Neogene vertebrates from the Gargano Peninsula, Italy

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Fissure-fillings in Mesozoic limestones in the Gargano Peninsula yield rich collections of fossil vertebrates, which are characterized by gigantism and aberrant morphology. Their age is considered to be Vallesian or Turolian. The special features of the fauna are probably due to isolation on an island. The vertebrate bearing fissure deposits are covered by a calcarenite which is dated as probably Serravallian on the basis of Foraminifera. This would mean that the continental Turolian may be older than the marine Serravallian, a conclusion which is in contrast with the general idea on the correlation of marine and continental Miocene and Pliocene in Europe.

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Introduction

In 1969 a group of paleontologists from the Rijksmuseum van Geologie en Mineralogie discovered a number of vertebrate bearing fossil localities on the Gargano Peninsula, prov. Foggia, Italy. This discovery appeared to be important enough to carry out a thorough investigation of the area. It was soon realized that this project would be of such magnitude that only international cooperation would make it possible to obtain results within a reasonable time. A team was formed comprising paleontologists from the universities of Bari (Italy), Montpellier (France), Utrecht (Netherlands) and the present author from the Rijksmuseum van Geologie en Mineralogie, who will cooperate in studying the rich Gargano faunas.

After the first discovery of fossiliferous localities in 1969, three larger campaigns were organized in the summers of 1969, 1970 and 1971. These ventures were financed by the Nederlandse Organisatie voor Zuiver-wetenschappelijk Onderzoek (Z.W.O.), the Consiglio Nazionale delle Ricerche (C.N.R.), and the Rijksmuseum van Geologie en Mineralogie. The support thus received is gratefully acknowledged. Moreover, thanks are due to Prof. A. Valduga (Bari) and Prof. A. Azzarolli (Florence), for their most valuable advice and aid. Last but not least I take great pleasure in thanking all of the inhabitants of Apricena and Poggio Imperiale who rendered our campaigns so successful through their generous and disinterested help.

Geological Setting

The Gargano promontory is essentially a block of uplifted Jurassic and Cretaceous limestones, which in places are exploited as 'marble'. This block appears to be bounded by faults and is cut by some major fault zones as well. Marine Tertiary deposits fringe the Mesozoic block. On its Western edge the Gargano High descends into the Foggia Graben via a number of fault-steps. The Graben, some thirty kilometers wide and topographically not much above sea-level, separates Gargano from the main Italian mountain ridges. It is conceivable that the uplifting of Gargano dates back to Cretaceous time, in view of the extensive bauxite deposits in the central Gargano highland, which are considered to be Cretaceous in age. Consequently, all over Gargano, karst development may have taken place throughout Cenozoic time.

Until now, our investigations have been practically confined to an area between the villages of Apricena and Poggio Imperiale, which forms the lowest visible fault step between the Foggia Graben and the Gargano Promontory. In this area limestone quarries abound, and in almost every one of them a number of karst fissures are exposed, filled with red deposits, which are often fossiliferous.

Up to now several hundred red fissure-fillings have been explored and well over fifty of these turned out to be more or less richly fossiliferous. Some fillings consisted of a rather hard calcified matrix, but many others contained a soft clayey sediment, which could easily be screened in water; the harder matrix had to be treated with acetic acid. As a result of the processing of many tons of matrix a
number of fine fossil collections has been obtained, which show an excellent state of preservation. Skulls are found quite often, and occasionally almost complete mammal skeletons.

Fauna and stratigraphy

The fauna collected so far consists of the following elements:

Amphibia: not specified,
Reptilia: Crocodilia, Testudinata, Serpentes, Lacertilia,
Aves: not specified,
Mammalia: Insectivora,
      Rodentia: Gliridae, Cricetidae, Muridae,
      Lagomorpha,
      Artiodactyla,
and some Eubranchiata, i.e. reworked foraminifera and gastropods, and some freshwater molluscs.

No thorough study of the collected material has been made to date, but a preliminary investigation of the mammal remains demonstrated quite clearly that they belong to a number of different biozones which may be defined by the degree of evolution of their faunas. It is also evident that these faunas represent a span of time which witnessed Gargano as an island, separated from the mainland and by the Foggia Graben then below sea level.

This conclusion is based on the fact that all groups of mammals found (except the Artiodactyla) show a remarkable tendency toward gigantism, and that the fauna is largely impoverished (Carnivora, Perissodactyla and Proboscidea appear to be absent). The same features, gigantism combined with impoverishment of the fauna, are not uncommonly found in island faunas, for instance of the Mediterranean Pleistocene, and may well be accepted as a proof for island conditions. Gargano remained separated from the mainland sufficiently long to permit evolution of the fauna involving both gigantism and considerable morphological changes, which can be followed step by step through the different biozones distinguished. This development may be summarized as follows:

INSECTIVORA

An insectivore of quite normal size and morphology, probably comparable to Miocene genera such as Pseudogalerix, is found in all localities. Another insectivore, however, evidently an Erinaceid, is quite unusual. In the oldest biozone recognized so far, it had already attained far larger dimensions than normally found in insectivores, but in the younger biozones it became truly gigantic: with a skull over 20 cm long and a body length of more than 60 cm it is certainly the largest insectivore known.
LAGOMORPHA

Lagomorpha are represented by the genus *Prolagus* which in the oldest biozone of Gargano shows the same general size as in all the numerous Miocene localities in Europe. In this biozone remains of *Prolagus* are very rare. Through the following zones their size increases progressively toward a form somewhat larger than the largest species known, *P. sardus* from the Pleistocene of Sardinia. Small individuals persist throughout the entire succession of biozones, and it is not yet clear whether these represent a separate species, or whether they are simply juvenile individuals of one and the same larger species. A second feature in the development of *Prolagus* is a progressive abundance, so that it is a dominant element of the younger faunas.

GLIRIDAE

The evolution of the Gliridae of Gargano Island remains obscure. In most localities two species are present, one of a rather normal size, while the other may attain the size of the Maltese *Leithia*. However, the relationships between the populations found in the different localities are not clear, and it is not even possible to attribute the material to any described genus. In the oldest locality discovered to date at least three different species of Gliridae, small, medium and large, are present. It may be added that the Gargano Gliridae do not show any signs of hypsodonty.

MURIDAE

The Muridae are abundant in all localities, and most of them show a most remarkable evolutionary trend.

In all localities a good many specimens of a small murid, morphologically comparable to *Apodemus* were found. In this group no evident morphological evolution has been recognized as yet, but there appears to be a moderate increase in size. More study will be needed to settle the point.

A second group of Muridae, belonging to a new genus, shows such a rapid and amazing evolution that it can be used conveniently to distinguish the different biozones mentioned before. In the oldest biozone it starts with two species, one somewhat larger than *Stephanomys*, the other considerably larger. Their ancestry might be found among some species of *Parapodemus*, although these are much smaller. A preliminary study of this new genus, carried out by Mr. R. Geesink, of Leiden University, permits me to give a short review of its evolution. A detailed study will undoubtedly alter some of the ideas expressed here, but the basic principles are likely to be confirmed.

Evolution is characterized by a considerable increase in size – in the youngest populations the skull length may attain nearly 10 cm – and by an enormous increase in length of *M*₁ and *M*₃. The longest specimens of *M*₁ found so far measure up to 10 mm. This increase in size is accompanied by progressive hypsodonty, and an addition of lobes in *M*₁ and *M*₃.

In the oldest localities *M*₁ still bears an aspect more or less comparable to that in other murids, but the anteroconid splits into two cusps which broaden
lingually and labially, while a little cusp is formed in front of the former. In the
next stage this little cusp is enlarged and split into two cusps as well, while again
a little cusp is formed in front of these. This process is continued until a maximum
of seven lobes is attained. It is conceivable that still higher numbers of lobes may
be found.

M³ in the oldest localities is a rather simple element consisting of a V-shaped
anterior part and one single lobe behind it, as is normal in Muridae. However, the
posterior lobe may form a constriction or valley in its centre, and thus be divided
into two parts, the anterior one developing into a simple transverse lobe, while in
the posterior one the same process of subdivision may be repeated. Finally the M³
may obtain up to seven lobes. The number of lobes in M₁ and M³ is more or less
balanced. This evolution of M³ is in full contrast with the situation in all other
Muridae in which M³ is generally a much reduced element.

These evolutionary trends in M₁ and M³ may be accompanied by an increase
in hypsodonty unequalled in any other murid. Complete hypsodonty, i.e. disap­
ppearance of roots, is not reached, but the length of the roots diminishes con­siderably in relation to the crown height.

This development of M₁ and M³ and the increase of hypsodonty are strongly
reminiscent of the Microtidae; moreover the shape of the mandible is typically
microtoid.

This overall pattern was noted in at least three different lineages which probably
originated from one or the other of the two species present in the oldest localities.
The most obvious difference between these lineages pertains to size. The lineage
of medium-sized species is the most important one because it is continuous and
the evolutionary trends mentioned are well developed in it. The increase of the
number of lobes and of the hypsodonty are the largest in this lineage.

The lineage of small size appears to be the most conservative one. Increase
of size takes hardly place, and the increase of the number of lobes is moderate,
as is the increase of hypsodonty.

This lineage is well represented in the higher biozones; in the lower biozones
it has been found in small numbers only which do not yet permit an evaluation
of its evolution. In the younger biozones populations may be primitive in some
respects, but modernized in others, so that it is not even certain that all these
populations can be placed in one single evolutionary line.

The lineage of large size shows an extreme increase in size and hypsodonty,
but an increase in the number of lobes which is somewhat less pronounced than
in the lineage of medium size. The lineage of large size seems to be restricted to
the younger biozones, and its appearance is quite abrupt. There is no population
of intermediate size which could serve as a linkage between the large and the
medium lineages. A possible explanation may be, that the lineage of large size
(and possibly also the one of small size) first developed on a neighbouring island
and subsequently could establish itself on Gargano after the difference in size from
the medium lineage had become sufficiently large.

The hypothesis of a development on some neighbouring island is supported
by the recent discovery of some similarly aberrant Muridae in a limestone quarry
between Barletta and Andria, on the Murge highland. This means that not only
Gargano, but also the Murge, were islands at the same time. Their faunas are
comparable if not identical. The problem to be solved is, whether Gargano and
the Murge formed one big island, or whether they were two neighbouring islands with limited faunal migration.

CRICETIDAE

In the oldest locality Cricetidae are abundantly represented by a species of about the same size as *Cricetus cricetus*. It possibly belongs to the same genus as ‘C.’ angustidens, ‘C.’ barrieri, and ‘C.’ kormosi. These species were originally assigned to the genus *Cricetus*, but probably represent a separate genus. The evolution of ‘Cricetus’ in Gargano is marked by a rapid increase in size, such that the youngest populations exceed in size the dimensions of *C. major* and *C. runtonensis*. The molar relief is sharpened in a way vaguely reminiscent of the pattern found in *Melissiodon*. In the biozone in which ‘Cricetus’ attains its maximum size it becomes less abundant, and in the highest two biozones no Cricetidae were found at all, though extensive collections from these zones are available. Apparently Cricetidae disappeared from Gargano sooner than other groups.

Apart from the abundant remains of ‘Cricetus’, a few specimens found in the oldest locality prove the presence of either a *Rotundomys* or a *Kowalskia*. Unfortunately no other remains of this stratigraphically important cricetid were found so far.

Apart from their purely paleontological value the Gargano faunas are highly interesting from a stratigraphical point of view. All the faunas mentioned have been found in fissure-fillings in the Mesozoic limestone. Both limestone and fissures are covered by a marine calcarenite, at least in a number of places. It seems probable that this calcarenite once covered the entire area, but that it has locally been removed by erosion. The calcarenite can be dated by means of its fossil content. A preliminary examination of the molluscs suggests an Upper Miocene or at the very least a Lower Pliocene age. In the recent edition of the geological map of Italy it is dated as probably Serravallian. As it is undoubtedly younger than the faunas from the red fissure-fillings, we are faced with the probability that genera like ‘Cricetus’, *Apodemus* and *Parapodemus* appeared in Europe well before the end of the Miocene. This would implicate a considerable change in the current opinions on the correlation between marine and continental Neogene.

The Mesozoic limestone and the overlying calcarenite rise above the surrounding country, where we find outcrops of Pliocene tuffs. These tuffs were evidently deposited against a cliff coast of limestone and calcarenite after a phase of uplift and tilt.

In several quarries it was possible to discern a second phase of karst development, this time affecting the calcarenite. The base of this karst phase appears to be the plane between the Mesozoic limestone and the calcarenite, and in at least one quarry an extensive cave system was observed on top of the limestone, in the calcarenite. This cave system is filled up with a yellowish sediment rich in quartz grains, which is remarkable considering that sand is lacking in the red fissure-fillings mentioned before. This sand must have been transported from the Italian mainland, across the Foggia Graben, since no likely source is present in the Gargano Promontory.
In these cave-fillings a rich mammalian fauna was found yielding: *Equus*, several species of Cervidae, Bovidae, *Sus, Elephas meridionalis, Hyaena, Machairodus, Ursus*, a Rhinocerotid, *Hystrix, Allophaiomys, Apodemus, Lepus*, and other vertebrates. This is a typically Lower Pleistocene fauna such as found in many localities all over Europe, without any indication of island conditions. In Lower Pleistocene time Gargano evidently formed part of the mainland. According to all available evidence the Foggia Graben was above sea level at that time.

Finally a few fissures were found which contain an Upper Pleistocene fauna; these are of little interest for the scope of this paper.

Cenozoic history of Gargano

In order to trace the post-Mesozoic history of Gargano the results obtained so far may be summarized as follows:

Karst development may have occurred throughout the Tertiary. The fissures thus formed may have been filled and emptied again repeatedly, and at a certain moment in Lower or Middle Miocene time an extensive fissure system existed in the lowest fault-step of the Gargano block, along the Foggia Graben. In this period Gargano was connected with the continent, thus permitting faunal migrations. This connection may have been either with the Central Italian mountain ridges, across the Foggia Graben, or Gargano may have been linked up with the Balkans by means of a threshold across the Adriatic sea. The connection most probably was not a continuous one, but a series of islands which merely offered a limited passage for the fauna. The lacking of many animal groups in the Gargano fauna may be explained in that way. The faunal components that eventually did reach Gargano encountered favourable conditions including an apparent absence of their natural enemies, and they developed rapidly. During this immigration Gargano was high above sea level, because the karst fissures were fully emptied, denoting a relatively low base of karst erosion; since the area under consideration is only a few kilometers from the sea, the base of karst erosion and the sea-level may be considered as almost identical. Subsequently the sea level rose, active karst development stopped, and the fissures were filled up, the deposits being rich in skeletal remains of the animals living on the island. The sea-level evidently rose at such a rate as to allow the observed evolution of the existing fauna. Finally the lower fault-step was entirely submerged and the fauna became extinct, at least in the area studied so far. This transgression deposited a calcarenite on top of the limestone and the fissure deposits. In several places limestone and calcarenite are separated by a stratified red and green deposit which may be interpreted as a fossil soil. After the deposition of the calcarenite (probably Middle or Upper Miocene) the limestone block with the overlying calcarenite was tilted and partly lifted above sea-level. Pliocene tuffs were then deposited around the uplifted block, and in the latter karst erosion set in again, affecting the calcarenite. This situation persisted until the end of Pliocene time. During the Pliocene Gargano was presumably an island – as suggested by Gignoux – but to-date no Pliocene mammalian faunas have been found. At the beginning of Pleistocene time Gargano became firmly connected with the Italian mainland, and the normal Pleistocene fauna invaded the area. Its remains are found in the cave-fillings in the calcarenite.
One of the main consequences of the discovery of the Gargano island faunas, is the change it causes in the ideas on the correlation of continental and marine stratigraphy. In this respect three genera are important: 'Cricetus', Apodemus, and the genus of aberrant Muridae mentioned before.

The first Muridae appear in Europe during the Vallesian; they probably emigrated from Asia. 'Cricetus' (i.e. species like angustidens, etc.) evolved locally from Democricetodon via Rotundomys or Kowalskia. A characteristic development in this evolution is the acquisition of a fourth root in M1. Vallesian species still have three roots, the fourth root appears in Turolian species for the first time. The oldest Gargano 'Cricetus' still has three roots, which makes it probable that its direct ancestor was a Vallesian Rotundomys or Kowalskia. As a consequence it seems logical that Gargano was populated not later than the early Turolian. The entire evolution of the Gargano faunas may have taken place during Upper Vallesian and/or Lower Turolian time.

According to marine stratigraphic standards the calcarenite overlying these faunas is dated as Middle or Upper Miocene. It is suggested that the Vallesian/ Turolian boundary is older than the marine Serravallian.

However, one should not forget that the composition of the Miocene micro-mammalian fauna of the Balkans is not known. Muridae invaded Europe toward the end of Miocene time, but possibly this invasion took place in the Balkans, including Gargano, in an earlier period. In other words, Gargano may have been populated from across the Adriatic sea, and not from the West or Northwest; the normal European Muridae may actually be younger than the Gargano murids. Future researches in Yugoslavia or Albania may solve this problem.

Notes on the field campaigns and future work

In early 1969, while discussing research projects, Dr. C. Beets, director of the Rijksmuseum van Geologie en Mineralogie, recommended reconnoitring Gargano Peninsula. Being broadly familiar with its geology and the regional framework, he suggested that Cenozoic island faunas might well be discovered there. Soon after, a reconnaissance was made in which participated Dr. Beets, Mr. H. J. W. G. Schalke, Rijksmuseum palynologist, and the writer. The survey was limited to only one week, but even this short period sufficed for the discovery of four abundantly fossiliferous localities, their faunas displaying gigantism to a remarkable degree. As gigantism is a characteristic of Pleistocene island faunas in the Mediterranean, their age was first thought to be Pleistocene. The calcarenite discussed above was also observed on this first trip and its importance realized, but lack of time did not permit our paying prolonged attention to it then. However, it was clear that the area, apart from its considerable palaeontological interest, offered splendid opportunities for correlating marine and continental deposits.

The overall results of the reconnaissance being so promising, we were fortunate in acquiring invaluable, timely support from the Netherlands Organisation for Pure Scientific Research (Z.W.O.) which enabled revisiting the Gargano area in the summer of the same year, for a period of one month. This second campaign too, was extremely successful. To a large degree this was due to enthusiastic cooperation in the field given by Mr. G. C. Abels, Utrecht, and Mr. A. W. Janssen,
of the Rijksmuseum, who paid special attention to the marine deposits, collecting mollusca for dating purposes. A total of nine new vertebrate localities were added and thoroughly exploited, as were the localities discovered in the first campaign. In the meantime contact had been made with Prof. A. Azzarolli, Florence, who forwarded my request for collaboration to Prof. A. Valduga, Bari. As a result we were joined in the field by geologists of the Geological Institute at Bari, and cooperation was soon agreed upon.

In the winter of 1969 evaluation of the preliminary results suggested that the differences between the vertebrate faunas found might well be due to evolutionary changes, and that so far three different biozones were involved. The marine mollusca suggested that the underlying vertebrate faunas were certainly not Pleistocene, but possibly Miocene or Lower Pliocene in age. The material collected was by then already so extensive that the forming of a larger team of vertebrate paleontologists appeared essential. Dr. J. Michaux of Montpellier, upon a visit to the Rijksmuseum happily agreed to partake in the next field campaign, and to join in preparing a publication on the Muridae from Gargano. In the course of a prolonged visit to the Rijksmuseum, Dr. Tina d’Alessandro, of Bari, ably prepared delicate specimens, sorted out wash residues and made a preliminary study of the Gliridae. One of the localities discovered in 1969 turned out to be of a Pleistocene age, and to contain some specimens of voles. Mr. A. J. van der Meulen, Utrecht, kindly undertook the investigation of this material.

In the summer of 1970 the writer spent another two months in Gargano, this time assisted by Mr. R. Geesink, Leiden, and Mr. H. Guldemond, Rijksmuseum technician. We were also joined by Dr. d’Alessandro, Bari, and Mr. M. van den Bosch, of the Rijksmuseum, who carried out field work in order to trace the relations of the fissure fillings to the marine sediments. Furthermore, Dr. J. Michaux and Dr. J. Sudre, Montpellier, and Mr. van der Meulen took part in this campaign. The overall results were once again quite overwhelming, and later evaluation led to the distinction of at least six biozones in the red fissure-fillings. A closer analysis of these biozones by Dr. Michaux, who visited the Rijksmuseum again in the spring of 1971, and the writer revealed that their sequence most probably was discontinuous. Evidently there were two fairly large hiatuses, a truly astonishing realization considering that by then the total number of fossil localities had risen to forty. It should be added that in 1970 also a large amount of matrix from the Pleistocene locality was screened, yielding a gratifyingly large collection of micromammals. In order to collect much needed additional material of larger mammals, Dr. d’Alessandro carried out another campaign in the autumn of 1970, with excellent results. The Pleistocene deposit now appears to be exhausted.

During the 1971 field campaign, finally, which lasted two months, the writer was assisted by Mr. J. van der Linden, Rijksmuseum technician, and Mr. J. Moltzer, Utrecht. Dr. Michaux again participated for several weeks, this time in the company of Miss L. Pasquier, Montpellier. We concentrated our efforts on closing the gaps in the sequence of biozones, apparently successfully so, by sampling no less than thirty new localities.

The present situation with regard to the description of the collections is as follows:

A preliminary paper by the present author on the giant insectivore is planned for the near future. The material, a complete skeleton and several hundred isolated teeth and postcranial elements, is available for further specialist studies, as are the small insectivores mentioned above.
The Muridae will be dealt with by Messrs. Michaux and Geesink, and the present writer, in a joint publication. The writer also plans to describe the Cricetidae.

The Gliridae, Lagomorpha, Artiodactyla, Reptilia, Amphibia and Aves are available for any specialist who is interested in studying them.

Mr. van der Meulen plans to examine the Pleistocene micromammals in detail. The larger mammals from the Pleistocene fauna finally, will be the subject of a preliminary investigation by Mr. G. Dagostino, of Bari.

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