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Deinogalerix: a giant hedgehog from the Miocene

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Abstract

During the Miocene the Abruzzo/Apulia region (Italy), isolated from the continent, was the theatre of the evolution of a vertebrate ecosystem in insular context. At the late Miocene the protagonists of this ecosystem called "*Mikrotia fauna*" show a high endemic speciation level with spectacular giant and dwarf species of mammals and birds. Most of the remains of this peculiar fauna are found exclusively in the "Terre rosse" of Gargano, except for the oldest genus: *Deinogalerix* and *Hoplitomeryx*, also found at Scontrone. *Deinogalerix* is one of the most uncommon forms of the "*Mikrotia fauna*". It's the largest Erinaceidea ever lived. *Deinogalerix* was described for the first by Freudenthal (1972) then by Butler (1980). Today the five species yet described are under discussion cause of the high intraspecific variations in an insular evolution context. In this study we valuated the information that could bring the new discoveries of *Deinogalerix* remains. The work was divided into three main parts: the preparation of the material, the drawing reconstructions and the anatomical description. The most important specimen was the second sub-complet skeleton ever found. We gave the most objective anatomical description for futures comparison with the first skeleton from a different specie. We put the finger on new juvenile features and on the relation between the growth of *Deinogalerix* and his feeding behaviours. We also isolate some problematic specimens at this time never described. In the future this new material will help us in the understanding of the evolution history of this giant Hedgehog.

Keywords: insularity, evolution, anatomy.

Introduction

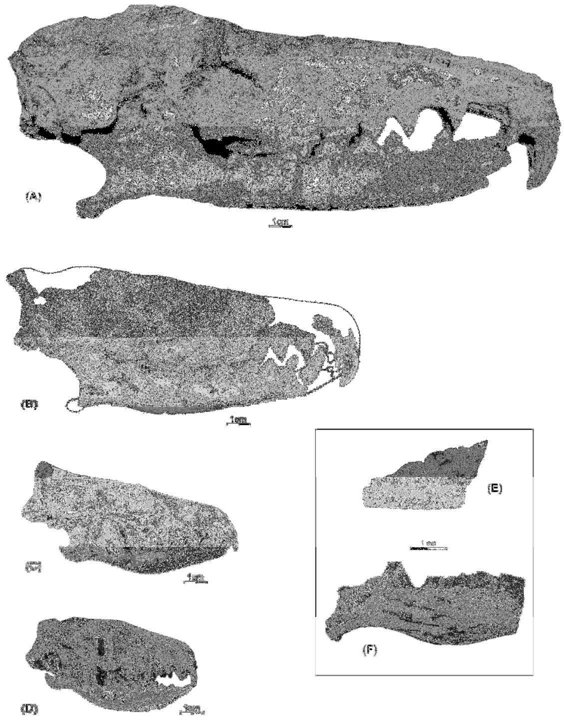
Across the time the island raised the interest of people. They once were sources of inspiration for writers, the horn of plenty for marines, new worlds for explorers and naturalists. Now they are seen as laboratories of evolution for the scientists. The actual studies about insular ecosystems (MacArthur & Wilson, 1967; MacNab, 1994a, 1994b; Meiri et al, 2006; Lomolino, 2005) show that the life on an island depends of weak balance. A balanced ecosystem depends mostly of the geography of the island, the resources (quantitatively and qualitatively speaking), the concurrences, the predation and the species' fitness.

The most spectacular insular adaptation is the dwarfism of large continental species (elephants, deer, hippos, etc) and gigantism of the small ones (rodents, birds). This phenomenon is called "Island law" (VanValen, 1973). Today most of the species with extreme insular features are extinguished. The most spectacular cases are observed by the palaeontologists in the fossil register (Sondaar, 1991).

The insular specie which we are interest in is *Deinogalerix sp.*. From the same family of hedgehogs (*Erinaceus sp.*) and moon-rats (*Echinosorex sp.*), it's the largest Erinaceidea ever lived (Plate 1). *Deinogalerix* occupied during the upper Miocene the Gargano Island, now part of the east coast of South Italy. And was part of the insular ecosystem kwon as "*Mikrotia fauna*" (*nomen novum* for *Microtia*, Freudenthal, 2006) after the endemic murid of the region.

The *Mikrotia fauna* was discovered at Gargano (Apulia, Italy) in 1969 by Freudenthal's team from the Rijksmuseum van Geologie en

Mineralogie (Netherlands), in the Miocene reddish clay (*terre rosse*). Among the most atypical species which composed the *Mikrotia fauna* there is the dwarf five horned deer *Hoplitomeryx matthei* (Leinders, 1984; Van der Geer, 2008), giant rodents as the murid *Mikrotia sp.* (Freudenthal, 1976) or the glirid *Sternomys sp.* (Daams & Freudenthal, 1985) and giant birds of prey as the eagles *Garganoaetus sp.* and the owls *Tyto sp.* (Ballmann, 1973). These species, *Deinogalerix* include, are endemics of Gargano at the genus level; this testified the long time isolation of this ecosystem.



Plat.1. Erinaceidea family. (A) *Deinogalerix koenigswaldi* Holotype RGM 177 777 & 779 (NNM, Leiden). (B) *Deinogalerix brevirostris* PU 100044 (DST, Torino). (C) *Echinosorex gymnura* 2007-422 (MNHN, Paris). (D) *Erinaceus europaeus* 1984 - 711 (MNHN, Paris). (E) PU 106955 (DST, Torino). (F) PU 106988 (DST, Torino).

Deinogalerix was attested for the first time by Freudenthal (1972), then Butler (1980) described five species and gave the following genus diagnosis: I^1 much larger than I^2 and I^3, I_3 absent; upper canine premolariform with two roots like P^1, P^2 and P_2; diastems between the teeth from C to P3; P3, P4 and the trigonid of M_1 enlarged, the other molars reduced; postglenoid part of skull shorter, face longer; mandible with small coronoid process, low condyle and a long angular process with a strong medial flange; vertebral centra comparatively short and broad. These features are more accentuated with the size increasing among species.

The unique sub complete skeleton found until now is the genus' and species' holotype of *Deinogalerix koenigswaldi*, the largest species with a skull up to 20 cm long (Plate 1A). *D. brevirostris* was his smaller contemporaneous. According with Butler phylogeny of *Deinogalerix*, base on the biochronology of Freudenthal (1976), the both previous species are the most derivate of there own evolutive lineages with *D. freudenthali*, the smallest specie, as common ancestor. *D. intermedius* (slightly larger than *D. Brevirostris*) and D. minor (slightly larger than *D. freudenthali*) are respectively the transition species leading to *D. koenigswaldi* and *D. brevirostris*. This model predicted a gradual size increasing along the time into two lineages from the oldest fissures Rinascita 1 and Biancone 1 where *D. freudenthali* was found to the youngest fissure San Giovannino where *D. koenigswaldi* and *D. brevirostris* were only and exclusively found. However, the variation of *Deinogalerix* has never been studied in detail, even though we know evolutive radiations occurs in island.

During the years 2000 the Dipartimento di scienze della Terra of the Università di Torino lead several excavation campaign in the Gargano *terre rosse*. Our study is focus on the new *Deinogalerix* material collected in aim to update the knowledge about this genus.

Regional, geological and chronological setting

The Thyrrhenian area's palaeogeography is mainly known through endemic faunal assemblages (Fig.1). The current knowledge does not allow sufficient resolution to determine maps of the evolution of the terrestrial and marine masses (Rook *et al.*, 2006). During the Late Miocene the Italy is divided into three major paleobioprovinces within the Tyrrhenian palaeo-archipelago (Masini *et al.* 2008): the paléobioprovince Tusco-sardenya, Calabria-Sicily and Abruzzi-Apulia. The latter is characterized by two major of Miocene sites each containing the endemic *Mikrotia fauna*: Gargano characterized by the continental deposits "Terre rosse" which partially fill the paleo-karstic fissures in the Mesozoic limestone substrate; and the tortonian lagoonal carbonates of Scontrone

(Abruzzo, Italy; Mazza & Rustioni 2008) where *Deinogalerix* and *Hoplitomeryx* were also found. This discovery enlarged the distribution area of the *Mikrotia fauna* until then restricted to Gargano.

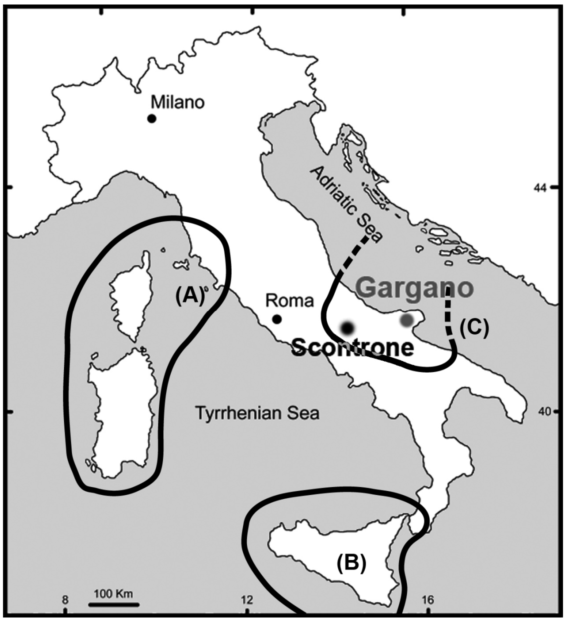


Fig.1. Palaeogeography of the Thyrrhenian area during the Miocene: paléobioprovince Tusco-sardenya (A), Calabria-Sicily (B) and Abruzzi-Apulia (C).

Our material is coming from the Miocene deposits filling the paleo-karstic fissures of the promontory of Gargano (Apulia, Italy) exposed in the limestone quarries between Apricena and Poggio Imperiale. The absolute age of the fossiliferous fissures of Gargano is still under debate. According with the stratigraphy (Abbazzi et al, 1996) these terrigenous deposits occurred during the late Miocene (Tortonian and Messinien) to the early Pliocene. At Pirro Nord some Miocene fissure were emptying and refilling by Plio-Pleistocene sediment rich in Villafranchian fauna. Some reworked *Deinogalerix* remains were found in the early layers of the succession.

A relative chronology of the fissures deposit was establish according with the evolution states of the *Mikrotia* base on size, hypsodonte level and number of cusp raw (Freudenthal, 1976; De Giuli et al, 1986). On this base the fissure San Giovannino was considered as the youngest one and Rinascita 1 and Biancone 1 as the oldest ones.

Our material was found in various fissures at Cava Pirro, Cava dell'Erba and Cava Chiro These fissures aren't yet integrated in the general bio-chronology. Cause of the quarrying work most of these fissures don't exist anymore.

Materiel and Methods

Our Deinogalerix material is composed by a sub-complete skeleton (Plate 2) and 77 isolate remains. The skeleton was found in the fissure *Mikrotia* 010 at Cava dell'Erba, without associated material. We give it a unique inventory number following by a secondary number (n) for each element. PU 100044-n.

The biggest part of the work concerned the skeleton. This skeleton is the second one ever found so it has a capital source of information for understanding the evolution of the genus. The work one has been divided in three main steps: preparation, reconstructions and anatomic description.

Fossil preparation

The highly fragmented skeleton required a long and meticulous preparation in particular for the skull. We use the acrylic resin paraloid B72 as coating and glue. For the skull we clean the brain case and reconstructed the sphenoid and occipital bones with half centimetre pieces. Then the maxillary were taking off and put back in anatomical position. Finally the brain case and the face were glued together.

Reconstruction

After preparation most of the bones were still uncompleted. Fortunately the missing elements of a bone were available on the opposite side homologous bone, so we could reconstruct virtually a complete bone by symmetry. As illustrated for the humerus (fig.2) we took pictures of the both bones in the same view. Then with the software Photoshop we constructed with different piece of bone a "chimera pictures" used after printing as drawing model. We realised drawing reconstructions following this methodology for most of the long bones (except for radio and ulna too much fractured; Plate 3)

For the skull we should used too the compared anatomy to reconstruct the premaxillary.

Additionally to the draw we performed a cast of the skull as it should been. Beforehand we model the missing part in wax easily removable at the end of the process. Moreover we made an endocast of the skull to get the morphology of the brain (fig.3).

Plat.2. Skeleton PU 100044.

Description

PU 100044.

Family ERINACEIDEA Fischer von Waldheim, 1817
Sub-family GALERICINAE Pomel, 1948
Genus *Deinogalerix* Freudenthal, 1972
Specie *brevirostris* Butler, 1980

The detailed description of the skeleton will be presented in a following paper; here we will give a brief description of the skull; adding descriptive elements will be given in results.

The skull (PU 100044-1) is relatively well preserved. It was preserved of the snoot part one fragment from the right premaxilla (PU 100044-6) with alveoli of I^1 and I^3, the right I^1 (PU 100044-2) and the left I^2 (PU 100044-3). In a general the left part of the skull is better conserved than the right part. It's missing the rights canine (C), P^2 and P^3. The base of the neurocrane and the cranial roof is fragmented. The right parietal is just represented by its rostral part which form the only portion of sagittal crest remained. It misses the internal face of the occipital and all the contact between parietal and occipital.

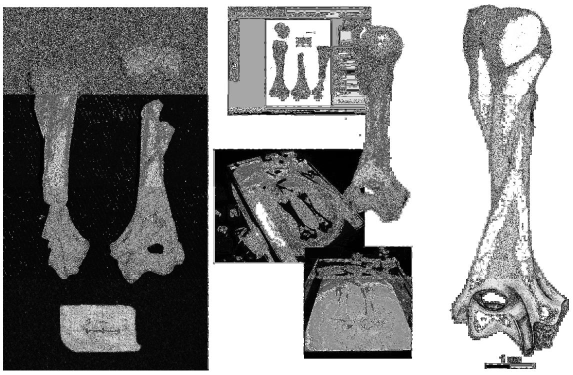


Fig.2. Steps of realisation for drawing plates.

On the both hemi-mandibles it miss the the part anterior to P$_1$. On the right one (PU 100044-4) the teeth row from the canine (c) to M$_3$ at the exception of the broken crown of P$_2$.The canine is isolated. The tip of the coronoid process (processus coronoideus) is broken and the lateral part of the condyle (*processus condyloideus*) is broken. On the left hemi-mandibles (PU100044-7) the teeth from P$_2$ to M$_2$ present, only miss the M$_1$ talonid. The coronoid and angular processes (*processus angularis*) and the median part of the condyle are broken.

Other material

Family ERINACEIDEA Fischer von Waldheim, 1817
Sub-family GALERICINAE Pomel, 1948
Genus *Deinogalerix* Freudenthal, 1972

On the other 77 remains, 4 are from larger specimen than PU 100044 and 65 are smaller than PU 100044. The material is principally composed by isolated teeth and long bones. Nevertheless we get maxillaries and mandibles from the smallest specimens with teeth in connections: PU 106954, left maxillary with P^4, M^1, M^2 and M^3; PU 106955, Left maxillary with P^3, P^4, M^1 and alveoli of P^2 and P^1 (Plate 1E); PU 106986, right maxillary with P^3, P^4, M^2 and alveoli of P^2, M^1 and M^3; PU 106988, left mandible with P$_4$, M$_1$, M$_2$ and M$_3$ (Plate 1F).

Results

Taxonomy

Our material was compared with the holotypes take at the Naturalis museum (Leiden, Netherlands). Most of our material could be determined: all the species are represented. The determination was mostly done according with size features cause of our fissure are not integrated inside the bio-chronology succession established by Freudenthal.

Nevertheless the taxonomic attribution of our smallest material remains problematic. All of them are smaller than *Deinogalerix freudenthali*. PU 106955 differs from the holotype in that: the hypocone is not divided into two smaller cusps; P2 longitudinal axe is slightly oriented linguo-bucally and not mesio-distally like in all other specimens; the palatine vault flatter. Moreover the mandibles were never described for *D. freudenthali*. The mature mandibles PU 106988 differ from the *Deinogalerix* material knows by the teeth proportion (M$_1$ is proportionally smaller), the wearing patter of the teeth (P$_4$ and P$_3$ are wearing), the shorter ascending ramus and the different morphology of the angular process.

The taxonomic attribution of the skeleton was also problematic. Due to the juvenile state of it we were constricted to do teeth comparison. The teeth size came inside the *D. brevirostris* and *D. intermedius* range. The both species differs by discrete size features unobservable on our specimen cause of the messing snoot or the immature state. The second difference between these species is the time repartition. *D. brevirostris* is supposed to occur in the later fissures deposit. To resume in fissures younger than San Giovannino we should find *D. brevirostris* and in the older ones *D. intermedius*. Unfortunately we are not allowed to date the fissure where was found PU 100044 cause of the missing associated microfauna.

We assumed that our specimen come under *Deinogalerix brevirostris* for the closer teeth size and cause of *D. intermedius* is only represented by mandibules and isolated teeth. The choice was also done to allow us to doubt about the linear evolution of *Deinogalerix*.

Juvenile features

The juvenile age of PU 100044 is attest by the epiphyses not fused, the teeth weakly worn; the I^1 in eruption (root not close; tip not worn) and the inter-sphenoid space don't close. During the preparation we didn't note any evidence of eruptive teeth (except for I^1) moreover all the teeth roots are closed. So we assumed that our specimen get his definitive denture. Comparing it with Deinogalerix material of Leiden we go further in juvenile features. We observed that on the juvenile specimens as well for *D. koenigswaldi* RGM 177777 and *D. brevirostris* PU 100044 the ascending ramus is proportionally shorter mesio-distally than the mature specimens and the angular process is shorter with muscular insertions less marked. The cranial distance between M^3 and glenoid fossa corresponding to the ascending ramus of the mandibule, is also proportionally shorter and there is no space between M^3 and the palatal ridge.

The specimen PU 106955 was again quite problematic the orientation of P^2 means that the snoot of PU 106955 was shorter. There are two hypotheses to explain this fact: it's an other specie, also support by the morphology of the hypocone of P^4; or the sorter snoot is a juvenile feature, it's mean that during the growth occur an elongation of the snoot at least for the small species.

Brain and sensorial system

We observed that the brain growth laterally in spit of longitudinally. On the external vault of the skull this lateral expansion is materialised by bulged squamosal bones, on the mature specimens the bulge out is less visible cause of the development of *muscle temporalis* insertion. The importance of the *paleopalium*, in particular of the pyriform cortex, compare to the *neopalium* is in part responsible of the brain's width shape. The pyriform cortex is involve in the olfactif sens. On actual Galericinea it's not so developed. The width size of the pyriform cortex in *Deinogalerix* should be an insular or ecological feature. In any case the *rhinarium* was an as important organ for this giant hedgehog as it's for the actual insectivores.

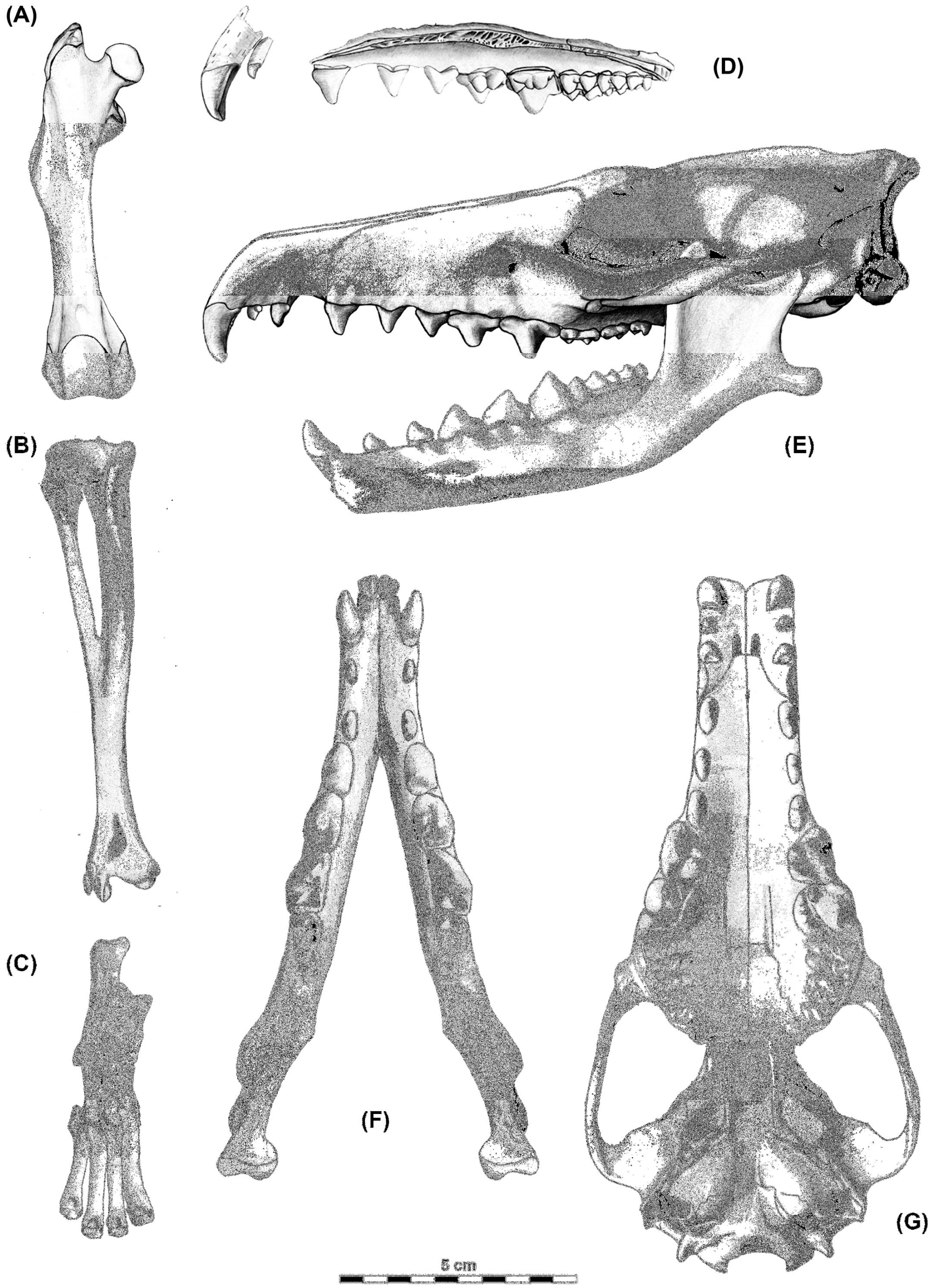
The inner part of the *petrosum* is also bigger than in actual species. With the large tympanic bulbs which occupied half space of the neuro-skull's ventral part. It's show that *Deinogalerix* has an acute hearing. This feature is commonly observed in species with low population density. That is not surprising to find it on insular specie like *Deinogalerix*.

The detailed comparison with the brain cast of *D. koenigswaldi* was impossible cause of the miss of resolution. But in preliminary observations the brain volumes seems to be closer than it was expected cause of the size differences between the species.

Like we saw before the inter-orbital constriction length increased during the growth. This part corresponds to the olvactive lobes of the brain. It's should be interesting to compare brain cast from matures and juveniles specimens to see if the growth affect also the brain development.

Mastication

The teeth of the snoot (upper C, P^1, P^2, P_1 and P_2) are similar, pointed and elongated and oriented mesio-distally. At the occlusion this teeth are not in contact. We presumed that this part has a prehensile function. P^4, P^3, P_4, P_3 and the trigonide of M_1 are massive and bunodonte. We note the analogy between the complex P^4/M_1 of Deinogalerix and the cutting complex of carnivores. The both teeth are the largest ones and for this raison they were considerate by the previous authors as principal functional complex. Nevertheless in spit of the carnassials analogy these teeth had a crushing function in spit of cutting function. The molars had cutting function assure by lateral movements of the mandibles. On each molar there are two transversal crests saw shaped. At the occlusion the interaction between the upper and lower crest by lateral shearing act like scissors. This fact is support by the wearing surface, the muscular insertion and the morphology of the mandible.



Plat.3. Plate 3: Drawing plates. (A) Right femur, frontal view. (B) Right tibiofibula, frontal view. (C) Right foot, dorsal view. (D) Right maxillary, median view (E) Skull and mandibles lateral view. (F) Mandibles, dorsal view. (G) Skull, ventral view.

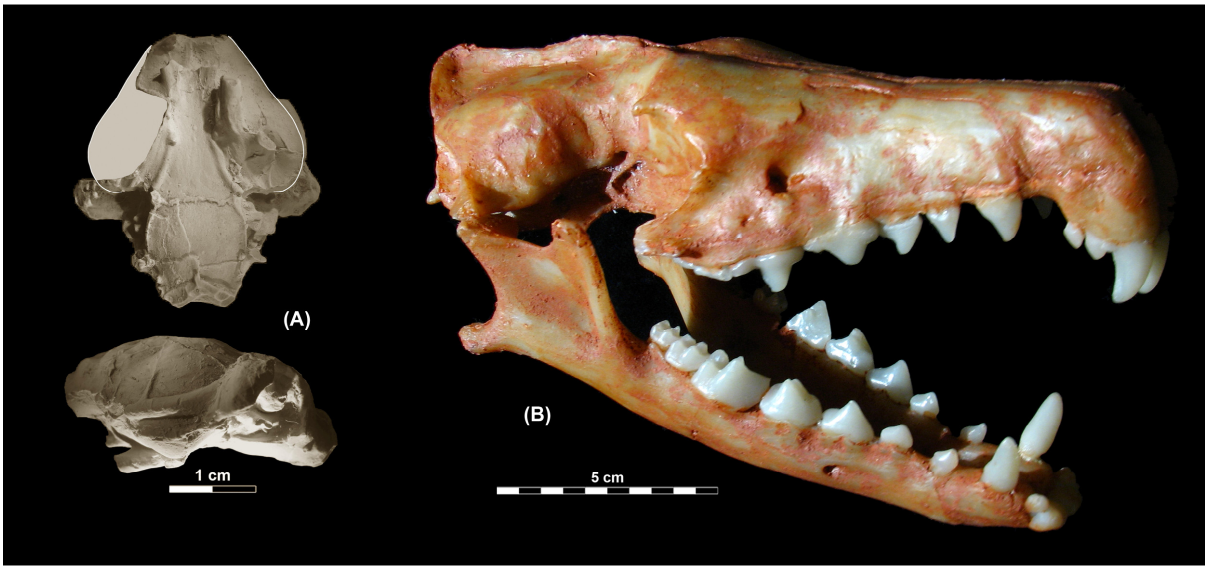


Fig.3. Cast pictures: endocast of PU 100044-1(A); reconstruction of the skull of PU 100044 (B).

The *muscle zygomatico-mandibularis* responsible of the transversal movement of the mandibles has a large surface of insertion on the median edge of the zygomatic arch, the lateral curvature of it increase the strange of the muscle. We note on the mandible and on occipital bone strong insertions for the *muscle digastricus* involve in lateral movements and antagonist muscle of the *m. temporalis*.

The *fossa glenoidalis* is flat so allowed a wider movement liberty of the condyle. The mandible's condyle has a median articulation surface, which articulated in the *processus post-tympanicus* (vertical, is borders medially the *fossa glenoidalis*) acts as pivot point.

This part of the masticator organ seems to be the most functional. On the mature specimens this cutting function of the molar is lost by extreme wearing. In the most advanced case the crown of the molars are worn until the roots while the premolars are slightly worn on the tip.
The little specimen PU 106988 has a wearing pattern different than all other *Deinogalerix* specimens described: the molar and premolar are homogeneously wearing.

Discussion

Deinogalerix was studied for the first and the last time in 1980 by Butler. Five species were described mostly on the base of chronological and size features. Since then the knowledge about insular fauna increased. We know that in insular context occurs evolutive radiation of the few colonizers and width intraspecific variations. That's why it's common to find on an island a large number of species for few families. With the new *Deinogalerix* material we start a revision of the genus and try to understand better this Giant Hedgehog.

The taxonomic determination remains problematic and doubtful cause of the missing data about the bio-chronology. In any case the addition of this material inside measurements' data set of *Deinogalerix* confirms a wide intraspecific variation also influenced by the maturation and probably by the sexual dimorphism. We observed a large overlapping in teeth size between *D. koenigswaldi* and *D. intermedius* and between *D. intermedius* and *D. brevirostris*. We can reasonably doubt about the reality of some species as *D. intermedius* which seems used as a "trash taxa". It should be more parsimonious to divide *Deinogalerix* in different morphotypes, as done for *Hoplitomeryx*, waiting for more information about this genus.

Butler evoked the fact that the masticator system of *Deinogalerix* was apt to fast mandibolar occlusion at the expense of the strength. We concord with these observations and we note morphological convergences between the ascending ramus of *Deinogalerix* and sabre-toothed tigers. Moreover we demonstrate that the laterally movement and molar are principally involve in the mastication.

The increasing length of the ascending ramus during the growth of juveniles *Deinogalerix* should play a role in the mandibolar strength. Deeper studies should be necessary to confirm and quantified the implications of this morphological change. We note also that the acquisition of the mature characters of the mandibles is following by a high wearing of the molars. There two hypotheses: this drastic change in wearing pattern is due to fossil gaps or to the insertion of harder aliments in the diet after weaning.

The ecological niche of *Deinogalerix* is still unclear. Microwear analyses on all species, as well juveniles as matures ones, are necessary to resolve these problems.

The particular case of PU 106955 and PU 106988 give us an ambiguous deal. The closest specie *D. freudenthali* is only knows by four isolated teeth supposed to come under the same individual. So the features of PU 106955 which differs from all the other material are they autapomorphic or due to the juvenile states? Moreover the mandible PU 106988 was never described before. These two specimens are they coming under a new specie or could they allow a redefinition of *D. freudenthali*? A comparative study with the material of Scontrone, where the presence *D. freudenthali* was attested, is necessary to resolve this deal.

Conclusion

The second sub-complet skeleton ever found is in itself a great discovery. This skeleton was totally restored and reconstructed. In this way we could obtain an objective anatomical description as complete as possible and divers detailed anatomic plate. This discovery will allowed us to made detailed anatomical comparison, also based on the post-cranial elements, between the both species *Deinogalerix koenigswaldi* and *D. brevirostris*.

This material allowed us to say that *D. brevirostris* and *D. koenigswaldi* weren't only present at San Giovannino; but didn't resolve the discussing question of the two lineages among the taxa cause of the inexistent chronology of our fissures.

We identified new juvenile features on the skull and discussed about the relation between growth and feeding behaviours.

Our collection contains the largest sample of the smallest morphotype of *Deinogalerix* only knows by four isolated teeth of *D. freudenthali*. Between these, the presence of an eventual new lineage was also testified by the specimens PU 106955 and PU 106988. In absence of spatio-temporally data we can't confirmed nothing. A comparative study with the material from Scontrone is necessary.

This new material provides elements for a better understanding of the evolutionary history of *Deinogalerix*. This preliminary study opens the way for a comparative study at larger scale, incorporating the material held in the collections of "Natuurhistorisch Nationaal Museum in Leiden (Holland), but also unpublished material in the collections of the University of Florence (Italy).

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