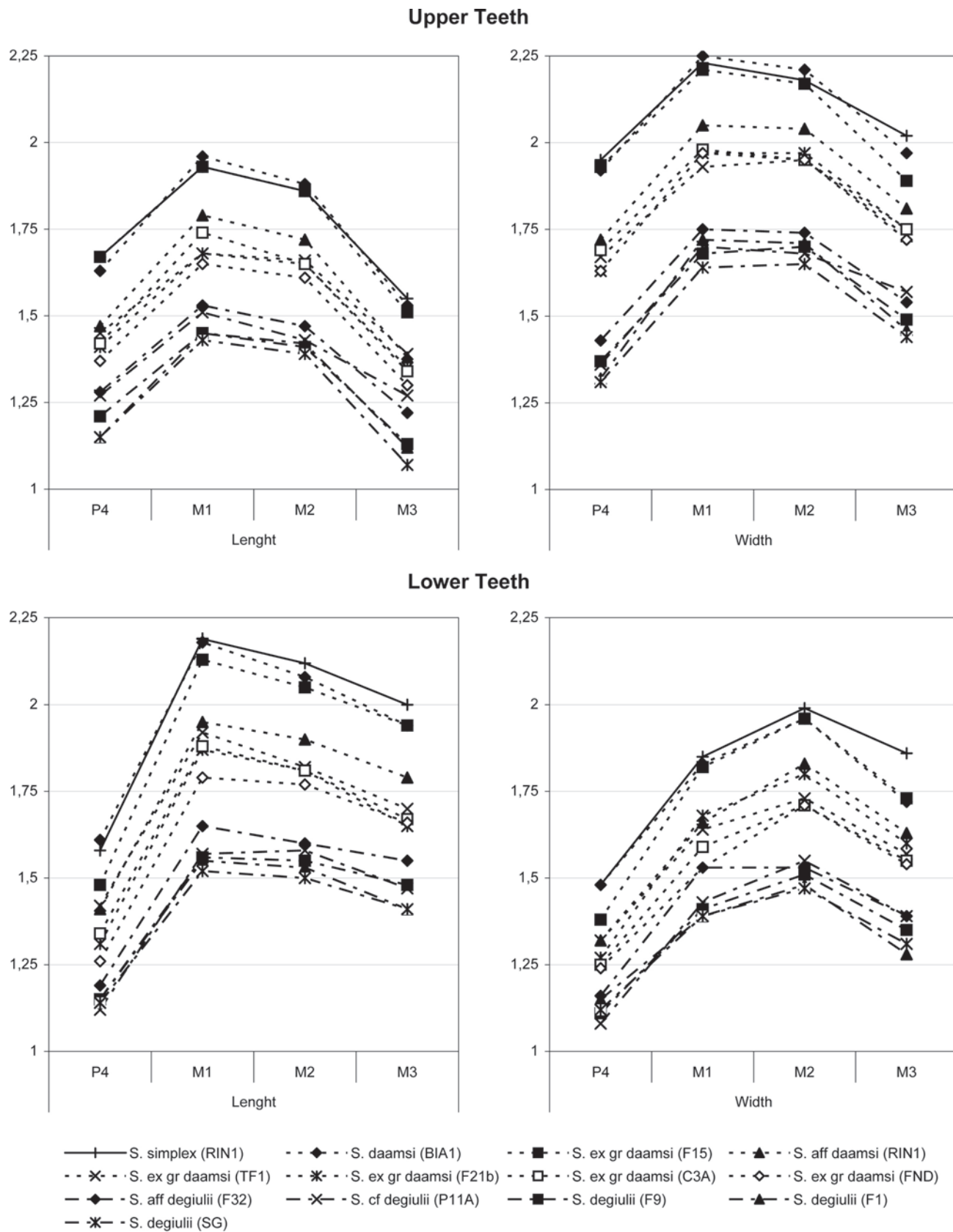
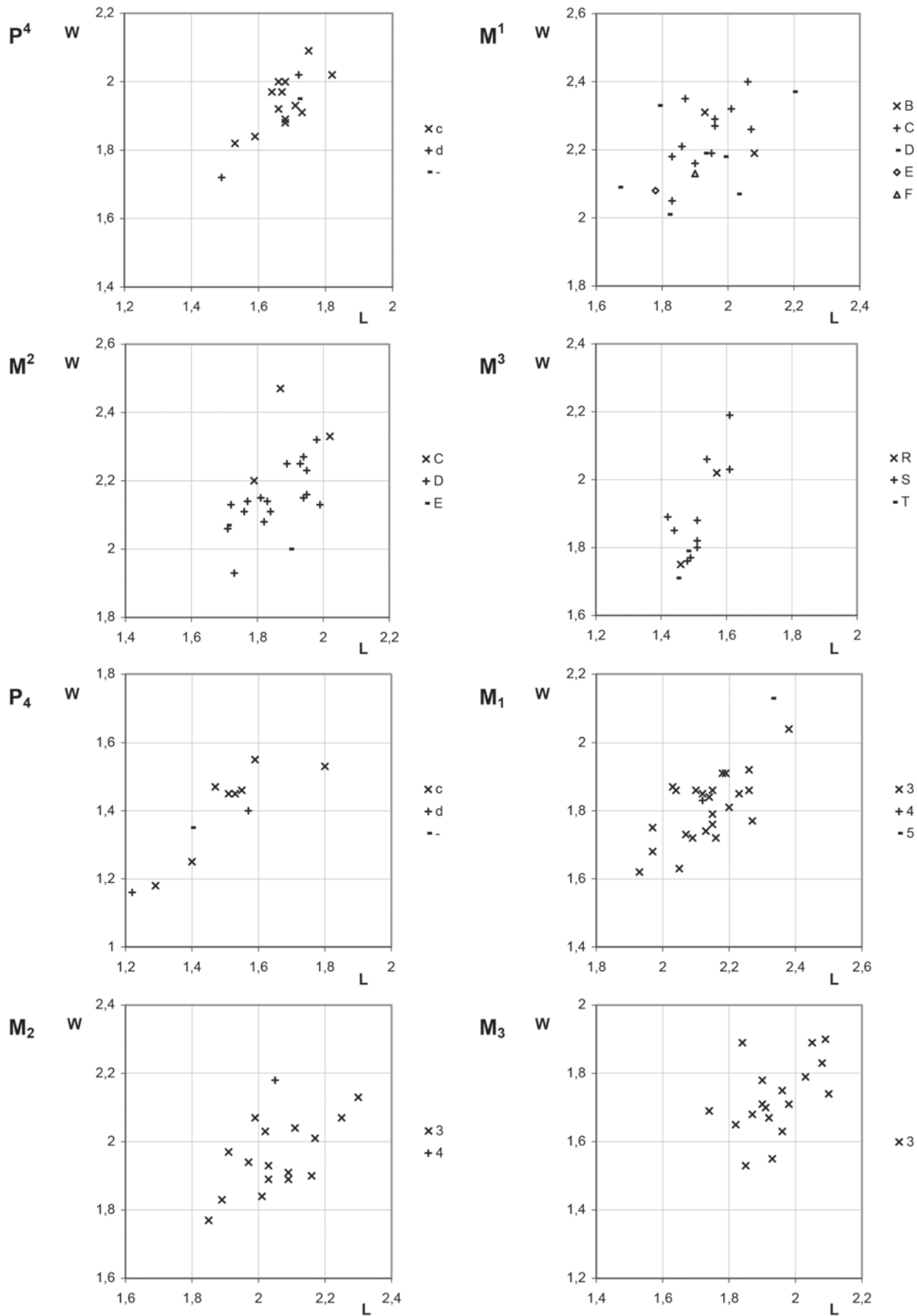
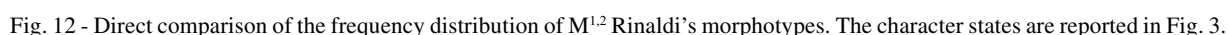


Fig. 10 - Length and width of upper and lower dental series of small-sized *Stertomys* samples. Data from Tabs. 4-5.

Fig. 11 - Length/width diagram for *Stertomys ex gr. daamsi* from F15. Specimens are indicated by their Daams' morphotype.



Locality - Fina D (FND).

Age - Late Miocene-Early Pliocene.

Material - 148 teeth (see Tab. 2, for details) (Pl. 2, figs. 37-55).

Measurements - See Tabs. 4-5.

Description - The specimens are comparable with those from the previously described samples. The Daams' morphotype distribution is similar to that of F15, with a very frequent morphotype C (Figs. 6, 13). In M¹, the trigon crests connect to the metaloph in four specimens, in three of which weakly; in M², the connection is present in six specimens, in two of which weakly (Figs. 7, 12). The lower teeth fit the general description. The M₁ have two roots, the anterior one is divided in all but one specimen. In three on thirteen M₁ the anterolophid tends to converge to the protoconid (Figs. 9, 14).

Tab. 6 - Chi-square test on M¹ Daams' morphotypes for samples Biancone 1, Rinascita 1 and F15. Complex morphotypes D, E and F are summed together. Statistically significant values are in bold.

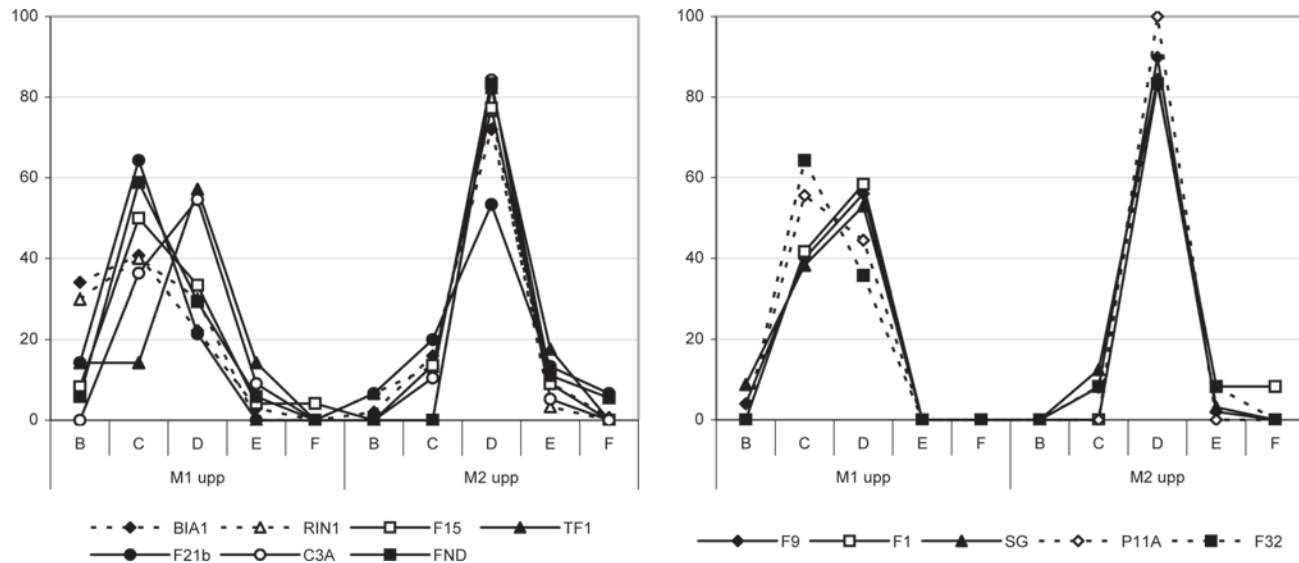


Fig. 13 - Direct comparison of the frequency distribution of $M^{1,2}$ Daams' morphotypes.

Discussion - All these samples have a quite similar morphology, but differ in size. Among the described *Stertomys* species, they are closer to *S. daamsi* from Biancone 1 (Freudenthal & Martín-Suárez, 2006) and *S. aff. daamsi* from Rinascita 1 (Martín-Suárez & Freudenthal, 2007), but they have a lower frequency of the simple Daams' morphotype B in M^1 (Figs. 6, 13). A statistical comparison of morphotype frequency has been computed for Biancone 1, Rinascita 1 and F15 only (Tab. 6), because of the low number of specimens in the other samples. The M^1 from F15 results significantly different with respect to those from Biancone 1 ($p = 0.03$), but the difference with Rinascita 1 is not significant ($p = 0.14$). However, Biancone 1 and Rinascita 1 are characterised by the same simpler (perhaps plesiomorphic) morphology. Even though it has not been statistically analysed, the occurrence of a very reduced frequency of the morphotype B in M^1 draws the samples Trefossi 1, F21b, Cantatore 3A and Fina D morphologically closer to F15, notwithstanding some differences occurring in the other morphotype frequencies. If the size is considered, however, two different groups can be recognised. Biancone 1 and F15 are characterised by a larger size, while Trefossi 1, F21b, Cantatore 3A and Fina D have a smaller size; Rinascita 1 is closer to the second group even though it is slightly larger (Tabs. 4-5, Fig. 10). By and large, Rinascita 1 is morphologically as simple as Biancone 1, but it is smaller in size; F15 is morphologically more complex than Biancone 1 and Rinascita 1, while it has the same size as Biancone 1; the other samples are characterised by a smaller size and are morphologically as complex as F15, or more.

All this considered, we prefer to identify all the described samples as belonging to *Stertomys* ex gr. *daamsi*. This solution avoids the formal institution of further taxa whose diagnostic features would be based on very subtle morphological differences (like morphotype frequencies) and, on the other hand, it implicitly suggests that those populations could belong to a single phyletic lineage.

Considering the adopted biochronology (see the paragraph "The adopted biochronological framework"), the primitive morphology of Biancone 1 and Rinascita 1 agrees with their oldest position and it supports the hypothesis that they are two populations belonging to the same evolutionary lineage. The younger F15 population, characterised by a slightly more complex (derived) morphology, could represent a further stage of the same lineage. The other samples (Trefossi 1, F21b, Cantatore 3A, and Fina D) might also be regarded as representatives of younger populations belonging to the same lineage. However, accepting this reconstruction, a problem with Rinascita 1 arises, regarding the trend in size variation. The small size of the Rinascita 1

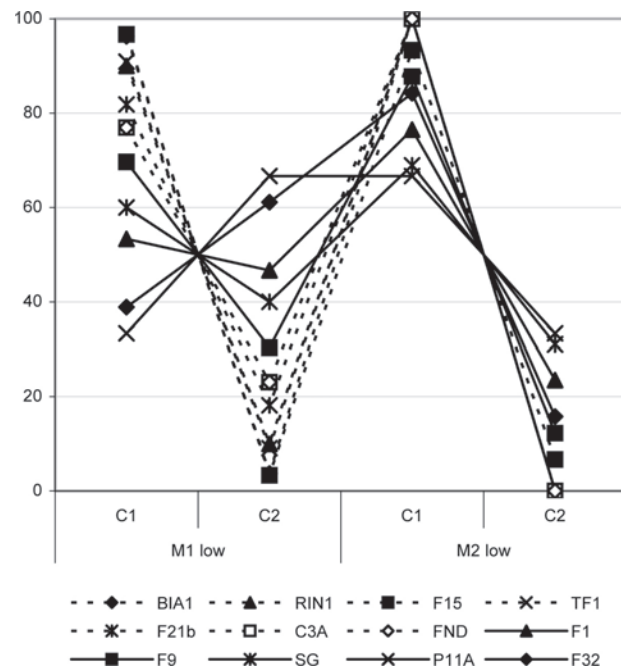


Fig. 14 - Direct comparison of the frequency distribution of $M^{1,2}$ Rinaldi's morphotype. The character states are reported in Fig. 3.

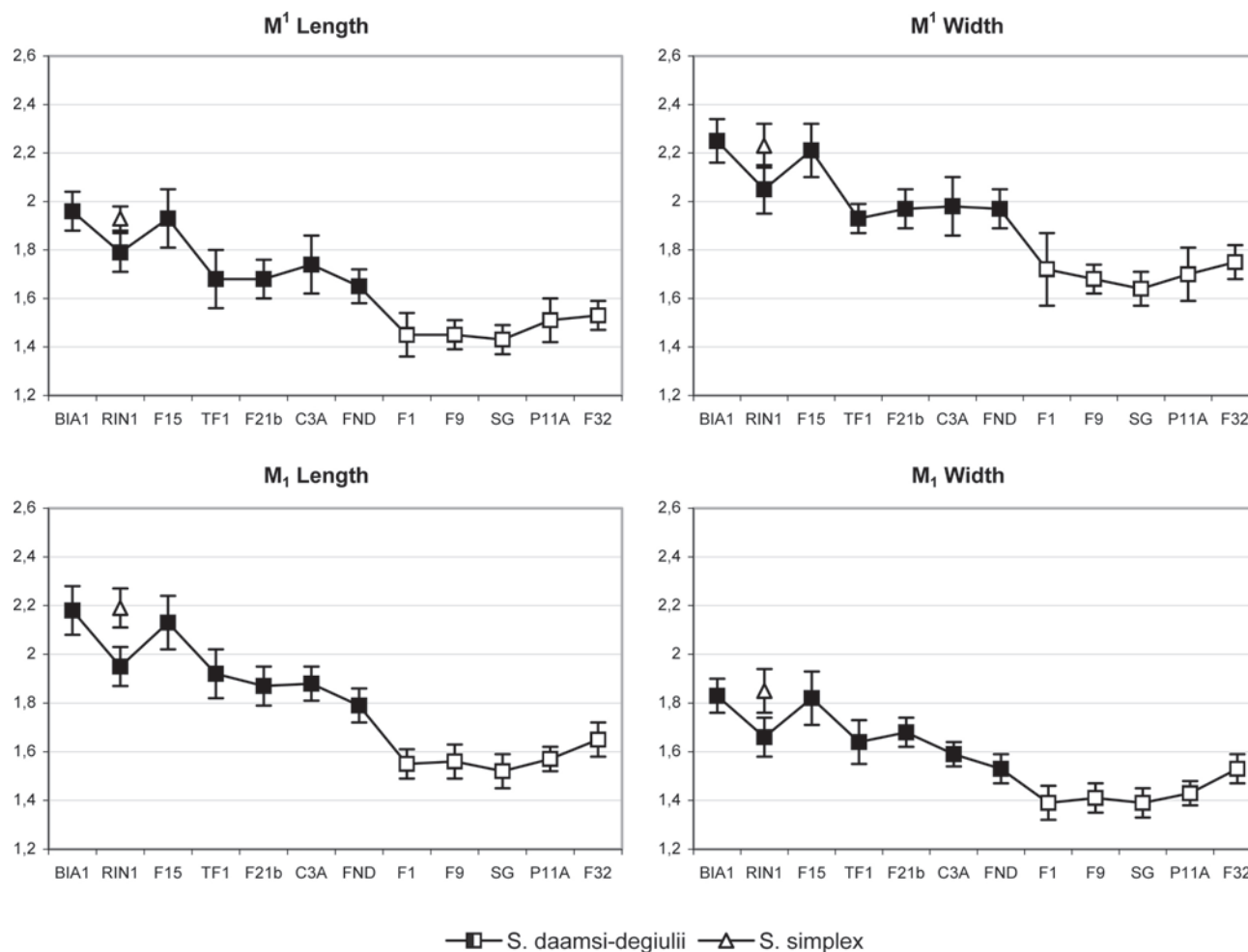


Fig. 15 - Size variation of small-sized *Stertomys* species. Vertical bars represent standard deviations. Samples are arranged according to the biochronological sequence resulting from this paper (see the paragraph "Biochronological remarks").

dormouse implies a double inversion of size variation: a reduction occurring from Biancone 1 to Rinascita 1, an increase in size in F15, followed by a definitive reduction occurring in the younger samples (Fig. 15). The small size of *S. aff. daamsi* from Rinascita 1 might be explained considering that this fissure is the only one containing three *Stertomys* species characterised by sizes that are close each other and partially overlapping (Martín-Suárez & Freudenthal, 2007). Indeed, in Rinascita 1 the species *S. simplex* occupies the size range of *S. daamsi* from Biancone 1 and *S. ex gr. daamsi* from F15. *Stertomys lyrifer* occupies a larger size range partially overlapping that of *S. simplex*, while *Stertomys aff. daamsi* occupies the smallest size range. Under those conditions, an ecological interaction among these three very similar taxa is likely. If the biochronological position of Rinascita 1 as younger than Biancone 1 is correct, we can infer that *S. simplex* is a new incomer from some neighbouring island and that the reduction in size of the resident *S. daamsi* could be an ecological response due to the competition between these two species very close in size. The release from the competition with *S. simplex*, possibly due to its extinction, could explain the recovery of the size of *S. ex gr. daamsi* in F15.

Stertomys degiulii nov. sp.

Type-locality - Apricena-Poggio Imperiale Limestone Quarries (Cava Fina), fissure filling F9.

Age - Late Miocene-Early Pliocene.

Geographical distribution - Endemic on the Gargano promontory (southern Italy).

Material - 576 teeth (see Tab. 2, for details) (Pl. 3, figs. 21-44).

Measurements - See Tabs. 4-5.

Repository - The material is stored in the collection of the Dipartimento di Scienze della Terra, Università degli Studi di Firenze, Italy.

Holotype - Left M² (F9-90) (Pl. 3, fig. 28).

Derivatio nominis - In honour of Claudio De Giuli (1938-1988) who, during the eighties of the past century, together with Danilo Torre, led the field survey and the research of the Florentine team on the Gargano Neogene, and brought fresh knowledge on the

mammalian endemics and on the palaeogeography of this palaeoarchipelago.

Diagnosis - *Stertomy*s of small size, the smallest observed among all *Stertomy*s species described so far. Dental pattern with well-developed secondary and accessory crests within the central valley of the upper molars. High frequency of connections between the trigon crests and the metaloph (Fig. 7).

Differential diagnosis - *Stertomy*s *degiulii* has a general morphological pattern similar to *S. daamsi* but it differs from the latter in having a higher frequency of connections of trigon crests with the metaloph in the upper molars (Figs. 7, 12) and in having a distinctly smaller size (Tabs. 4-5, Fig. 10). *Stertomy*s *degiulii* also shows a higher frequency of connections between the anterolophid and the protoconid, determining, with wear, a complete closure of the anterior valley in the lower molars (Fig. 14). It differs from *S. simplex* by the smaller size and the more complex morphology. It is clearly separated from *S. lyrifer* by its smaller size, simpler morphology and by the absence of the lyre-shape connection in the lower molars. It differs from *S. daunius* by its much smaller size, its distinctly simpler morphology and in having protoloph and metaloph always connected; from *S. laticrestatus* by the much smaller size, the narrower and higher crests and in having protoloph and metaloph always connected.

Description of the material from the type-locality - Dental features are typical of small-sized *Stertomy*s (see "General description" above in this paragraph). The Daams' morphotypes distribution for upper and lower teeth is reported in Figs. 6 and 8 respectively.

The most important characters are the following.

P^4 - The metaloph is usually connected to the protoloph, except in three specimens. Trigon crests join the metaloph in four specimens and the protoloph in two specimens. The labial end of the protoloph joins a small precentroloph in a hook shape only in few specimens.

M^1 - Only one specimen lacks the connection between the metaloph and the protoloph at the protocone. Centrolophs are connected to each other lingually in twelve specimens. Fourteen specimens present a well-defined prototrope (they belong to Daams' morphotype D). The prototrope is usually slightly shorter than the centrolophs. Trigon crests join the metaloph in fourteen specimens, in five of them this connection is weak.

M^2 - Centrolophs are connected to each other lingually in 21 specimens. 45 of 49 specimens have a well-developed prototrope. It is usually as long as the centrolophs; these three crests are also quite parallel and they are connected lingually in an E-shaped structure. Trigon crests join the metaloph in 32 specimens, in eight of which this connection is weak.

M^3 - In six specimens the anterolabial root and the lingual one fuse. Five specimens have a well-developed endoloph. Centrolophs are usually connected to each other lingually. The prototrope is usually long and it is connected labially to the precentroloph in 38 specimens, while it is connected to the paracone in 30 specimens. The postcentroloph usually joins the metacone. Trigon

crests join the metaloph in 40 specimens, while in eleven this connection is weak.

P_4 - The anterior part of the tooth shows a high variability of crests length and of their connections. Eight specimens have a well-developed endolophid.

M_1 - Only seven specimens have three roots, two anterior and one posterior. 67 specimens have two roots: in 27 specimens the anterior root partially splits and in seven specimens the root is undivided. The anterolophid tends to converge on the protoconid, closing, with wear, the anterior valley in 27 specimens. Generally the centrolophid slightly exceeds half the tooth width, it usually joins the metaconid lingually and in 27 specimens it labially joins the metalophid. Two specimens have a well-developed endolophid.

M_2 - Only two specimens have two roots, a split anterior one and a posterior one. The anterolophid tends to converge towards the protoconid enclosing, with the wear, the anterior valley in thirteen specimens. The centrolophid length generally ranges between half and one third of the tooth width, it usually joins the metaconid lingually while on the labial side it joins the metalophid in ten specimens. Only one specimen has a well-developed endolophid.

M_3 - Only one specimen has two roots, a split anterior one and a simple posterior one. The anterolophid tends to converge to the protoconid in ten specimens. The centrolophid generally is extended about one third of the tooth width; it usually joins the metaconid lingually, while labially it joins the metalophid in eight specimens and the mesolophid in six specimens. Three specimens have a well-developed endolophid.

Locality - Fl.

Age - Late Miocene-Early Pliocene.

Material - 91 teeth (see Tab. 2, for details) (Pl. 3, figs. 1-20).

Measurements - See Tabs. 4-5.

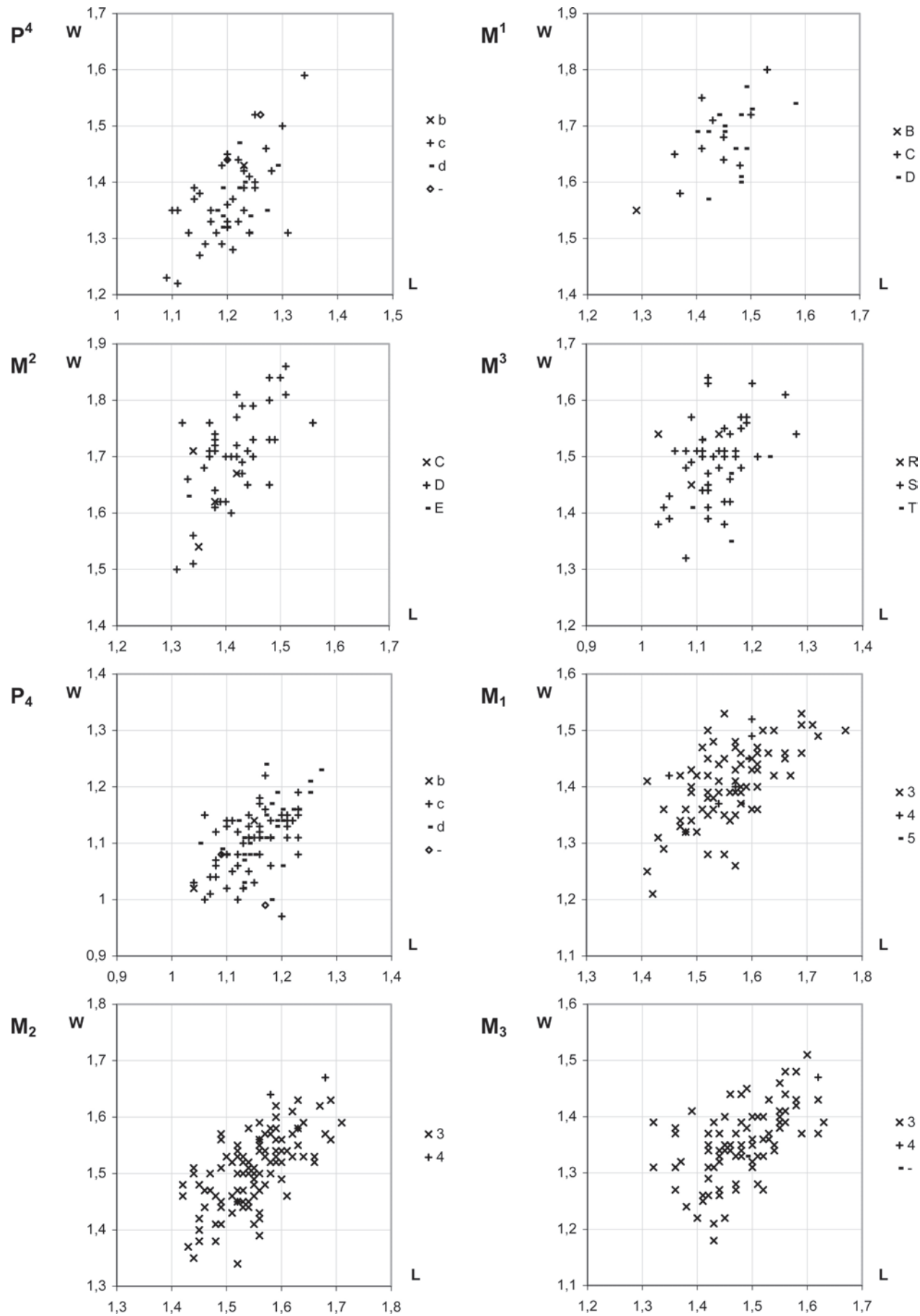
Description - The specimens fit the size and the morphology of the type-locality. The P^4 presents a very high frequency of the complex Daams' morphotype d. The trigon crests of the M^1 connect to the metaloph in six specimens (two of which weakly), the same datum is recorded for the M^2 (Fig. 7). The M_1 presents a higher frequency of complex morphotypes (Daams' morphotypes 4 and 5) than the type-locality (Fig. 8). In M_1 the anterior root is undivided in two specimens of eight, where it is preserved. The anterolophid converges to the protoconid in seven of fifteen M_1 and in four of seventeen M_2 (Fig. 9).

Locality - San Giovannino (SG).

Age - Late Miocene-Early Pliocene.

Material - 189 teeth (see Tab. 2, for details) (Pl. 3, figs. 45-63).

Measurements - See Tabs. 4-5.

Fig. 16 - Length/width diagram for *Stertomys degiulii* type-population from F9. Specimens are indicated by their Daams' morphotype.

Description - The specimens fit the size and the morphology of those from the type-locality. The M^1 presents a slightly higher frequency of the Daams' morphotype B respect to the other samples belonging to this taxon (Figs. 6, 13). In 20 of 33 M^1 the trigon crests connect to the metaloph (of which seven weakly), this character is present in 22 of 32 M^2 (of which seven weakly) (Fig. 7). Complex Daams' morphotypes are absent in the lower molars. All the M_1 have two roots; the anterior one is undivided in one specimen. In ten of 25 M_1 and nine of 29 M_2 the anterolophid converges on the protoconid tending to close the anterior valley (Fig. 9).

Discussion - The sample from fissure F9 is the richest here examined. Both size and morphological variations are moderate and evenly distributed (Fig. 16). This sample can be considered as not affected by major taphonomic biases and this condition confirms that F9 sample is particularly suitable for the description of a new species.

The distinct smaller size distinguishes the F9 population from *S. daamsi*, and also from the smaller representative of that species (*S. ex gr. daamsi* from Trefossi 1, F21b, Cantatore 3A and Fina D; Fig. 10). The morphological distinction from *S. gr. daamsi* is rather subtle and it is based mainly on the different frequency distribution of morphotypes. In the upper molars of *S. degiulii*, the Daams' morphotype D is dominant (56% in M^1 and 90% in M^2); the other morphotypes, namely B, E and F, are extremely rare or absent (Fig. 13). Unfortunately the small sample-size for the single dental elements in same samples, and in particular the absence of some morphotypes, challenges the possibility to make a reliable statistical test on Daams' morphotype frequencies with *S. gr. daamsi*. On the other hand, the higher frequency of the connection between trigon crests and metaloph in M^1 and M^2 (Rinaldi's morphotypes B, Fig. 3) clearly distinguishes *S. degiulii* from *S. gr. daamsi* (Fig. 12). These frequencies in F9 have been compared with those in Biancone 1, Rinascita 1, and F15 by a chi-square test that yielded significant results ($p < 0.01$).

The specimens from F1 and San Giovannino are close in size and similar in morphology to those from the type-locality F9 (Figs. 12-14). Small variations in the morphotype frequencies occur. The San Giovannino sample has a slightly higher frequency of Daams'

morphotype B in M^1 (Fig. 13); F1 has a slightly lower frequency of connections between the trigon crests and the metaloph (Rinaldi's morphotype B1; Fig. 12). However, the frequency of the other characters fits well that of the type population. Considering that the samples have a close size to the type-locality (Fig. 10), it is possible to refer the material from these two fissures to the species *S. degiulii*.

Stertomya aff. *degiulii*

Locality - F32.

Age - Late Miocene-Early Pliocene.

Material - 116 teeth (see Tab. 2, for details) (Pl. 4, figs. 9-27).

Measurements - See Tabs. 4-5.

Description - The specimens are morphologically comparable with those from F9, but slightly larger in size. This sample presents a higher frequency of Daams' morphotype C respect to morphotype D in M^1 (Figs. 6, 13). It has a high frequency of the "weakly connected" trigon crests in M^1 (Rinaldi's morphotype B2) and of "connected" crests (Rinaldi's morphotype B3) in M^2 (Figs. 7, 12). The anterolophid converges to the protoconid, closing the anterior valley, in eleven of eighteen M_1 and three of nineteen M_2 (Fig. 9). In M_1 , all but one specimens have two roots; the anterior one is undivided in only two specimens. The M_1 is proportionally wider than the other teeth (Fig. 10).

Discussion - The differences of the morphotype frequencies in the upper molars do not yield significant results in a chi-square test, possibly also because some of the samples are poorly represented. However, the frequency of closed anterior valley in M_1 (Rinaldi's morphotype C2) in F32 resulted significantly higher than in F9 (Tab. 7). This result, together with the slightly larger size and the relatively wider M_1 , suggests that the F32 dormouse is distinct from the type-population of *S. degiulii* and from the other populations referred to this taxon. We prefer, therefore, to refer this sample as *S.*

Observed frequency							Chi-square test: $p=0,01$ (significant)				
	F1	F9	SG	P11A	F32	tot	Cross chi-square test for pairs of samples				
C1	8	62	15	7	7	99					
C2	7	27	10	14	11	69					
tot	15	89	25	21	18	168					
Expected frequency											
	F1	F9	SG	P11A	F32	tot	F9	F1	SG	P11A	
C1	8,8	52,4	14,7	12,4	10,6	99	0,21	0,68	0,36		
C2	6,2	36,6	10,3	8,6	7,4	69	0,23	0,002	0,07		
tot	15	89	25	21	18	168	0,41	0,01	0,17	0,72	

Tab. 7 - Chi-square test on frequency of connection between anterolophid and protoconid in M_1 (Fig. 3) for *S. degiulii*. Statistically significant values are in bold.

aff. *degiulii*. This taxon might represent the most derived population of the *S. degiulii* lineage.

Stertomys cf. *degiulii*

Locality - Pirro 11A (P11A).

Age - Late Miocene-Early Pliocene.

Material - 89 teeth (see Tab. 2, for details) (Pl. 4, figs. 1-8).

Measurements - See Tabs. 4-5.

Description - The upper teeth are poorly represented compared to the lower ones (25 and 64 specimens respectively). Half the P^4 specimens are characterised by the connection of the metaloph and the posteroloph on the labial side (at the metacone). In all the M^1 the trigon crests are connected to the metaloph, in four of these specimens the connection is weak, while in M^2 this connection is recorded in four of six specimens (Fig. 7). The number and the morphology of the roots is not analysed because all the teeth are inserted in their alveoli.

In M_1 the frequency of complex morphotypes is very low (Fig. 8). In fourteen of twenty-one M_1 the anterolophid converges to the protoconid, closing with wear the anterior valley, while in M_2 this character is present in six of eighteen specimens (Fig. 9).

Discussion - Though the sample is fairly comparable with the type-locality F9, the difference of the morphotype frequencies in Pirro 11A respect to F9 is greater than that observed in the above reported samples. In this case, the evaluation of the morphological variation is severely affected by the low number of specimens, particularly for the upper teeth (e.g. six M^2 specimens). Pirro 11A is the only sample in which the trigon crests are always connected, weakly or fully, to the metaloph in M^1 (Fig. 12). In M^2 it apparently lacks the “weakly connected” morphotype. However, it is hard to state if those differences reflect the actual morphology of the population, or if they are an effect due to the low number of specimens. Conversely, a significant difference respect to the type-population (chi-square test: $p = 0.002$) is found in the lower first molar that shows the highest frequency of the enclosed anterior valley, a feature shared with the sample F32 (Figs. 9, 14, Tab. 7). The scant number of upper teeth prevents to define

EXPLANATION OF PLATE 1

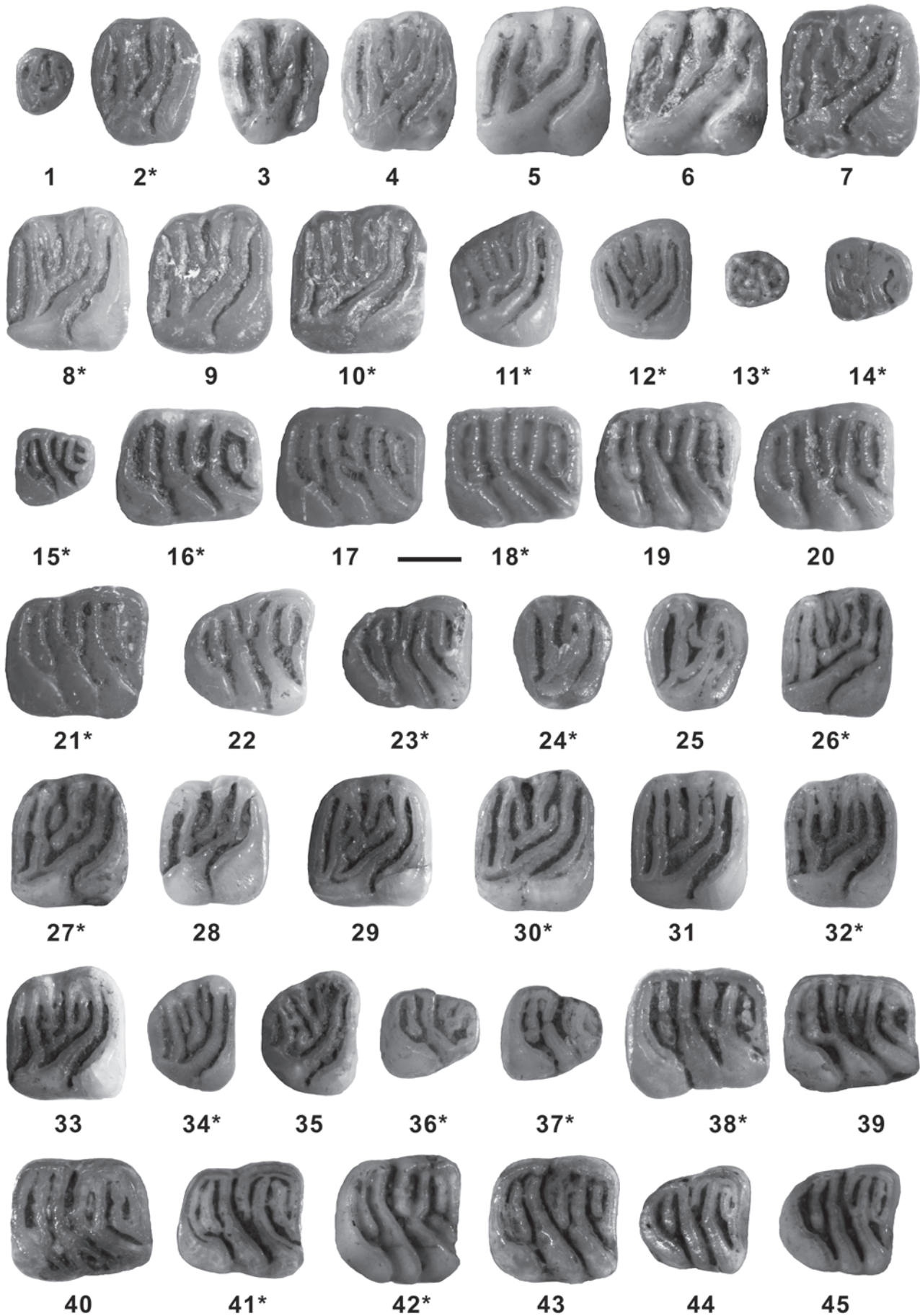
figs. 1-23 - *Stertomys* ex gr. *daamsi*. F15.

- 1 - D^4 r.
- 2 - P^4 l.
- 3 - P^4 r.
- 4-7 - M^1 r.
- 8 - M^2 l.
- 9 - M^2 r.
- 10 - M^2 l.
- 11-12 - M^3 l.
- 13 - D^4 l.
- 14-15 - P^4 l.
- 16 - M_1 l.
- 17 - M_1 r.
- 18 - M_1 l.
- 19-20 - M_2 r.
- 21 - M_2 l.
- 22 - M_3 r.
- 23 - M_3 l.

figs. 24-45 - *Stertomys* ex gr. *daamsi*. Trefossi 1.

- 24 - P^4 l.
- 25 - P^4 r.
- 26-27 - M^1 l.
- 28-29 - M^1 r.
- 30 - M^2 l.
- 31 - M^2 r.
- 32 - M^2 l.
- 33 - M^2 r.
- 34 - M^3 l.
- 35 - M^3 r.
- 36-37 - P^4 l.
- 38 - M_1 l.
- 39-40 - M_1 r.
- 41-42 - M_2 l.
- 43 - M_2 r.
- 44-45 - M_3 r.

Scale bar = 1 mm. All specimens are right-hand represented. (*) Left-hand specimens.



Stertomyx from Pirro 11A as a distinct taxonomic unit respect to *S. degiulii*. On the other hand, the occurrence of a shared character with F32 might suggest that Pirro 11A represents a transition between *S. degiulii* and *S. aff. degiulii*. Taking into account all these considerations, the use of an “open” taxonomical referral, such as *S. cf. degiulii*, appears to be a suitable solution.

DESCRIPTION OF THE OUTLIERS OF THE SMALL-SIZED *STERTOMYS* SPECIES

A total number of 18 outliers occurs in seven of the ten samples of small-sized *Stertomyx* species here described (Tab. 3). The outliers do not display peculiar

morphologies and fall into the range of morphological variation observed in the group of small-sized *Stertomyx*. Even though the size fits the overall range of this group, the outliers can be identified by their different size respect to the bulk of specimens of each fissure. The outliers from F15 and Pirro 11A are smaller in size, those from Fina D and F1 are larger in size, while in F21b, Trefossi 1 and Cantatore 3A outliers either larger or smaller occur.

Locality - F15.

Number of outliers - One (Pl. 4, fig. 28). See Tab. 3 for measurement and Daams' morphotype.

EXPLANATION OF PLATE 2

figs. 1-17 - *Stertomyx* ex gr. *daamsi*. F21b.

- 1-2 - P⁴ l.
- 3 - M¹ r.
- 4 - M¹ l.
- 5 - M² r.
- 6 - M²-M³ r.
- 7 - M³ l.
- 8 - D₄ r.
- 9 - P₄ r.
- 10 - P₄ l.
- 11 - M₁ l.
- 12 - M₁ r.
- 13 - M₁ l.
- 14 - M₂ l.
- 15 - M₂ r.
- 16-17 - M₃ l.

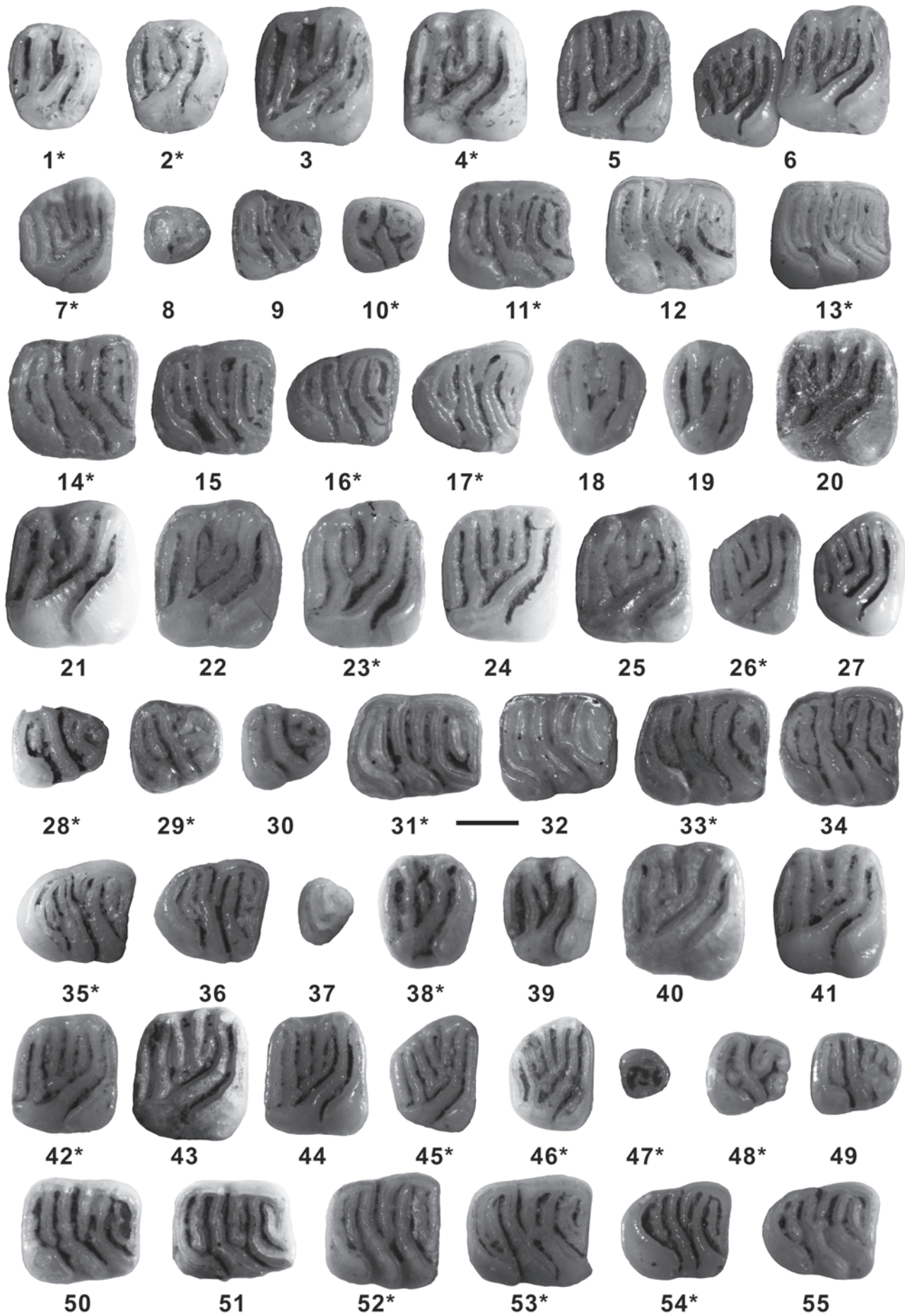
figs. 18-36 - *Stertomyx* ex gr. *daamsi*. Cantatore 3A.

- 18-19 - P⁴ r.
- 20-22 - M¹ r.
- 23 - M² l.
- 24-25 - M² r.
- 26 - M³ l.
- 27 - M³ r.
- 28-29 - P₄ l.
- 30 - P₄ r.
- 31 - M₁ l.
- 32 - M₁ r.
- 33 - M₂ l.
- 34 - M₂ r.
- 35 - M₃ l.
- 36 - M₃ r.

figs. 37-55 - *Stertomyx* ex gr. *daamsi*. Fina D.

- 37 - D⁴ r.
- 38 - P⁴ l.
- 39 - P⁴ r.
- 40-41 - M¹ r.
- 42 - M² l.
- 43-44 - M² r.
- 45-46 - M³ l.
- 47 - D₄ l.
- 48 - P₄ l.
- 49 - P₄ r.
- 50-51 - M₁ r.
- 52-53 - M₂ l.
- 54 - M₃ l.
- 55 - M₃ r.

Scale bar = 1 mm. All specimens are right-hand represented. (*) Left-hand specimens.



Description - The M_2 F15-58 is a small-sized outlier and shows a high degree of wear. This specimen has well-developed main crests and centrolophid. The latter is half-tooth-width long. Both the anterotropid and the posterotropid are present. The former reaches the anterolophid at its labial end. The latter tends to reach the entoconid.

Locality - Trefossi 1 (TF1).

Number of outliers - Two (Pl. 4, figs. 29-30). See Tab. 3 for measurement and Daams' morphotype.

Description - The P^4 RGM436051 is a large-sized outlier and shows a very simple morphology. Only the

main crests are present. The protoleph, the metaloph and the posteroloph join the protocone on the lingual side. RGM436025 is a small M_1 with well-developed main crests. The centrolophid, slightly exceeding half of the tooth width, ends on the lingual side without connections. However, a small spur at the lingual end of the metalophid tends to reach the centrolophid. The anterolophid slightly connects the metalophid at the protoconid. A well-developed anterotropid tends to connect the anterolophid on the labial side. A well-developed posterotropid is present as well.

Locality - F21b.

Number of outliers - Eight (Pl. 4, figs. 31-38). See Tab. 3 for measurement and Daams' morphotype.

EXPLANATION OF PLATE 3

figs. 1-20 - *Stertomys degiulii* nov. sp. F1.

- 1 - P^4 l.
- 2 - P^4 r.
- 3-5 - M^1 l.
- 6-7 - M^2 l.
- 8 - M^2 r.
- 9-10 - M^3 r.
- 11-12 - P_4 r.
- 13 - M_1 r.
- 14-15 - M_1 l.
- 16-17 - M_2 l.
- 18 - M_2 r.
- 19 - M_3 r.
- 20 - M_3 l.

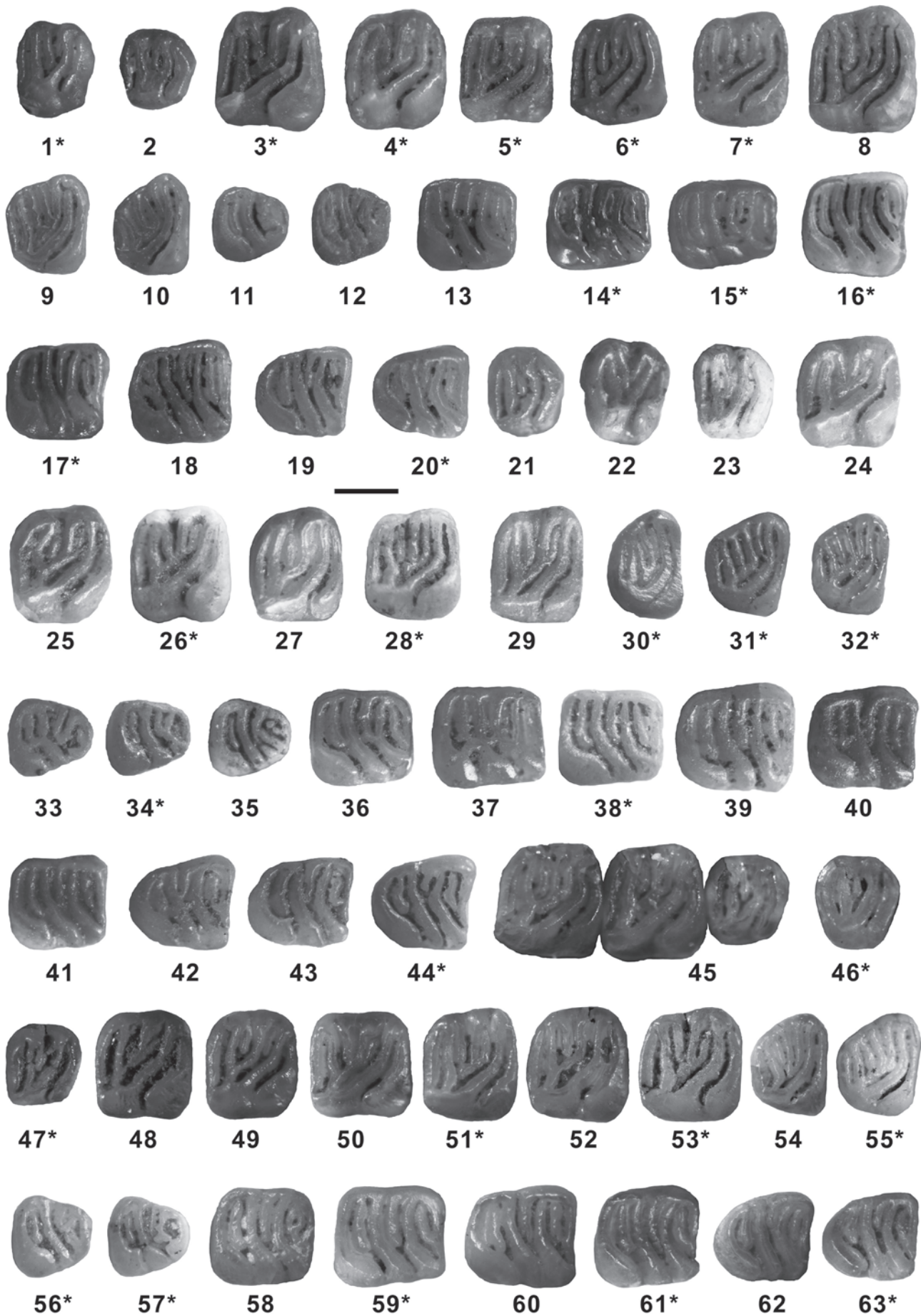
figs. 21-44 - *Stertomys degiulii* nov. sp. F9.

- 21-23 - P^4 r.
- 24-25 - M^1 r.
- 26 - M^1 l.
- 27 - M^2 r.
- 28 - M^2 l (holotype).
- 29 - M^2 r.
- 30-32 - M^3 l.
- 33 - P_4 r.
- 34-35 - P_4 l.
- 36-37 - M_1 r.
- 38 - M_1 l.
- 39-41 - M_2 r.
- 42-43 - M_3 r.
- 44 - M_3 l.

figs. 45-63 - *Stertomys degiulii* nov. sp. San Giovannino.

- 45 - P^4 - M^3 r.
- 46-47 - P^4 l.
- 48-50 - M^1 r.
- 51 - M^2 l.
- 52 - M^2 r.
- 53 - M^2 l.
- 54 - M^3 r.
- 55 - M^3 l.
- 56-57 - P_4 l.
- 58 - M_1 r.
- 59 - M_1 l.
- 60 - M_2 r.
- 61 - M_2 l.
- 62 - M_3 r.
- 63 - M_3 l.

Scale bar = 1 mm. All specimens are right-hand represented. (*) Left-hand specimens.



Description - The large P⁴ F21b-58 shows a high degree of wear. The anteroloph is interrupted in the middle. The protoloph is short and does not reach the labial edge of the tooth. It slightly joins the long centroloph. The latter converges to the paracone. Three M¹ exceed the size of the bulk of specimens. F21b-45a has well-developed main crests, two well-developed centrolophs, separated on the lingual side, and a short, thin prototrope connected lingually to the precentroloph. F21b-51 shows a high degree of wear. It has well-developed main crests and centrolophs. A very short, thin prototrope is present. The centrolophs connect each other on the lingual side and tend to connect the metaloph. F21b-53 has a well-developed precentroloph and a reduced postcentroloph. Two M³ are larger than the bulk of specimens. F21b-2 has well-developed main crests. Inside the trigon there are a long prototrope and a long

precentroloph, connected lingually, and in a more distal position there is a shorter postcentroloph, which does not reach the labial border of the tooth. F21b-61 presents the same pattern of the previous described tooth. In this specimen, however, the prototrope is slightly shorter and the postcentroloph reaches the labial border of the tooth. F21b-34 is a large M₁ with well-developed main crests. A long anterotrope and a long posterotrope are present. An oblique spur leaves the metaconid to join the mesolophid. The latter crest is slightly connected to the entoconid. Between the metalophid and the centrolophid there is a small tubercle slightly connected to the latter crest. The centrolophid stretches not longer than two third of the tooth width. F21b-73 is a small-sized, worn M₂. Long anterotrope, posterotrope and centrolophid are present. The pattern of connection is quite regular.

EXPLANATION OF PLATE 4

figs. 1-8 - *Stertomys* cf. *degiulii* Pirro 11A.

- 1 - P⁴-M² l.
- 2 - P⁴-M² r.
- 3 - M₁-M₃ l.
- 4 - P⁴-M³ r.
- 5 - M₁-M₂ l.
- 6 - P₄, M₂-M₃ r.
- 7 - M₁, M₃ l.
- 8, M₁-M₃ r.

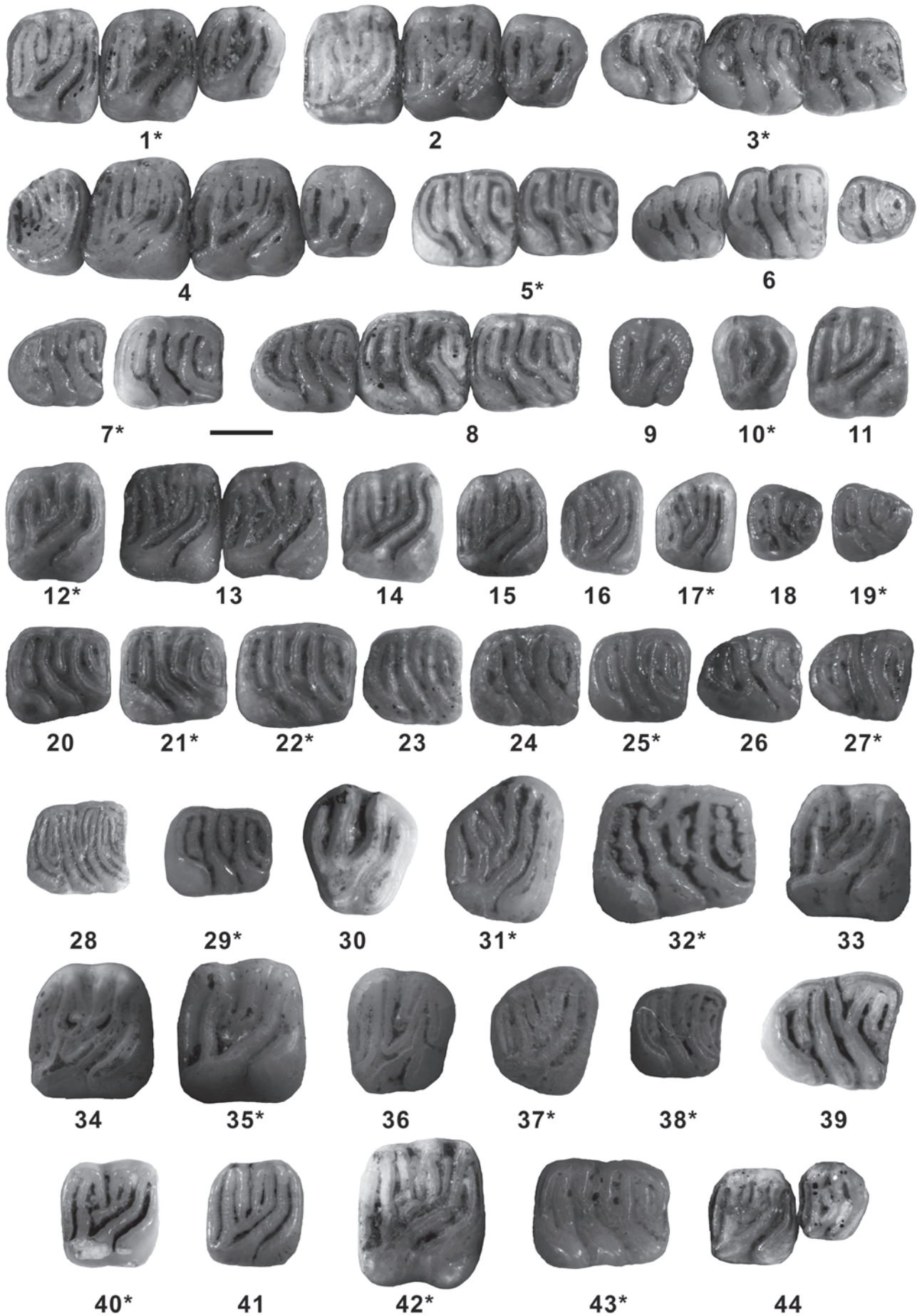
figs. 9-27 - *Stertomys* aff. *degiulii*. F32.

- 9 - P⁴ r.
- 10 - P⁴ l.
- 11 - M¹ r.
- 12 - M¹ l.
- 13 - M¹-M² r.
- 14-15 - M² r.
- 16 - M³ r.
- 17 - M³ l.
- 18 - P₄ r.
- 19 - P₄ l.
- 20 - M₁ r.
- 21-22 - M₁ l.
- 23-24 - M₂ r.
- 25 - M₂ l.
- 26 - M₃ r.
- 27, - M₃ l.

figs. 28-44 - Outliers.

- 28 - F15-58 (M₂ r).
- 29 - TF1-RGM436025 (M₁ l).
- 30 - TF1-RGM436051 (P⁴ r).
- 31 - F21b-02 (M³ l).
- 32 - F21b-34 (M₁ l).
- 33 - F21b-45a (M¹ r).
- 34 - F21b-51 (M¹ r).
- 35 - F21b-53 (M¹ l).
- 36 - F21b-58 (P⁴ r).
- 37 - F21b-61 (M³ l).
- 38 - F21b-73 (M₂ l).
- 39 - C3A-RGM435895 (M₃ r).
- 40 - C3A-RGM435912 (M¹ l).
- 41 - C3A-RGM435929 (M² r).
- 42 - FND-RGM436221b (M¹ l).
- 43 - F1-2.20 (M₁ l).
- 44 - P11A-RGM436016a-b (P⁴-M¹ r).

Scale bar = 1 mm. All specimens are right-hand represented. (*) Left-hand specimens.



Locality - Cantatore 3A (C3A).

Number of outliers - Three (Pl. 4, figs. 39-41). See Tab. 3 for measurement and Daams' morphotype.

Description - RGM435912 is a small M¹ with well-developed main crests. The paracone is placed on the anterior border of the tooth. The three trigon crests are connected lingually. The prototrope is labially limited by a forward spur of the precentroloph on the labial edge of the tooth. The latter crest is very long and tends to converge lingually to the central portion of the metaloph. The long postcentroloph joins the metacone. A small tubercle is present in a slightly distal position respect to the metaloph. RGM435929 is smaller than the bulk of the sample. This M² has well-developed main crests. Within the trigon, three crests are well-developed and lingually connected forming a E-shaped structure. The precentroloph and the prototrope join each other labially. The postcentroloph converges to the metacone. A M₃ (RGM435895) exceeds in size the bulk of the sample. The main crests are well-developed. A long anterotripid and a long posterotripid are present. Two crests are present between the metalophid and the mesolophid: a very short one, which connects lingually to the metaconid, and a longer one, in a more distal position, not connected to the metaconid, which leaves the lingual border of the tooth and reaches the metalophid at its half.

Locality - Fina D (FND).

Number of outliers - One (Pl. 4, fig. 42). See Tab. 3 for measurement and Daams' morphotype.

Description - RGM436221b exceeds in size the bulk of the sample. This M¹ has well-developed main crests and four crests within the trigon: prototrope, precentroloph, centrotrope and postcentroloph. The narrow prototrope does not reach the labial border of the tooth; on the lingual side it slightly connects the long backward-curved precentroloph. The centrotrope is short and placed in the middle of the trigon, between the two centrolophs. The postcentroloph connects lingually the other centroloph, labially it reaches the metacone, although the connection with the metaloph is weak. The trigon crest complex tends to connect the metaloph.

Locality - F1.

Number of outliers - One (Pl. 4, fig. 43). See Tab. 3 for measurement and Daams' morphotype.

Description - F1-2.20 is larger than the other M₁ of the sample. There are well-developed main crests, a long anterotripid and a long posterotripid. The centrolophid is long and it connects the metalophid both at the lingual end and at its middle. A short crest is present between the centrolophid and the mesolophid.

Locality - Pirro 11A (P11A).

EXPLANATION OF PLATE 5

figs. 1-13 - *Stertomys daunius*. F15.

- 1 - P⁴ r.
- 2 - M¹ r.
- 3-4 - M² l.
- 5-6 - M³ l.
- 7 - M³ r.
- 8 - P₄ r.
- 9 - M₁ l.
- 10 - M₂ r.
- 11 - M₂ l.
- 12 - M₃ r.
- 13 - M₁-M₃ r.

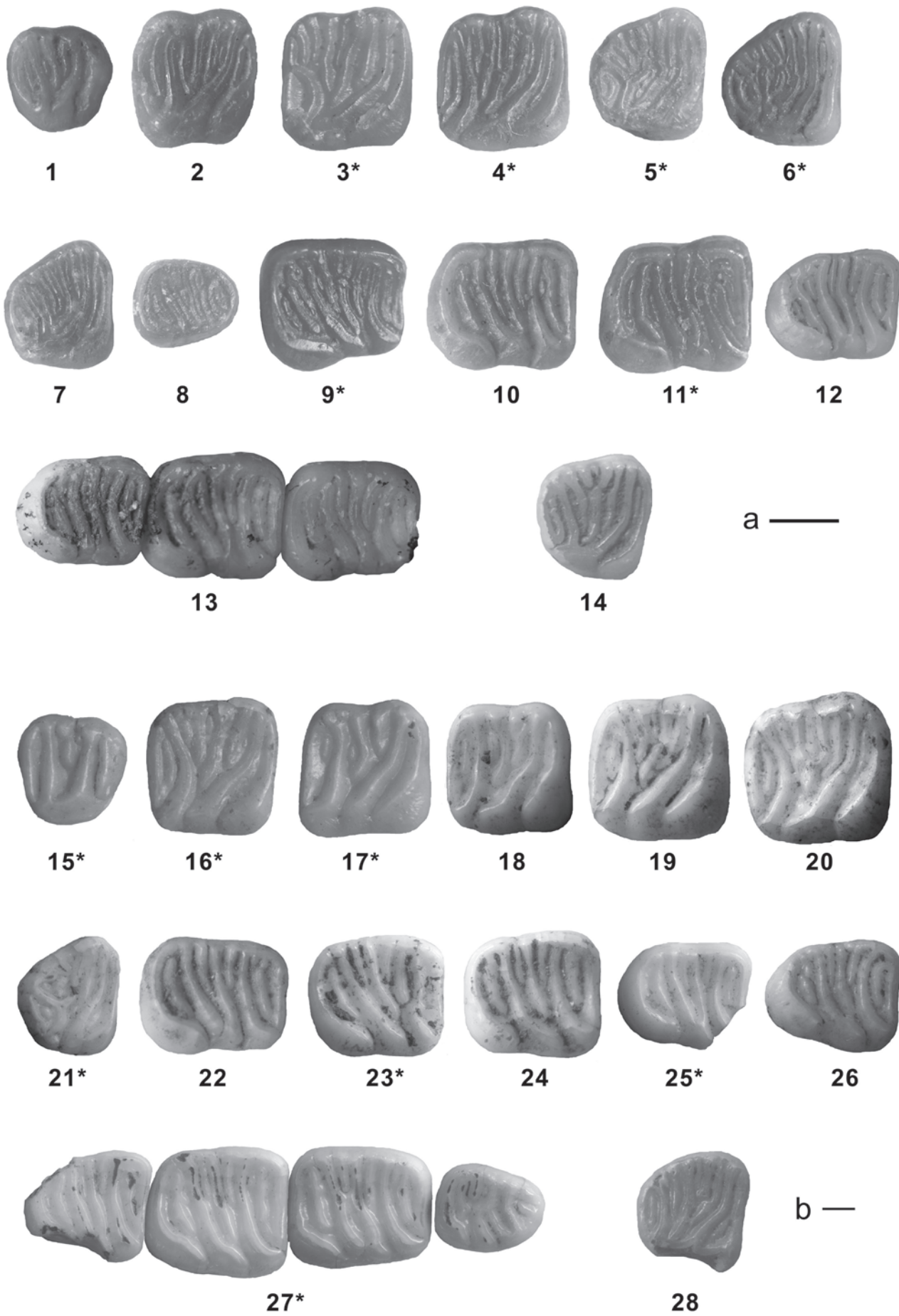
fig. 14 - *Stertomys daunius*. F21a, M³ r.

figs. 15-27 - *Stertomys laticrestatus*. F9.

- 15 - P⁴ l.
- 16-17 - M¹ l.
- 18-20 - M² r.
- 21 - M³ l.
- 22 - M₁ r.
- 23 - M₂ l.
- 24 - M₂ r.
- 25 - M₃ l.
- 26 - M₃ r.
- 27 - P₄-M₃ l.

fig. 28 - *Stertomys* aff. *laticrestatus*. F1, M³ r.

a) Scale bar for figs. 1-14 = 1 mm; b) Scale bar for figs. 15-28 = 1 mm. All specimens are right-hand represented. (*) Left-hand specimens.



Number of outliers - Two (Pl. 4, fig. 44). See Tab. 3 for measurement and Daams' morphotype.

Description - The P^4 and the M^1 of the dental series RGM436016 are smaller in comparison with the rest of the sample. The P^4 has well-developed main crests and a single isolated centroloph. The proto-loph is divided in two parts. The M^1 has well-developed main crests, two centrolophs and a small prototrope. The centrolophs are isolated, and the precentroloph is the longest one. The prototrope is reduced to a small tubercle in a mesial position at the half of the precentroloph length. The third element of the series (RGM436016c), however, falls within the variation range of the M^2 .

Discussion - As reported in the description, the outliers fall within the range of morphological variation of the two small-sized *Stertomys* species. The larger outliers from F21b, Trefossi 1, Cantatore 3A, and Fina D fall within the variation range of *S. daamsi* from Biancone 1 and *S. ex gr. daamsi* from F15, while the smaller ones fall within the range of *S. degiulii* from the type-locality (F9). Also the small outlier from F15 falls within the range of *S. degiulii*. The large outlier from F1 is intermediate between *S. ex gr. daamsi* from F21b and *S. ex gr. daamsi* F15. Eventually, the outliers from Pirro 11A are the smallest-sized *Stertomys* specimens so far recovered.

It is difficult to state if each outlier (or group of outliers) found in each fissure may represent a distinct species or if all the larger-sized and small-sized outliers belong to two evolutionary lineages differing in size. For that reason and because of the very small number of outliers in each sample, a precise taxonomic status is not given in this paper, while an informal taxonomy based on the size is provided (Tab. 3).

Martín-Suárez & Freudenthal (2007) give three possible explanations for the occurrence of the outliers at fissure Rinascita 1. Firstly, the outliers might represent individuals belonging to different species evolved in neighbouring islands, that by chance reached the Apricena-Poggio Imperiale area during phases in which faunal exchanges within the archipelago were easier. Secondly, the outliers might be rare specimens belonging to different species evolved in neighbouring islands whose remains are introduced by chance by birds preying in those islands. Finally, some fissure fillings might be heterogeneous and present a mixture of fossils of different ages. We suggest that outliers might also represent individuals belonging to relict populations of species formerly widespread on the island.

Our analysis shows that the outliers occur more frequently in the older samples (for instance they reach 10% of the whole sample in F21b). In those samples the possible occurrence of faunal exchanges from neighbouring islands is suggested also by other taxonomic groups, i.e. *Mikrotia* (see the paragraph "Biochronological framework"). Those arguments support the interpretation of a direct faunal exchange, or an introduction of allochthonous faunal elements by the activity of bird of prey. Nevertheless, such older samples are also those in which the probability of some

reworking due to the infiltration of fossils derived from younger deposits is higher. On the other hand, if the small-sized outliers in fissures F15, Trefossi 1, F21b and Cantatore 3A were reworked from older fissure fillings we would expect glirids of the same size to have occurred in such fissures. However, no remains of comparable size are found in Biancone 1 and Rinascita 1, considered as the oldest sites of the palaeoarchipelago (Freudenthal & Martín-Suárez, 2006; Martín-Suárez & Freudenthal, 2007). Thus, the possibility that those small-sized outliers could be derived by infiltration of younger material should be taken into account. However, the occurrence in the same fissures of large-sized outliers comparable with *S. daamsi* from Biancone 1 contradict the hypothesis that all outliers are derived from infiltration of younger material, since specimens of such large size are absent in the younger fissures. The possibility that small-sized outliers derive from reworking of younger fissures while the large-sized ones come from older fissures is definitely not realistic. Therefore, the occurrence of sporadic small-sized teeth in the samples belonging to the population phase 1 (F15, Trefossi 1, F21b, and

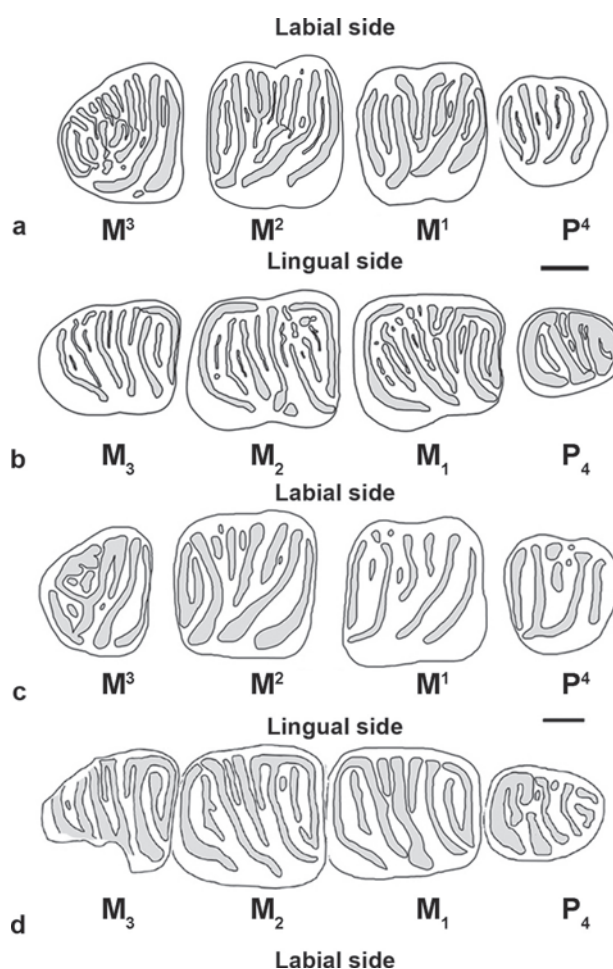


Fig. 17 - Dental row of large-sized *Stertomys* species. a) *S. daunius* upper teeth; b) *S. daunius* lower teeth; c) *S. laticrestatus* upper teeth; d) *S. laticrestatus* lower teeth. All specimens are right-hand drawn with the anterior side facing to the right. Scale bar = 1 mm.

Cantatore 3A) suggests that a taxon of the same size as *S. degiulii* was already present in some other island in the Gargano archipelago during this time slice. The possibility that this small *Stertomys* species is the direct

ancestor of *S. degiulii* cannot be excluded. However, the small-sized outliers from the younger Pirro 11A could suggest that a small *Stertomys* lineage was still present in another island at least till the populating phase

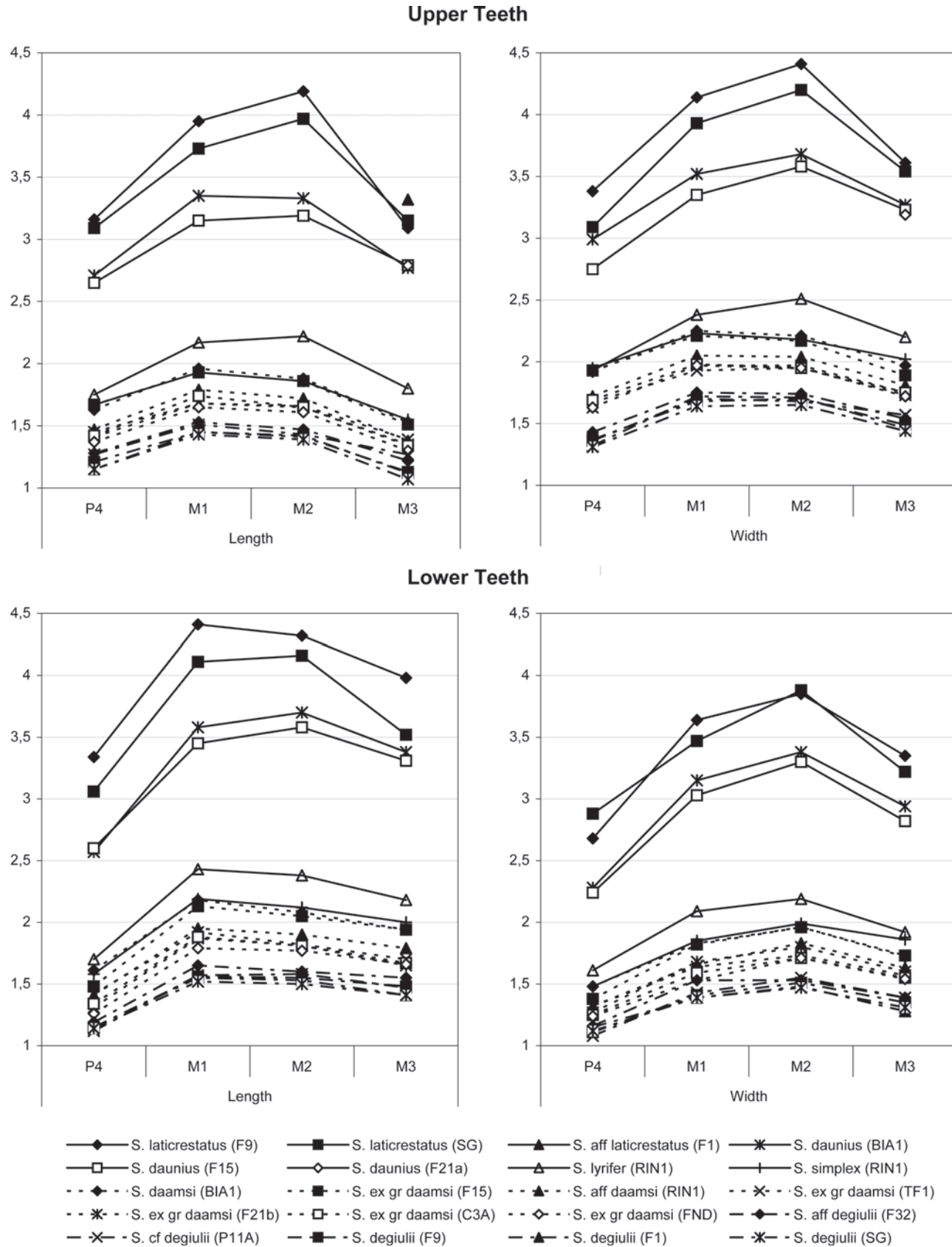


Fig. 18 - Length and width of upper and lower dental series of *Stertomys* species. Data from Tabs. 4-5, 8.

3. Following this line of interpretation, also the large-sized outliers might represent parallel lineages of *S. daamsi* in other islands of the archipelago.

Description of the large-sized Stertomys species

Large-sized species of *Stertomys* have a similar teeth outline as that observed in small-sized species. The occlusal pattern is very complex (Fig. 17) and characterised by the occurrence of eight or more crests (up to fourteen in some *S. daunius* molars). The pattern of connections between crests is simpler than that observed in the small-sized *Stertomys* species. The number of roots differs from the small-size species only in M_1 : the *S. daunius* specimens have two roots of which the anterior one is split; in *S. laticrestatus*, however, almost 50% of specimens have two completely divided anterior roots.

The teeth rows differ from *S. daamsi* and *S. degiulii* in having smaller P^4 - P_4 , particularly in the lower row, reduced M^3 - M_3 and M^2 - M_2 that tend to be the longest molars of the rows (Fig. 18).

Stertomys daunius Freudenthal & Martín-Suárez, 2006

Locality - F15.

Age - Late Miocene-Early Pliocene.

Material - 43 teeth (see Tab. 2, for details) (Pl. 5, figs. 1-13).

Measurements - See Tab. 8.

Description and discussion - Teeth show a very complex morphology (Fig. 17a, b). Both upper and lower teeth have well-defined, long primary, secondary and accessory crests, usually isolated. A high variability occurs in size and position of the additional crests. Although this dormouse belongs to Myomiminae (Freudenthal & Martín-Suárez, 2006; Rinaldi, 2006), the metaloph tends to separate from the protoloph lingually. In the lower molars the centrolophid occupies almost the entire width of the tooth and it tends to be separated from the mesolophid at the metaconid, in contrast to what is observed in *S. lyriifer* from Rinascita 1 (Martín-Suárez & Freudenthal, 2007). Unlike the small-sized *Stertomys* species, the hypoconid is positioned at the labial edge, so the posterolophid completely surrounds the posterolabial edge of the tooth. This character is found in all large-sized *Stertomys*.

The morphology of the F15 large dormouse fits the description of *S. daunius* from the type-locality Biancone 1 (Freudenthal & Martín-Suárez, 2006). The F15 specimens fall within the size range of Biancone 1, the average values are, however, a bit smaller (Fig. 18, Tab. 8). A statistical comparison of length and width of the upper and lower teeth yielded only four significant differences (t-test: $p = 0.02$ for P^4 width, $p = 0.03$ for M^1 length, $p = 0.02$ for M^1 width, $p = 0.03$ for M_3 width). Such result should not be considered significant for a

taxonomical difference at the species level. Therefore this material can confidently be referred to *S. daunius*.

Locality - F21a.

Age - Late Miocene-Early Pliocene.

Material - One tooth (M^3) (Pl. 5, fig. 14).

Measurements - See Tab. 8.

Description and discussion - Metaloph joins the protoloph lingually. Anteroloph splits in two parts. A well-developed prototrope is present. Centrolophs do not connect to each other. Two small additional crests join the postcentroloph at the labial edge; a small mesostyl is present between these two crests. Trigon crests do not have connections among themselves or with other crests. The posterotrope is long. The posterior part of the tooth has a more rounded outline compared with what is observed in the other samples referred to *S. daunius*.

The size (Fig. 18, Tab. 8) and the morphology of this single tooth fit those observed both in F15 and Biancone 1 specimens.

Stertomys laticrestatus Daams & Freudenthal, 1985

Locality - F9.

Age - Late Miocene-Early Pliocene.

Material - 35 teeth (see Tab. 2, for details) (Pl. 5, figs. 15-27).

Measurements - See Tab. 8.

Description and discussion - Very large teeth with a complex morphology (Fig. 17c, d). Crests are low, wide and smooth; accessory crests are usually absent. In the lower molars the long, well-developed centrolophid tends to separate from the mesolophid at the mesoconid. Few specimens show the lyre-shape structure described by Martín-Suárez & Freudenthal (2007) in *S. lyriifer*. In the upper molars the metaloph does not converge to the protocone. This character, found also in some specimen of *S. daunius* and *S. lyriifer*, may be considered as a real autoapomorphy of *S. laticrestatus*. The material from F9 may be assigned to *S. laticrestatus* because the morphology is very similar to that of the sample from the type-locality San Giovannino (Daams & Freudenthal, 1985).

The specimens from F9 are larger than those from the type-locality (Tab. 8, Fig. 18). The teeth length in F9 and San Giovannino has been statistically analysed by t-test. The test yielded significant results in three of six analysis (M^2 : $p = 0.01$; M_1 : $p = 0.01$, M_3 : $p < 0.001$), while the result is not significant for P^4 ($p = 0.41$), M^1 ($p = 0.33$) and M_2 ($p = 0.08$). The analysis has not been performed on M^3 and P_4 , because these teeth are represented by single specimens in F9 sample. This result cannot be considered significant for taxonomical

			Length							Width						
			n	min	mean	max	sd	95% ci		n	min	mean	max	sd	95% ci	
D ⁴	<i>S. lyrifer</i>	<i>Rinascita 1</i>	1		1,22							1,35				
	<i>S. daunius</i>	<i>Biancone 1</i>	2	1,73	1,78	1,84	-			2	1,85	1,92	1,99	-		
P ⁴	<i>S. lyrifer</i>	<i>Rinascita 1</i>	28	1,61	1,75	1,95	0,08	1,72	1,78	29	1,81	1,93	2,07	0,08	1,90	1,96
	<i>S. daunius</i>	<i>Biancone 1</i>	4	2,65	2,71	2,78	0,06	2,65	2,77	4	2,90	2,99	3,15	0,11	2,88	3,10
		F15	4	2,51	2,65	2,85	0,14	2,51	2,79	4	2,65	2,75	2,88	0,11	2,64	2,86
	<i>S. laticrestatus</i>	F9	3	3,02	3,16	3,29	0,14	3,00	3,32	3	3,26	3,38	3,47	0,11	3,26	3,50
<i>San Giovannino</i>		8	2,99	3,10	3,24	0,09	3,04	3,16	8	3,00	3,17	3,35	0,12	3,09	3,25	
M ¹	<i>S. lyrifer</i>	<i>Rinascita 1</i>	16	2,01	2,17	2,36	0,09	2,13	2,21	16	2,24	2,38	2,58	0,10	2,33	2,43
	<i>S. daunius</i>	<i>Biancone 1</i>	9	3,20	3,35	3,53	0,10	3,28	3,42	9	3,33	3,52	3,68	0,06	3,48	3,56
		F15	3	2,98	3,15	3,32	0,17	2,96	3,34	3	3,29	3,35	3,40	0,10	3,24	3,46
	<i>S. laticrestatus</i>	F9	6	3,79	3,95	4,10	0,11	3,86	4,04	5	3,97	4,14	4,25	0,11	4,04	4,24
<i>San Giovannino</i>		10	3,85	3,91	3,99	0,05	3,88	3,94	10	3,89	4,15	4,34	0,13	4,07	4,23	
M ²	<i>S. lyrifer</i>	<i>Rinascita 1</i>	17	2,13	2,22	2,36	0,07	2,19	2,25	16	2,39	2,51	2,68	0,09	2,47	2,55
	<i>S. daunius</i>	<i>Biancone 1</i>	8	3,12	3,33	3,56	0,14	3,23	3,43	8	3,43	3,68	3,81	0,11	3,60	3,76
		F15	5	3,16	3,19	3,24	0,04	3,15	3,23	5	3,55	3,58	3,60	0,02	3,56	3,60
	<i>S. laticrestatus</i>	F9	6	3,86	4,19	4,45	0,21	4,02	4,36	5	4,28	4,41	4,52	0,09	4,33	4,49
<i>San Giovannino</i>		11	3,88	3,97	4,18	0,11	3,90	4,04	11	3,92	4,23	4,36	0,14	4,15	4,31	
M ³	<i>S. lyrifer</i>	<i>Rinascita 1</i>	31	1,50	1,80	1,97	0,10	1,76	1,84	31	1,96	2,20	2,39	0,10	2,16	2,24
	<i>S. daunius</i>	<i>Biancone 1</i>	10	2,64	2,77	2,98	0,12	2,70	2,84	10	3,15	3,27	3,46	0,10	3,21	3,33
		F15	5	2,65	2,79	2,98	0,13	2,68	2,90	6	3,16	3,23	3,37	0,07	3,17	3,29
		F21a	1		2,79					1		3,19				
	<i>S. laticrestatus</i>	F9	1		3,09					1		3,61				
		<i>San Giovannino</i>	7	3,03	3,24	3,35	0,11	3,16	3,32	7	3,32	3,71	3,93	0,20	3,56	3,86
D ₄	<i>S. aff. laticrestatus</i>	F1	1		3,32					0		-				
	<i>S. lyrifer</i>	<i>Rinascita 1</i>	3	1,18	1,28	1,34	-			3	0,76	0,91	1,07	-		
P ₄	<i>S. daunius</i>	<i>Biancone 1</i>	4	1,60	1,72	1,91	0,14	1,58	1,86	4	1,36	1,43	1,51	0,06	1,37	1,49
	<i>S. lyrifer</i>	<i>Rinascita 1</i>	23	1,48	1,70	1,85	0,09	1,66	1,74	23	1,43	1,61	1,76	0,08	1,58	1,64
		<i>Biancone 1</i>	8	2,37	2,57	2,74	0,14	2,47	2,67	7	1,99	2,28	2,4	0,14	2,18	2,38
	<i>S. daunius</i>	F15	2	2,56	2,60	2,65	0,06	2,52	2,68	2	2,22	2,24	2,26	0,03	2,20	2,28
<i>S. laticrestatus</i>		F9	1		3,34					1		2,68				
	<i>San Giovannino</i>	2	2,86	3,07	3,27	0,29	2,67	3,47	2	2,75	2,88	3,00	0,18	2,63	3,13	
M ₁	<i>S. lyrifer</i>	<i>Rinascita 1</i>	23	2,14	2,43	2,60	0,10	2,39	2,47	23	1,95	2,09	2,27	0,08	2,06	2,12
	<i>S. daunius</i>	<i>Biancone 1</i>	8	3,33	3,58	3,85	0,17	3,46	3,70	6	2,90	3,15	3,27	0,13	3,05	3,25
		F15	4	3,29	3,45	3,61	0,15	3,30	3,60	4	2,92	3,03	3,21	0,13	2,90	3,16
	<i>S. laticrestatus</i>	F9	5	4,26	4,41	4,53	0,13	4,30	4,52	5	3,42	3,64	3,8	0,14	3,52	3,76
<i>San Giovannino</i>		6	3,82	4,11	4,33	0,18	3,97	4,25	5	3,20	3,47	3,71	0,18	3,31	3,63	
M ₂	<i>S. lyrifer</i>	<i>Rinascita 1</i>	28	2,24	2,38	2,58	0,09	2,35	2,41	28	2,01	2,19	2,40	0,10	2,15	2,23
	<i>S. daunius</i>	<i>Biancone 1</i>	8	3,52	3,70	3,81	0,09	3,64	3,76	9	3,18	3,38	3,54	0,11	3,31	3,45
		F15	8	3,4	3,58	3,72	0,14	3,48	3,68	8	3,14	3,30	3,53	0,13	3,21	3,39
	<i>S. laticrestatus</i>	F9	8	4,11	4,32	4,71	0,21	4,17	4,47	8	3,65	3,85	4,05	0,16	3,74	3,96
<i>San Giovannino</i>		10	3,78	4,17	4,27	0,14	4,08	4,26	9	3,47	3,88	4,19	0,19	3,76	4,00	
M ₃	<i>S. lyrifer</i>	<i>Rinascita 1</i>	29	1,93	2,18	2,43	0,11	2,14	2,22	29	1,72	1,92	2,09	0,09	1,89	1,95
	<i>S. daunius</i>	<i>Biancone 1</i>	6	3,15	3,38	3,66	0,18	3,24	3,52	6	2,81	2,94	3,10	0,10	2,86	3,02
		F15	7	3,16	3,31	3,44	0,10	3,24	3,38	7	2,74	2,82	2,93	0,07	2,77	2,87
	<i>S. laticrestatus</i>	F9	6	3,79	3,98	4,2	0,15	3,86	4,10	5	3,16	3,35	3,46	0,12	3,24	3,46
		<i>San Giovannino</i>	5	3,32	3,52	3,71	0,14	3,40	3,64	4	2,96	3,22	3,42	0,20	3,02	3,42

Tab. 8 - Measurements and descriptive statistical parameters of the large-sized *Stertomys* teeth. Data from Biancone 1 and Rinascita 1, according to Freudenthal & Martín-Suárez (2006), Martín-Suárez & Freudenthal (2007) respectively. Parameters of San Giovannino are computed on the original analytic data of Daams & Freudenthal (1985), kindly provided by Freudenthal. Abbreviations: n: number of specimens; min: minimum value; max: maximum value; sd: standard deviation, 95% ci: 95% confidence interval. Measurements are in millimetres.

purposes, but likely reflects a trend of size reduction from the older F9 to the younger San Giovannino population.

Stertomys laticrestatus is actually the largest Gliridae so far described in the extant and fossil record, excepted for the giant M₃ found in Baccinello V1 described by Engesser (1983).

Stertomys aff. *laticrestatus* Daams & Freudenthal, 1985

Locality - F1.

Age - Late Miocene-Early Pliocene.

Material - One tooth (M³) (Pl. 5, fig. 28).

Measurements - See Tab. 8.

Description and discussion - This M³ lacks the lingual part and the posterolabial corner. It presents a total of eleven crests. A short anterotrope occurs in the lingual part of the anterior valley. The anteroloph does not reach the paracone. A long prototrope is weakly connected labially to the postcentroloph. The precentroloph is clearly shorter than the prototrope; the postcentroloph and the metatrope tend to connect the prototrope labially. A small centrotrope is present; the metatrope is long. An additional crest occurs between the metatrope and the metaloph. In the posterior valley an isolated posterotrope occurs.

This specimen slightly exceeds the size of the single M³ from F9 but falls within the upper range of the size distribution of the type-locality San Giovannino (Daams & Freudenthal, 1985) (Tab. 8, Fig 18). It presents a more complex pattern than M³ from F9 and San Giovannino; however, the disposition of the crests and their low and wide aspect strongly suggests a close

Biochronological phases*				1					2		3			4
Fissure		BIA1	RIN1	F15	TF1	F21a	F21b	C3A	FND	F1	F9	SG	P11A	F32
Small-sized group	<i>S. daamsi</i>	Θ	aff						○					
	<i>S. gr. daamsi</i>			○	○	○	○	○		○				
	<i>S. degiulii</i>										Θ	○	cf	aff
	<i>S. simplex</i>	Θ												
Large-sized group	<i>S. lyrifer</i>	Θ	Θ		-			-	-				-	
	<i>S. daunius</i>	Θ		○		○			-	-			-	
	<i>S. laticrestatus</i>				-			-	-	aff	○	Θ	-	

Tab. 9 - Distribution of *Stertomys* taxa within the chronological sequence of fissure. RIN1 (Rinascita 1): Martín-Suárez & Freudenthal, 2007; BIA1 (Biancone 1): Freudenthal & Martín-Suárez, 2006; SG (San Giovannino): Daams & Freudenthal, 1985 and this paper; other samples: this paper. The sign “Θ” indicates the type-locality of each species. The sign “-” indicate fissures in which large-sized species have been not examined. *: *sensu* Masini et al. (2008).

relation with *S. laticrestatus*. Therefore this specimen is provisionally assigned to *S. aff. laticrestatus*.

DISCUSSION

Taxonomical remarks

Six species of *Stertomys* are now known from the Gargano assemblages: five previously described (Daams & Freudenthal, 1985; Freudenthal & Martín-Suárez, 2006; Martín-Suárez & Freudenthal, 2007) and a new species described in this contribution (Tab. 9, Fig. 19). Two species are large-sized with a complicated dental pattern, while three are small-sized with a simpler dental pattern. *Stertomys lyrifer*, even though has a slightly larger size respect to simple group, may be considered as belonging to the large-sized, complicated group for the complexity of its dental pattern (see also Martín-Suárez & Freudenthal, 2007).

Fig. 19 reports an outline of the results of the present work. This scheme shows size changes of the *Stertomys* taxa along the biochronological succession and the possible phylogenetic lineages. The M_1 length has been used as a rough proxy for the size variation. The outliers are also reported to give a more complete picture. For the samples in which the M_1 is absent, the size of a “virtual” M_1 has been estimated with a regression method based on the length of the available specimens (see the caption of Fig. 19 for further details).

Among the large-sized group of species, in the eleven fissure fillings here examined, *Stertomys daunius*, described by Freudenthal & Martín-Suárez (2006) from the fissure Biancone 1, has been recognised in the fissures F15 and F21a. The specimens from Biancone 1 are slightly larger than those from F15 (Figs. 18-19, Tab. 8). This might suggest the occurrence of a trend towards size reduction from the older Biancone 1 to the younger F15. *Stertomys laticrestatus*, occurring in San Giovannino (Daams & Freudenthal, 1985; Florence collection, undescribed), has also been identified in fissure F9, where it is represented by a population of slightly larger size (Figs. 18-19, Tab. 8). The statistical significance of the size difference again suggests a trend

toward size reduction from F9 to San Giovannino. In F1 a specimen identified as *S. aff. laticrestatus* occurs. *Stertomys lyrifer* is absent in all the fissure fillings here examined, even in the oldest ones, thus confirming the rarity of this species whose occurrence is limited to Rinascita 1. The results of the present study confirm what observed by Martín-Suárez & Freudenthal (2007) regarding the difficulty of arranging the three large-sized, complicated *Stertomys* species within a single progressive evolutionary lineage. *Stertomys daunius*, notwithstanding its older age, has a more complex pattern than the other two species, but it is closer to *S. lyrifer* by the lower frequency of the connection between the protoloph and metaloph in the upper molars, and in the aspect of the crests that are not low and wide as in *S. laticrestatus*. However, the occurrence of *S. daunius* in fissures considered both older and younger than Rinascita 1 shows that *S. lyrifer* and *S. daunius* belong to independent lineages. The new material shows the occurrence of size variations within *S. daunius* and *S. laticrestatus*, but does not give further morphological evidences to support the hypothesis of a direct ancestry of *S. daunius* with respect to *S. laticrestatus*. A solution to this question might be found in samples belonging to the second phase of population of the Gargano area. A clue towards a possible solution is the single specimen from fissure F1. This upper third molar is characterised by a size comparable to *S. laticrestatus*, but a morphology that is more complex than the latter species and simpler than *S. daunius*. It may be interpreted as a representative of a transitional form between *S. daunius* and *S. laticrestatus*, or, more likely, as a distinct species close to the direct ancestor of *S. laticrestatus*.

The study of the small-sized *Stertomys* yielded more significant results. A rather complex taxonomic situation can be observed in the older samples belonging to the population phase 1 (Tab. 9, Fig. 19). The most ancient small-sized species is *Stertomys daamsi* from Biancone 1. This taxon also occurs in Rinascita 1 with a smaller-sized form, *S. aff. daamsi*, together with the closely related species *Stertomys simplex*. The latter species has not been found in any of the oldest samples here examined, confirming that it is rare and apparently limited to Rinascita 1 (Tab. 9). This taxon seems to be the less derived *Stertomys* of all “Terre Rosse” samples. Within the new examined material, fissure F15 yielded a *Stertomys* with morphology and size very close to *S. daamsi* from the type-locality Biancone 1. The study of M^1 and M^2 morphotypes and size of these three samples shows that *S. daamsi* from Biancone 1 and *S. aff. daamsi* from Rinascita 1, notwithstanding the difference in size, are statistically undistinguishable on the basis of morphotype frequency. On the other hand, F15 differs significantly from Biancone 1, having a lower frequency of the primitive Daams’ morphotype B, though both dormice have the same size. Thus, on a morphological basis, Biancone 1 and Rinascita 1 can be considered closer to each other than to F15. *Stertomys* from Trefossi 1, F21b, Cantatore 3A and Fina D have a quite homogeneous size, distinctly smaller than those from Biancone 1 and F15. The morphology, though not statistically analysed because of the low number of

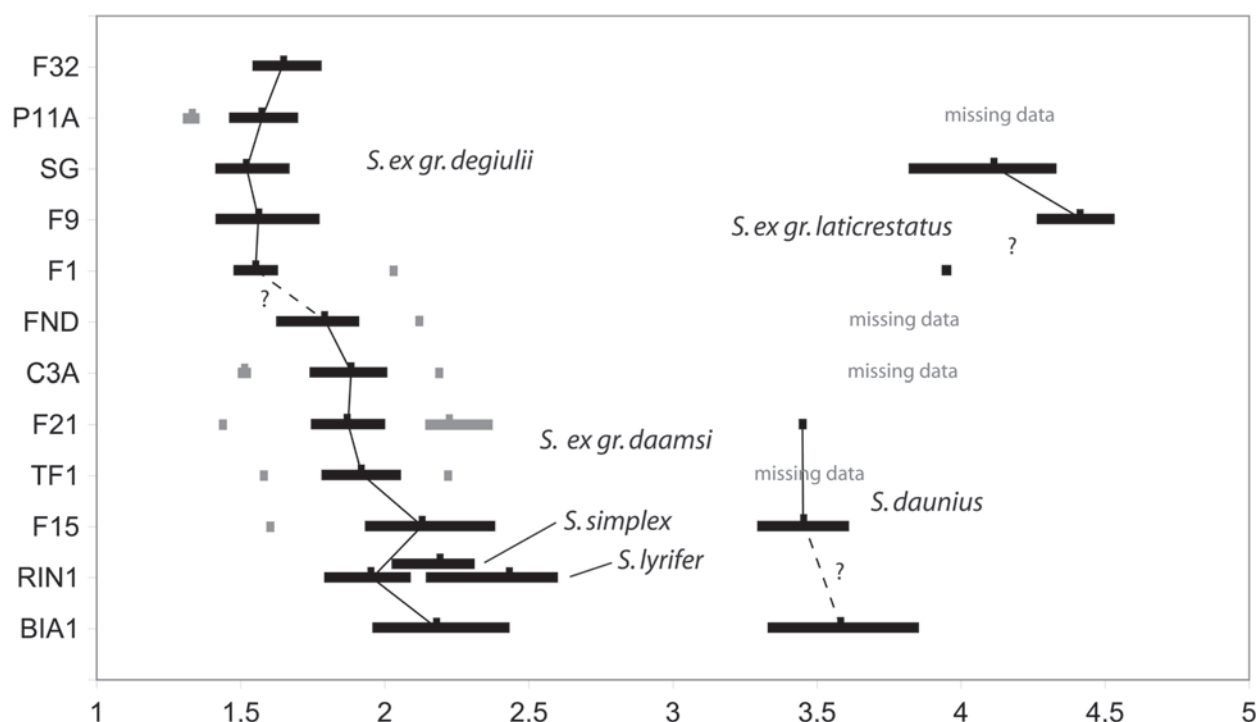


Fig. 19 - Plot of M_1 length of *Stertomys* taxa in the biochronological sequence. Detailed taxonomy is in the text and synthesised in Tab. 9. Measurements (in mm) are from Tabs. 5 and 8. The length of the horizontal bars represents the size range; the dot corresponds to the mean value. Grey lines indicate the outliers occurring in each sample. "Missing data" indicates samples for which the occurrence of large-sized species has not been checked. The thin lines joining the samples represent phyletic lineages as discussed in the text. Tooth length of *S. daunius* from F21a, of *S. aff. laticrestatus* from F1, and of all the outliers, except but three M_1 (RGM436025 from TF1, F21b-34 from F21b, F1-2.20 from F1), has been inferred using linear regression method based on the length of the specimen(s) available in each case. First, considering all the available populations, the mean length of M_1 vs. that of the other tooth elements (M^1 , M_2 , etc) have been plotted, in order to estimate the relationship between the size of the couples of teeth. Then, a linear regression has been computed. In all the cases the very strong linear relationship between the lengths of the couples of teeth is confirmed by a high value of R^2 ranging from 0.975 to 0.99. The lengths of the "virtual" M_1 s have been computed inserting in the regression equation the value of the element occurring in the considered sample. The confidence interval of the regression coefficients has been also computed but not reported since the inferred values are used only for a qualitative evaluation on the plot.

specimens, is somewhat variable, but the low frequency of Daams' morphotype B suggests that those populations are closer to F15 than to Biancone 1 and Rinascita 1. All the examined *Stertomys* samples, including F15, have been identified as *S. ex gr. daamsi*. These results suggest that *S. daamsi* underwent some evolutionary modification and all these taxa might represent a single phyletic lineage (Fig. 19). An ecological explanation of the reduction in size of *S. aff. daamsi* from Rinascita 1 has been discussed in the previous section.

The small dormice from F1, F9, San Giovannino, Pirro 11A and F32 are distinct from *S. gr. daamsi* by their smaller size (Figs. 15, 19) and by the higher frequency of the connection between the trigon crests and the metaloph in M^1 and M^2 (Rinaldi's morphotype B; Fig. 12). A further subtle difference regards the distribution of the Daams' morphotypes in the same teeth, i.e. the higher frequency of morphotype D and the rarity or absence of morphotypes B, E and F (Fig. 13). Those differences suggest that these populations should be considered as a taxon different from *S. gr. daamsi*. The F9 population, that is the most numerous and homogeneous, is the most suitable for the

description of the new species *Stertomys degiulii*. Among the other samples, F1 and San Giovannino can be referred to the same species. The dormouse from F32, which is the youngest sample of the whole succession, has been identified as *S. aff. degiulii* because it differs from the type-population by a slightly larger size, by the relatively wider M_1 and by the higher frequency of connection between the anterolophid and the protoconid in M_1 and M_2 (Rinaldi's morphotype C, Fig. 14). The latter character is shared with the glirid from Pirro 11A, here referred to *S. cf. degiulii*, which appears to have intermediate features between San Giovannino and F32. By and large, the dormice samples belonging to *S. degiulii* are quite homogeneous; the most recent samples F32 and Pirro 11A, however, present some differences that might be suitable for a taxonomical distinction.

A limited number of specimens have been identified as outliers. These specimens fall within the morphological range of *S. daamsi* and/or *S. degiulii* and they are distinguishable in two size group that roughly correspond to the same *S. gr. daamsi* and *S. degiulii* (see the paragraph "Description of the outliers of the small-sized *Stertomys* species", Tab. 3, and Fig.

19). We might suggest that those outliers represent parallel evolutionary lineages evolved in some neighbouring island of the palaeoarchipelago.

Biochronological remarks

The taxonomical results agree on a large scale with the biochronological framework adopted in the paragraph "Biochronological framework". The species related to *S. daamsi* occur in the older fissure fillings, where they are usually associated with *S. daunius*, while those related to *S. degiulii* are found in the younger fillings, usually associated with *S. laticrestatus* (Tab. 9). However, the details of the results allow, on the one hand, to refine the chronology of the populating events, but on the other hand they require some revision of the adopted chronology and cause some further problems. The discussion of the populating phases of the Gargano fauna integrated with the data on *Stertomys* follows.

Phase 1 - Several problems arose concerning the relative position of the oldest fissure fillings, particularly Rinascita 1. In fact, this fissure is different from the supposedly older Biancone 1 and the younger F15 in several aspects. (1) *S. daunius*, which occurs in Biancone 1 and F15, is absent in Rinascita 1 where it is replaced by *S. lyrifer*, a morphologically complex, but much smaller species, whose occurrence is limited to Rinascita 1 itself (Tab. 9). (2) *S. simplex*, the morphologically simplest small-sized species, very close in size to *S. daamsi*, occurs only in Rinascita 1 (Tab. 9). (3) *S. aff. daamsi* from Rinascita 1 is smaller in size with respect to the related taxon in Biancone 1 and F15 (Fig. 15). Placing Biancone 1 as the oldest sample and Rinascita 1 as older than F15 implies several bioevents to have occurred: the local extinction and reimmigration of *S. daunius*; the dispersal and extinction of *S. lyrifer* and *S. simplex*; the reduction and the increase in size of *S. gr. daamsi*. Applying the principle of parsimony to the glirid assemblage, the position of Rinascita 1 as the oldest fissure would have been more suitable, since it would imply a lesser number of bioevents. In such a case, *S. lyrifer* and *S. simplex* could be assumed as resident taxa that became extinct in Biancone 1; *S. daunius* would have dispersed only once on the island in Biancone 1 and the size of the *S. daamsi* lineage would have increased once passing from Rinascita 1 to Biancone 1. The occurrence in Rinascita 1 of the simplest *Stertomys* species, closer to the supposed continental ancestor, would also sustain the hypothesis that this fissure is the oldest. Unfortunately, such hypothesis conflicts with the information derived from *Mikrotia*, exhaustively discussed by Freudenthal (1976). A detailed analysis of some further taxa from Rinascita 1, Biancone 1 and F15 (i.e. *Galerix*, *Apodemus*, *Prolagus*, etc.) could help in resolving this tangle. The results of the present work can therefore not be considered as conclusive for this question and the biochronological position of Rinascita 1 proposed by Freudenthal (1976) is provisionally maintained.

The characteristics of *Stertomys* from the other samples belonging to this phase (Trefossi 1, F21b and Cantatore 3A) do not contradict the assumed chronology. *Stertomys ex gr. daamsi* from these samples represents a fairly homogeneous group characterised by a smaller size with respect to Biancone 1 and F15

(Figs. 15, 19). The position of Trefossi 1 is, however, affected by some uncertainties. The specimens from this sample are smaller than those from Rinascita 1 and much smaller than those from F15; however, in Trefossi 1 *S. simplex* does not occur and *S. ex gr. daamsi* seems to be morphologically as derived as in F15. Considering these observations, Trefossi 1 could be regarded as younger than Rinascita 1 and close in age to F15. However, the size of *S. ex gr. daamsi* from Trefossi 1 is comparable with the younger samples F21b, Cantatore 3A and Fina D, and therefore a position younger than F15 is more likely.

Phase 2 - In the two samples referred to this phase two different species of small-sized *Stertomys* occur: *S. ex gr. daamsi* in Fina D and *S. degiulii* in F1. This phase appears, therefore, to be transitional for what regards the glirids. Unfortunately the large-sized *Stertomys* species are here poorly defined. The occurrence of large-sized *Stertomys* in Fina D has not been checked, and the single specimen in F1 is distinct from *S. daunius* and *S. laticrestatus*, and more related to the latter species. Considering F1 as belonging to the following phase, as suggested by the occurrence of *S. degiulii*, it is, however, not consistent with the occurrence of a single *Mikrotia* species instead of the three species usually found in the other samples containing *S. degiulii*. Moreover, the occurrence of *S. aff. laticrestatus* confirms that F1 represents a different phase with respect to phase 3. The occurrence of *S. ex gr. daamsi* in Fina D is an evidence that the latter fissure is older than F1 and it also suggests that Fina D could even be considered the youngest sample of the previous phase 1.

Phase 3 - This phase is well characterised by the occurrence of *S. degiulii* and *S. laticrestatus*. The characteristics of *S. cf. degiulii* from Pirro 11A bring some new data on the position of this fissure. This *Stertomys* is significantly different from *S. degiulii* type-population and it is closer to *S. aff. degiulii* from the fissure F32, the latter belonging to the younger phase 4. The morphological analysis suggests that Pirro 11A should be considered younger than San Giovannino, contrarily to what previously assumed in this paper. Indeed, Freudenthal (1976) already suggested for Pirro 11A an age very close to San Giovannino, perhaps younger.

Phase 4 - This phase is documented only by the sample from the fissure F32 and it is characterised by the absence of *S. laticrestatus* and by the occurrence of *S. aff. degiulii*. This *Stertomys* is fairly different from the type-population of *S. degiulii*, in particular for the features discussed yet for Pirro 11A (see "Taxonomic remarks" above in this paragraph). *Stertomys aff. degiulii* is a bit larger in size than the populations of the previous phase. These differences are a further confirmation that phase 4 is clearly distinct from the previous one. The strict relationship of *S. aff. degiulii* with the population from Pirro 11A suggests a possible phyletic evolution, and it further confirms the younger age of sample F32 with respect to those belonging to the phase 3.

The Myomiminae assemblage confirms phase 1 as the most intensively affected by extinctions and dispersals, likely due to interchanges among islands and possibly with

the mainland. The presence of several outliers among glirids reinforces this interpretation. On the basis of the observations on the glirid assemblage, phase 1 might be divided in two different parts. The number of species of *Stertomys* found in the early part (Biancone 1, Rinascita 1 and F15) is fairly high (four species, three of which coexisted in Rinascita 1). The second part, including Trefossi 1, F21b and Cantatore 3A, is characterised by the occurrence of two species only, a rare large-sized one and a smaller one, with fairly stable size. A fairly analogous range of distribution of species is observed for *Mikrotia* (Freudenthal, 1976; De Giuli et al., 1987a), while *Prolagus* is apparently represented by a single taxon (Mazza, 1987a, b). The cricetids (Freudenthal, 1985) support that phase 1 could be subdivided in two parts. Trefossi 1, however, would belong to the first part by the occurrence of *Cricetulodon* and *Hattomys beetsi*, found also in Biancone 1 and Rinascita 1, while in Cantatore 3A a different species of *Hattomys* occurs, *H. nazarii*.

Phase 2 was defined by the presence of a single *Mikrotia* species with a derived morphology (De Giuli et al., 1987a). In the fissure here considered as the oldest of this phase (Fina D) (see the paragraph “The adopted biochronological framework”), *S. ex gr. daamsi* occurs, while in the other sample (F1) the first occurrence of *S. degiulii* and *S. aff. laticrestatus* renews the Myomiminae assemblage. These occurrences seem to precede the dispersal of the small and large-sized *Mikrotia* species that are found in phase 3. Fina D is close to Cantatore 3A because of the occurrence of *H. nazarii* and of *S. ex gr. daamsi*.

Phase 3 seems to be the most stable phase for what concerns the composition of the small mammal assemblage. Nevertheless, several taxa present phyletic evolutionary trends that allow to define a detailed succession of samples within this phase. *Stertomys* still occurs with two species: *S. degiulii* and *S. laticrestatus*. *Prolagus* is also affected by a trend. This lagomorph is present with two taxa in San Giovannino. This is the only new occurrence in this phase, at least for the small mammal assemblages. However, it is difficult to state if it is an *in situ* speciation or a dispersal from some neighbouring island. Unlike what was observed for *Mikrotia* and *Prolagus* (Freudenthal, 1976; De Giuli et al., 1987a; Mazza, 1987a, b), the morphology of *S. degiulii* seems to be more stable. In the sample that we consider as the most recent one of this phase, Pirro 11A, *S. cf. degiulii*, however, presents some derived features. According to Freudenthal (1985), in the samples with three *Mikrotia*, the cricetid assemblage is characterised by the occurrence of *Hattomys nazarii-gargantua* in the oldest fissures, followed by the occurrence of *Hattomys gargantua*. The cricetids, however, disappear in the late part of the phase (namely San Giovannino and Pirro 11A). On the other hand, De Giuli et al. (1987a, 1990) report the occurrence of *Hattomys* sp. also in San Giovannino. A careful re-examination of the latter sample in the Florence collection would be helpful in solving this contradiction.

The absence of a large-sized *Stertomys* and the derived morphology of *S. aff. degiulii* confirm that phase 4 is clearly distinct from the previous one.

Stertomys aff. *degiulii* seems to derive from *S. degiulii* through *S. cf. degiulii* from Pirro 11A. In F32, *Stertomys*, like all the other surviving small mammal taxa, is characterised by a slightly larger size than in the older fissures (De Giuli et al., 1987a, 1990). This phase is characterised by a marked drop in faunal diversity due to the disappearance of largest-sized “small mammal” taxa (*Mikrotia magna*, *Mikrotia* sp. resident lineage, *S. laticrestatus*). This might suggest that an environmental deterioration occurred.

The above mentioned considerations evidence that the changes in the Myomiminae assemblages do not correspond precisely to those observed for *Mikrotia*, *Prolagus*, and cricetids. Each clade is characterised by a different rate of evolution and of dispersal. It is reasonable to assume that these small mammals have different ecology and therefore a different response to the environmental changes in the palaeoarchipelago is expected for each clade.

The age of the colonization events of the ancestors of the “Terre Rosse” taxa is widely debated and cannot be exhaustively discussed in this contribution. By and large, there are two different positions on this topic (see also de Vos et al., 2007). The first one envisages that the forerunners of the elements of the “*Mikrotia* fauna” entered the insular domain during the Messinian, possibly with a single event of colonization (Freudenthal, 1976, 1985; Freudenthal & Martín-Suárez, 2008). The second approach foreshadows that the colonization of the archipelago is polyphasic, i.e. it is the result of different biogeographic mechanisms, vicariant or dispersive, that acted during time slices of widely different ages, from the Early Miocene to the Early Pliocene (De Giuli et al., 1986b, 1987c; Masini et al., 2002b, 2008; Mazza & Rustioni, 2008).

For what regards *Stertomys*, an ancestor could be traced in the *Peridyromys-Myomimus* lineage that represents the main branch of the Myomiminae diversification. Freudenthal & Martín-Suárez (2006) propose that the ancestor is traceable in some Messinian *Myomimus* species, e.g. *Myomimus dehmi* (MN9-13) or *Myomimus maritsensis* (MN13). Rinaldi (2006) listed a number of possible ancestors for the Gargano Myomiminae including the same *M. dehmi* and the older *Peridyromys lavocati* (Paşalar, Turkey, MN6) or *Myomimus* nov. sp. (Çandır, Turkey, MN6; de Bruijn et al., 2003). We feel that this question might be positively answered when further data will be available on the *Peridyromys-Myomimus* distribution in the Miocene.

Evolutionary remarks

The quality and quantity of evolutionary differentiation that affected the hypothetical common ancestor of *Stertomys* after the entrance in the insular domain is noteworthy. Even though the phyletic relationships among the six species so far described are not exhaustively reconstructed, if we accept the origin of *Stertomys* from a single forerunner (Freudenthal & Martín-Suárez, 2006), it is evident that the endemic evolutionary processes produced an adaptive radiation and some marked morphological changes, with the appearance of new characters and strong increases in size. This evolutionary process

seems to have produced two branches (Tab. 9, Fig. 19): the first one acquired more complex morphologies and very large size, while the second one remained simple, or acquired moderately complex morphologies, and a moderately larger size respect to the hypothetical ancestor.

Stertomyss daamsi, *S. simplex*, and *S. degiulii* belong to the latter group. These three species, however, cannot be arranged in a single lineage (Fig. 19). In fact, *S. simplex*, the less derived, i.e. morphologically simplest, species occurs together with *S. aff. daamsi* in Rinascita 1. *Stertomyss simplex* may be considered by its morphology as the species closer to the hypothetical common ancestor of the genus. A larger amount of data, most of which are original in this paper, is available for *S. daamsi* and *S. degiulii*. The former is distributed in the older samples, while the latter occurs in the younger ones. Even the oldest representative of *S. daamsi* has acquired more complex morphologies in comparison with *S. simplex*. *Stertomyss daamsi* and *S. degiulii* likely represent two segments of the same evolutionary lineage (Fig. 19). This interpretation is, however, affected by some uncertainties due to the occurrence of some finds, here mentioned as outliers, with a very similar size and morphology that could represent further lineages evolved in neighbouring islands (see "Description of the outliers of the small-sized *Stertomyss* species" and Fig. 19). Such lineages may have dispersed to the Apricena-Poggio Imperiale island, giving rise to *S. degiulii*. However, the rarity of the occurrence of these outliers that are always found together with a more numerous resident population renders the hypothesis of an *in situ* phyletic evolution more likely. *Stertomyss* gr. *daamsi* and *S. gr. degiulii* are close morphologically and remain rather stable, while their size underwent several changes, as already outlined by De Giuli et al. (1987a) (Figs. 15, 19). If we accept the hypothesis of a single phyletic lineage connecting *S. daamsi* from Biancone 1 to *S. aff. degiulii* from F32, we observe that the size of the molars underwent a marked reduction. Within the *S. gr. daamsi* segment the older samples are the largest of the group, although a fluctuation in size can be observed in Rinascita 1, likely due to the effects of the ecological interaction with *S. simplex* (see "Taxonomical descriptions" in paragraph "Description of small-sized *Stertomyss* species"). A first drop in size occurs in the younger populations of the *S. gr. daamsi* segment, while the most marked size reduction separates the populations belonging to *S. degiulii* from those belonging to *S. daamsi*. On the other hand, the morphological phyletic evolution along this lineage is moderate and regards only changes in frequencies of the same morphotypes.

The size decrease emerged from this reconstruction requires further discussion, since it apparently contradicts the assumption that small mammals tend always to achieve giant size on islands: the so called "island rule". Recently, this rule has been critically revised by the studies of the size variation patterns in taxa from extant archipelagos by Lomolino (2005). The latter author evidences that such patterns are conditioned by the influence of island characteristics (area and geographical isolation) on different selective forces,

such as barriers to immigrations, resource availability and interactions among and within species. It can be assessed that the body-size of particular species and size variation within single species are responses controlled by the changing states of the ecosystem. In this perspective the size variation observed in *S. daamsi-degiulii* group is, therefore, not surprising, but this trend, however, is worth to be further investigated, particularly in its relationships to changes in biodiversity and body-size of the whole vertebrate assemblages occurring in the sequence of population phases. Up to date, only two papers were devoted to this topic by De Giuli & Torre (1984) who analysed the specific interrelationships among *Prolagus* and *Mikrotia* and by Millien & Jaeger (2001) who studied the variation of size of *Mikrotia* and related it to interspecific competition.

The group of large-sized *Stertomyss* species with complex morphology includes *S. lyrifer*, *S. daunius*, and *S. laticrestatus*. These species likely represent three distinct but strictly related lineages (Fig. 19). *Stertomyss lyrifer*, the smallest of these species, is restricted to a single fissure (Rinascita 1) belonging to the oldest population phase and might represent a species very close to the common ancestry with *S. daunius*. *Stertomyss laticrestatus*, occurring in the younger samples, has acquired the largest size, but its morphology is relatively simpler with respect to *S. daunius*, which occurs in the older phase. Therefore, it seems difficult to interpret *S. daunius* and *S. laticrestatus* as two segment of the same evolutionary lineage (Fig. 19). The low number of samples and specimens prevent to reconstruct the details of the possible phyletic changes within these two lineages. Apparently, however, a trend toward a slight reduction in size occurs independently within the two segments (Fig. 19). Unfortunately, these observations are based only on a couple of samples for each lineage and they would require more data in order to be confirmed. Some further issue regards the evolution of the dental pattern of *S. laticrestatus*. This dormouse is distinct from the other large-sized *Stertomyss* species, apart from the largest size and the slightly simpler morphology, in having low, wide, and smooth profile of the crests. One can speculate that the increase in the size of the teeth, most likely, requires a change in the dental morphology in order to maintain chewing efficiency. *Stertomyss* could have responded to this problem in two different ways. *Stertomyss daunius* maintained the narrow and high profile of the crests and increased the grinding surface complicating the dental pattern by adding accessory and additional crests. *Stertomyss laticrestatus*, instead, modified the profile of the crests turning them low, wide and smooth but maintaining a moderately complex pattern, adding only one crest with respect to the small-sized species. In such way, the low and wide crests would guarantee a wide abrasive enamel surface, without excessively complicating the dental pattern.

Eventually, an interesting evolutionary and taxonomic issue regards the changes in the pattern of connection between the metaloph and the protoleph on the lingual side of the upper molars. The occurrence of this

connection is considered as a key for the identification of the Myomiminae subfamily (Freudenthal & Martín-Suárez, 2006; Rinaldi, 2006). In *S. simplex*, *S. daamsi*, and *S. degiulii* this character is stable, but in the populations of *S. lyrifer* and *S. daunius* there are some specimens in which this connection is weak or absent. The latter condition is the only one present in *S. laticrestatus*. In the taxonomical practice the latter feature is considered as typical of Glirinae, the reason why Daams & Freudenthal (1985) classified *Stertomy*s within this subfamily. Therefore, this case shows that microevolutionary processes occurring in an insular domain can produce modifications in some characters that are considered as stable in the evolutionary history of glirids on the continent. The relatively easy switch from a Myomiminae to a Glirinae-like pattern, documented by the Gargano *Stertomy*s, invites the specialists to consider cautiously the dental pattern in the high rank taxonomy, as already suggested by Daams & de Bruijn (1995) and by Vianey-Liaud (2003).

The data produced in this contribution give ground to further evolutionary remarks. Comparing the evolutionary history outlined above, with those of *Prolagus* and particularly of *Mikrotia*, it appears that documented phyletic change in *Stertomy*s is limited mainly to size, while the morphology within the single species, or lineage segments, is rather stable. Most of the evolutionary divergence is observed between lineages, particularly in the differences between the two main branches of large and small-sized taxa, and among the large-sized species. Apparently this reconstruction evidences some gradualistic process, but, most of all, it matches the predictions of punctuated equilibria, i.e. the major evolutionary changes occur in correspondence of cladogenetic process (Eldredge & Gould, 1972, 1993). Apparently such cladogenetic processes did not occur in the Apricena-Poggio Imperiale island, or were not documented by the available set of samples.

CONCLUSIONS

One of the problems faced by the present contribution regards the integration of the biochronologies of the Gargano fissure fillings proposed by Freudenthal (1976) and De Giuli et al. (1987a). The elaboration of such an integrated chronology is necessary to compare the material of the dormice stored in the Leiden Museum and in the Florence Department. As a matter of fact this paper contains the first attempt to combine the two collections that have always been studied separately. The integrated biochronological framework here proposed is based on the scheme elaborated by De Giuli et al. (1987a) in which the fissures of the Leiden Museum are arranged. However, many difficulties have been encountered and only partially solved. Possibly, a careful analysis of the other mammals of the assemblages occurring in each fissure filling could help in solving some of the problems encountered during the work.

Notwithstanding the above-mentioned difficulties, this study permitted to enhance significantly the knowledge of the Myomiminae dormice from the

Gargano “Terre Rosse” fissure fillings, whose information was previously limited to the taxa occurring in two fissures (Biancone 1 and Rinascita 1) described by Freudenthal & Martín-Suárez (2006) and Martín-Suárez & Freudenthal (2007) and to *Stertomy*s *laticrestatus*, described from San Giovannino by Daams & Freudenthal (1985). In this contribution the material from eleven further fissure fillings has been examined and described. These fillings, together with Biancone 1 and Rinascita 1 that are considered as the oldest fissure fillings so far recovered, represent a consistent record of the populating history of the Gargano palaeoisland. In the present contribution seven taxa have been identified: *Stertomy*s *daunius*, *Stertomy*s *laticrestatus*, *S. aff. laticrestatus*, *Stertomy*s ex gr. *daamsi*, *Stertomy*s *degiulii* nov. sp., *S. cf. degiulii* and *S. aff. degiulii* (Tab. 9). Only two of the four species described in the oldest population phase by the quoted authors, *S. daamsi* and *S. daunius*, have been identified in the examined material, while *Stertomy*s *simplex* and *Stertomy*s *lyrifer* apparently are limited to Rinascita 1. The new species, *S. degiulii*, has been described in samples from more recent deposits, where it is associated with *S. laticrestatus*. *Stertomy*s aff. *degiulii*, a closely related form, occurs in the youngest fissure. The new material confirms the occurrence of two groups of *Stertomy*s (Martín-Suárez & Freudenthal, 2007): one is characterised by small size and simple to moderately complex morphology and the other is large-sized and morphologically moderately to very complex. The analytic study of the small-sized species suggests that *S. daamsi* and *S. degiulii* might belong to a single phyletic lineage, in which a marked reduction in size occurs along with moderate morphological change (Fig. 19).

The integration of data derived from *Stertomy*s in the biochronological framework results in a better definition of the populating phases of the Gargano palaeoisland, even though some details remain problematic particularly in the oldest phase. The major problem regards the biochronological position of Rinascita 1. As our results confirm, these difficulties may be due to the fact that during the oldest phase faunal exchanges among neighbouring islands frequently occurred rendering the reconstruction of the succession of the bioevents rather complex. On the other hand, the results show that in the most recent phases the faunal exchanges stopped and the faunal assemblage was stable, while minor phyletic changes occurred. Eventually, the last phase recorded some phyletic evolution and a marked drop in faunal diversity, due to extinction of the large-sized endemic micromammals, possibly related to environmental changes in the palaeoisland.

A preliminary reconstruction of the evolutionary history suggests that an early radiation occurred in the Myomiminae of the palaeoarchipelago, producing at least five lineages, three of which are found together in Rinascita 1. Those lineages are: *S. daamsi-degiulii*, *S. simplex*, *S. lyrifer*, *S. daunius*, and *S. laticrestatus* (Fig. 19). Even though their phyletic relationships are still not defined in detail, the lineages can be arranged in two main branches characterised by different size. Usually a large-sized and a small-sized species occur

together in the same sample, with the exception of the youngest fissure (F32), in which only the small-sized species occurs, and of the problematic fissure Rinascita 1, in which the three species are closer in size. Analogous radiation processes are documented for several other clades of mammals, such as *Mikrotia*, *Prolagus*, *Hoplitomeryx*, and *Deinogalerix* (see Masini et al., 2008 and references therein). These recurrent radiations render the endemic “Terre Rosse” fauna unique in the Mediterranean area and they make the Gargano case history of the utmost importance for evolutionary and biogeographical topics.

The present contribution does not pretend to be exhaustive but leaves the door open to some further study on the forerunner(s) of *Stertomys* and the age of its dispersal in the Gargano area.

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