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THE GARGANO TERRE ROSSE INSULAR FAUNAS: AN OVERVIEW

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Abstract. After forty years from its discovery, the history of the field surveys and of the researches on the fossiliferous deposits of Gargano is briefly reported.

The Gargano fauna belongs to the Abruzzo-Apulian Palaeobioprovince (including also Scontrone and Palena, Abruzzo). The fossil assemblage comprehends all the classes of terrestrial vertebrates: Reptilia, Amphibia, Aves and Mammalia. The faunal composition is unbalanced and presents the features of a typical insular endemic fauna. The bulk of the assemblage is composed of small mammals and birds. Based on literature, we report the most characteristic features, phylogenetic relationships, and evolutionary remarks on a list of mammals, focusing particularly on the adaptations of the most endemic taxa. Moreover, a biochronological scheme of the major faunal events is proposed and illustrated. Although still imperfect, the scheme is the first synopsis of all the biochronological and taxonomical information on mammals so far available. Eventually, the hypotheses on the origin and modes of colonisation are summarized and shortly discussed.

From this overview the Gargano fauna is indeed of great interest for studies of evolution and biogeography. Nonetheless, there are persistent uncertainties on its age and origin, as well as on the age of infilling of the karstic fissure system of this unique fossiliferous locality.

Riassunto. I depositi di riempimento delle fessure carsiche nel Gargano nord-occidentale (Terre Rosse) contengono una ricca fauna endemica. Faune simili sono state ritrovate in zone limitrofe del Gargano, ma anche nella zona di Andria (Puglia), a Palena e a Scontrone (Abruzzo). Tali faune endemiche sono state riunite nella paleobioprovincia Abruzzo-Apula.

In questo contributo si presenta una breve storia delle ricerche sul Gargano, con particolare riferimento alla composizione della fauna e a considerazioni biocronologiche e biogeografiche. I primi resoconti delle ricerche sulla fauna delle Terre Rosse risalgono all'inizio degli anni '70, quando Matthijs Freudenthal pubblicò una nota preliminare sui ritrovamenti di vertebrati nell'area garganica, individuandone il carattere endemico insulare.

Seguirono, ad opera di diversi autori, la descrizione delle avifaune e delle forme a carattere endemico più marcato: *Mikrotia, Hoplitomeryx, Hattomys, Stertomys, Deinogalerix, Paralutra*. Negli anni '80, il Dipartimento di Scienze della Terra di Firenze, accanto agli aspetti tassonomici (*Prolagus*), affronta alcuni aspetti evolutivi, paleogeografici e biocronologici che permettono di identificare le faune garganiche come rappresentanti di una bioprovincia distinta con forti caratteri endemici. Gli anni '90 rappresentano un momento di approfondimento su aspetti evolutivi di *Mikrotia* e altri taxa. Al contempo, una campagna, in cui sono coinvolte competenze multidisciplinari, porta a una più dettagliata comprensione della stratigrafia delle coperture sedimentarie locali e delle modalità di riempimento delle fessure. Tale lavoro è stato ripreso recentemente in occasione delle attività di ricerca finalizzate allo studio dei depositi quaternari a cui cooperano varie università italiane, la Soprintendenza e gli enti locali. L'ultimo decennio è dedicato agli studi tassonomici sui gliridi, sull'avifauna e sull'erpetofauna. Sono frequenti, infine, lavori in cui le faune endemiche del Gargano vengono citate come esempio particolarmente interessante per la continuità della documentazione o per l'evidenza e la dinamica dei processi evolutivi.

La fauna delle Terre Rosse comprende tutte le classi di vertebrati terrestri: Rettili, Anfibi, Uccelli e Mammiferi. La composizione presenta tutti i caratteri tipici di una fauna endemica insulare, anche se le fessure più antiche contengono taxa non endemizzati. I taxa endemici vengono qui tratteggiati nelle loro linee essenziali, evidenziando possibili relazioni con antenati continentali e i principali trend evolutivi.

Viene quindi proposto per la prima volta un quadro biocronologico, suddiviso in fasi di popolamento, in cui si è cercato di riunire tutte le informazioni relative ai mammiferi finora descritti in Gargano. Questo quadro ha tuttora un carattere preliminare per le difficoltà incontrate nell'integrare informazioni tassonomiche e cronologiche da lavori fatti da diversi specialisti e per la incompletezza delle conoscenze su alcuni taxa e sulle faune di numerose fessure.

Infine, viene ripercorsa la storia delle ipotesi sull'origine delle faune della paleobioprovincia Abruzzo-Apula, con particolare attenzione al settore garganico. Le ipotesi sull'età e le modalità di provenienza sono poi confrontate e discusse.

Questa panoramica mostra che, dopo quarant'anni di ricerche, la fauna del Gargano è, da un lato, un caso di studio molto interessante per gli aspetti evolutivi e biogeografici, ma, dall'altro, ancora presenta aspetti d'incertezza che riguardano principalmente l'età e la provenienza dei taxa e in secondo luogo anche l'età dei depositi fossiliferi stessi.

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Introduction

Red soil deposits (Terre Rosse) fill most of the extensive palaeokarst network in the Mesozoic limestone on the North-Western slopes of Mount Gargano. Several fissure fillings yielded a very rich amount of fossil remains of a very diversified assemblage of vertebrates. These fossils attest to a succession of faunal settlement events, which occurred when the area was isolated and inhabited by endemic taxa. Most of the fossiliferous deposits have been exposed by intensive quarrying in a small area, of about 20 square kilometres, included between the towns of Apricena and Poggio Imperiale (Fig. 1). Similar fauna, however, was also found out of this area, i.e., at S. Nazzario (about 5 km northward), Monte Granata (25 km South-East), as well as in an unidentified locality between Barletta and Andria (Freudenthal 1971), about 100 km South-East of the quarry area. The Terre Rosse fauna, together with those recovered from Scontrone and Palena-Capo di Fiume (Abruzzo, central Italy), are believed to prove the existence of the so-called Abruzzo-Apulian Palaeobioprovince (cf. Mazza & Rustioni 2008). This contribution intends to be a state-of-the-art report of the knowledge on the Gargano fauna.

A brief history of the researches in Gargano

Field surveys were first conducted in the Apricena-Poggio Imperiale area from 1969 to 1974 (Freudenthal pers. comm.) by Matthijs Freudenthal (Naturalis, Nationaal Natuurhistorisch Museum, of Leiden, the Netherlands). In his first report, Freudenthal (1971) identified the peculiar "*gigantism and aberrant morphologies*" of some of the taxa, thus acknowledging the insular features of the Terre Rosse fauna. Moreover, Freudenthal reported the occurrence of an early Pleistocene (Calabrian) fauna characterized by *Allophaiomys*, which has later on been called Pirro Nord Fauna by De Giuli et al. (1987a). The find of stone tools associated with this fauna raised considerable interest in the scientific community (Arzarello et al. 2006).

Freudenthal (1971) actually anticipated most of the results that were to be published on the Terre Rosse fauna. In the following years Freudenthal described some endemics, exhibiting most peculiar features, such as *Deinogalerix* (Freudenthal 1972) and *Mikrotia* (Freudenthal 1976). Meanwhile, he proposed the first biochronological arrangement of the fissure fillings (Freudenthal 1976). Freudenthal's (1971) influential study triggered a flurry of studies.

Several monographs were published on the Gargano fauna: Ballmann (1973, 1976) described the bird remains, Butler (1980) revised the genus *Deinogalerix*, Willemsen (1983) analyzed the otter *Paralutra garganensis*, Leinders (1984) the endemic ruminant *Hoplitomeryx*, Freudenthal (1985) studied the cricetids, and Daams & Freudenthal (1985) described the giant dormouse *Stertomys laticrestatus*.

During the 80s, researchers of the Department of Earth Sciences of Florence (Italy) conducted new field surveys, and gave new impulse to the studies on Gargano analyzing the evolution of the fauna (in particular *Mikrotia* and *Prolagus*), as well as the palaeogeography of the area, but they also proposed a new biochronological arrangement of the fissure fillings (De Giuli et al. 1986a, b, 1987a, c; Mazza 1987a, b, c; Mazza & Zafonte 1987). From these studies the Gargano fauna was acknowledged to belong to a distinct endemic bioprovince which was called the Apulo-Dalmatic Realm (De Giuli et al. 1987c). De Giuli & Torre (1984) interpreted the evolutionary trends observed in *Mikrotia* and *Prolagus* as the result of competitive interrelationships between them, while Torre (1986) stressed the gradualistic aspects of the their evolution. Valleri (1984) gave a substantial contribution proposing a Pliocene age to the marine deposits locally sealing the fissure fillings. These marine sediments were previously dated to the Tortonian by D'Alessandro et al. (1979). Other studies followed, devoted especially to the evolution of specific taxa, namely *Mikrotia* (Zafonte & Masini 1992; Abbazzi

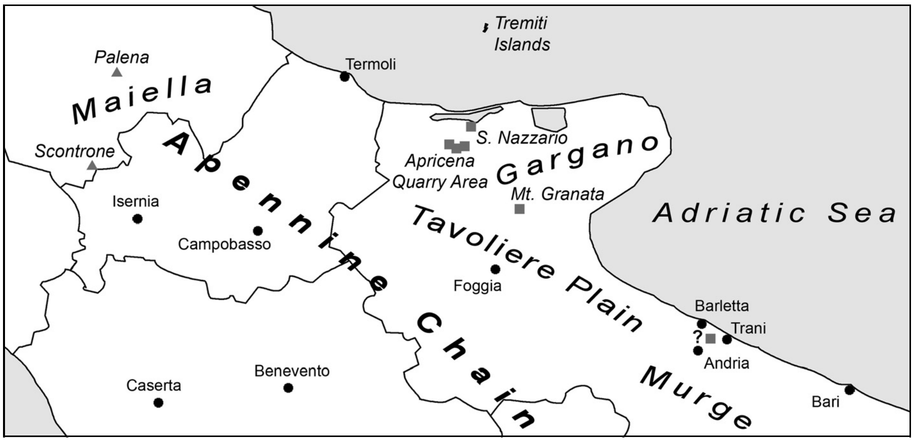


Fig. 1 - Location of the sites of the Abruzzo-Apulian Palaeobioprovince. Squares indicate localities with Terre Rosse fauna, found in fissure deposits in the foreland domain. Triangles indicate localities with remains found in beach to marine deposits in the chain domain.

et al. 1993; Parra et al. 1999; Millien-Parra 2000; Millien & Jaeger 2001), *Prolagus* (Angelone 2005), the insectivores (Fanfani 1999; van den Hoek Ostende 2001), and *Hoplitomeryx* (van der Geer 1999, 2005, 2008).

Meanwhile, at the beginning of the 90s, further field surveys were conducted jointly by the universities of Florence, Pisa, and Camerino. The results of these surveys were summarized in Abbazzi et al. (1996) multidisciplinary report, which reconstructs the evolution of the karst system, as well as the origin and stratigraphy of the whole outcropping succession, from the Terre Rosse soils up to the Pleistocene (Calabrian to Recent) deposits. The study includes also a detailed stratigraphy of the marine sedimentary cover that locally seals the fissures, together with an interpretation of the palaeogeographic evolution of the area.

Over the last ten years, interest on the Gargano fauna bursted again. Delfino (2002) and Delfino et al. (2007) studied the herpetofauna for the first time, while Göhlich & Pavia (2008) identified a new species of bird. Glirids, twenty years after Daams & Freudenthal's (1985) description of *Stertomys laticrestatus*, received the attention of several researchers, i.e., Freudenthal & Martín-Suárez (2006), Rinaldi (2006), Martín-Suárez & Freudenthal (2007) and Rinaldi & Masini (2009). In these papers five new *Stertomys* species are described. Rinaldi & Masini (2009) also proposed a correlation between the fissure biochronologies proposed by Freudenthal (1976) and De Giuli et al. (1987b).

Starting from 1990, the Terre Rosse fauna is considered an example of utmost interest, because of the continuity of its documentation and of the promising potentials it has to provide accurate, reliable and seamless information on evolutionary processes. It is often mentioned with Scontrone in papers devoted to the Neogene palaeogeography of the Mediterranean (e.g.: De Giuli et al. 1990; Moyà-Solà et al. 1999; Masini et al. 2002a, b, 2008; Rook et al. 2006, 2008; de Vos et al. 2007; Mazza & Rustioni 2008).

The fauna

The rich Terre Rosse fauna includes all classes of terrestrial vertebrates: Reptilia, Amphibia, Aves and Mammalia. It is highly unbalanced, however, and presents all the features of an insular population. The bulk of the assemblage is composed of endemic micromammals and birds, some of which of gigantic size. Macromammals are poorly represented: they include a group of ruminants of the endemic family Hoplitomericidae, together with several species of the giant insectivore *Deinogalerix*, which is mentioned as a large mammal because of its anomalous size. Carnivora are represented only by the marine otter *Paralutra garganensis*. However, the predators are fairly common and represented by crocodiles, snakes and particularly by birds of prey. The latter are represented by two endemic species of eagle (*Garganoaetus*) and six species of owl, among which three barn owl including the very large-sized *Tyto gigantea*. Non-endemic small mammals are also found in the assemblage. The faunal list of the mammalian taxa, with some taxonomical details and evolutionary remarks, is reported in Tab. 1.

Endemic taxa. Hoplitomericidae are most peculiar endemic ruminants. They are represented by several species of different size, at least two of which very small. They are characterized by the fusion of tarsal bones (navico-cuboid and metatarsal), which functionally limits lateral movements of the articulation (Leinders & Sondaar 1974), suggesting locomotion on ragged terrains. The most remarkable feature, however, is the occurrence, at least in some species, of five cranial appendages (one on the rear end of the nasal bone, and two couples upon each orbit) coupled with long, sabrelike upper canines (Fig. 2). The morphological distance from the other ruminant families, together with the occurrence of a set of diagnostic features, which is not found in the other ruminants, led Leinders (1984) to refer these endemics to a new family. The phylogenetic relationships of these ruminant are still debated, as well as the age of their continental ancestor. According to Mazza & Rustioni (2008), the ancestor might be traced back in the Late Oligocene before the divergence between Cervidae, Bovidae and Giraffidae. Other authors (e.g. Moyà-Solà et al. 1999) suggested the possibility of an early Late Miocene ancestor (*Micromeryx*), while Leinders (1984) suggested the Early Miocene *Amphimoschus* as a suitable candidate to the ancestry of the family. Eventually, van der Geer (2008) and van den Hoek Ostende et al. (2009) are in favor of a Palaeomerycidae ancestor.

Deinogalerix is an insectivore belonging to the Echinosoricinae, a subfamily nowadays restricted to Southern Asia. Extant Echinosoricinae include small to medium sized species that live in tropical or subtropical forests in humid environments. The subfamily was widespread in Europe at least from the Oligocene to the Early Pliocene, particularly with representatives of the tribe Galericini. *Deinogalerix* is characterized by short and strong legs, a large head with elongated muzzle, and highly specialized chewing apparatus with strong, sharp incisors, stout "*third and fourth premolars, with blunt cusps, adapted for crushing*" (Butler 1980), and short, strong row of molars. The rear part of the mandible shows a very low condyle, which suggests that this moonrat could widely open and rapidly snap its jaws. In Gargano, *Deinogalerix* is present already in the most ancient fissures with a single, small-sized and short-

Order and Family	Genus	Characteristics	Species	Age of the forerunners	Source
Carnivora Mustelidae	*Paralutra*	Slightly endemic, very rare. A single occurrence in fissure Fina H.	*P. garganensis*	Late Miocene (?)	Willemsen 1983
Artiodactyla Hoplitomericidae	*Hoplitomeryx*	Strongly endemic, common. Only one species is formally described[1]. It includes, however, several species with different size and adaptation arranged in four differen size groups[2], often found in the same assemblage. Present also in Scontrone with archaic features[3].	*H. mathei*	Oligocene-Early Miocene[3] Late Miocene[4]	[1]Leinders 1984 [2]van der Geer 2005, 2008 [3]Mazza & Rustioni 2008 [4]Moyà-Solà et al. 1999
Insectivora Erinaceidae	*Deinogalerix*	Strongly endemic, common. It includes five species belonging to at least two evolutionary lineages, very often coexisting in the same assemblage[1]. Present also in Scontrone with archaic features[4].	*D. freudenthali* *D. minor* *D. intermedius* *D. brevirostris* *D. koenigswaldi*	Oligocene-Early Miocene[1,4] Middle to Late Miocene[3] Late Miocene[2]	[1]Butler 1980 [2]Freudenthal 1972 [3]van den Hoek Ostende 2001 [4]Mazza & Rustioni 2008
	Galerix (*Parasorex*)	Endemic, very common. It is possibly represented by a single lineage.	*G.* (*P.*) *pusillus*	Late Miocene[1,2]	[1]De Giuli et al. 1987b, c Fanfani 1999 Fanfani & Masini unpub. [2]van den Hoek Ostende 2001
Insectivora Soricidae	*Lartetium*	Not endemic, rare. Single lineage. It occurs in the oldest fissures.	*L.* cf. *dehmi*	Middle Miocene	Fanfani 1999
Rodentia Gliridae	*Stertomys* (small-sized)	Endemic, very common. Moderately large size, with simple to complex dental morphology. An evolutionary trend could be recognised only in *S. daamsi-degiulii*[5]. Rinascita 1 is the only fissure in which two small-sized species occur[4].	*S. daamsi* *S. simplex* *S. degiulii*	Early-Middle Miocene[1,3] Middle (?)-Late Miocene[2] Messinian[2]	Daams & Freudenthal 1985 [1]De Giuli et al. 1987c [2]Freudenthal & Martín-Suárez 2006 [3]Rinaldi 2006 [4]Martín-Suárez & Freudenthal 2007 [5]Rinaldi & Masini 2009
	Stertomys (large-sized)	Endemic, rare. Large to very large size, with complex to very complex dental morphology. It is associated with the small-sized species.	*S. daunius* *S. lyrifer* *S. laticrestatus*		
	Dryomys	Not endemic, very rare. Represented by a single species. It is found in the oldest fissures.	*D. apulus*	Messinian[2]	
Rodentia Cricetidae	*Hattomys*	Endemic, common. Represented by three species, likely belonging to the same evolutionary lineage increasing in size and dental complexity. Absent in the most recent fissures.	*H. beetsi* *H. nazarii* *H. gargantua*	Late Miocene	Freudenthal 1985
	Neocricetodon	Not endemic, very rare. It occurs in the most ancient fissures.	*Neocricetodon* sp.	Messinian-Early Pliocene	
	Apocricetus	Not endemic, very rare. It occurs only in Rinascita 1.	*Apocricetus* sp.		
Rodentia Muridae	*Mikrotia*	Endemic, widespread. Represented by at least four lineages, two or three of which cohabiting on the same island. It underwent important size increase and changes in dental morphology. Only three species have been formally described: *M. maiuscola*, limited to the oldest fissure, *M. parva*, belonging to the "resident evolutionary lineage", and *M. magna*, belonging to the very large-sized lineage[2]. A very small-sized and simple lineage is limited to the oldest fissures (Lineage 1 in [1]) while a small-sized, morphologically derived lineage occurs in modern fissures[1,2].	*M. maiuscola* *M. parva* (L2[1]) *M. magna* (L4[1]) *Mikrotia* L1[1] *Mikrotia* L3[1]	Late Miocene[1,2]	Abbazzi et al. 1993 [1]De Giuli et al. 1987b, 1990 [2]Freudenthal 1976 Zafonte & Masini 1992
	Apodemus	Not endemic, very common. It is likely represented by a single lineage. In the most recent fissure, the dentition tends to be specialised.	*Apodemus* sp.	Messinian-Early Pliocene	De Giuli et al. 1987b, 1990
Lagomorpha Ochotonidae	*Prolagus*	Endemic, widespread. Represented by two lineages. It underwent important size increase and changes in dental morphology. The largest-sized lineage occurs in the most recent fissures. A taxon with similar endemic features occurs in Palena-Capo di Fiume[2].	*P. apricenicus* *P. imperialis*	Middle Miocene[1,2] Late Miocene[3]	Mazza 1987a, b, c Mazza & Zafonte 1987 [1]De Giuli et al. 1987c [2]Mazza et al. 1995 [3]Angelone 2007

Tab. 1 - Overall taxonomic composition of the mammalian assemblages of the *Mikrotia fauna* (after De Giuli et al. 1990 and Masini et al. 2008, updated). *Mikrotia* lineages are numbered after De Giuli et al. (1987b).

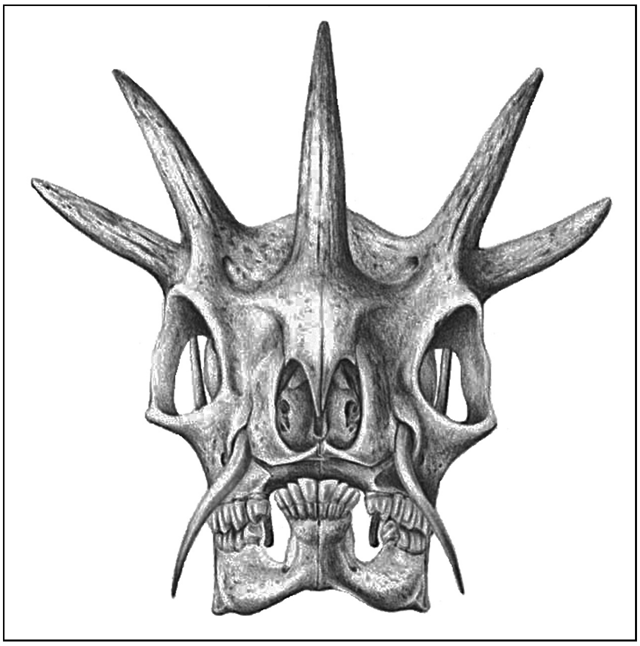


Fig. 2 - Reconstruction of the cranium of *Hoplitomeryx matthei*, an unusual anterior view (from Leinders 1984).

muzzled species (*Deinogalerix freudenthali*). It underwent a radiation which produced at least two lineages, differing in size and in the shape of the fore-muzzle.

Another Galericini species, smaller than the Miocene representatives of the tribe, is very common in the Terre Rosse fissure fillings. Also this tiny gymnure shows some endemic features, such as an enlarged and stout premolar series. It is phylogenetically related to the *Parasorex-Schizogalerix* group (Fanfani 1999; Masini unpublished). The phylogenetic relationships of *Deinogalerix* are still discussed. Butler (1980) suggested a possible derivation from an Oligocene-Early Miocene unknown Asian ancestor, while van den Hoek Ostende (2001) proposed a Middle-Late Miocene *Parasorex*-like ancestor, assuming a common ancestry for both the gigantic *Deinogalerix* and the very small-sized gymnure. Also the adaptation of *Deinogalerix* is discussed. Freudenthal (1972) regarded this moonrat as a scavenger, whereas, according to the elaborated argumentation of Butler (1980), it could have been an active predator, possibly specialized in hunting fishes as well as crustaceans.

Stertomys is an endemic dormouse of the subfamily Myomiminae, with dental morphology complicated by an increased number of crests on the occlusal surface of the teeth (e.g. five to fourteen crests in the upper molars). The genus includes six species which can be arranged in two different groups. The first includes large- to very large-sized species with complex to very complex dental morphology (*S. daunius*, *S. lyrifer* and *S. laticrestatus* - the latter may be the largest glirid so far known), while the second includes medium-sized species with simpler dental morphology (*S. daamsi*, *S. simplex* and *S. degiulii*). These groups likely represent two independent evolutionary branches stemming from a common, probably non-endemic, ancestor (Martín-Suárez & Freudenthal 2007; Rinaldi & Masini 2009). Both a small and a large-sized species usually occur together, with few exceptions: fissure Rinascita 1, where three small species occur, partially overlapping in size, two of which of the simpler-toothed group (*S. daamsi* and *S. simplex*), and fissure F32, where only the small-sized *S. degiulii* occurs. Rinaldi & Masini (2009) recognized the occurrence of five distinct phyletic lineages: three of the complex-toothed group and two of the simpler one. Only the evolution of the *S. daamsi-S. degiulii* lineage can be followed throughout the succession of fissures. It changed modestly in morphology and it presents a reduction in size that is apparently opposite to what is imposed by the so-called "island rule". The ancestry of *Stertomys* is discussed: Freudenthal & Martín-Suárez (2006) suggested a Messinian *Myomimus* ancestor, whereas Rinaldi (2006) considered a most likely Middle-early Late Miocene ancestor of the *Peridyromys-Myomimus* lineage.

Prolagus is widespread European Miocene ochotonid (a very far relative of extant pikas), which is present in Gargano too. Mazza (1987a, b, c) shows that Gargano *Prolagus* underwent significant evolutionary changes in the dental morphology, coupled with a marked increase in size compared to its continental counterparts. A less-derived and smaller species (*Prolagus apricenicus*) is widespread in all fissure fillings, whereas in the youngest fissures a larger and more derived species (*Prolagus imperialis*) also occurs. According to Mazza et al. (1995) Gargano *Prolagus* derived from *Prolagus oeningensis* and colonized the bioprovince in the Middle Miocene. Angelone (2007) holds a eastern European *P. oeningensis*-like ancestor for the Gargano endemic, and suggests a Late Miocene (early Messinian) colonization. An articulated skeleton tentatively referred to *Prolagus* cf. *apricenicus* has been recovered in early Messinian lagoon sediments in Palena-Capo di Fiume (Mazza et al. 1995).

Mikrotia is an ubiquitous murid of the Terre Rosse fissure fillings, and perhaps the most characteristic genus of the assemblage. The endemic evolution of this murid is characterized by a very marked growth in size, accompanied by an increase in hypsodonty and complexity of the dental crowns. Starting from the basic murid pattern, as crown height increases tubercles unite forming transversal crests in lower molars and in the upper third molar, while the circular stephanodont pattern of the first and second upper molars is accentuated. The most significant feature in the dental evolution of *Mikrotia*, however, is the increase of crown complexity, resulting from the addition of up to five new transversal crests in the first lower and in the third upper molars. The advanced species from San Giovannino possess the most highly modified teeth. Hypsodonty, transversal crests and increasing complexity of the M_1 and M^3 are characters shared also by Microtinae rodents: for this reason Freudenthal (1976) coined the original name *Microtia*. Unfortunately, the name had to be changed in "*Mikrotia*" by Freudenthal 2006, since it was pre-occupied by a Lepidoptera genus. The macroscopic morphological changes in the teeth are accompanied by modifications in the pattern of enamel microstructure: progressive increase in prism inclination causes a switch from the primitive radial pattern to proto-tangential bands (Zafonte & Masini 1992). Both morphological and microstructural changes suggest that the dentition of *Mikrotia* become highly specialized for an abrasive diet. This specialization could be linked to the acquisition of a fossorial habit (Parra et al. 1999). Excavating, living, and possibly feeding, in burrows likely forced these murids to grind high percentages of coarse items (e.g., soil particles). *Mikrotia* underwent several speciation events producing a rather complex branching phylogeny, of which at least five lineages are better known (Fig. 3). Parallel morphological evolution occurred in the different lineages, although the major phylogenetic trend characterizes the so-called "resident lineage". In those that are considered the most ancient fissures, *Mikrotia* shows simpler morphology, close to the basic murid pattern, although already with a certain degree of hypsodonty and larger size. In younger fissures two non-resident species, which likely evolved in some neighbouring islands, reached the Gargano island by dispersal, envisaging the so-called "archipelago effect" (Freudenthal 1971; De Giuli et al. 1986a). The morphological evolution of *Mikrotia* is striking, to a point that, if it had developed in non-insular context, it would have justified the creation of a thoroughly distinct supra-generic taxon, i.e., a tribe. The forerunner of *Mikrotia* is somewhat uncertain. Freudenthal (1976) suggested a possible ancestry from *Stephanomys* (see also Abbazzi et al. 1993). Freudenthal & Martín-Suárez (1999) suggested that *Apodemus* could be considered a suitable ancestor, too. This opinion is sustained by Freudenthal & Martín-Suárez (2010) considering the occurrence of an unpaired tubercle in the anterior part of the M_1 of *Apodemus* and *Mikrotia* and that in the latter genus "*all successive additions of crests pass through a stage with such an anterior cusp*".

Hattomys is an endemic hamster of the Terre Rosse fissure fillings, lacking only in the younger fissures of phases 3 and 4 (see below). It shows a marked endemic tendency toward ever larger sizes, accompanied by a progressive complication of the anterior part of the first molars. According to Freudenthal (1985), other characteristic features of this genus are the flanges that develop on the labial border of the molars, as well as the "*crests that tend to became dominating on the cusps*", which give the teeth a carved-in aspect. Apparently, this endemic evolved along a single phyletic lineage (*H. beetsi-H. nazarii-H. gargantua*).

Freudenthal (1985) recognises a certain affinity of *Hattomys* with *Cricetulodon (Neocricetodon* in Freudenthal & Martín-Suárez 2010), but the third molars that persist to be large in the endemic genus rules out a direct ancestry. Recently, Freudenthal & Martín-Suárez (2010) proposed a possible ancestry from *Cricetus* (*Apocricetus* in Freudenthal & Martín-Suárez 2010), which is still another genus present in the Gargano assemblage.

Non-endemic taxa. The Terre Rosse assemblage includes also non-endemic taxa. With the exception of *Apodemus*, they all occur only in the older fissures.

Dryomys apulus is scarcely represented only in three fissures (Biancone 1, Rinascita 1 and F15). This dormouse had been identified as *Eliomys* in earlier reports; then it was given its correct taxonomic description by Freudenthal & Martín-Suárez (2006). These authors included it in *Dryomys* on the basis of the morphology of the lower molars, though admitting, however, that *Eliomys* and *Dryomys* are quite indistinguishable dentally. Both genera are known since the Middle Miocene (Daams & de Brujin 1995); *Eliomys* was more common in Europe as opposed to *Dryomys* which was widespread in North Africa and Near East.

Neocricetodon (*Cricetulodon* in Freudenthal 1985) is known from three fissures (Biancone 1, Rinascita 1 and Trefossi 1), whereas *Apocricetus* (*Cricetus* in Freudenthal 1985) occurs only in Rinascita 1. Cricetids of the De Giuli collection have recently been checked by Andrea Savorelli (work in progress). According to Freudenthal (1985), both those cricetids are similar to their congenerics from the Turolian fauna of Crevillente (de Bruijn et al. 1975), where also *Eliomys* is present.

Megacricetodon is yet another cricetid, represented by only one specimen in Rinascita 1, which Freudenthal (1985) and Freudenthal & Martín-Suárez (2010) considered due to contamination. *Megacricetodon* occurred in Europe from the middle Orleanian (MN4) to the early Vallesian (MN9).

Lartetium cf. *dehmi* has been retrieved in fissures F15 and F21a-c (Fanfani 1999); its occurrence in the Leiden collection has not been checked. This shrew is known in Europe from Early to Middle Miocene.

The murid *Apodemus* is the most widespread non-endemic taxon at Gargano. Unlike the other continental taxa, which had gone extinct precociously, *Apodemus* became resident, and underwent evolutionary modifications that, according to De Giuli et al. (1987b, 1990), are quite significant in the last phase of

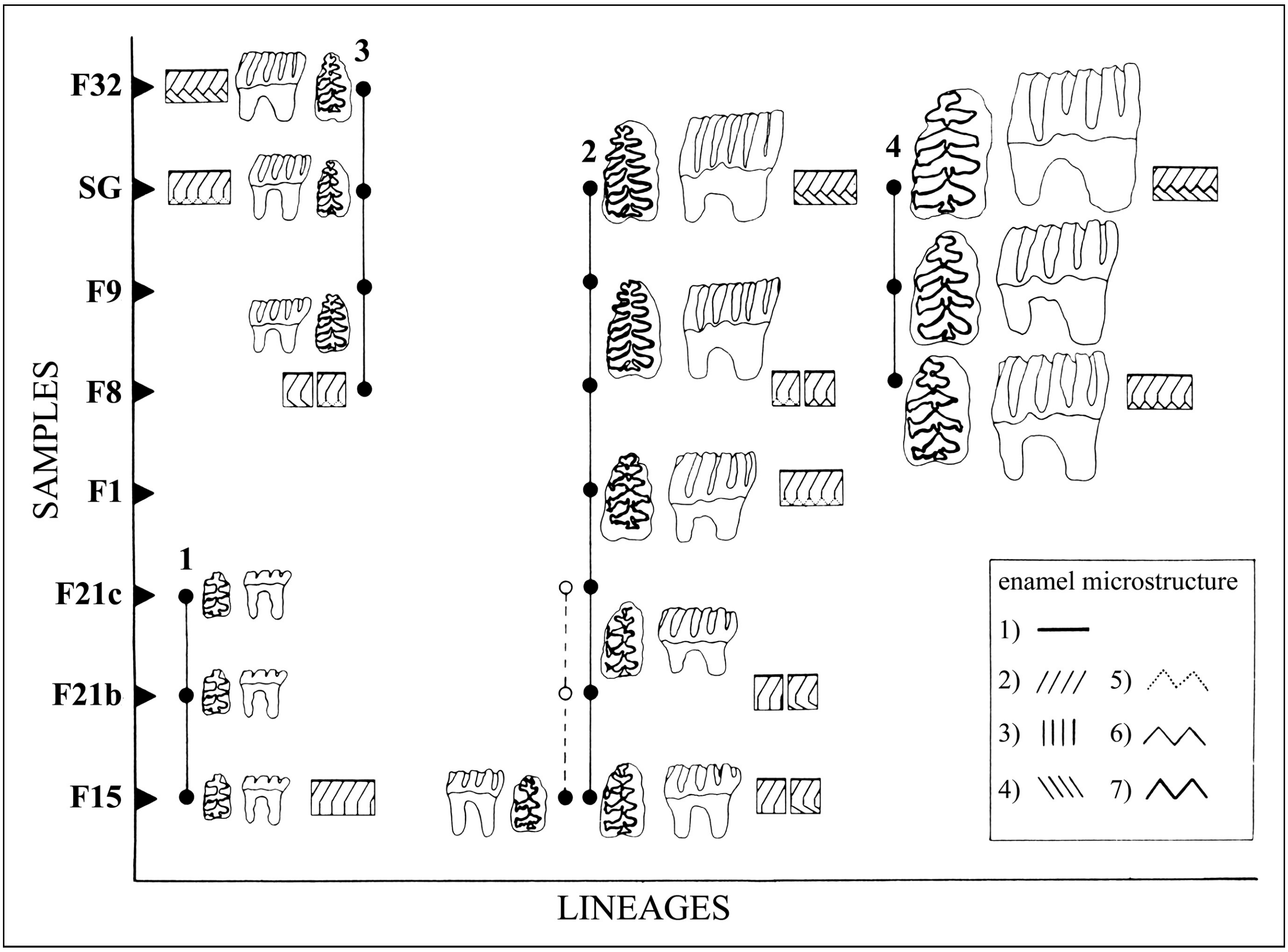


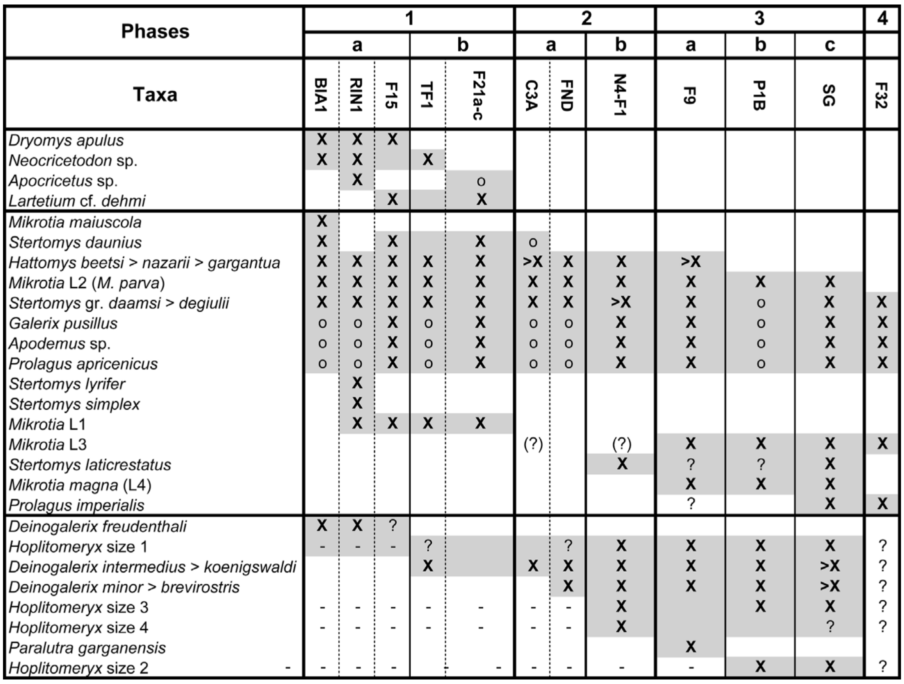
Fig. 3 - Scheme showing the evolution of the dental morphology and enamel microstructure of the first lower molar of *Mikrotia* (after Abbazzi et al. 1993 modified).
1: dentine; 2: radial enamel with axially inclined prisms; 3: radial enamel with prisms normal to the occlusal surface; 4: radial enamel with ab-axially inclined prisms; 5: primitive tangential enamel stage A; 6: primitive tangential enamel stage B; 7: tangential enamel.

faunal settlement (fissure F32, Fig. 4). It has never been analyzed in detail, although both Freudenthal (1985) and De Giuli et al. (1987b) recognized advanced features recalling those of the late Turolian-early Ruscinian mainland counterparts. More details on the ancestry of this mouse are reported below.

Biochronology and outline of the phases of faunal settlement

Because the deposits from the different fissures are not ordered stratigraphically, researchers had to sequence them biochronologically on an evolutionary basis. This was possible because the faunal composition and endemic features of the taxa from the different fissures vary in a fairly coherent way.

Freudenthal (1976) and De Giuli et al. (1987b) followed two slightly different biochronological strategies. The former tried to arrange chronologically all possible fissures on the basis of the evolution of both *Mikrotia* and *Hattomys*, assuming an irreversible increase of size of the *Mikrotia* main lineage. De Giuli et al. (1987b), in contrast, selected the richest samples, pinpointing a succession of faunal settlement pulses, based primarily on the evolution of *Mikrotia* and *Prolagus*, and selecting the most parsimonious among the alternative solutions (see Rinaldi & Masini 2009 for a detailed discussion). The biochronological sequences obtained using these two methods are fairly comparable, with minor inconsistencies. Rinaldi & Masini (2009) tried to integrate De Giuli et al.'s (1987b) samples with some of Freudenthal's (1976), obtaining a summary succession which includes also data on the evolution of *Stertomys*. They also extensively discussed the difficulties they had come up with trying to combine the two biochronologic solutions. One for all, Freudenthal (1976) had not considered the evolution of *Prolagus*, and De Giuli et al. (1987b) had not included that of cricetids. In the present contribution updated data on



Phases	1					2			3			4
	a			b		a		b	a	b	c	
Taxa	BIA1	RIN1	F15	TF1	F21a-c	C3A	FND	N4-F1	F9	P1B	SG	F32
Dryomys apulus	X	X	X									
Neocricetodon sp.	X	X		X								
Apocricetus sp.		X			o							
Lartetium cf. *dehmi*			X		X							
Mikrotia maiuscola	X											
Stertomys daunius	X		X		X	o						
Hattomys beetsi > nazarii > gargantua	X	X	X	X	X	>X	X	X	>X			
Mikrotia L2 (*M. parva*)	X	X	X	X	X	X	X	X	X	X	X	
Stertomys gr. *daamsi > degiulii*	X	X	X	X	X	X	X	>X	X	o	X	X
Galerix pusillus	o	o	X	o	X	o	o	X	X	o	X	X
Apodemus sp.	o	o	X	o	X	o	o	X	X	o	X	X
Prolagus apricenicus	o	o	X	o	X	o	o	X	X	o	X	X
Stertomys lyrifer		X										
Stertomys simplex		X										
Mikrotia L1		X	X	X	X							
Mikrotia L3						(?)		(?)	X	X	X	X
Stertomys laticrestatus								X	?	?	X	
Mikrotia magna (L4)									X	X	X	
Prolagus imperialis									?		X	X
Deinogalerix freudenthali	X	X	?									
Hoplitomeryx size 1	-	-	-	?			?	X	X	X	X	?
Deinogalerix intermedius > koenigswaldi				X		X	X	X	X	X	>X	?
Deinogalerix minor > brevirostris							X	X	X	X	>X	?
Hoplitomeryx size 3	-	-	-	-	-	-	-	X		X	X	?
Hoplitomeryx size 4	-	-	-	-	-	-	-	X			?	?
Paralutra garganensis									X			
Hoplitomeryx size 2 -	-	-	-	-	-	-	-	-	-	X	X	?

Fig. 4 - Tentative distribution of the mammalian assemblage in the Terre Rosse deposits. The chronological order derived from De Giuli et al. (1987b) integrated by several sources of data. Shaded rows indicate the distribution of the taxa; X: occurrence reported in the literature; o: occurrence not reported in the literature, and based on unpublished data; ?: doubtful occurrence reported in the literature; (?): doubtful identification; no symbol means inferred occurrence; >: phyletic transition within an evolutionary lineage. BIA1, Biancone 1; RIN1, Rinascita 1; TF1, Trefossi 1; C3A, Cantatore 3A; FND, Fina D; N4, Nazzario 4; P1B, Posticchia 1B; SG, San Giovannino.
Broad columns represent groups of fissures: F21a-c = F21a to F21c; N4-F1 = Nazzario 4, Biancone 2, Chirò 3, Chirò 7A, Pizzicoli 4, Chirò 11B, Chirò 5A and F1; F9 = F9, Monte Granata 1, Chirò 6, Chirò 14A, Chirò 12, Chirò 10A-B, Chirò 2S-N, Chirò 9, Fina H and Chirò 27; P1B = Posticchia 1B, Gervasio 1, Chirò 4, Chirò 20A-E, Chirò 24 and Gervasio 2; SG = San Giovannino and Pirro 11A. *Mikrotia* lineages are numbered after De Giuli et al. (1987b).

cricetids of the De Giuli collection are considered (Savorelli, work in progress).

Figure 4 is an attempt to combine both sequences into a single chronological scheme, based on the highest possible number of mammalian taxa. It obviously founds mainly on *Mikrotia*, *Stertomys*, *Hattomys* and *Prolagus*, but it also includes *Hoplitomeryx* and *Deinogalerix*. Not all fissures reported in the literature can be fit into the sequence: we have included only the best controlled ones which yielded the richest and most reliable information. Some fissures with roughly similar assemblages containing taxa at similar evolutionary degree are grouped together. This is a reasonable simplification when comparable assemblages occur in different fissures, which is not so infrequent (see Masini & Abbazzi 2006 and Petruso et al. 2008 for a discussion on this principle). In order to manage the highest possible amount of biochronological information, De Giuli et al.'s (1987b) four phases of faunal settlement have been articulated in sub-phases, following Masini et al. (2008).

Phase 1 fissures contain varied faunal assemblages not easy to group in sub-phases, especially because of the incoherent faunal composition of fissure Rinascita 1 (see Freudenthal 1976, 1985 and Rinaldi & Masini 2009 for a discussion on this fissure). It is characterized by the scattered occurrence of non-endemic, continental taxa, as well as by not too endemic small mammals, such as *Mikrotia parva*, *Mikrotia* evolutionary lineage 1, *Hattomys beetsi*, etc. This phase is also characterized by a primitive *Deinogalerix*, whereas information on *Hoplitomeryx* is scant or not available. A larger and more advanced *Deinogalerix* occurs in the late part of this phase. This phase of faunal settlement foreshadows the occurrence of faunal arrivals from the mainland and possibly faunal exchanges with the neighbouring islands of the palaeoarchipelago, but it also documents evolutionary trends in the resident taxa. Masini et al. (2008) believe that all “continental” taxa, but *Apodemus*, became extinct because of their inability to adapt to the insular biotope, the other face of the medal of the “advantage of the resident”.

De Giuli et al.'s (1987b) Phase 2 can be considered transitional from the oldest fissures to the more recent ones and it has been articulated in two sub-phases. Resident taxa underwent phyletic evolutionary changes, such as those observed in *Hattomys*, *Mikrotia* and the small-sized *Stertomys*. The arrival of endemics from neighbouring islands, such as *Stertomys laticrestatus*, cannot be excluded. In this phase, apparently three different sizes of *Hoplitomeryx* (van der Geer 2005, 2008) and two species of *Deinogalerix* occur.

Phase 3 is the best documented one. It is characterized by the occurrence of taxa with derived endemic features. Three *Mikrotia* lineages are present; the largest is a new incomer (*M. magna*). Several taxa underwent phyletic changes in the late part of this phase, e.g. the small-sized *Stertomys* and the resident lineage of *Mikrotia*. At the same time cricetids became extinct and *Prolagus imperialis* appears, either by dispersal or by in situ evolution. The most recent part of the phase records also the phyletic transition of *Deinogalerix minor* into

D. brevirostris and of *D. intermedius* into *D. koenigswaldi*: both cases exhibit size increase. Up to four different sized *Hoplitomeryx* taxa occur.

Phase 4 is documented, to date, only by fissure F32 (De Giuli et al. 1987b). The small mammal assemblage is poorly diversified. Larger-sized *Mikrotia* and *Stertomys* species became extinct, whereas smaller-sized ones, along with *Apodemus* and *Galerix* (*Parasorex*), underwent phyletic modification and slightly increased in size. *Prolagus* still occurs with two different species. Both *Hoplitomeryx* and *Deinogalerix* are present, but they have not been studied in the detail. The drop in diversity of the small mammals has been interpreted as a signal of a trophic crisis, possibly due to the shrinking of the island (De Giuli et al. 1987b, 1990; Masini et al. 2008).

The origin and age of the fauna

Theories, models, and related assumptions on the mechanisms and processes that originate the island faunas, are particularly relevant – and intimately tangled – to the question of the age of the faunas. Actually, the deposition of the fossiliferous sediments, together with the colonisation events by the ancestors of the insular taxa might have been scattered in time. The two questions should therefore be examined separately, even though they are often discussed jointly in the literature. The different opinions of the authors on the origin of insular taxa reflect, in part, two contrasting theoretical approaches, vicariance and dispersalism. Unfortunately, there is a certain amount of confusion in the use of these concepts, as stressed also by Masini et al. (2002b, 2008, 2009).

Freudenthal (1971) suggested that the Gargano was populated via dispersals from the mainland through a sort of continental bridge, possibly "*a series of islands which merely offered a limited passage for the fauna*" (filtering corridor). The area of origin of the fauna could have been either the emerged Apennine chain, across the Foggia Graben, or the Balkans, through a threshold across the Adriatic Sea. He first believed that migrations occurred in the late Vallesian-early Turolian, which he considered older than the Serravallian on the basis of incorrect dating of the calcarenites that seal the Terre Rosse deposits. A late Vallesian-early Turolian age of colonization was also supposed by Moyà-Solà et al. (1999) based on Freudenthal (1971, 1976). Later on, Freudenthal (1985) assumed the same mode of colonization, but at a different time. He recognized a general affinity of the Gargano fauna with those of some Messinian localities, such as Crevillente (Freudenthal 1985), El Arquillo, Maramena (Freudenthal & Martín-Suárez 2006), and he considered the Messinian low sea-level phase as a suitable condition for the dispersals onto the Gargano islands. Recently, following the claims of van den Hoek Ostende et al. (2009) on the Scontrone fauna (see below), Freudenthal & Martín-Suárez (2010) admitted that the most suitable mechanism to explain the unbalanced fauna of the Gargano is sweepstake dispersal which, however, should had occurred during the favourable low-stand conditions of the Messinian. Freudenthal & Martín-Suárez (2006, 2010) refused the hypothesis that Gargano could have been reached by successive waves of migration, insisting that mammals "*may have reached Gargano simultaneously*" (Freudenthal & Martín-Suárez 2009), de facto contradicting the sweepstake mechanism.

Butler (1980) argued that the unbalanced composition of the Gargano fauna could be explained by sweepstakes, but he concluded that this mechanism was not exclusive, since it would not account for the occurrence of Amphibia, which cannot cross expanses of salt sea water. To resolve this inconsistency, he interpreted the Gargano fauna as being composed of a core of an "*impoverished relic of an older fauna*" (actually a vicariance process), to which new faunal elements were added by later invasions (a dispersalist process). Butler was, indeed, the first who considered the Gargano fauna as the result of different events scattered in time and with different modes.

De Giuli et al. (1987c) also considered the Gargano fauna as the result of different dispersal events scattered through time. The events that brought the ancestors of *Prolagus*, *Deinogalerix, Hoplitomeryx* and *Stertomys* into the insular domain, were believed to have occurred in not-better defined moments during the Early Miocene-early Middle Miocene. A second wave of dispersals, involving the ancestors of *Dryomys, Mikrotia* and *Apocricetus*, was assumed to have occurred during the regressive phase of the late Messinian-earliest Zanclean. The dispersal of *Apodemus* is considered by the authors as a key to define the age of the Terre Rosse fissures. In a first reconstruction, *Apodemus* is assumed to have reached the islands together with the other non-endemic rodents (*Dryomys*, etc.) during the Messinian-Early Pliocene. An alternative possibility (I hypothesis in De Giuli et al. 1987c) is based on the morphological affinity of Gargano *Apodemus* with *Apodemus dominans* from Csarnota 2, and envisages a dispersal of this single murine at the very beginning of the Piacentian, during a marine regression documented locally, as well as elsewhere in the Mediterranean basin.

According to the latter interpretation, the fossiliferous fissures together with the whole history of the endemic fauna would have been concentrated in the Piacentian. Following Freudenthal (1971), De Giuli et al. (1987c) pinpointed the major sea level regressions, and indicated them as the most suitable occasions for dispersion onto Gargano, when the so-called "Mid Adriatic Ridge" (a submarine structural high across the Adriatic Sea) emerged. De Giuli et al. (1987c) did not specify explicitly whether dispersals occurred via land bridges, filtering barriers, or sweepstakes concentrated during the low-stand intervals. They were the first, however, who considered the Gargano faunas and islands within a wider palaeogeographical context, attempting a synthesis of marine stratigraphy, tectonics, palaeogeography of lands, and terrestrial mammal distribution.

The discovery of the Scontrone fossil fauna (Rustioni et al. 1992) had a deep impact on the discussions on the origin of the Gargano fauna. Scontrone is located in the Apennine chain about 115 km W of Gargano (Fig. 1). It yielded a fauna composed of large-sized vertebrates found in coastal sediments which were dated by the authors to the early Tortonian. The occurrence of *Hoplitomeryx* and *Deinogalerix*, although exhibiting more archaic features, testifies the strict affinity with the Gargano fauna (Mazza & Rustioni 1996, 2008). Mazza et al. (1995) and Mazza & Rustioni (1996) suggested that the colonization of the Abruzzo-Apulian area would have occurred during two intervals, Late Oligocene-Early Miocene and Messinian, in conjunction with major marine regressions. During the first interval the ancestor of *Hoplitomeryx* (and *Deinogalerix*, according to Mazza & Rustioni 2008) would have reached the insular domain, while in the second interval most of the small mammals typical of the Terre Rosse fauna would have reached the Gargano area from the mainland (Mazza et al. 1995).

Abbazzi et al. (1996) considered that Gargano "*was what remained of a bioprovince that was, at least in the Late Miocene, considerably larger*", of which Scontrone represents an older record. By and large, they considered the Gargano fauna as the relic of an older faunal settlement, resulting from multiple dispersal events. Rook et al. (2006) interpreted the Gargano area as a rather stable structural high, being part of the foreland of the Apennine orogene, while Scontrone was involved in the tectonic disruption linked to the edification of the chain. This interpretation is fully consistent with the vicariance model.

Masini et al. (2002b, 2008) approached the question of the origin of the Gargano communities distinguishing taxa as strongly endemic, intermediate/moderately endemic and non-endemic.

The first category includes *Hoplitomeryx* and *Deinogalerix*. These two taxa, following previous interpretations, are considered as survivors from the older phase of faunal settlement of the Abruzzo-Apulian Palaeobioprovince. For intermediate/moderately endemic as well as for non-endemic faunas, Masini et al. suggested a sort of sweepstake mechanism (rafting or floating islands) which occurred in two time intervals when the barriers separating the islands from the mainland were easier to be crossed. The older period is not clearly defined, because it would span from the late Middle Miocene to the Late Miocene, involving the whole Palaeobioprovince (both the Abruzzo and Apulia sectors). The second phase is assumed to have occurred in the late Messinian, involving only the relic Gargano area, as suggested by De Giuli et al. (1987c). Sweepstakes are preferred respect to full connection by land bridges, since they permit filtered arrivals of small mammals. Moreover, in the opinion of the authors, full connections with the mainland are to be excluded since they would likely have caused the extinction of the endemic fauna (see the late Pleistocene of Sicily, as an example). Masini et al. (2002b) introduced the concept of "polyphasic population" to indicate faunal settlements derived by bioevents scattered in time, which in turn may involve different mechanisms (vicariance or dispersalist). Polyphasic populations are very common in the Mediterranean area (e.g., Plio-Pliestocene of Sicily and Sardinia). Moreover, Masini et al. (2002b, 2008, 2009) remarked the difficulties in operating a clear-cut distinction between vicariance and dispersalist mechanisms when a detailed reconstruction is required, stressing that, for instance, a temporary land bridge (a peculiar case of vicariance) or a filtering barrier (dispersalist) do not have easy distinguishable effects on the fauna of the islands.

Recently, Mazza & Rustioni (2008) reconsidered the question of the Abruzzo-Apulian Bioprovince in the light of the discovery of *Deinogalerix* at Scontrone, and of the very careful on-shore and off-shore geological investigations in the Abruzzo-Apulian area and Adriatic Sea by Patacca et al. (2008a, b). The Early Tortonian age of the Scontrone fauna is confirmed by Patacca et al. (2008a) who referred the fossiliferous layer to an age slightly younger than the First Regular Occurrence of *Neogloboquadrina acostaensis*, some 10.5 Ma, even though some uncertainty still persists, as stressed by Freudenthal & Martín-Suárez (2010).

Palaeogeographical interpretations by Mazza & Rustioni (2008) and Patacca et al. (2008b) confirmed also the occurrence of two major regressions during the Late Oligocene-Early Miocene and the Messinian, and permitted to identify a structural high (Central-Adriatic Bridge =? Mid Adriatic Ridge of De Giuli et al. 1987c) which was likely fairly emerged during the marine low-stands, connecting Dalmatia and the Abruzzo-Apulian area "*either in the form of stripe of land or as a chain of islands*" (Mazza et al. 2009). Mazza & Rustioni (2008) adopted the model of land bridges, to justify the arrivals of mammals and, as in their previous paper, they sustained two migration waves: the older one, allowing the arrival of the ancestors of *Hoplitome-*

ryx and *Deinogalerix*, and the second one bringing small mammals into the Gargano area. By and large, Mazza & Rustioni (2008) interpreted the fauna of Gargano as the result of both a pure vicariance mechanism (the relic of a wider and older Palaeobioprovince), and a dispersalist mechanism via filtering bridge in the Messinian.

Angelone (2007) considered *Prolagus* unable to cross marine barriers, and she sustained that this ochotonid dispersed on islands via land bridges in the Messinian.

Van den Hoek Ostende (2001) suggested that both Gargano Erinaceidae (the giant *Deinogalerix* and the small gymnure) have a *Parasorex* ancestor, whose immigration should be younger than MN9 (early Vallesian). Finally, van den Hoek Ostende et al. (2009), criticising Mazza & Rustioni (2008), focused on the tempo and mode of colonization of the Abruzzo-Apulian area. They assumed a sweepstake mechanism, considering that this model should be the most suitable to explain the unbalanced features of the Gargano fauna, which in their opinion is equivalent to the faunas that are commonly found on the oceanic islands. The arrivals were supposed to be concentrated in a definite time interval when all the ancestors of the Gargano-Scontrone fauna, including rodents and other small mammals (not found at Scontrone), reached the Abruzzo-Apulian area. They dated this interval to the early Tortonian, adopting the Scontrone chronology by Mazza & Rustioni (2008), and strongly claiming against the possibility that the Abruzzo-Apulian fauna may be derived from dispersals and/or vicariance scattered throughout time (polyphasic populations).

Freudenthal & Martín-Suárez (2010) refuse the early Tortonian dating of Scontrone bone beds making a very detailed criticism of Patacca et al. (2008a). By and large, they conclude that the fossiliferous layers should be consistently younger of 10.5 Ma and older than 6.4 Ma (FRO of *Turborotalia multiloba*). In this time interval, Freudenthal & Martín-Suárez (2010) consider the occurrence of suitable ancestors of the Abruzzi-Apulian fauna, and conclude that the MN12 zone (late Tortonian-early Messinian) could be a suitable interval for the immigration of the fauna onto the insular domain. Freudenthal & Martín-Suárez (2010), as yet reported before, share the interpretation of van den Hoek Ostende et al. (2009) of a single migration possibly occurred by sweepstakes, even though they admit that the palaeontological data prevent to state if the migration wave originates from eastern or western Europe.

This overview evidently shows that the question of the age of the fossiliferous deposits of Gargano and of the dating of the faunal migrations are still not completely settled. Focussing, at first, only on the age of the Gargano fauna and not on its origin, we should add some comments.

The late Early Pliocene age of the base of the marine deposits that locally seal the Terre Rosse karst fissures (Valleri 1984; Abbazzi et al. 1996; Pavia et al. 2010) is an upper chronological constraint for the endemic fauna. The lower boundary, instead, is more problematic, also because the succession of phases of faunal settlement likely involved a substantial time interval. In this context the non-endemic taxa from the older fissures are most suitable for inferring the age of the beginning of the fossil record. According to De Giuli et al. (1987b) and Freudenthal & Martín-Suárez (2010), the occurrence of *Apodemus* would imply that the oldest "*Mikrotia* fauna" could not be older than the Turolian, because the first occurrence of *Apodemus* in Europe is in MN12. However, the above mentioned affinities with late Turolian-early Ruscinian continental species (Freudenthal 1985; De Giuli et al. 1987b) also suggested the possibility of a younger age (MN13-MN14). For that reason there is a general agreement on the Late Miocene-Early Pliocene age of the "*Mikrotia* fauna". Only van den Hoek Ostende et al. (2009) have sustained an early Tortonian age for both Scontrone and Gargano. Unfortunately, they did not consider that the oldest record of *Apodemus* in Europe is some 2 Ma later and apparently ignore the papers containing substantial discussion on the age of the Gargano fauna. The attribution at an early Tortonian age to the Gargano fauna is therefore untenable, in our opinion.

Further comments can be added on the mode of origin of the faunas. De Giuli et al. (1986b, 1987b) and Mazza & Rustioni (1996, 2008) tried to identify the most favourable palaeogeographic conditions for vertebrate dispersals to the insular domain, on the basis of geological data. This method has been exhaustively discussed by Azzaroli (1996) and applied to several insular faunas. Even though the aforementioned authors use typical dispersalist concepts, their approaches are at the boundary with vicariance biogeography, as stressed by Masini et al. (2002b). On the other hand, van den Hoek Ostende et al. (2009) adopted the typical dispersalist model of sweepstakes, adapted to the island theory by Dermitzakis & Sondaar (1978) as discussed by de Vos et al. (2007). Freudenthal first adopted the Simpson's (1940) model of land bridges (Freudenthal 1971, 1976, 1985) but, recently, he also embraces sweepstakes (Freudenthal & Martín-Suárez 2010). However, all the authors, with the exception of van den Hoek Ostende et al. (2009), agreed that, when vicariance is ruled out, faunas disperse only under very favourable palaeogeographic conditions, i.e., when the coasts of source-lands and target-islands are relatively close each other (see also Masini et al. 2002b). From this point of view, if colonization is via land bridges, filtering barriers or sweepstakes, is not particularly relevant. Especially in the case of faunas like those of Gargano, for which the knowledge of "surrounding" palaeogeographical setting and coeval faunas is very scant and imprecise.

The assumption of oceanic island by van den Hoek Ostende et al. (2009) also requires some criticisms. Sweepstakes onto oceanic islands are expected to be scattered in time, and not concentrated in particularly favourable intervals. Even if we assume that arrivals are concentrated, too many taxa, i.e., some ten genera of mammals, would have dispersed on Gargano following a stochastic mechanism, such as a typical sweepstake. Freudenthal & Martín-Suárez (2010) have an apparently similar position, but they look for favourable conditions in which sweepstakes occurred, and they assume a lesser number of incomers, considering many of the endemic taxa as derived from less endemic counterpart found in the same Terre Rosse assemblage, e.g. *Mikrotia* originated from *Apodemus*, *Hattomys* from *Apocricetus* and *Deinogalerix* from the very small *Galerix*. In our opinion, however, considering how widely different is endemism in Gargano, ranging from highly endemic to non-endemic, "continental" species, it seems very hard to suppose a single migration wave.

Conclusion

This overview shows that after forty years of researches the Gargano fauna is, on one hand, a most interesting study case for evolution and biogeography, but, on the other, it still presents a considerable amount of uncertainty, especially regarding age and provenance of the taxa, as well as the age of the fossiliferous deposits. By and large, this compilation shows that over the last years interest on this ancient insular system is rising again. Several new publications and works in progress are supplying new tesserae to the mosaic of the Gargano history, even though the details are far to be exhaustively reconstructed. At the state of the art, Gargano, like many other palaeontological objects, recalls an Impressionist painting, which is clear enough if seen from a distance, but blur when the canvas is observed in the details.

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