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Original article

New data on the Cricetidae from the Miocene “Terre Rosse” of Gargano (Apulia, Italy)[☆]

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ARTICLE INFO

Article history:

Received 1 December 2011

Accepted 11 October 2012

Available online 10 January 2013

Keywords:

Late Miocene

Biochronology

Endemic mammals

Cricetidae

Southern Italy

ABSTRACT

The Gargano “Terre Rosse” deposits are paleokarst fissure fillings found in the Mesozoic limestone of the Apricena-Poggio Imperiale area. They are an important source of information for evolutionary and paleobiogeographic studies. The Late Miocene-Early Pliocene assemblages found in the Terre Rosse attest the complex history of endemic faunal distribution in a paleoarchipelago. Based on the cricetid samples from six distinct fissures (F15, F21a, F21b, F21c, F1, F9, NBS) stored in the Department of Earth Sciences of the University of Florence, three species of endemic cricetids are described: the small-sized *Hattomys beetsi*, the middle-sized *Hattomys nazarii*, and the large-sized *Hattomys gargantua*. The specimens from fissure F15 are attributed to *H. beetsi*, those from F21a-b to the transitional form *Hattomys beetsi-nazarii*, those belonging to NBS are ascribed to *H. nazarii*, whereas those from F1 and F9 are classified as *H. gargantua*. F21c is considered contaminated with material from different fissures. In line with previously published results, the analysis confirms that the endemic cricetids underwent a remarkable increase in size through time. The morphological variations show a marked trend towards increasing enamel thickness, but also the tendency of the cusps to assume a carved-in aspect. The variations of the morphological characters confirm that the three species likely belong to the same lineage.

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1. Introduction

The Gargano “Terre Rosse” consists of fossiliferous deposits that fill a network of karst fissures developed in the Mesozoic platform carbonate. The remains of endemic fauna retrieved from these deposits document events of settlement in an isolated land. They therefore represent a significant source of information for evolutionary and paleobiogeographic studies. Most of these fissure fillings crop out in an area of intense quarrying activities between Apricena and Poggio Imperiale. Together with the fauna recovered from Scontrone and Palena-Capo di Fiume (Abruzzo, central Italy), the Terre Rosse assemblages document the existence of the so-called Abruzzo-Apulian Paleobioprovince (Mazza and Rustioni, 1996, 2008; Rook et al., 2006).

The Terre Rosse fauna was discovered and sampled by Matthijs Freudenthal (Naturalis, Nationaal Natuurhistorisch Museum, Leiden, Netherlands) and his team during excavations carried out between 1969 and 1974 (Freudenthal, 1971). The Italian expeditions (Department of Earth Sciences of the University of

Florence) began in the late 1970's and continued during the 1980's (De Giuli and Torre, 1984).

The tetrapods assemblages yielded by the Terre Rosse deposits present many taxa with different degree of morphological modification derived from evolution in insular conditions. All the classes of vertebrates are represented (Masini et al., 2010): Amphibia, Reptilia (Delfino, 2002; Delfino et al., 2007), Aves (Ballman, 1973, 1976; Göhlich and Pavia, 2008), and Mammalia. The fauna, as often happens in insular settings, is highly unbalanced: it consists primarily of endemic small mammals and birds, some of which of gigantic size. The fauna draws its name from the extremely abundant and strongly endemic murid *Microtia*, later renamed *Mikrotia* by Freudenthal (2006).

The biochronology (sensu Lindsay, 1990) of the fissure fillings elaborated by Freudenthal (1976) is based on the evolutionary modifications of *Mikrotia*, but also on those of the giant endemic cricetid *Hattomys* (Freudenthal, 1985). De Giuli et al. (1987) also worked on *Mikrotia*, as well as on *Prolagus*. Until now, Freudenthal (1985) was the only one to deal with the endemic cricetids of Gargano. In this paper the results of a morphological and morphometric analysis of dental, maxillar and mandibular remains of Gargano cricetids are presented. The material is kept at the Department of Earth Sciences of the University of Florence. This study is aimed at comparing the results with those of

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Freudenthal (1985) for a more complete knowledge and understanding of the Gargano cricetids.

2. Biochronology of the fissure fillings

Because the karst fissures are not lithostratigraphically superposed, they need to be sequenced biochronologically. This can be obtained by reconstructing the morpho-evolutionary trends of the taxa that compose the Terre Rosse faunal assemblages.

Freudenthal (1976) was the first to propose a biochronology of the Terre Rosse fissures, based mainly on the evolutionary modifications of *Mikrotia* and on a preliminary study of the cricetids. In that paper, the author recognized the important increase in size of *Mikrotia* as well as the remarkable variation in teeth morphology, especially of the first lower and third upper molars. Teeth change primarily by increasing the number of crests and becoming more hypsodont. Assuming smaller and simpler species to be older than the larger and more complex ones and that size increased through time, Freudenthal (1976) ordered the fissures using the mean value of the length of the first lower molar of *Mikrotia* from each fissure as a guideline. He thus outlined three evolutionary lineages. The “medium size line of evolution” (lineage 2) is the only lineage present in all the fissures. Freudenthal used it as his major reference to reconstruct the relative chronological position of the samples. Lineage 1 includes a small-sized *Mikrotia*, whereas lineage 3 a very large-sized one. Over time, they grow increasingly smaller and larger, respectively. Lineage 1 and 3 are not present in the oldest fissures, where other primitive *Mikrotia* species accompany the *Mikrotia* of lineage 2, the main line of evolution.

De Giuli et al. (1987) presented the biochronological succession of eight of the richest fissures they had sampled. To build this scheme, alongside *Mikrotia* and *Prolagus*, they used also preliminary data on *Galerix*, *Myomiminae* and *Apodemus*. The rationale adopted by these authors was similar to that used by Freudenthal (1976), but with some important differences: in contrast with Freudenthal (1976), who analysed sub-samples of 20 specimens for each fissure (with the exception of Biancone 1 of which he studied 100 specimens), De Giuli et al. (1987) studied only a few, but very rich samples. Moreover, the latter authors put more emphasis on morphological modifications than on size changes.

Rinaldi and Masini (2009) were the first who tried to integrate the biochronological successions elaborated by Freudenthal (1976) and De Giuli et al. (1987). Fig. 1 shows the fissures ordering proposed by De Giuli et al. (1987), with the integration of some of the fissures studied by Freudenthal (1976). The scheme is

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

Fig. 1. Tentative correlation of the biochronological successions by De Giuli et al. (1987) and by Freudenthal (1976), from Masini et al. (2013).

organized in different phases characterized by different taxonomical composition and evolutionary stages. A detailed description of the phases is given by Masini et al. (2013).

As previously stated, one of the difficulties of this correlation is that different authors studied different taxa and researchers from Florence ignored the cricetids. The fissures of the Florence collection analyzed in this paper are those published by De Giuli et al. (1987) and included in Rinaldi and Masini's (2009) chronological scheme, namely F15, F21a, F21b, F21c, F1 and F9. Another fissure was added, called “Nazario Bivio Sinistra” (NBS). It is quite rich in cricetid remains, and it has never been analyzed before. Considering the size and morphology of *Mikrotia*, this new fissure results to be somewhat older than fissure F1. Nazario Bivio Sinistra's chronological position was defined by Savorelli (2010). Fissure F21c, as explained later in this paper, is very rich in outliers. The fossil content of this fissure devoid of outliers, is referred to as F21c pro parte. Outliers of F21c are fully described in section 6.1. Because of their similar fossil content, fissures F21a, F21b and F21c pro parte are often considered as one, and referred to as fissures F21a-b-(c).

3. Taxonomy of the Gargano cricetids

The endemic cricetids of Gargano were studied in detail by Freudenthal (1985), who defined three species of the same lineage: the small and primitive *Hattomys beetsi*, the middle-sized and more advanced *Hattomys nazarii*, and the largest and most complex *Hattomys gargantua*. The specimens from fissures Biancone 1 (type locality), Rinascita 1, Trefossi 1, and Chiro 19 were attributed to *H. beetsi*; those from Fina D, Cantatore 3A, Chiro 7A, Nazario 2A, Nazario 2B (type locality), and Nazario 4 to *H. nazarii*; those from Chiro 27, Chiro 5A, and Chiro 29 to a chronospecies called *Hattomys nazarii-gargantua*; and those from Pizzicoli 11, Pepo 1A, Chiro 10 C, Chiro 12, Chiro 10B, and Chiro 2 N (type locality) to *H. gargantua*. Specimens become larger throughout the given sequence of the fissures. Therefore, the fissures with *H. beetsi* are the oldest, and those with *H. gargantua* the youngest. Older fissures yielded remains of continental taxa such as *Neocricetodon* (Biancone 1, Rinascita 1, and Trefossi 1) and *Apocricetus* (Rinascita 1 only). Basic statistic parameters for the size measurements of each one of Freudenthal's (1985) samples are reported in Table S1, alongside those of the samples of the collection of Florence.

4. Material and methods

The samples studied are stored in the Department of Earth Sciences of the University of Florence and are labelled F (“fissure”) followed by a progressive number that indicates the sampling order. The only exception is “Nazario Bivio Sinistra” which is referred to with the acronym “NBS”. A lower-case letter next to the number (e.g., F21a, F21b, F21c) indicates different fissures from the same complex. Other terms or numbers next to the acronym of the fissure (e.g., “F1 SA” or “NBS3,5”) indicate different sub-samples of the same fissure. The specimens are indicated by a progressive number; the mandibulae and maxillae that preserve more than one molar are indicated by the code of the specimen plus a letter that refers to the dental element (a: first molar; b: second molar; c: third molar).

Length and width of the molars are measured with a Wild Heerbrugg MMS 235 system mounted on a Leitz Wetzlar Elvar microscope with calibration at 2.5 mm; measurements are in millimetres. The maximum and minimum length and width were measured as shown by the dashed lines on Fig. 2. The width of the first upper molar (M^1) has been taken measuring from the tangent to the lingual side to the labial end of the metacone. Broken or very worn molars have not been measured.

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