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Original article

When and how did the *Mikrotia* fauna reach Gargano (Apulia, Italy)?☆

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ABSTRACT

The time and mode of colonization of Gargano have been a subject of debate. Taking into account the temporal distribution of the ancestors of the *Mikrotia* fauna, a Late Tortonian age represents the best fit for the time of migration. How these animals reached the island is even harder to decide. In the past some scholars embraced rafting as an important mechanism enabling small mammals to reach the islands, whereas others rejected this hypothesis, considering it an improbable mode of colonization. The recent record of oceanic rafts indicates that rafting is indeed a very plausible method for small-sized animals to reach islands, and the most probable method for the colonization of Gargano. A polyphasic model, as proposed by Masini and colleagues, is rejected in the case of Gargano, as it is based on a misinterpretation of the adaptive radiations within the *Mikrotia* fauna.

1. Introduction

Miocene fissure fillings on the Gargano peninsula (Fig. 1) have yielded a fauna that bears clear characteristics of insular evolution. It contains various giant rodents, such as the dormouse *Stertomys* Daams and Freudenthal, 1985, the hamster *Hattomys* Freudenthal, 1985, and the murid *Mikrotia* Freudenthal, 2006. The latter is particularly abundant, and therefore these Miocene faunas are often referred to as the *Mikrotia* faunas. Apart from the giant rodents, *Deinogalerix* Freudenthal, 1972, a giant gymnure inhabited the palaeo-island. Large mammals are represented by the endemic ruminant *Hoplitomeryx* Leinders, 1984, and some sparse finds of the otter *Paralutra* Roman and Viret, 1934.

Mazza and Rustioni (2008) suggested that the fauna reached the island in different stages by means of land bridges. This argument is based on their assumption that *Hoplitomeryx* represents an ancient stock of ruminants which, according to Mazza and Rustioni's model, would have reached the island as early as the Late Oligocene. As murids appear in Europe only in the Late Miocene, the ancestor of *Mikrotia* obviously arrived in Gargano much later.

Van den Hoek Ostende et al. (2009) argued that the colonization of the island is better explained by sweepstake dispersal, and suggested that such a colonization took place in the earlier part of the Late Miocene. Freudenthal and Martín-Suárez (2010) agreed that sweepstake dispersal was the most probable mode of colonization. Moreover, in reviewing the entire faunal composition, they came to the conclusion that the palaeo-island was probably colonized at the end of the Late Miocene.

Paramount in this discussion is whether the two different models of colonization are viable. This is a hard task considering that there is almost no evidence of land bridges or sweepstake dispersal events in the record. Geology can provide indications for a possible land bridge, but such a structure itself would be prone to erosion, and unlikely to be preserved. The sweepstake dispersal model basically assumes that colonization took place as a freak accident, which did not leave any trace in the record, other than the colonization of the island itself. In this paper, we review the evidence of the time in which the ancestors of the *Mikrotia* fauna reached Gargano, and then we analyse the plausibility of the different models of colonization.

2. The age of the colonization of Gargano

Freudenthal (1971) supposed a Vallesian or Turolian age for the Gargano faunas. Agustí (1986) concluded a Vallesian (early Tortonian) origin of the faunas. Freudenthal and Martín-Suárez (2010) gave a detailed analysis of the biostratigraphic distribution of the possible ancestors of the components of the Gargano faunas. They concluded that a Late Tortonian or Early Messinian age (limit MN11/MN12, 7.5–7.0 Ma) was most likely for the colonization of Gargano. This was partly based on the record of *Apodemus* Kaup, 1829, a genus present from MN12 onwards. However, Mein et al. (1993) and Martín-Suárez and Mein (1998) mentioned the presence of *Apodemus* in the Early Vallesian (MN9) of Buzhor (Moldavia). Here, we present a modified version of fig. 1 of

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Fig. 1. Location of the area with the fossiliferous fissure fillings in Gargano, Southern Italy.

Freudenthal and Martín-Suárez (2010) (Fig. 2). During the meeting held in Scontrone (1–3 March 2011), Masini and colleagues presented a cricetid, similar to *Cricetodon* Lartet, 1851, from a new Gargano fissure filling labelled "M013", which is believed to contain the oldest known Gargano fauna to date (Masini et al., 2013). Although not yet published at this time, we introduced *Cricetodon* in Fig. 2, together with *Hispanomys* Mein and Freudenthal, 1971, a close relative of *Cricetodon*.

On the basis of these modified data, we now suppose that the immigration occurred in a Late Tortonian age (MN11, 8.8–7.5 Ma), in agreement with the position of the Scontrone mammal locality (Mazza and Rustioni, 2008) within the *Lithothamnium* Limestone, with an age ranging between 10.5 and 6.4 Ma (Fig. 2). For the moment this is the most parsimonious solution, even though the presence of *Megacricetodon* Fahlbusch, 1964 and *Cricetodon* are in conflict with this interpretation. We should in this respect mention that the presence of *Megacricetodon* may be due to contamination (Freudenthal, 1985), as Gargano material was processed in Leiden at the same time as Spanish *Megacricetodon* faunas.

Dr Masini kindly sent us photographs of what he interpreted as *Cricetodon* material. It shows similarities with *Cricetodon*, but there are also important differences, which of course may be the result of the evolution of the taxon on the island. Nevertheless, it is possible that it does not belong to *Cricetodon* and that the similarities are the result of local evolution. We will have to await the publication of this new cricetid to be able to study it further (Masini et al., 2013).

According to Mazza and Rustioni (1996, 2008), the primitive characteristics of *Hoplitomeryx* suggest a very early colonization by the ancestors of this ruminant. However, interpretations of this genus in the literature differ vastly (Mazza and Rustioni, 1996, 2008; van der Geer, 2005; van den Hoek Ostende et al., 2009). We note that there is a remarkable parallel between *Hoplitomeryx* and *Homo floresiensis* Brown et al., 2004. The latter was also considered to be too primitive to be derived from the generally assumed ancestors (Argue et al., 2009). Meijer et al. (2010) explained this by the reversal to primitive characters, a phenomenon more often noted in insular forms (Palombo, 2003). As yet, derivation of *Hoplitomeryx* from a palaeomerycid stock seems still a plausible hypothesis, worthy of further testing.

An additional problem in determining the time of arrival of the *Mikrotia* fauna is that no data are known from the Balkans, which could be the source area of the fauna.

3. Dispersal and speciation mechanisms

Various models have been proposed for the colonization of islands by mammals. Of course, for each individual island we need to assess which of these models best fits the available data. In this

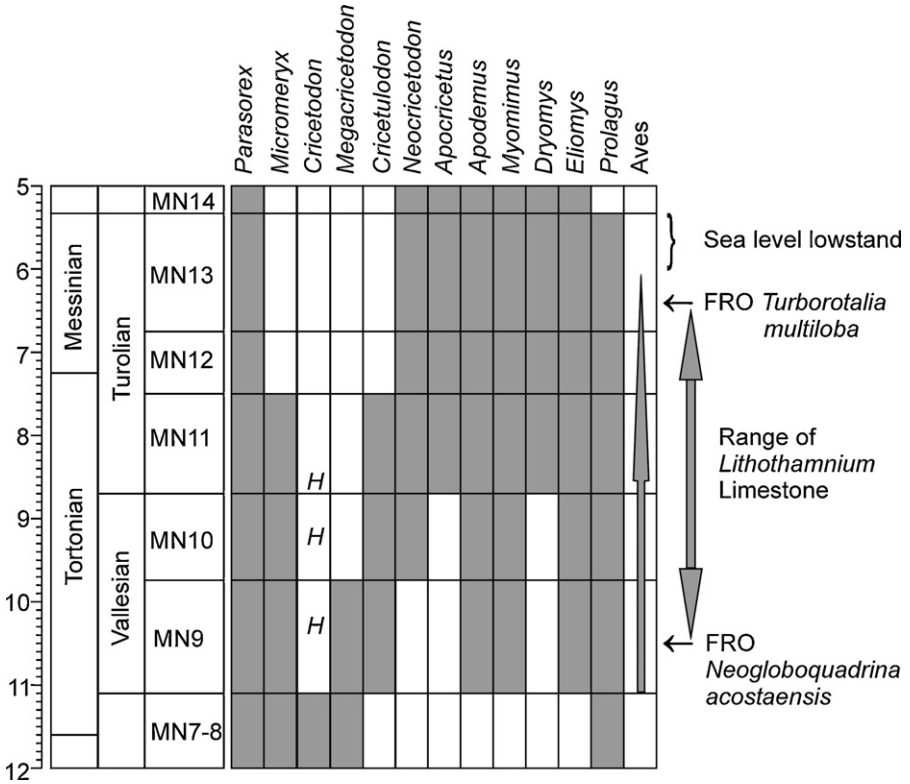

Fig. 2. Time distribution of the potential ancestors and related taxa of the *Mikrotia* faunas. H: *Hispanomys*, a descendant of *Cricetodon* (modified after Freudenthal and Martín-Suárez, 2010: fig. 1).

section we discuss the different models for the colonization of Gargano and their likelihood.

3.1. Vicariance

The island was populated while it formed part of the mainland and got isolated afterwards, which led to speciation. This is the model proposed by Mazza and Rustioni (2008) to justify the presence of *Hoplitomeryx* in Scontrone and Gargano. Since it is based on a doubtful taxonomic hypothesis it was rejected by van den Hoek Ostende et al. (2009) and Freudenthal and Martín-Suárez (2010).

3.2. Filter connection: land bridge, island hopping

The animals dispersed actively, but only a selection of species reached the island due to the filtering effect of geographical, climatic or any other kind of barrier. In view of the paleogeography of the studied area, this may have happened in Gargano, but given its position this would only have been possible after the sea level lowering of the Late Messinian and at that time various possible ancestors had already become extinct on the mainland.

3.3. Rafts or floating islands

The animals reach the island passively, being transported on entangled masses of vegetation, washed out into the sea and transported by sea currents and wind. Renner (2004) stated that such a floating island may cross the Atlantic Ocean in two weeks, i.e., at a speed of about 200 km per day.

In the case of Gargano and Scontrone this means that rafts may have crossed the Adriatic Sea from the Croatian Coast in one day, if sea currents were favourable. One single mechanism, pluviosity, may determine whether conditions were favourable: high precipitation values in the North Adriatic may have washed vegetation mats into the sea, on the one hand, and produced strong currents which transported them rapidly southward, on the other hand. An additional effect of this situation may be a decrease in the salinity of the sea surface water (Measey et al., 2007), which might be positive for the survival of the travelers on the floating island.

3.3.1. The Gargano case

We believe rafting is the most likely mechanism to explain the colonization of Gargano. All potential ancestors of the fauna components are small (body mass < 100 g) and may easily be transported on a floating island. Only for the artiodactyls this might have been more problematic in case they were large in size. However, the youngest *Micromeryx* (= *Hispanomeryx* in Sánchez and Morales, 2006) from MN11 of Puente Minero (Spain) were small. Costeur and Legendre (2008) estimated the body mass of *Micromeryx* at plm. 10 kg. Van der Geer (2008) estimated 5–6 kg for the smallest *Hoplitomeryx*. In view of their body mass, rafting is more probable than swimming, though some tragulids of similar size are reported to be good swimmers (Meijaard et al., 2010). Butler (1980) stated that the presence of Amphibia on Gargano is incompatible with the sweepstake model, because they cannot cross expanses of salt sea water. However, Measey et al. (2007) demonstrated they could, due to the decreased salinity of sea water.

3.3.2. Recent cases of rafting

Masini et al. (2002) stated that colonization by natural raft is a far from common phenomenon. In an attempt to determine the plausibility of the rafting method, we looked for documentation of recent cases of floating islands, with some amazing results: van Duzer (2006) gave many examples of floating islands in rivers and lakes and a few newspaper citations of floating islands in oceans. van Duzer (2004) reported a floating island from the Congo river 240 km offshore and examples from other rivers, like the Sepik River (Papua New Guinea), the Río Paraná and Río de la Plata (Argentina). He gave an account of floating islands seen at sea with trees, monkeys, parrots, etc. on them, sighted in 1898, 1902, 1908 (two islands seen on consecutive days), 1910 and 1924. Censky et al. (1998) reported a floating island, drifted ashore on Anguilla in 1995 some 350 km from its origin on Guadeloupe, with 15 individuals of the lizard *Iguana iguana* L., 1758 on it.

Apparently, floating islands are rare on a human scale, but these examples show that, geologically speaking, they are certainly not exceptional: six sightings and one demonstrated colonization in 100 years. Furthermore, in many cases rafting is the only reasonable explanation: the shrews and amphibians on the island of São Tomé (Measey et al., 2007), the endemic murid *Nesoryzomys* Heller, 1904 on Galapagos, and many other cases.

3.4. Mono/polyphasic island populations

Masini et al. (2002: 172) introduced the term *polyphasic island populations* for "a faunal population in which, in a given time zone, faunal elements derived from more ancient population phases coexist with elements of more recent events". As such, this model does not give a dispersal method per se, but only states that a fauna is composed of elements from multiple dispersal events. Masini et al. (2002) built a convincing case that the sequence of faunal complexes of Sicily can be explained by assuming temporal connections with some kind of filter barrier to the mainland. Given the topography of the island, such connections across the Strait of Messina are highly likely. In the younger faunal complexes, the Sicilian insular faunas are rather atypical in, e.g., the presence of mammalian carnivores.

Masini et al. (2002, 2008) also advocated the polyphasic model for Gargano, but along a somewhat different line of argument. They argued that the "degree of endemicity" represents different phases in the colonization of the island. This line of argument was implicitly followed by Mazza and Rustioni (2008), who assumed a colonization of the Apulia platform in the Late Oligocene by *Hoplitomeryx* and *Deinogalerix*, the only two taxa indicated by Masini et al. as "strongly endemic". However, in biology, endemic means restricted to a specific area, which may be large (S. America) or small (Galapagos). When speaking about a single species a possible qualifier is the geographic area in which it is endemic, but not the degree of endemism. Degree of endemism can be used when speaking about fauna composition, but not in the context of a single species. Since none of its taxa is found on the mainland, the Gargano fauna is 100% endemic (*Apodemus* may be non-endemic, but has not yet been determined at species level). Some species are very different from mainland forms and others are more similar, but that is not a measure of endemism.

4. Discussion

In trying to assign an age to the colonization of Gargano, we have already assumed implicitly that the colonization is, in geological terms, a single event. Nevertheless, considering the use of polyphasic model for Gargano in literature (Masini et al., 2002, 2008; Mazza and Rustioni, 2008), we need to further examine this model. Unlike in Sicily, where the polyphasic model was proposed on the basis of a series of faunal changes in consecutive faunas, in the case of Gargano the model was based on "degrees of endemism". As said before above, the allocation to different degrees of endemism only indicates the degree of morphological divergence from continental forms: the giant forms of Gargano differ more from their presumed ancestors than from the species

that remained small. This, however, has no consequences for the timing of the migrations. Cucchi et al. (2006) described a new species of *Mus* L., 1758, from Cyprus. This species is so much like mainland species, that the first clue to its separate status derived from molecular genetics, after which the species status was confirmed using morphometric analyses. Moreover, the genetic data indicated that the species had separated from *Mus macedonicus* Petrov and Ruzic, 1983, between 650–350 ky ago, clearly indicating that rodents can also maintain an ordinary continental size in an insular environment. The same holds true for the genera *Paulamys* Musser, 1986, and *Komodomys* Musser and Boeadi, 1980, on the Indonesian island of Flores. These belong to the same clade as the giant rats of the genus *Papagomys* Sody, 1941 (Musser and Carleton, 2005), but are comparable in size to *Rattus rattus* L., 1758, and were in fact originally identified as a subspecies of the Black Rat (Musser, 1981). Even though island evolution in rodents is generally linked to gigantism, small-sized species are quite common in insular environments. They form part of the array of sizes that fill up the ecological space available on an island after its colonization. These adaptive radiations also yield the giant forms which we have come to recognize as separate island genera.

In our opinion, different degrees of morphological deviation from mainland forms are no argument for polyphasic colonization. The faunal composition is best explained by adaptive radiations from a chance colonization, similar to the radiations found on oceanic islands as exemplified by the deer from Crete (de Vos and van der Geer, 2002) and the murids from Flores.

A model that predicts fewer colonizations seems to be preferable over one based on multiple colonizations, particularly when an intermittent route such as the one between Sicily and Calabria is not available. We agree with Masini et al. (2002) that island colonizations are not randomly distributed through time. Certainly, with the sea level changes of the Quaternary, chances for colonizing islands differ greatly, especially because of the reduced distance either between islands or between island and continent during sea level lowstand. Whether or not a lowering of the erosion base would also give an increase in the formation of floating islands we can only speculate, but given the increased erosion and the increased length of rivers, this seems well possible. High pluviosity may well be a key factor.

In any case, a punctuated colonization of an island does not necessarily imply the presence of a land bridge, but could equally indicate favorable conditions for other means of crossing open water. It is highly unlikely that all the different ancestors of the lineages on Gargano arrived on a single raft, but rafts appear to be sufficiently frequent to explain their arrival within a single time window, in which the ecological space on the island was not completely occupied and newcomers had chances.

Indeed, the polyphasic model seems to have its merits for islands close to the coast. Nevertheless, there is evidence that it can also play a role in oceanic islands. The majority of the fossil murids on Flores belong to a single clade. However, apart from these, remains have been found of the giant rat *Spelaeomys* Hooijer, 1957, which has a completely different origin. Musser (1981) referred to this genus as belonging to the old group, indicating that it is a survivor of an older fauna as suggested by Masini et al. (2002). The same holds true for the shrew rat, of which scarce remains have also been found on Flores.

5. Conclusions

Determining the age and mode of colonization of Gargano is, and will probably remain, largely a matter of conjecture. All we can do is try to find the most parsimonious model which fits all the geological and biological data. Thus, we believe that the data fit a single (or a number of temporary close) colonization events. Based on the stratigraphic distribution of the presumed ancestors, the best fit for this event lies in the Late Tortonian age (MN11, 8.8–7.5 Ma). However, the presence of a *Cricetodon*-like hamster is problematic for this age estimate. Furthermore, we lack data on the Balkan, which is a possible source area for the *Mikrotia* fauna. Should, for instance, the genera *Apocricetus* Freudenthal, Mein and Martín Suárez, 1998, and *Dryomys* Thomas, 1906, appear in southeastern Europe earlier than in the west, an older migration event could be considered possible.

Rafting as a mode of colonization is embraced by some scholars (van der Geer et al., 2010 and references therein) and considered unlikely by others (Masini et al., 2002, 2008). Our literature search shows that natural rafts indeed occur even in the present, and are a very plausible means of transportation to islands. Taking into account the body mass of the members of the *Mikrotia* fauna, we consider rafting the most plausible explanation for the colonization of Gargano.

We find no evidence for a polyphasic colonization of Gargano, as proposed by Masini et al. (2002, 2008). The presumed differences in endemism on which these studies were based, are in fact end members of a radiation which may or may not deviate largely from the ancestral form. This does not mean we reject the polyphasic model as such. However, this model seems to be better applicable to insular environments with an intermittent connection to the continent, such as Sicily.

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