



New species of *Deinogalerix* (Mammalia, Eulipotyphla) from the late Miocene of Scontrone (Abruzzo, central Italy)

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ABSTRACT

Deinogalerix is a typical component of the late Miocene insular fauna of Gargano (south-eastern Italy). Remains of this taxon had also been found over the last 20 years at the early Tortonian site of Scontrone (Abruzzo, central Italy), but they had never been described in detail. Two new species are introduced. One of them, *D. samniticus* sp. nov., is larger sized and better documented, and received a formal description. The other entity is clearly distinct from *D. samniticus* sp. nov., but it is merely represented by a single mandible. It is therefore presented here as a different, but undetermined species, *Deinogalerix* sp. Comparative analyses show that the new species have exclusive dental proportions that distinguish them from all the other species of *Deinogalerix* and seem to exclude them from the direct ancestry of the Gargano clade. Consistent with its early stratigraphic age, *D. samniticus* sp. nov. bears a suite of primitive characters of the genus. Besides these, however, it also bears the autapomorphic relative proportion between p3 and p4.

The analysis of the erinaceids from Scontrone supports the assumption that *Deinogalerix* presumably descended from a hypothetical early – middle Miocene 'Parasorex-like' galericine. On the other hand, it seems to rule out the supposed common ancestry of the giant *Deinogalerix* and the small gymnure *Apulogalerix* from Gargano. Because the presumed ancestor of *Deinogalerix* dates back to the early – middle Miocene, the study corroborates the asynchronous colonization of the Apulia Platform.

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INTRODUCTION

The ‘terrible’ erinaceid *Deinogalerix* Freudenthal, 1972, was first described over 40 years ago from the Gargano Promontory (Apulia, south-eastern Italy). It was found associated with a variety of large and small vertebrate taxa, with different degree of endemization, which now form the so-called ‘Terre Rosse’ faunal complex, otherwise known as the ‘*Mikrotia* fauna’ (Freudenthal, 1971; Masini et al., 2010). This faunal complex was largely found in the infillings of a set of karstic fissures. It includes an array of biochronologically ordered assemblages extended over an evolutionary time period (Freudenthal, 1976; De Giuli et al., 1987; Masini et al., 2013). The fissures are carved through Mesozoic limestones in the area included between Apricena and Poggio Imperiale, in the province of Foggia (Savorelli and Masini, 2016; Savorelli et al., 2016, with references therein). The limestones are actively quarried, exposing the fissures.

In the early 1990s remains of a fauna similar to that from Gargano and also containing *Deinogalerix*, but more ancient (see below) and less

diversified, was found at Scontrone (Abruzzo, central Italy, Figure 1). The Scontrone and Gargano fossil records indicate the existence of a land, called the Apulia Platform, that has been repeatedly isolated from neighbouring mainland areas for long periods of time (Patacca et al., 2008a, 2008b, 2013). This land is an important natural laboratory for advancing our understanding of adaptation and evolutionary diversification of species in large islands (Freudenthal, 1971, 1976; De Giuli et al., 1987; Masini et al., 2010, 2013, and references within).

Deinogalerix is a multispecific genus. It was first described by Freudenthal (1972), based on an almost complete skeleton, which is the holotype of the largest species, *Deinogalerix koenigswaldi* Freudenthal, 1972. A few years later, Butler (1980) added four more species: *D. brevirostris* Butler, 1980, *D. intermedius* Butler, 1980, *D. minor* Butler, 1980, and *D. freudenthali* Butler, 1980. In that paper, Butler proposed a phylogeny of the genus, grounded on Freudenthal’s (1976) biochronology of the mammalian assemblages of Gargano, where the smallest species, *D. freudenthali*, is the com-

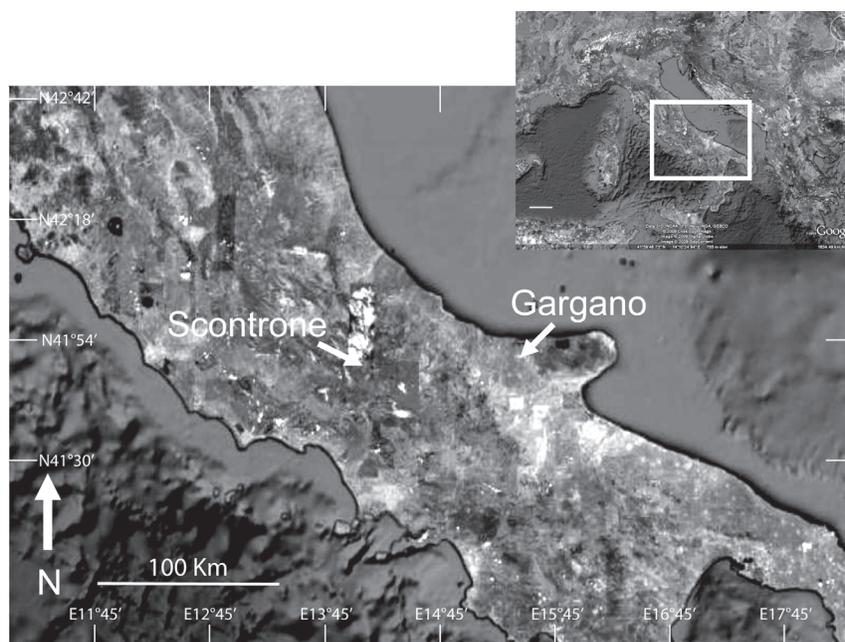


FIGURE 1. Location map of Scontrone and Gargano. From Mazza (2013a), modified.

mon ancestor to all the other species. According to Butler (1980, p. 36), two lineages stem from *D. freudenthali*: one includes the larger-sized representatives and leads to the advanced *D. koenigswaldi* through the transitional *D. intermedius*; the second passes through *D. minor* and ends with *D. breviostris*, which is coeval with, but smaller than, *D. koenigswaldi*. This scheme imposes an increase in size in both lineages, from the oldest to the most recent karstic fissure fillings.

Over forty years after Butler's (1980) monograph, Villier (2012) re-examined the taxonomy of the genus and downgraded *Deinogalerix freudenthali* and *D. minor* from species to morphotype rank, including them, together with a third *koenigswaldi*-morphotype, within the genus' type species *Deinogalerix koenigswaldi*. Villier et al. (2013) also introduced a new species, *D. masinii*, based on remains from the Gargano's most ancient fissure, M013 (Masini et al., 2013). Villier et al. (2013) remarked the morphological primitiveness of the new species, but excluded it from the direct ancestors of Butler's (1980) species. Villier et al. (2013, p. 74) reconsidered Villier's (2012) taxonomic revision and regarded the Gargano species of *Deinogalerix* described in Butler (1980) as a "...more modern [than *D. masinii*, note added by the present writers] group of *Deinogalerix* represented by *D. koenigswaldi* and *D. freudenthali* at the extreme." Later on, Villier and Carnevale (2013, p. 902) agreed with Villier et al. (2013) stating "[...] that only two former species [besides *D. masinii*, note added by the present writers] can be interpreted as valid: *D. koenigswaldi*, the largest, most derived, and most variable in size; and the smaller and less derived, *D. freudenthali*." Finally, Villier (2012) and Villier and Carnevale (2013) informed about a second, nearly complete skeleton of *D. koenigswaldi* from the fissure Mikrotia 010 at Cava dell'Erba (Gargano).

Butler (1980), van den Hoek Ostende (2001), and Ziegler (2005) worked on the genus' phylogenetic relationships, and McKenna et al. (1997) on its classification. All four of these studies agreed in including *Deinogalerix* in Galericipini. Butler (1980) thought that it derived from a still unknown gymnure from Asia, which he assumed was the most likely source area for these erinaceids. Butler (1980), however, rejected that *Deinogalerix* could be closely related either to the galericipines known at those times in Europe, or to *Lanthanותרium* Filhol, 1891, which he considered as a relative of modern moonrats of southern Asia. Van den Hoek Ostende (2001) assumed that *Deinogalerix* derived

from a middle – late Miocene 'Parasorex-like' ancestor and showed that *Deinogalerix* clusters with *Schizogalerix* Engesser, 1980, and *Parasorex* von Meyer, 1865, the latter including *P. socialis* von Meyer, 1865, *P. depereti* (Crochet, 1986), and *P. ibericus* (Mein and Martín-Suárez, 1993). Ziegler (2005) stated that *Deinogalerix* is sister taxon to *Schizogalerix* and *Parasorex*. Villier in Villier et al. (2013), although sharing the opinion that *Deinogalerix* stemmed from *Parasorex*, argued for an earlier forerunner than that supposed by van den Hoek Ostende (2001).

Deinogalerix was first reported from Scontrone by Mazza and Rustioni (2008), based on the fragmental right maxillary SCT 232, with associated M3 and fragmental M2. The two authors attributed the specimen to *D. freudenthali*, because of its apparent morphological primitiveness, relatively small size, and old stratigraphic age.

Several issues on the taxonomy of *Deinogalerix* are still unsettled. Butler (1980, p. 36) distinguished the different species of *Deinogalerix* based primarily on size, with the addition of only few morphological features. He stressed that the specimens from fissures FH, G1 and San Giovannino range too widely in size to be included all in one species, and supposed the co-existence of two different entities. Villier and Carnevale (2013) simplified Butler's (1980) taxonomy, as explained above. We find Butler's (1980) opinions fairly convincing and share many of his considerations. Hence, we adopt a conservative option and provisionally deem his species legitimate. *Deinogalerix* from Scontrone is thus compared with the species introduced by Butler (1980) and Villier et al. (2013) and described here as *D. samniticus* sp. nov. and as *Deinogalerix* sp. Besides SCT 232, all the other remains of *Deinogalerix* that have been recovered from Scontrone over the last 20 years have never been analysed in detail. In this paper we present a formal taxonomic description of these erinaceids, together with a discussion on their relation within the other species of the genus. Piecing together all the available information, we also address the issues of the potential continental origin of the genus, as well as of its dispersal to the Apulia Platform.

GEOLOGICAL SETTINGS AND ORIGIN OF THE FAUNA

The Scontrone faunal remains come from tidal-flat aeolian calcarenites at the base of the Lithothamnion Limestone, a Miocene carbonate ramp widespread in the central-southern Apen-

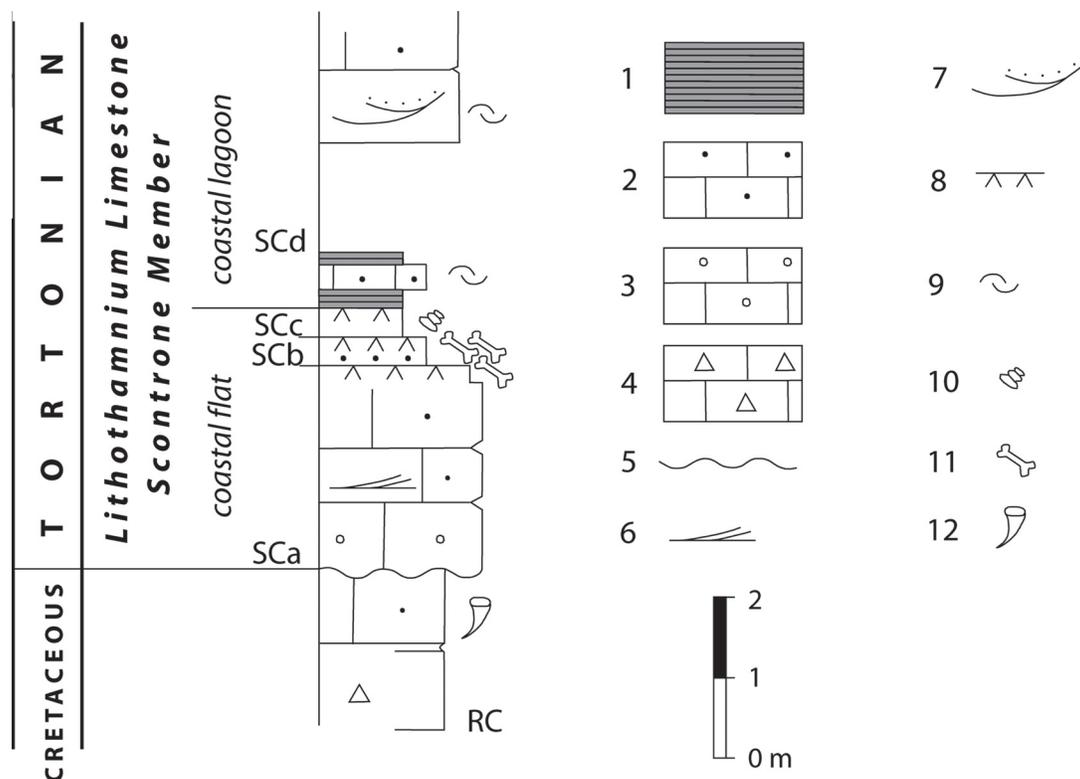


FIGURE 2. Schematic stratigraphy of the early Tortonian site of Scontrone (from Patacca et al., 2008a, modified). Succession showing the stratigraphic position of the bonebeds within the Scontrone Member of the Lithothamnium Limestone Formation. RC Rudist-bearing Calcarenites; SC Scontrone Member of the Lithothamnium Limestone Formation; SCa–SCd facies units of the Scontrone Member recording major shifts in the depositional setting and biotic associations (SCa = costal bar deposits; SCb = tidal creek deposits; SCc = marsh deposits; SCd = lagoon deposits). 1-Calcareous marls; 2-Bioclastic calcarenites; 3-Bioclastic calcarenites with oversized well-rounded lithoclast lags; 4-Lithoclastic calcirudites; 5-Major disconformity; 6-Low-angle cross-bedding; 7-Trough cross-bedding; 8-Root traces; 9-Oyster shell lags; 10-Hydrobiids; 11-Bonebeds; 12-Rudists. For further details see Patacca et al. (2008a).

nines. Based on its well-established stratigraphic location (Figure 2), the vertebrate bearing level is dated to about 9 m.y. (Patacca et al., 2013). In contrast, like for many other insular vertebrate assemblages from karstic fissure fillings, the age of the Gargano fauna is uncertain and hotly debated. It is notorious that fissure fillings can be exposed to reworking processes. Nonetheless, the Terre Rosse yielded a rich fossil record, quite coherent from the evolutionary viewpoint and from that of the composition of the assemblages. For this reason, reworking has been considered negligible (Masini et al., 2010). There is a general consensus that the fossiliferous fissure fillings are upper Miocene (Freudenthal et al., 2013; Masini et al., 2013; Savorelli et al., 2016), but unfortunately, the data available is of no aid in determining the exact chronology of the fauna within this time span. Over the years, the authors (e.g., Freudenthal, 1971; Agustí, 1986; De Giuli et al., 1987; Freudenthal

and Martín-Suárez, 2010; Freudenthal et al., 2013; Savorelli et al., 2016) dated the Gargano fossils relying on biostratigraphic-biochronological methods, which use the stratigraphic range of the presumed continental ancestors of the endemic taxa to set chronological constraints on the history of the insular faunas and of the fossil-bearing fissure fillings. A drawback of this method is that the different scholars (e.g., Freudenthal et al., 2013; Masini et al., 2013; Savorelli and Masini, 2016; Savorelli et al., 2016) dispute the identity of the continental ancestors, which does not contribute to a clear understanding of the origin and modes of colonization of the insular fauna.

The Terre Rosse karst fissures are locally sealed by late lower Pliocene marine deposits (Valleri, 1984; Abbazzi et al., 1996; Pavia et al., 2010), which impose an upper chronological constraint to the Gargano fossil records. Establishing their earliest age is far more problematic. They

were originally dated to a time older than the Serravallian by Freudenthal (1971) founded on the chronological attribution, erroneous at the time, of the marine deposits capping the karstic fissures.

The time of first arrival of the forerunners of the Gargano species has been variously dated as late Tortonian (Freudenthal et al., 2013), late Tortonian or early Messinian (Freudenthal and Martín-Suárez, 2010), Messinian (Freudenthal, 1985), and Messinian or early Pliocene (De Giuli et al., 1987). Hence, based on present knowledge, and until new convincing evidence will be published, the Scontrone fauna is to be considered more ancient than the Gargano assemblages.

Still discussed is the origin of the Scontrone-Gargano fauna and, more specifically, the number of events that gave rise to the endemic assemblages (Masini et al., 2010). One model theorizes that the fauna reached the Apulia Platform with a single colonizing event, or through several events very close in time (Freudenthal, 1971, 1985; Freudenthal and Martín-Suárez, 2006, 2010; van den Hoek Ostende et al., 2009; Freudenthal et al., 2013). The alternative model corresponds to Masini et al.'s (2002) so-called 'polyphasic' hypothesis, which assumes that the fauna is a palimpsest built up over time through a set of diachronous bio-events, which involve multiple (vicariant and/or dispersalist) mechanisms (Butler 1980; De Giuli et al., 1987; Mazza et al., 1995, 2009; Abbazzi et al., 1996; Mazza and Rustioni, 1996, 2008; Masini et al., 2002, 2008, 2010, 2013; Rook et al., 2006). Freudenthal et al. (2013) sponsor the single dispersal model and propose a Mammal Neogene (MN) zone 11 time frame for the colonization of the insular domain. In their opinion, this time period is the most suitable based on the overlapping ranges of distribution of the possible ancestors of the Gargano taxa. Nonetheless, the site of Scontrone is older (Patacca et al., 2013) than the time of colonization proposed by Freudenthal et al. (2013).

Supporters of the polyphasic model suggested the asynchronous dispersal of the Apulia Platform's colonizers. The ancestor of *Hoplitomeryx* arrived supposedly during the late Oligocene – early Miocene (Mazza, 2013b), that of the puzzling cricetid *Mystemys* during the MN 1-9 interval (Savorelli and Masini, 2016), that of *Apulogalerix* during the MN 9-10 time span (Masini and Fanfani, 2013), that of *Mikrotia* during the MN 11-13 time period (Tesakov, personal commun., 2016), and that of *Apatodemus* at the time of the MN 13 zone (Savorelli et al., 2016).

MATERIAL AND METHODS

Material

The material from Scontrone examined for this study consists of two fragmental right maxillaries (SCT 19, SCT 232), two fragments of horizontal rami of left hemimandibles (SCT 243, SCT 246), and a well preserved, isolated, left m1 (SCT 347). The specimens are stored at the Centro di Documentazione Paleontologica *Hoplitomeryx*, at Scontrone. The numerous remains of *Deinogalerix* found in Gargano over the past years and considered here, are now housed in the National Museum of Natural History (Naturalis) of Leiden (Netherlands) and in the Italian Departments of Earth Sciences of the Universities of Turin (DSTT) and Florence (DSTF).

The Scontrone material was compared with original specimens from the collection of the DSTF and casts made by the staff of the Naturalis. The comparative material of *Deinogalerix* is reported in Table 1. The casts are stored in the laboratories of the Archaeological Superintendency of Abruzzo (ASA) in Chieti. The material from the collection of Florence (fissures F15, F21c, P81D, NBS, F1, F8, F9) is stored in the DSTF. Pending future detailed analyses of the latter specimens, most of the remains from fissure F15 are here referred to as *D. freudenthali*, based on direct observations of their sizes and morphologies by the authors, but also on preliminary indications by Villier (2012). The material from fissures F21c, P81D, NBS, F1, F8, and F9, which is still not formally attributed taxonomically, has been also used for comparison purposes. These specimens permitted the formulation of the revised diagnosis of the genus included below.

Comparisons were also made with *Deinogalerix masinii*, from the fissure Mikrotia 013 (= M013), and *D. koenigswaldi* (PU100044), from the fissure Mikrotia 010, based on Villier (2012), Villier et al. (2013), and Villier and Carnevale (2013), where the extent of the morphological and size variability of these taxa is presented in detail. Fissures Mikrotia 013 and Mikrotia 010 are located at Cava dell'Erba, Gargano. The remains from these deposits are preserved at the DSTT.

Finally, comparisons were also made with uncatalogued specimens of *Parasorex socialis* and *Galerix exilis* from La Grive Saint Alban, but also of *Apulogalerix* from fissures F1 and F32 from Gargano. All these remains are preserved at the DSTF.

TABLE 1. Comparative material used for the present study; (h) = holotype; (p) = paratype.

Species	Deposit	Inventory	Description
<i>D. minor</i>	Fina H	RGM 178184 (h) cast	fragmental right jaw with p2-m3
	Gervasio 1	RGM 179174 (p) cast	fragmental left jaw with p3-m3
<i>D. intermedius</i>	Nazario 4	RGM 179063 (h) cast	fragmental left jaw with p3-m1
	Chiro 20 C	RGM 177982 (p) cast	fragmental right maxillary with P3-M2
<i>D. brevisrostris</i>	SG	RGM 179134 (h) cast	skull with right P1, both P2s, P3s, P4s, M1s, right M2-M3
	SG	RGM 179237 (p) cast	fragmental right premaxillary with I1, I3
	SG	RGM 179232 (p) cast	fragmental left jaw with p3-m2 (broken m1)
<i>D. koenigswaldi</i>	SG	RGM 177777 (h) cast	skull with both I1s, I3s, Cs, P1s, P3s, P4s, M1s, M2s, M3s and right P2
	SG	RGM 177778 (h) cast	fragmental left jaw with p1-m3
	SG	RGM 177779 (h) cast	fragmental right jaw with p1-m3
	SG	RGM 179194 cast	skull with right C, P1, P4 both P3s
	SG	RGM 179147 cast	fragmental right jaw with p3-m3
<i>D. freudenthali</i>	F15	F15-015	fragmental left jaw with p2-p4
	F15	F15-016	fragmental left jaw with m3
	F15	F15-031	isolated left p4
	F15	F15-032	isolated right M1
	F15	F15-033	isolated right M2
	F15	F15-034	isolated right m3
	F15	F15-036	isolated left M3
	F15	F15-037	isolated left M3
	F15	F15-038	fragmental left maxillary with P3-M2
	F15	F15-039	fragmental left jaw with m1, m3
	F15	F15-041	isolated right P4
	F15	F15-042	fragmental right jaw without teeth
	F15	F15-043	isolated right m1
	F15	F15-044	isolated right m2
	F15	F15-045	isolated right m2
F15	F15-046	isolated right p3	

Methods

Upper teeth are indicated with capital letters (e.g., M1, M2, M3), lower ones with lower case letters (e.g., m1, m2, m3). Figure 3 depicts the tooth nomenclature used in this paper. In the upper molars, the mesial cuspule between protocone and paracone, which is sometimes reported as paraconule in the literature, is here called protoconule following Engesser (1980). Moreover, the distal arm of metacone is indicated as metastylar crest (metastylar spur in Gould, 1995). We introduce in this paper the name postparacristid for the disto-lingual prologment of the paracone in p4–m1–3.

Measurements were performed using a Mitutoyo Dial Calipers and are expressed in millimetres. Size measurements are reported in Table 2. Length (L) and width (W) of the upper and lower teeth from Scontrone and of the specimens preserved in the DSTF have been measured following Prieto et al. (2010). In the lower teeth and in P3 and P4, W corresponds to Prieto et al.'s (2010) W2. In the third upper molar, L is the minimum length from the mesial border to the distal angle of the crown (L2 in Prieto et al., 2010; LmM3 in Masini and Fanfani, 2013). The measurements of the specimens kept in Naturalis and DSTT collections were drawn from Butler (1980), Villier (2012), and

TABLE 1 (continued).

Species	Deposit	Inventory	Description
<i>Deinogalerix</i> sp.	F21c	F21-001	isolated left M1
	F21c	F21-002	isolated right p4
<i>Deinogalerix</i> sp.	P81D	P81D-001	fragmental left jaw without teeth
	P81D	P81D-002	fragmental left jaw without teeth
	P81D	P81D-003	fragmental right jaw without teeth
	P81D	P81D-004	fragmental left jaw with m2-m3
	P81D	P81D-009	isolated left m1
	P81D	P81D-023	left jaw with p3
	P81D	P81D-024	left jaw with p3-p4
	P81D	P81D-025	fragmental right maxillary with P4
	P81D	P81D-026	isolated left P3
	P81D	P81D-027	isolated left p3
	P81D	P81D-028	isolated right p4
<i>Deinogalerix</i> sp.	NBS	NBS-001	isolated left p4
<i>Deinogalerix</i> sp.	F1	F1-006	isolated left P4
	F1	F1-007	isolated left P4
	F1	F1-009	isolated left m2
<i>Deinogalerix</i> sp.	F8	F8-040	left jaw with c, p3-m3 (broken m1)
<i>Deinogalerix</i> sp.	F9	F9-014	fragmental skull with left C, both P1s, P3s, P4s, M2s and M3s
	F9	F9-017	fragmental left maxillary with P1-P2, P4
	F9	F9-018	isolated left M1
	F9	F9-022	fragmental right jaw with p4

Villier et al. (2013). Butler (1980) did not report the analytical data of the remains of *Deinogalerix koenigswaldi*. The latter were therefore obtained from Villier (2012).

A Wild Heerbrugg microscope type 308700 was used for the morphological analyses. Photographs were taken with a Canon Powershot S70 and with a Panasonic Lumix DMC-TZ20 digital cameras, both mounted on a stand.

As explained in the introduction, we primarily adopted Butler's (1980) size-discrimination to distinguish the different species of *Deinogalerix*. Because the largest and smallest of Butler's (1980) species (i.e., *D. freudenthali* and *D. koenigswaldi*, respectively) are also the easiest to distinguish morphologically, they have been used as reference species for the differential diagnosis of the present paper. *D. samniticus* sp. nov. is also compared there with the most recently and very well-described species *D. masinii* (Villier et al., 2013).

SYSTEMATIC PALAEOONTOLOGY

Class MAMMALIA Linnaeus, 1758

Superorder INSECTIVORA sensu Novacek, 1986

Order EULIPOTYPHILA Waddell, Okada, and Hasegawa, 1999

Family ERINACEIDAE Fischer, 1814

Subfamily GALERICINAE Pomel, 1848

Tribe GALERICINI Pomel, 1848

Genus DEINOGALERIX Freudenthal, 1972

Type Species. *Deinogalerix koenigswaldi* Freudenthal, 1972 from the Messinian (latest Miocene) of Gargano (Apulia, south-eastern Italy), fissure San Giovannino (Foggia, south-eastern Italy; Freudenthal, 1972).

Included Species. *Deinogalerix brevisrostris* Butler, 1980; *Deinogalerix freudenthali* Butler, 1980; *Deinogalerix intermedius* Butler, 1980; *Deinogalerix minor* Butler, 1980; *Deinogalerix masinii* Villier et al., 2013; *Deinogalerix samniticus* sp. nov.

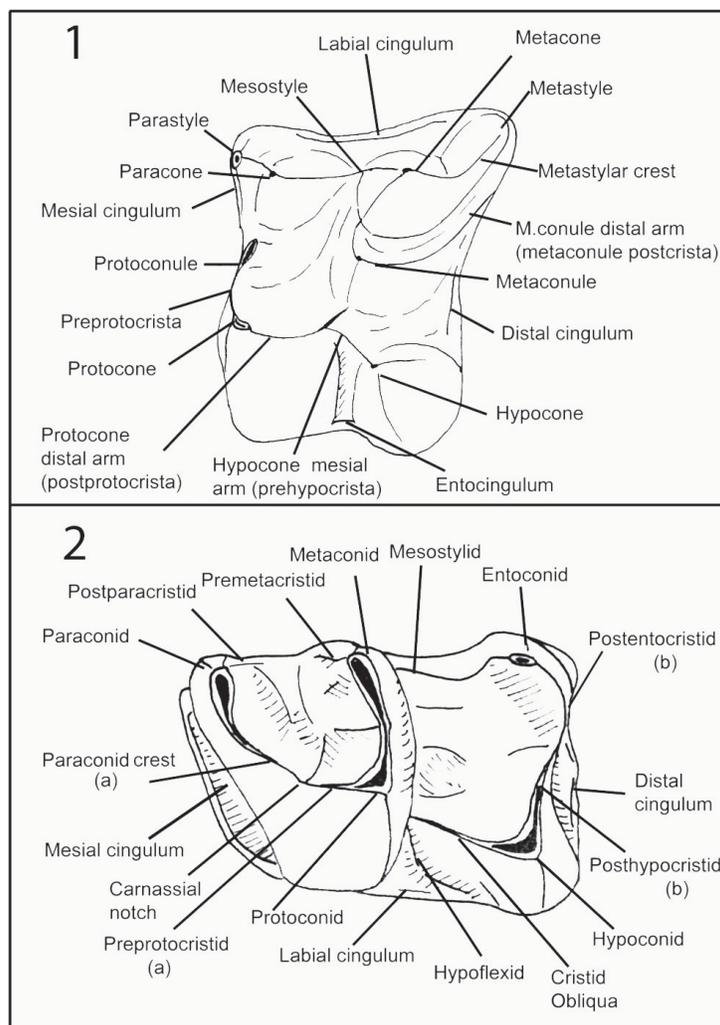


FIGURE 3. Guide to dental morphology terms used in this paper, drawn from Engesser (1980), Gould (1995), Lopatin (2006) by Masini and Fanfani (2013), and slightly modified here. **1**, Upper molar. **2**, Lower molar; (a) paralophid (paracristid) = paraconid crest + preprotocristid sensu Lopatin (2006); (b) postcristid (hypolophid) = postentocristid + posthypocristid sensu Lopatin (2006).

Distribution. Early Tortonian (early late Miocene) of Scontrone (Abruzzo, central Italy) to Messinian (late late Miocene) of Gargano (south-eastern Italy).

Original diagnosis. See Freudenthal (1972).

Emended Diagnosis (from Villier et al., 2013, p. 65). 'Large galericini; I1 much larger than I2 and I3; P3, P4, p3, p4, and the trigonid of m1 enlarged; posterior molars reduced; P3 and p4 bunodont; on p4 the trigonid is well-defined, the paralophid is absent or partially developed and the metaconid and the distal-ridge form a continuum via a bulbous metacristid; hypocone and protostyle on P3 invariably present; hypoconule present on P4; connection protocone-metaconule usually absent on M1 and M2; on M1 and M2 the postcrista of the

metaconule reaches the bucco-distal corner of the tooth, distal cingulum bipartitionated; mesostyle of M1 and M2 round and not divided; metastylar crest of M3 well-developed and inflated; mandible with small coronoid process and low condyle; supra-orbital processes present and formed by the frontal'.

Revised Diagnosis. Large galericini; I1 much larger than I2 and I3; P3, P4, p3, p4, and trigonid of m1 enlarged; posterior molars reduced; P3 and p4 bunodont; p4 with well-delineated trigonid, weak mesial part of paracristid, preprotocristid blunt, metaconid and distal cingulum joined by bulbous mesostylid; hypocone constantly present in P3; protocone and metaconule usually not connected in M1 and M2; in M1-2 distal cingulum interrupted, or distal arm of metaconule sometimes confluent

TABLE 2. Odontometrics of *Deinogalerix samniticus* sp. nov. and *Deinogalerix* sp. (SCT243). Measurement: L: length; W: width, Lm: minimum length (only M3), aL: alveolar length, H (m1, p2): height of mandible below m1 and p2, W m1: width of the mandible below m1. Italics: inferred value.

	Dental Measurements									
	L	W	L	W	L	W	L	W	L	W
	p3		p4		m1		m2		m3	
SCT246	8.8	5.0	12.1	7.6	12.25	/	6.5	/	5.8	/
SCT243	7.1	3.5	10	6.7	10.3	6.5				
SCT347					12.1	8				
	L	W	L	W	L	W	L	W	Lm	W
	P3		P4		M1		M2		M3	
SCT19	10.3	8.9	/	10.9						
SCT232									5.85	6.3
	Mandible Measurements									
	aL	aL	aL	aL	H m1	W m1	H p2			
	m1-m3	p2-p4	p4-p3	p4-p3						
SCT246	27.55	32.7	21.1	20.6	18.5	14.5	>15			

with uninterrupted distal cingulum (Figure 4.1-2); bulging and undivided mesostyle in M1 and M2; metastylar crest of M3 well-developed and inflated; supraorbital processes present and formed by frontal bone; mandible with small coronoid process, low condyle, and mental foramen under mesial root or between roots of p3.

Deinogalerix samniticus sp. nov.

Figure 5, Figure 6

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Diagnosis. Medium-sized *Deinogalerix* with proportionally very small p3 and large p4, p4 as long as m1. Trigonid of m1 broad, with mesiolingual bulge (Figure 4.3-4) dipping downward and protruding lingually. M3 with well-developed parastyle. Strong and continuous mesiolabial cingulum in m2. P3 narrow, with relatively small protocone. In p4 paraconid imperfectly defined and trigonid valley closed lingually (Figure 4.5-6).

Differential Diagnosis. *Deinogalerix samniticus* sp. nov. differs from all the other species of *Deinogalerix* by having proportionally a smaller p3 and a larger p4. Compared to *D. koenigswaldi*, *D. samniticus* sp. nov. has smaller overall size; smaller p3, m1, and m2; cheek teeth lower-crowned, imperfectly divided protocone-hypocone in P3 (Figure 4.7-8); lower protocone in P4; more acute anterolabial corner in M3; lingually-closed trigonid basin and less-defined paraconid in p4; m1 with broad, trigonid not concave lingually, and with mesiolingual bulge dipping downward and protruding lin-

gually; strong and continuous mesiolabial cingulum in m2; labially-prominent hypoconid in m3.

Deinogalerix samniticus sp. nov. differs from *D. freudenthali* by being larger sized, but also by possessing: larger p4 and m1; slightly more bunodont teeth; M3 with faint protoconule and more developed parastyle; trigonid of m1 with slightly lower lingual enamel wall and mesiolingual bulge dipping downward and protruding lingually; m2 with longer mesiolabial cingulum.

Deinogalerix samniticus sp. nov. differs from *D. masinii* by having: larger teeth (especially p4 and m1); smaller protocone, imperfectly divided protocone-hypocone and not well defined parastyle in P3; faint protoconule and more developed parastyle in M3; stronger and longer mesiolabial cingulum in m2.

Etymology. After the Samnites, an Italic people living in Samnium, the ancient region where Scontrone is located. Because the genus *Deinogalerix* is masculine (Zijlstra and Flynn, 2015), the species name is treated here as masculine.

Synonymy. 2008, *Deinogalerix freudenthali*, Mazza and Rustioni, p. 209, figure 6. 2013, *Deinogalerix freudenthali*, Villier et al., p. 64.

Material. Holotype: SCT 246, fragment of horizontal ramus of left hemimandible, still partly embedded in rock, preserving p3, p4, alveoli of p2, and most of the molar row, except m1, which is largely broken (Figure 5.1-2, Figure 6). Paratypes: fragmental right maxillaries SCT 232, with M3 and postero-lingual portion of M2 (Figure 5.8), and SCT 19,

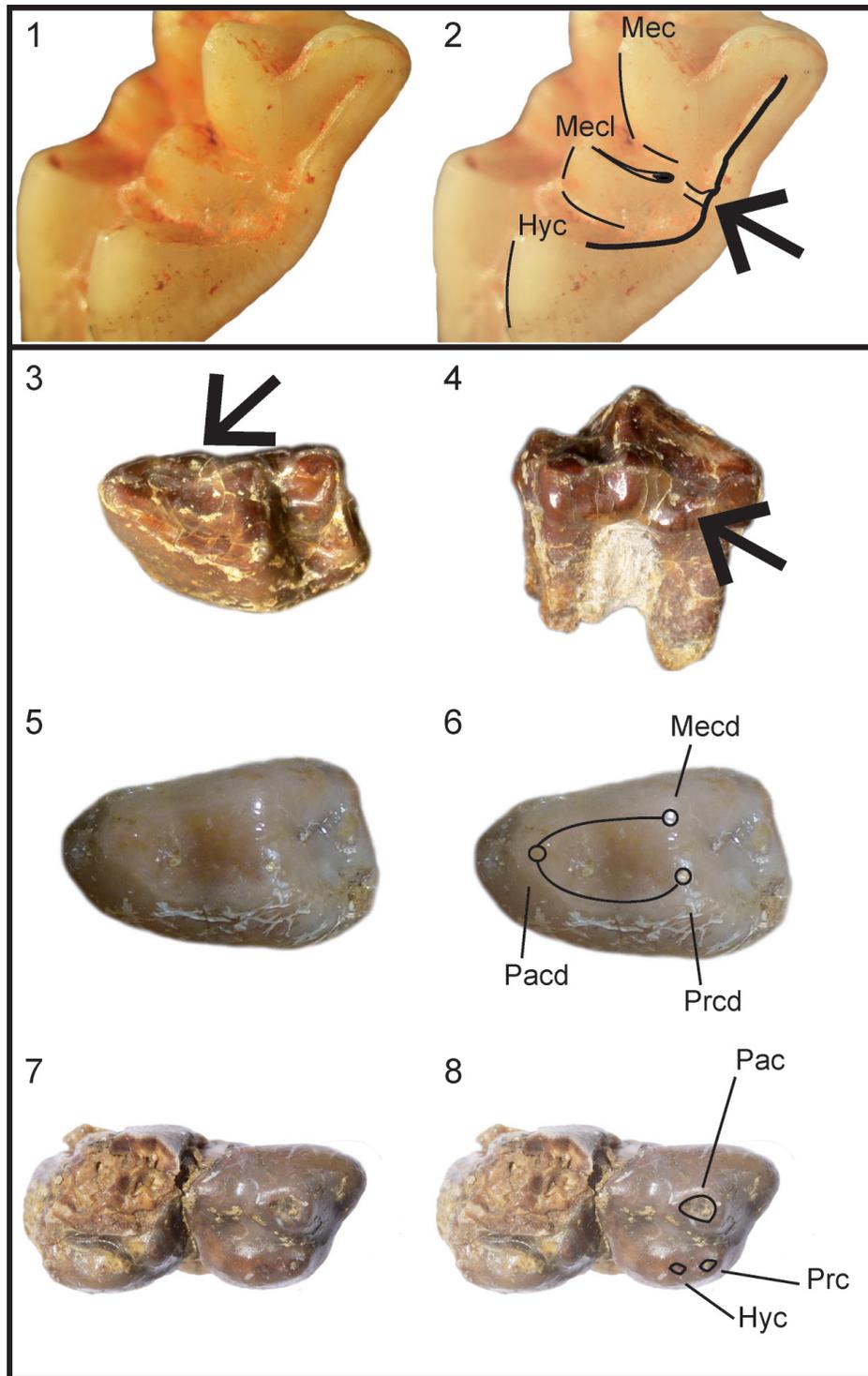


FIGURE 4. 1, Left M1 (F9-018), undetermined *Deinogalerix* sp. from fissure F9, oblique, occluso-distal view. 2, same as 1 with sketch showing contact of the distal arm of the metaconule with the uninterrupted distal cingulum. 3, left m1 (paratype SCT 347), *Deinogalerix samniticus* sp. nov., occlusal view. 4, same specimen as 3, lingual view. Arrows in 3 and 4 showing mesiolingual bulge. 5, left p4 (holotype SCT 246), *Deinogalerix samniticus* sp. nov., occlusal view. 6, same as 5, with sketch showing roundish, delimited lingually, trigonid valley. 7, right P3-P4 (paratype SCT 19), *Deinogalerix samniticus* sp. nov., occlusal view. 8, same as 7 with sketch showing the weak separation of protocone and hypocone. Hyc = Hypocone, Mecl = Metaconule, Mec = Metacone, Mecl = Metaconid, Pac = Paracone, Pacd = Paraconid, Prc = Protocone, Prcd = Protoconid. Figures not to scale.

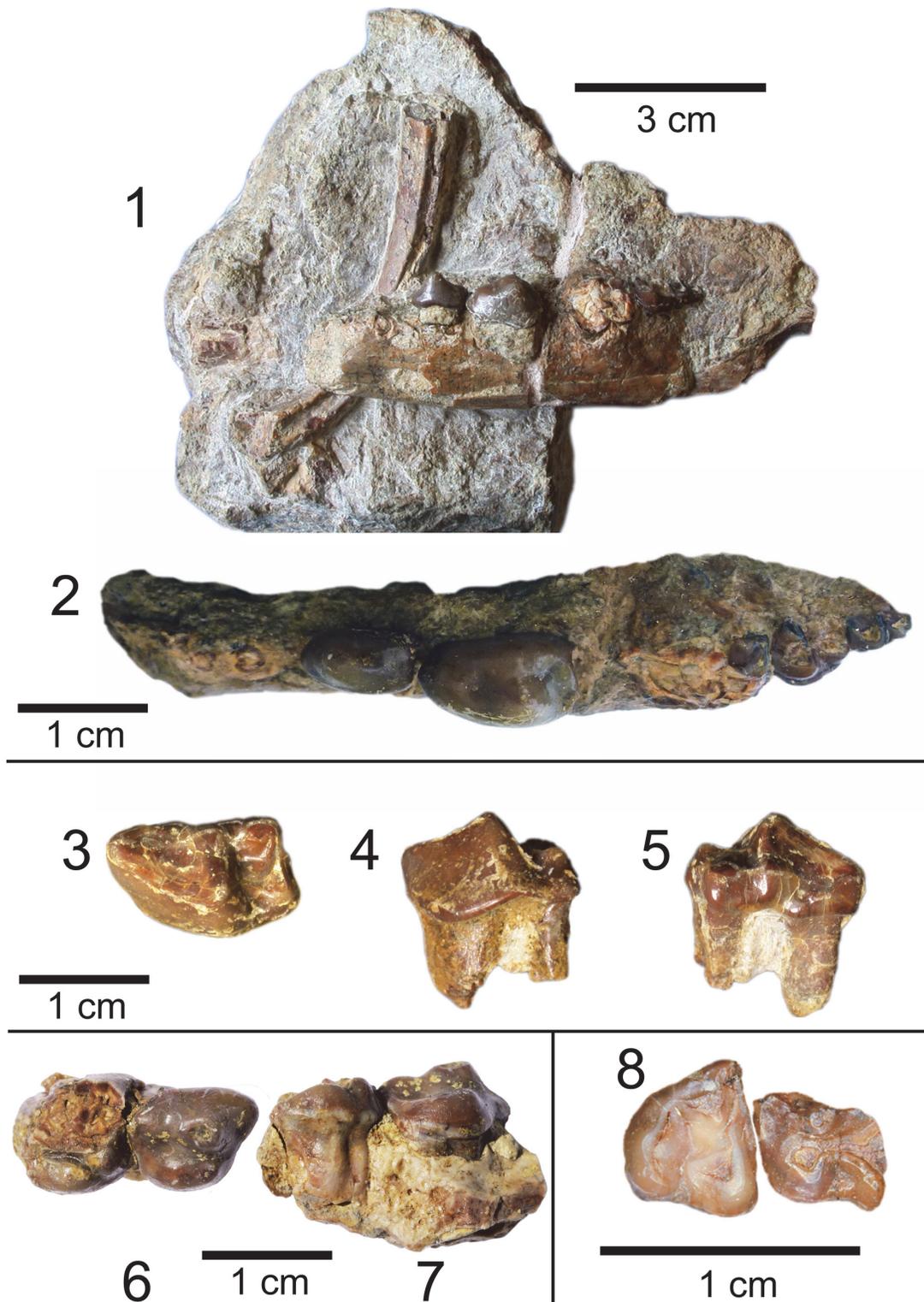


FIGURE 5. *Deinogalerix samniticus* sp. nov., from Scontrone. **1–2**, Holotype, fragment of left hemimandible, with p3, p4, alveoli of p2, broken m1, m2, and m3 partially embedded in the rock (SCT 246). **1**, labial view; **2**, occlusal view. **3–5**, Paratype, isolated left m1 (SCT 347). **3**, occlusal view; **4**, labial view; **5**, lingual view. **6–7**, Paratype, fragmental right maxillary with complete P3 and fragmented P4 (SCT 19). **6**, occlusal view; **7**, lingual view. **8**, Paratype, fragmental right maxillary, with M3 and postero-lingual portion of M2 (SCT 232).



FIGURE 6. 1–3, Holotype SCT 246 during its preparation from the rock matrix by vibrotool. The figure shows the pre-molars still partially encased in the rock matrix.

with complete P3 and fragmented P4; left m1 SCT 347.

Type Locality. Outskirts of Scontrone, southern border of the National Park of Abruzzi, L'Aquila, central Italy (41°45'15.54"N, 14°2'13.14"E).

Horizon. Scontrone Member, *Lithothamnion* Limestone.

Age. Lower Tortonian (lower upper Miocene) (Patacca et al., 2008b).

Measurements. See Table 2.

Description SCT 246 (Figure 5.1-2). Fragment of horizontal ramus of left hemimandible still partly embedded in rock. Specimen broken in front of p2 alveoli and aborally to m3, but still preserving p3, p4, alveoli of p2, and most of the molar row, except m1, whose dental crown is largely broken. Mesial root of p2 slightly smaller than distal one. Tooth presumably somewhat smaller than p3 based on relative proportion of roots. In ventral view (specimen not observable in medial view) distal end of mandibular symphysis extended to mesial root of p3. Mental foramen located under mesial root of p3 and elongated mesially by groove. Horizontal ramus particularly thick latero-medially under molar section.

p3. Unworn, blunt, fairly low-crowned, dominated by protoconid triangular and symmetrical in side view. Metaconid absent. Labially, protoconid relatively swollen at the base. Two roots apparently straight and not divergent mesio-distally from one another. In occlusal view crown with sub-oval outline and with talonid represented by blunt and small cuspule, prominent disto-lingually. p3 narrower and markedly smaller than p4 (Table 2) and separated from alveoli of p2 by short diastema.

p4. Moderately worn, large, and massive, quite more massive and larger than p3. Occlusal profile sub-oval, slightly wider distally, distal margin of tooth straight and transverse labio-lingually to horizontal ramus. Crown formed mesially by three

fairly low and blunt cuspids, i.e., paraconid, protoconid, and metaconid. Protoconid dominant, metaconid somewhat lower than protoconid. Cleft between protoconid and metaconid clearly visible distally. Paraconid robust and low mesially. Protoconid connected with paraconid by blunt and low paralophid. Trigonid valley roundish, very shallow, and delimited lingually by very blunt and robust mesial border of metaconid (premetacristid?) and postparacristid. Distal side of crown slightly concave, distal cingulum very inclined labially and bearing small cuspule disto-lingually. Metaconid with bulbous disto-lingual mesostylid fused with cingulum.

m1–m3. Molars in typical fashion of *Deinogalerix*. Crown of m1 almost completely broken, with only entoconid, mesio-labial part of cingulum, and general outline of crown preserved. m2 and m3 largely visible, except entoconid of m2 and part of lingual enamel wall and of entoconid of m3, still embedded in rock. m1 largest tooth (approximately same length as p4) with very elongated trigonid. m2 and m3 quite worn. m2 much smaller and with shorter trigonid than m1, m3 slightly shorter, but quite more slender than m2. m2 with strong continuous mesial and labial cingulum prolonged distally to base of hypoconid. m3 with relatively narrower talonid than m2, hypoconid prominent labially, robust mesial cingulum, small labial cingulum at hypoflexid, from which issues very small enamel pillar.

Specimen SCT 347 (Figure 5.3-5). Two-rooted left m1, well preserved, but rather worn. Marked disproportion between trigonid and talonid, typical of *Deinogalerix*. Trigonid with dominant, high and continuous, blade-like paralophid, formed by fusion of paraconid crest and preprotocristid, carnassial notch lacking. Lingual wall of trigonid high. Mesial part of lingual enamel wall between paraconid and metaconid (i.e., postparacristid) slightly protruding lingually forming a mesiolingual bulge (Figure 4.3-

4) and dipping downwards towards collar. Upper margin of lingual enamel profile indented by wear at distal end of postparacristid. Metaconid and protoconid transversally aligned in occlusal view. Talonid narrower and much lower than trigonid. Hypoconid low and connected mesially with protoconid by cristid obliqua and lingually with entoconid by postcristid. Entoconid slightly higher than hypoconid. Hypoconulid absent. Presence of faint labial cingulum. Weak and short distal cingulum, not connected with postentocristid. Enamel much thinner in trigonid than in talonid. Mesial root much larger than distal root.

Specimen SCT 19 (Figure 5.6-7). Fragmental right maxillary with complete P3 and fragmented P4.

P3. Bulbous tooth with typical *Deinogalerix* morphology. Trapezoidal outline, with labio-distal margin slightly inclined lingually. Crown very low and blunt, dominated by large and high paracone, placed in labial position. Shallow depression separating paracone from small, distally prominent metastyle (metacone of Villier and Carnevale, 2013). Tooth elongated mesially by shoulder-shaped parastyle. Lingual side of tooth formed by protocone-hypocone complex. Small protocone and large hypocone, separated by very shallow depression, which is rapidly obliterated by wear (Figure 4.7-8). Based on wear pattern, protocone apparently slightly higher than hypocone. Hypocone bulbous, elongated and declining gently towards distal margin of crown, where it prolongs in cingular fashion. Lingual root with faint furrow not extended to lingual enamel wall, which appears complete.

P4. Only mesio-lingual half of tooth preserved. Larger than P3, with small mesio-lingual protocone. Differs from P3 by having shallow notch between protocone and crest-like hypoconal structure. Notch opens in valley between paracone and lingual cusps. Evident groove in lingual root, which corresponds to separation between protocone-hypocone.

Specimen SCT 232 (Figure 5.8). Fragmental right maxillary, with M3 and postero-lingual portion of M2.

M2. Hypocone only cusp preserved. Mesial arm of hypocone connected with distal arm of protocone, distal arm of hypocone lacking. Metaconule partially preserved and well developed, placed in more mesial position than hypocone. Fragment of distal arm of metaconule apparently still preserved. Short entocingulum in valley between hypocone and pro-

tocone. Protocone and metaconule separated. Enamel thick.

M3. Sub-triangular outline. Mesial margin almost straight, disto-labial margin markedly arched, lingual margin slightly concave. Tooth somewhat broader than long. Protocone larger than all other cusps of tooth, and prolonged labially in narrow preprotocrista, which bears very reduced protoconule extended towards antero-lingual corner. Paracone connected with well-developed parastyle. Parastyle projected mesiolabially and labial margin of paracone slightly concave. Angle between mesial and labial margins of crown acute. Metacone strongly shifted to disto-lingual position, disto-labial part of tooth with distal arm of paracone and metacone joined to form continuous and arched crest, ending in inflated metastylar crest, separated from distal arm of protocone. Trigon valley deep and opened lingually. Very short entocingulum at outlet of the trigon valley. Short mesial cingulum. Protocone with flat wear surface. Enamel thick.

Comparison. The specimens from Scontrone have the typical characters of the genus: very large size, enlarged P3, P4, p3, p4, and trigonid of m1, very reduced m2 and m3, bunodont P3 and p4, well-developed metastylar crest in M3. Nonetheless, a number of differences exclude these teeth from those of all the known species. In particular *Deinogalerix samniticus* sp. nov. has a set of unusual dental proportions. Its middle-sized mandible bears a proportionally very large p4 (as large as those of *D. intermedius* and *D. koenigswaldi*), smaller p3 (in the size ranges of *D. freudenthali*, *D. minor*, and *D. brevirostris*), and large m1 and M3 (see Figure 7, Figure 8, Table 3, Table 4, Table 5).

Morphologically, the occlusal outline of p3 is somewhat less stretched disto-lingually than in the other species. The crown of p3 is lower than in *D. koenigswaldi* (RGM 179147, 177778, 177779) and than in the specimens of *Deinogalerix* sp. from fissures F8 and P81D.

In p4, the difference in height between the protoconid-metaconid complex and the paraconid is similar to that visible in the p4s of *Deinogalerix freudenthali* from F15 and *D. masinii*; it is somewhat lesser in the p4s of the other species of *Deinogalerix*. The paraconid is also less well-identified than in other species, but it is connected with the metaconid and protoconid, similarly to *D. freudenthali* from F15. In contrast, the paraconid tends to be more isolated in all the other species (*D. masinii* included). In labial view, the profile of the distal face of the protoconid is less steep than in *D.*

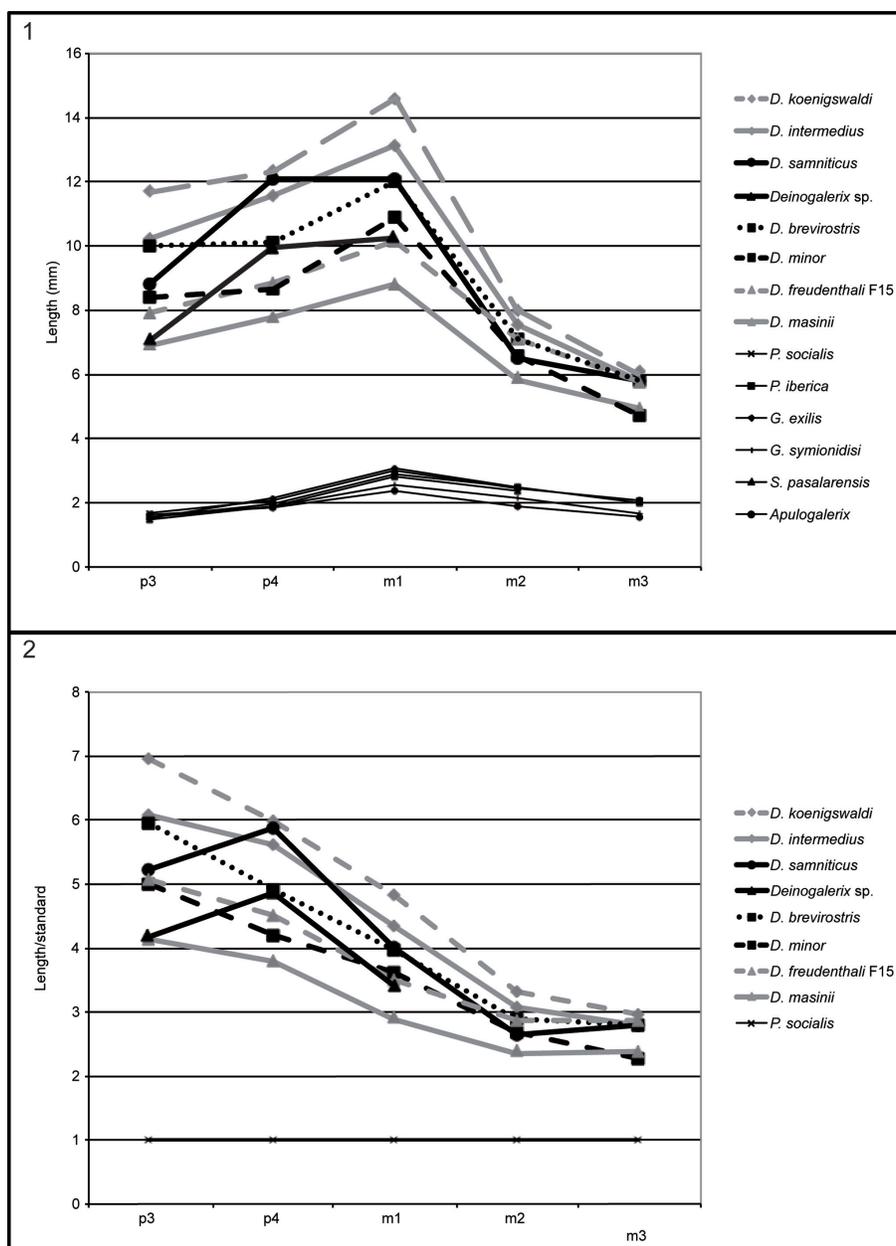


FIGURE 7. Comparisons of p3–m3 lengths in the different species of *Deinogalerix*, as well as in *Parasorex*, *Galerix*, *Schizogalerix*, and *Apulogalerix* (measurements and abbreviations in Table 3). **1**, The graph shows that in *Apulogalerix*, *Parasorex* and other continental galericines molars grow progressively larger towards m1, which is the largest tooth of the row. The fourth lower premolar is larger than p3, which, in contrast, is the smallest of the toothrow (it is somewhat smaller than m3). Compared to the mainland counterparts, *Deinogalerix* bears a very large m1 (due to the increase of the trigonid length) and larger premolars, that grow progressively smaller moving rostrally, but less than in the continental genera (p3 intermediate in size between m1 and m2). The Scontrone specimen shows the size increase from m3 to m1 typical of *Deinogalerix*. In contrast, it bears a very large p4, similar in size to m1 and in the dimensional ranges of *D. koenigswaldi*, and a very reduced p3, more similar to those of the smaller and more primitive species of *Deinogalerix* from Gargano. **2**, Ratio diagram comparing the p3–m3 lengths (see Table 4) in *Deinogalerix samniticus* sp. nov. with other species of *Deinogalerix*, using *Parasorex socialis* from La Grive as the standard (horizontal line). All the *Deinogalerix* specimens show a similar trend where the proportions of m2 and m3 are parallel to the standard, whereas, starting from m1, the teeth proportionally increase in size respect to the standard. It is noteworthy that this trend reaches its maximum expression in *D. koenigswaldi*. Compared to the other species of *Deinogalerix*, the curve of *D. samniticus* sp. nov., shows a steeper rise toward p4, and it is the only one that drops toward p3.

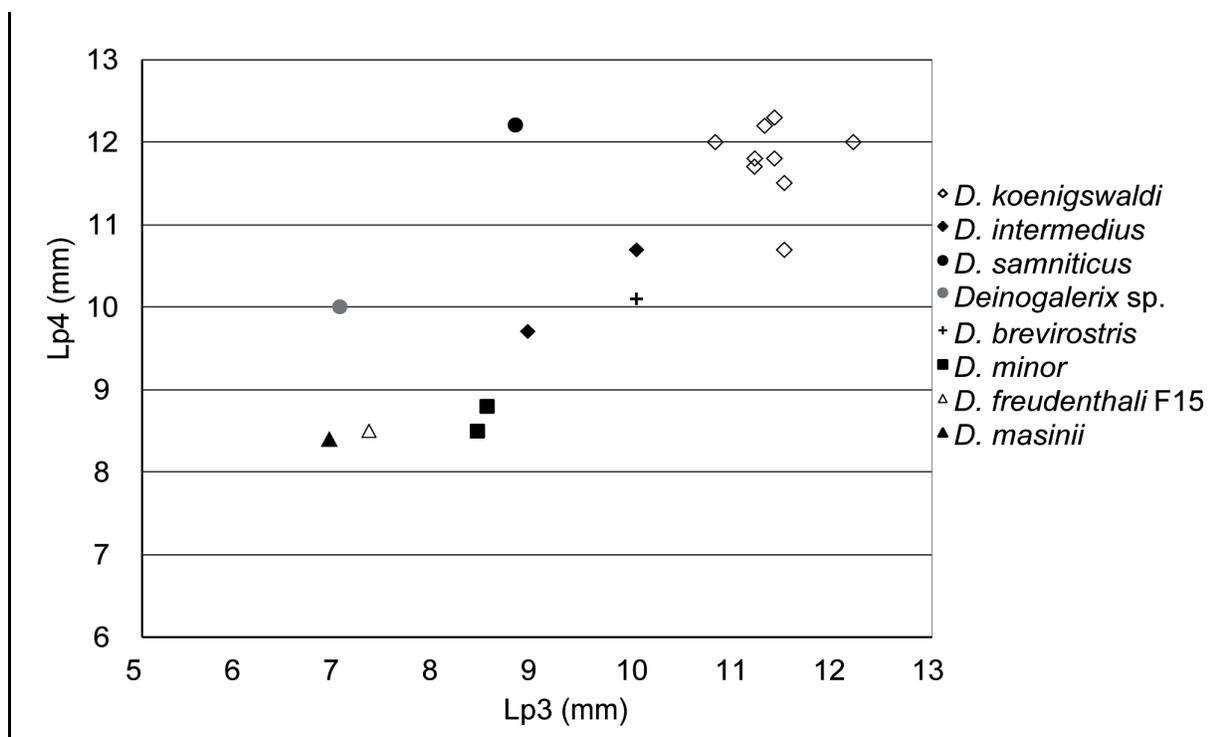


FIGURE 8. Scatter plot of Lp4 vs Lp3 (values in Table 5) for the species of *Deinogalerix*. The *Deinogalerix* specimens from Gargano align roughly in a linear trend. *D. samniticus* sp. nov. and *Deinogalerix* sp., in contrast, display an anomalously short p3. It is worth noting that also the smaller and more primitive species, e.g., *D. freudenthali* from F15 and *D. masinii* from M013, have fairly short p3s. Measurements in mm.

koenigswaldi and closer to *D. freudenthali* from F15.

The lingual side of the m1 of *Deinogalerix samniticus* sp. nov. is characterized by the downward dip of the enamel margin of the mesiolingual bulge, which causes an unusual wear pattern. In all the other species but *Deinogalerix masinii*, this enamel profile is continuous and straight. In *D. masinii* the mesiolingual bulge never dips downward and lingually as much as in *D. samniticus* (Villier, personal commun., 2015). Because of the mesiolingual bulging, in occlusal view the trigonid of m1 of *D. samniticus* appears somewhat broader than those of the m1s of most of the other species, which in contrast have an outline more concave lingually. Without detailed descriptions of this feature at hand, inspection of Villier et al.'s (2013) figure 3 suggests that also the m1 of *D. masinii* has a broad trigonid. m1 is relatively lower-crowned than in the more advanced species (e.g., *D. koenigswaldi*). In *D. samniticus* sp. nov. the talonid is proportionally longer than in *D. koenigswaldi*. It does not present a mesial and labial cingulum at the base of the trigonid, as in the other species except *D. masinii*.

The m2 of *Deinogalerix samniticus* sp. nov. has a strong and continuous mesio-labial cingulum that extends distally to the base of the hypoconid. A similar, but shorter cingulum is possessed by all the small species of *Deinogalerix* (i.e., *D. freudenthali* and *D. masinii*). This cingulum is generally weaker and discontinuous, and only sporadically uninterrupted (i.e., PU 100044: Villier and Carnevale, 2013) in *D. koenigswaldi*.

The m3 of *Deinogalerix samniticus* sp. nov. is bounded by a stronger cingulum than in the other species. In *D. koenigswaldi* this cingulum is virtually absent. m3 of *D. samniticus* sp. nov. has a hypoconid prominent labially, similar to that of *D. freudenthali* and *D. masinii*. In contrast, *D. minor* and *D. koenigswaldi* have a less prominent hypoconid, which gives the tooth a more rounded disto-labial outline.

P3 is lower-crowned than in the other species. It is proportionally somewhat narrower than in *D. masinii* and *D. koenigswaldi*. The protocone is very small. It falls, dimensionally, at the lower end of the size ranges of the genus. RGM 177982 (paratype of *D. intermedius*) and a specimen from fissure Pirro 81/D (P81/D-026) possess P3s with proto-

TABLE 3. Basic statistic parameters of lengths in mm of lower teeth (p3-m3) of the different *Deinogalerix* species, as well as in *Parasorex*, *Galerix*, *Schizogalerix*, and *Apulogalerix*. The mean values of *Apulogalerix* are actually grand means (i.e., mean of the means) of six different populations. The ranges have been approximated to the decimal digit to make them comparable to those reported by Butler (1980) and Doukas (1986). N = number of specimens; \bar{x} = mean values; σ = standard deviations. * Inferred from diagrams and figures. Raw data for Figure 7.1.

Genus Species	Locality	Source	Length							
			p3				p4			
			N	\bar{x}	σ	range	N	\bar{x}	σ	range
<i>Deinogalerix</i>										
<i>D. masinii</i>	M013	Villier, 2012; Villier et al., 2013	6	6.97	0.225	6.6-7.2	5	7.82	0.559	6.9-8.4
<i>D. freudenthali</i>	F15	This paper	2	7.90	0.849	7.3-8.5	2	8.85	0.495	8.5-9.2
<i>D. minor</i>	Various fissures	Butler, 1980	3	8.40	0.100	8.3-8.5	2	8.65	0.212	8.5-8.8
<i>D. brevirostris</i>	SG Low	Butler, 1980	1	10.00	/	/	1	10.10	/	/
<i>D. samniticus</i>	Scontrone	This paper	1	8.80	/	/	1	12.10	/	/
<i>Deinogalerix</i> sp.	Scontrone	This paper	1	7.10	/	/	1	10.00	/	/
<i>D. intermedius</i>	Various fissures	Butler, 1980	6	10.23	0.728	8.9-11	7	11.56	1.108	9.7-12.6
<i>D. koenigswaldi</i>	SG, SG Low	Butler, 1980	6	11.70	0.360	11.3-12	7	12.34	0.560	11.5-13
<i>Galerix</i>										
<i>G. symeonidisi</i>	Aliveri	Doukas, 1986	3	1.56		1.5-1.6	14	1.90		1.7-2.1
<i>G. exilis</i>	Goldberg	Ziegler, 1983	123	1.55	0.095	1.3-1.8	100	2.08	0.098	1.9-2.4
<i>Parasorex</i>										
<i>P. socialis</i>	La Grive	Masini & Fanfani, 2013	15	1.68	0.137	1.5-1.9	39	2.06	0.088	1.9-2.3
<i>P. ibericus</i>	Otura 1	Mein & Martin Suarez, 1993	2	1.56		1.5-1.6	3	1.96		1.9-2
<i>Schizogalerix</i>										
<i>S. pasalarensis</i>	Pasalar	Engesser, 1980 (*)	1	1.48	/	/	7	1.88	0.040	1.8-1.9
<i>Apulogalerix</i>	All fissures	this paper	6	1.64		1.6-1.7	6	1.85		1.8-1.9

cones of approximately the same size, whereas *D. masinii* has P3s with the proportionally largest protocones of the genus. Accessory cusps that are sporadically present in the P3s of other species are absent in SCT 19. *D. samniticus* sp. nov. differs from *D. masinii* by having an imperfectly defined parastyle.

P4 bears a low protocone, like in *Deinogalerix masinii* and *D. freudenthali* from F15. In contrast, *D. brevirostris*, *D. intermedius*, and *D. koenigswaldi* have a quite higher protocone. The hypocone is comparatively as high as it is in smaller species, and quite lower than those of *D. brevirostris*, *D. intermedius*, and *D. koenigswaldi*. It is not split. In the other species the hypocone can be either complete, or variably split. It is quite more split in *D. koenigswaldi*. The tooth bears no accessory cusps.

In M3 of *Deinogalerix samniticus* sp. nov. the parastyle is somewhat more developed than in the other species, giving the labial wall a slightly concave profile. The parastyle is projected mesio-labially as in the small species *D. masinii* and *D. freudenthali* from F15 and not mesially as in *D. koenigswaldi* and the F9 specimens. Moreover, the angle between the mesial and labial margins is acute in *D. samniticus* sp. nov., *D. freudenthali* from F15, and *D. masinii*, and more open in *D. brevirostris*, *D. koenigswaldi*, and in a still undetermined species, *Deinogalerix* sp. from F9.

Deinogalerix sp.

Figure 9

Material. Left hemimandible SCT 243.

TABLE 3 (continued)..

Genus Species	Length											
	m1				m2				m3			
	N	\bar{x}	σ	range	N	\bar{x}	σ	range	N	\bar{x}	σ	range
<i>Deinogalerix</i>	9	8.77	0.308	8.3-9.2	10	5.88	0.467	5.3-6.5	5	4.86	0.363	4.1-5.5
<i>D. masinii</i>												
<i>D. freudenthali</i>	2	10.14	0.325	9.9-10.4	2	7.10	0.566	6.7-7.5	3	5.77	0.221	5.5-5.9
<i>D. minor</i>	2	10.90	0.141	10.8-11	3	6.57	0.208	6.4-6.8	1	4.70	/	/
<i>D. brevisrostris</i>	1	12.00	/	/	2	7.05	0.071	7-7.1	1	5.80	/	/
<i>D. samniticus</i>	2	12.18	0.106	12.1-12.25	1	6.50	/	/	1	5.80	/	/
<i>Deinogalerix</i> sp.	1	10.30	/	/								
<i>D. intermedius</i>	7	13.13	0.916	12-14.5	6	7.53	0.344	7.1-8	2	5.80	0.000	5.8-5.8
<i>D. koenigswaldi</i>	7	14.57	0.650	13.5-15.3	7	8.14	0.480	7.6-9	5	6.16	0.470	5.8-6.9
<i>Galerix</i>												
<i>G. symeonidisi</i>	2	2.55		2.5-2.6	8	2.14		2-2.3	4	1.65		1.5-1.8
<i>G. exilis</i>	150	3.07	0.077	2.8-3.4	150	2.49	0.100	2.4-2.8	150	2.11	0.093	1.7-2.3
<i>Parasorex</i>												
<i>P. socialis</i>	49	3.02	0.082	2.9-3.2	72	2.46	0.063	2.2-2.6	40	2.08	0.100	1.9-2.3
<i>P. ibericus</i>	5	2.90		2.9-3	2	2.47		2.4-2.5	3	2.01		2-2.1
<i>Schizogalerix</i>												
<i>S. pasalarensis</i>	3	2.80	0.098	2.7-2.9	2	2.39	0.021	2.4-2.4				
<i>Apulogalerix</i>	6	2.39		2.3-2.5	6	1.91		1.8-2	6	1.57		1.5-1.7

Type Locality. Outskirts of Scontrone, southern border of the National Park of Abruzzi, L'Aquila, central Italy (41°45'15.54"N, 14°2'13.14"E).

Horizon. Scontrone Member, *Lithothamnion* Limestone.

Age. Lower Tortonian (lower upper Miocene) (Patacca et al., 2008b).

Measurements. See Table 2.

Description Specimen SCT 243 (Figure 9.1-2).

Still partly embedded in rock. Specimen broken in front of mesial root of p3 and at level of m2. p3, basal parts of p4 and m1, and mesial part of m2 still preserved. Part of both roots of p2 visible. p2 presumably somewhat smaller than p3 based on relative proportion of the roots. Specimen cut by fracture between p3 and p4 that displaces rostral portion of horizontal ramus ventrally. Mental foramen under mesial border of distal root of p3 and elongated mesially by groove. Horizontal ramus

quite high and thick under molar section and tapering rostrally.

p3. Slightly worn, blunt, fairly low-crowned, dominated by protoconid triangular and symmetrical in side view. Metaconid absent. Labially, protoconid with relatively swollen base. Two roots straight and divergent mesio-distally from one another. In occlusal view crown slender mesio-distally with subtriangular outline and talonid extended distally and with blunt and small cuspule, prominent disto-lingually. p3 narrower and markedly smaller than p4 (Table 2) and separated from alveoli of p2 by short diastema.

p4. Crown badly damaged, only lingual and mesio-labial part of enamel wall preserved. Tooth large and massive, much more than p3. Occlusal outline sub-triangular, slightly wider distally, distal margin of tooth straight but obliquely inclined disto-labially.

m1. General outline of crown and mesio-labial part of cingulum preserved. m1 largest tooth (approx-

TABLE 4. Ratios of lower teeth length (p3-m3) in *Deinogalerix samniticus* sp. nov. with other species of *Deinogalerix* respect to the standard (*Parasorex socialis* from La Grive). Raw data for Figure 7.2.

Genus Species	Locality	Length ratio				
		p3	p4	m1	m2	m3
<i>Deinogalerix</i>						
<i>D. masinii</i>	Fissure M013	4.14	3.80	2.91	2.39	2.34
<i>D. freudenthali</i>	Fissure F15	5.08	4.52	3.50	2.87	2.87
<i>D. minor</i>	Various fissures	4.99	4.20	3.61	2.68	2.26
<i>D. brevirostris</i>	Fissure SG Low	5.94	4.91	3.98	2.87	2.79
<i>D. samniticus</i> sp. nov. SCT246	Scontrone	5.23	5.88	4.04	2.65	2.79
<i>Deinogalerix</i> sp.	Scontrone	4.22	4.86	3.41		
<i>D. intermedius</i>	Various fissures	6.08	5.61	4.35	3.07	2.79
<i>D. koenigswaldi</i>	Fissures SG and SG Low	6.95	5.99	4.83	3.32	2.97
<i>Parasorex</i>						
<i>P. socialis</i>	La Grive	1.00	1.00	1.00	1.00	1.00

TABLE 5. Lengths of p3 and p4 of single specimens of *Deinogalerix*. Raw data for Figure 8.

Species	Locality	Specimen	Source	Lp3	Lp4
<i>D. masinii</i>	Fissure M013	PU128502	Villier et al., 2013	6.9	8.4
<i>D. freudenthali</i>	Fissure F15	F15-015	This paper	7.3	8.5
<i>D. minor</i>	Fissure Fina H	RGM178184	Butler, 1980	8.5	8.8
	Fissure Gervasio	RGM179174	Butler, 1980	8.4	8.5
<i>D. intermedius</i>	Fissure Nazario 4	RGM179063	Butler, 1980	10.0	10.7
	WG 354 294	RGM178085/086	Butler, 1980	8.9	9.7
<i>D. brevirostris</i>	Fissure SG Low	RGM179232	Butler, 1980	10.0	10.1
<i>D. koenigswaldi</i>	Fissure SG	RGM177778	Villier, 2012	11.3	12.2
	Fissure SG	RGM177779	Villier, 2012	11.2	11.8
	Fissure SG	RGM179145	Villier, 2012	10.8	12.0
	Fissure SG	RGM179147	Villier, 2012	11.4	12.3
	Fissure SG	RGM179148	Villier, 2012	12.2	12.0
	Fissure SG	RGM179149	Villier, 2012	11.4	11.8
	Fissure SG	RGM179193	Villier, 2012	11.5	10.7
	Fissure SG Low	RGM179206	Villier, 2012	11.2	11.7
<i>D. samniticus</i> sp. nov.	Fissure SG Low	RGM179224	Villier, 2012	11.5	11.5
	Scontrone	SCT 246	This paper	8.8	12.1
	Scontrone	SCT 243	This paper	7.1	10.0

mately same length as p4) with very elongated trigonid. Mesial part of lingual enamel wall between paraconid and metaconid, i.e., postparacristid, slightly concave lingually and with no mesiolingual bulge.

m2. Undescribable fragment.

Comparison. SCT 243 shares with *Deinogalerix samniticus* sp. nov. the relative proportions of p3, p4, and m1. It differs from it by its smaller overall

size, and by having a rostrally tapering horizontal ramus. p3 is more slender and not roundish as in *D. samniticus* sp. nov., and p4 has an oblique and not transverse distal edge. The trigonid of m1 is uniformly concave lingually without any trace of mesiolingual bulge.

SCT 243 has p3 as large as that of *D. masinii*, p4 the same size as that of *D. brevirostris*, and m1

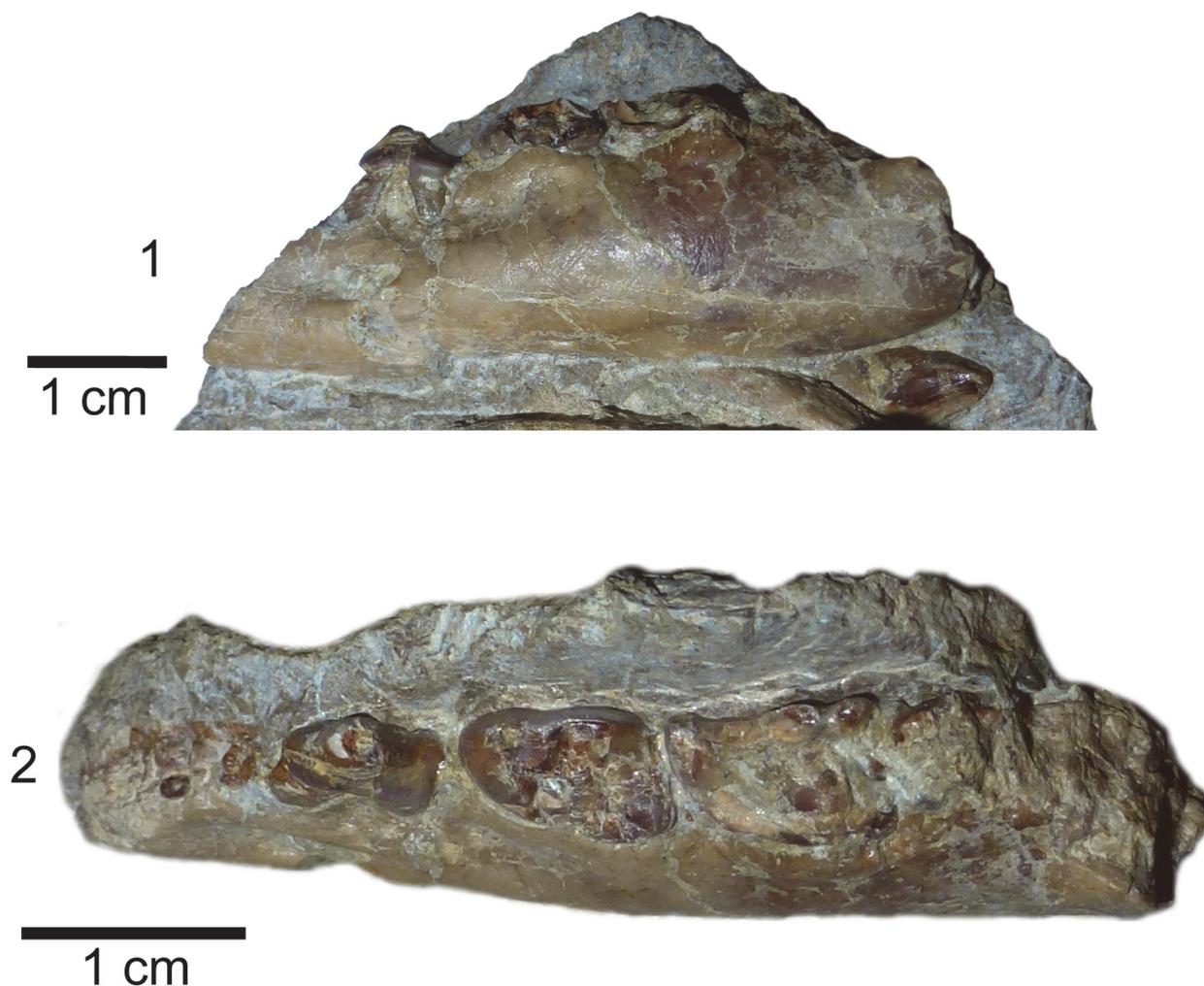


FIGURE 9. Left mandible (SCT 243), *Deinogalerix* sp. 1, lateral view; 2, dorsal view.

slightly larger than that of *D. freudenthali* (Figure 7).

DISCUSSION

Interrelations with the Gargano *Deinogalerix*

The comparative analyses performed in this study indicate that *Deinogalerix samniticus* sp. nov. and *Deinogalerix* sp. from Scontrone differ from all the other species of the genus described so far because of their possessing a small p3 associated with a proportionally much larger p4 (same size as m1, see Figure 7.1, Table 3). *Deinogalerix* sp. is significantly smaller than *D. samniticus* sp. nov. Both could possibly be extreme variants of the same species. Nonetheless, the marked odontometrical difference (roughly 20%), which exceeds that between sexes (approximately 10%) indicated by Butler (1980), but also important morphological distinctions, such as the quite high and rostrally

tapering horizontal ramus of *Deinogalerix* sp., as well as the different features of the trigonid of m1 in the two species, seem to rule out this possibility. *Deinogalerix* sp. is distinct from *D. samniticus* sp. nov., but the writers believe that a formal description of another new species based only on a single and badly preserved specimen is impracticable. Based mainly on dimensional criteria, all the remains of *Deinogalerix* from Scontrone but SCT 243 are attributed to the new species *D. samniticus* sp. nov.

Deinogalerix samniticus sp. nov. is characterized by having m1 with trigonid enlarged by the mesiolingual bulge of the postparacristid, and M3 with well-developed parastyle and slightly concave labial profile of the paracone, which give the tooth its characteristic profile. A set of dental features near *D. samniticus* sp. nov. to the primitive species of the genus (*D. masinii* and *D. freudenthali*): p4 with enclosed trigonid compared to more advanced

species basin, protoconid and metaconid low, and paraconid imperfectly identified; m1 with talonid slightly larger proportionally than the trigonid; m2 with robust and complete mesiolabial cingulum; m3 with well-developed mesiolabial cingulum; P4 with low protocone and hypocone; M3 with acute mesiolabial corner. Another primitive trait is its blunt and low-crowned cusps/ids. In contrast, the small protocone in P3 seems an advanced morphotype of the genus.

Not only *Deinogalerix samniticus* sp. nov. has features in common with primitive representatives of the genus. Also *Deinogalerix* sp. shares a primitive character, which is the rostrally tapering horizontal ramus like *D. masinii*. The primitive characters of *D. samniticus* sp. nov. and *Deinogalerix* sp. are consistent with Scontrone's older age, compared to the Gargano fissure fillings (Mazza and Rustioni, 2008, but see also Freudenthal et al., 2013).

However, despite being the earliest representatives of the genus, the species from Scontrone cannot candidate for direct ancestors of the Gargano species. Morphologically, several primitive features of *Deinogalerix samniticus* sp. nov. (i.e., proportionally longer talonid in m1, well-developed mesiolabial cingulum in m2 and m3, enclosed trigonid basin in p4, blunt and low-crowned cusps/ids) do not contrast this possibility.

However, dimensionally, both the species from Scontrone possess a very large p4, approximating the size of m1, and a proportionally very small p3 (see Figure 7, Figure 8, Table 3, Table 4, Table 5). In contrast, the Gargano species are characterized by a gradual increase in length from p3 to m1, which is a typical trait of the galericines that are supposed to be the ancestors of *Deinogalerix*. Moreover, *D. samniticus* sp. nov. is larger than the most primitive species from Gargano. Therefore, the peculiar relative proportions of p3, p4, and m1, make the *Deinogalerix* species from Scontrone a very unlikely ancestor to those from Gargano, as this derivation would involve a set of evolutionary inversions. The hypothetical transition from *D. samniticus* sp. nov. and *Deinogalerix* sp. to the small-sized Gargano species (i.e., *D. masinii* and *D. freudenthali*) imposes a drop in the dimensions of p4, and the passage to the larger species (i.e., *D. intermedius* and *D. koenigswaldi*) a new growth of p4. At the same time, p3 should grow relatively larger, compared to p4 (Figure 7.2, Table 5). In addition, the small protocone in the P3 of *D. samniticus* sp. nov. might be considered an advanced character weighing against the hypothet-

ical derivation of the Gargano species from it. This scenario is quite more complicated than if *D. samniticus* sp. nov. and *Deinogalerix* sp. were considered sister taxa of the Gargano species.

Based on these lines of evidence, we can speculate that the peculiar proportions of *Deinogalerix samniticus* sp. nov. and *Deinogalerix* sp. result from an independent evolutionary path from a close common ancestor which, in turn, is not the forerunner of the Gargano representatives. In contrast, both these hypothetical ancestors probably derived from a mainland ancestral species characterized by a regular increase in length of the teeth from p3 to m1.

The presence of two strongly endemized *Deinogalerix* species at Scontrone, which are not the direct ancestors of the other primitive representatives of the genus, implies that the fossil record from this locality is a late step along what was an already intricate evolutionary pathway. The high diversification of *Deinogalerix* documented by the earliest fossil records from the Apulia Platform (e.g., Scontrone, M013) allows us to speculate that these animals underwent a strong radiation and possibly had already a (relatively?) long history behind them.

New Insights from the Mental Foramen

The mental foramen of the Scontrone *Deinogalerix* and of the other species of *Deinogalerix*, is a character that has not been given the attention it deserves and that nonetheless offers a helpful clue in the search for the possible continental ancestor of the genus. *Deinogalerix* has the mental foramen constantly located under the mesial root of the p3, or between the two roots of this tooth. In contrast, its position is highly variable within the galericines. In *Parasorex* it is more frequently observed under the mesial root of p4, or between the roots of p3 and p4. The foramen often opens more rostrally in *Galerix* Pomel, 1948 [e.g., *Galerix exilis* (de Blainville, 1839): see Ziegler, 1983], but its position is also quite variable in this genus (e.g., under the mesial root of p4 in *Galerix aurelianensis* Ziegler, 1990, see van den Hoek Ostende and Fejfar, 2006; Ziegler, 1990). *G. stehlini* (direct observation by the writers) and *G. exilis* (Ziegler 1983) may occasionally show two foramina. In *Apulogalerix* the mental foramen is positioned approximately like in *Parasorex*, but the morphotypes with the foramen under p3 are quite less frequent.

We can speculate that the foramen constantly located in rostral position in *Deinogalerix* is a founder effect, or a by-product of the stretching of

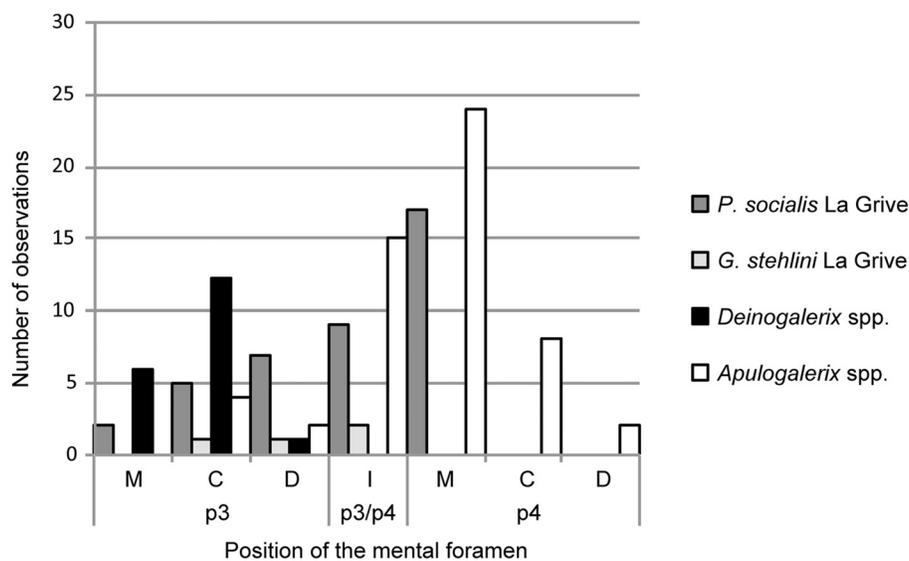


FIGURE 10. Histogram of the positions of the mental foramen in *Deinogalerix* and in other galericines. M = foramen located under the mesial root of p3 or p4, D = under the distal root of p3 or p4, C ("Central") = between the roots of p3 or p4, I ("Intermediate") = Foramen located between p3 and p4.

the muzzle somehow connected with its evolution in isolation. This second option, however, seems quite unlikely. In spite of the significant elongation of the rostral portion of the mandible from *D. masinii* to *D. koenigswaldi*, which involves, above all, the symphyseal region, the position of the foramen remains unchanged, constantly under p3. Whereas the p1–p2 diastema progressively stretches, the rear margin of the symphysis is invariably located under the mesial root of p3.

Actually, very primitive Galericiini, such as *Eogalericius* Lopatin, 2004, and *Microgalericulus* Lopatin, 2006, from the middle Eocene of Mongolia, often possessed two rostrally-positioned mental foramina, under p3 and/or p2 (Lopatin, 2006). Even if the position of the mental foramen seems variable in the galericines, a foramen constantly located in a rostral position is suggestive of a primitive status for this character. A summary of the different positions of the mental foramen in some of the galericines cited above is reported in Figure 10.

Whether the location of the foramen is inherited, or the result of endemization, it supports the polyphyletic origin of *Deinogalerix* and *Apulogalerix*, because in the latter genus the foramen is prevalently located under the mesial root of p4, as often occurs in *Parasorex* (Figure 10). This supports van den Hoek Ostende's (2001) and Masini and Fanfani's (2013) supposed derivation of *Apulogalerix* from a late Miocene *Parasorex*. At the same

time, however, it suggests that *Deinogalerix* had a distinct and more primitive ancestor.

The Origin of *Deinogalerix*

Butler (1980), van den Hoek Ostende (2001), Ziegler (2005), and Villier et al. (2013) addressed the issues of the continental origin of *Deinogalerix* and of its possible phylogenetic relationships. Butler (1980) favoured the hypothesis that the genus derived from a still unknown gymnure from Asia. Van den Hoek Ostende (2001) suggested that *Deinogalerix* derived from a middle – late Miocene species of *Parasorex*, namely *P. socialis*, *P. iberica*, and *P. depereti*, based on a set of common features, which are shared also with *Schizogalerix* (i.e., hypocone on P3, absence of protocone-metacoenule connection in M1–2, p3 larger than p2, p4 with trigonid-like paraconid-protoconid-metacoenid complex). Van den Hoek Ostende (2001) underscored that *Parasorex* and *Deinogalerix* lack typical synapomorphies of *Schizogalerix* (i.e., M1–2 diagonally elongated and with split mesostyle, distal cingulum often connected with entoconid and free posthypocristid in lower molars). According to van den Hoek Ostende (2001, p. 691) "the development of a metastylar crest on the M3 and a shorter distal arm of the metaconule of the M1 and M2 in *Deinogalerix* are interpreted as secondary developments." Based on preliminary observations van den Hoek Ostende (2001, p. 691) assumed

that the “smaller Gargano gymnure” (which is currently ascribed to *Apulogalerix* Masini and Fanfani, 2013) is sister-taxon to *Deinogalerix* and affirmed that this solution is the most parsimonious, because it involves only one migration event to the insular domain.

Van den Hoek Ostende’s (2001) hypothesis found an apparent later support (van den Hoek Ostende and de Vos in Viller et al., 2013) in the derivation of *Apulogalerix* from recent (Mammal Neogene faunal zone 10 = MN 10, late Miocene) representatives of *Parasorex*, as proposed by Masini and Fanfani (2013). In contrast, Ziegler (2005) argued that *Deinogalerix* stemmed from taxa that had achieved a hypocone-bearing P3 before the appearance of the *Parasorex-Schizogalerix* clade.

Villier in Villier et al. (2013) contended that the most advanced species of the *Parasorex socialis* group, e.g., *Parasorex ibericus*, are more recent, stratigraphically, than the Scontrone *Deinogalerix*, which at those times was ascribed to *D. freudenthali*. He also shared van den Hoek Ostende’s (2001) opinion (i.e., a derivation from *Parasorex*), but focused on a set of morphological characters of *Deinogalerix* (i.e., the absence of the paralophid in p4 and the presence, though rare, of a protocone-metaconule connection in M1, which are interpreted as primitive character states by Villier et al., 2013) to claim the descent of *Deinogalerix* from earlier representatives than the late Miocene ones supposed by van den Hoek Ostende (2001).

The present detailed analysis of the Scontrone *Deinogalerix* cannot conclusively settle this question; it nonetheless adds new evidence to the debate. The remnant of paralophid in the mesial part of p4 in *D. samniticus* sp. nov. suggests the derivation of *Deinogalerix* from a taxon bearing such structure, as already remarked by van den Hoek Ostende (2001). Nonetheless, some features possessed by the Gargano species of *Deinogalerix*, but unfortunately not visible in the fragmental Scontrone remains, seem to contrast the supposed stemming of *Deinogalerix* from the late Miocene *Parasorex* and to support Villier’s (Villier et al., 2013) opinion. The first is the protocone-metaconule connection, which is very rare, but nonetheless present in M1s of *Deinogalerix*, as noted by Villier et al. (2013). This connection is absent in all the species of *Parasorex* but *Parasorex kostakii* Doukas and van den Hoek Ostende, 2006, which is one of the earliest species of the genus (middle Miocene, MN 5). The second feature in contrast with the stemming of *Deinogalerix* from a late Miocene *Parasorex* is the continuous

distal cingulum in the majority of the M1s and M2s of *Deinogalerix*, which is a character stressed by Butler (1980) and van den Hoek Ostende (2001). According to Villier et al. (2013), in *D. masinii* the distal cingulum is discontinuous and the distal arm of the metaconule extends to the disto-labial corner of the tooth, reaching the metastyle. The same pattern is present in *Parasorex*. Nonetheless, examining the pictures in Villier et al. (2013, figure 3g, PU128531), the distal arm of the metaconule of M1 seems fused to the wall of the metastylar crest, more lingually than the disto-labial corner of the crown. Furthermore, in Villier (2012, figure 5.18) specimen PU128533 seems to show M1–2 with a distal arm of the metaconule confluent with an uninterrupted distal cingulum. These two specimens indicate that the relationship between the distal arm of the metaconule and the distal cingulum is variable in *D. masinii*, as it is in the whole genus (e.g., *Deinogalerix* sp. from F9, Figure 4.1-2). The unsteadiness of this feature distinguishes *Deinogalerix* from the late Miocene representatives of *Parasorex*. Nonetheless, this trait is included in the variability of *Galerix iliensis* (Kordikova, 2000). Also the position of the mental foramen contrasts the supposed derivation from a late Miocene *Parasorex*.

Piecing together the evidence, we support a hypothesis, similar to that proposed by Villier in Villier et al. (2013), in which *Deinogalerix* likely descended from a still unknown ‘*Parasorex*-like’ taxon, more primitive than the late Miocene representatives of this genus. Possible examples of these ‘*Parasorex*-like’ species are the MN 5 (early – middle Miocene) *Parasorex kostakii*, or *Galerix iliensis* (Kordikova, 2000). The former bears features (e.g., weak protocone-metaconule connection) that Prieto et al. (2012, p. 231) affirmed being primitive traits of that genus, which had previously been believed exclusive to *Galerix*. *Galerix iliensis* has characters (i.e., hypocone on P3 and absence of connection between protocone and metaconule) that, in spite of its assignment to *Galerix*, evoke *Parasorex*, according to Kordikova (2000) and Doukas and van den Hoek Ostende (2006). Unfortunately, the generic attribution of this speculative ancestor of *Deinogalerix* to either *Galerix* or *Parasorex* is complicated by the imperfect definition of *Galerix*. Important diagnostic characters of the latter genus, such as the size of p2, are still unknown in some of its species (e.g., *Galerix iliensis*).

As a consequence of all this information, the hypothesis of a late Miocene arrival in the insular domain of the presumed common forerunner of

Deinogalerix and *Apulogalerix* seems unlikely. The accumulated evidence weakens the assumption that there was a unique event of colonization of the Scontrone-Gargano area (sweepstake dispersal model, as proposed by Freudenthal, 1985; Freudenthal and Martín-Suárez, 2006, 2010; van den Hoek Ostende et al., 2009; Freudenthal et al., 2013). In contrast, the results of this study seem to weigh in favour of a polyphasic mode of colonization, as supposed by Butler (1980), De Giuli et al. (1987), Mazza et al. (1995, 2009), Abbazzi et al. (1996), Mazza and Rustioni (1996, 2008), Masini et al. (2002, 2008, 2010, 2013), Rook et al. (2006), and Savorelli and Masini (2016).

CONCLUSIONS

Although based on a limited number of remains, the new species from Scontrone, *Deinogalerix samniticus* sp. nov. and *Deinogalerix* sp., are warranted by quite distinctive morphologic and morphometric features. Their discovery revives interest in the giant erinaceids of the Apulia Platform, and in particular in their origin. The early Tortonian age of the Scontrone fossil-bearing deposits (Patacca et al., 2008a, 2008b, 2013) makes the species from Scontrone the earliest representatives of these weird erinaceids. However, independently from their stratigraphic location, the Scontrone representatives have characters that rule them out from the direct ancestry of the Gargano lineages. *Deinogalerix* was supposed to have stemmed either from late Miocene (van den Hoek Ostende, 2001), or from earlier representatives (Villier in Villier et al., 2013) of *Parasorex*. The results of the present study are in line with the latter hypothesis, indicating that *Deinogalerix* would have presumably descended from a hypothetical early – middle Miocene ‘*Parasorex*-like’ galericine. These results also dispute the assumption of a common origin of the giant *Deinogalerix* and the small gymnure *Apulogalerix* from Gargano.

Recent and ongoing studies on the different components of the peculiar Apulia Platform fauna seem confirming asynchronous colonization events (De Giuli et al., 1987; Masini et al., 2002, 2008), which challenge the presumed unique wave of colonization of the area claimed by Freudenthal (1985), Freudenthal and Martín-Suárez (2006, 2010), van den Hoek Ostende et al. (2009), and Freudenthal et al. (2013). The precursor of the hoplitomerycids, for example, is stated to have arrived in Oligocene times (Mazza and Rustioni, 2011; Mazza, 2013b), whereas the forerunners of various micromammals reached the Apulia Plat-

form at least in the course of the early Miocene and during the Messinian (Savorelli and Masini, 2016; Savorelli et al., 2016). The results of the present study bring new evidence that calls into question the hypothesis of a late Miocene arrival of the lineage of the giant erinaceid *Deinogalerix* and seems rather to indicate an early – middle Miocene dispersal.

These discoveries add further tiles to the still imperfect mosaic of the evolution of the Apulia Platform’s palaeoinsular fauna. They not only reveal that *Deinogalerix* had a longer history than previously supposed, they also show that, similar to other taxa of the Apulia Platform, like the ruminant family Hoplitomerycidae (Mazza and Rustioni, 2011; Mazza et al., 2014), this erinaceid was monophyletic and radiated into a set of strongly endemized species.

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REFERENCES

- Abbazzi, L., Benvenuti, M., Boschian, G., Dominici, S., Masini, F., Mezzabotta, C., Piccini, L., Rook, L., Valleri, G., and Torre, D. 1996. Revision of the Neogene and Pleistocene of the Gargano region (Apulia, Italy). The marine and continental succession and the mammal faunal assemblages in an area between Apricena and Poggio Imperiale (Foggia). *Memorie della Società Geologica Italiana*, 51:383-402.
- Agustí, J. 1986. Dental evolution in the endemic glirids of the Western Mediterranean islands. *Mémoires du Muséum d’Histoire Naturelle de Paris (C)*, 53:227-232.
- Butler, P.M. 1980. The giant erinaceid insectivore *Deinogalerix* Freudenthal from the Upper Miocene of the Gargano, Italy. *Scripta Geologica*, 57:1-72.
- Crochet, J.Y. 1986. Insectivores pliocènes du Sud de la France (Languedoc-Rous-sillon) et du Nord-Est de l’Espagne. *Palaeovertebrata*, 16:145-171.

- de Blainville, H.M.D. 1839. *Osteographie des Mammifères*. Tome I, Livraison 6-H, insectivores. J.B. Bailliere et Fils, Paris.
- De Giuli, C., Masini, F., and Valleri, G. 1987. Paleogeographic evolution of the Adriatic area since Oligocene to Pleistocene. *Rivista Italiana di Paleontologia e Stratigrafia*, 93:109-126.
- Doukas, C.S. 1986. The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). Part 5. The Insectivores. *Proceedings Of The Koninklijke Nederlandse Akademie Van Wetenschappen Series B-Palaeontology Geology Physics Chemistry Anthropology*, 89:15-38.
- Doukas, C.S. and van den Hoek Ostende, L.W. 2006. Insectivores (Erinaceomorpha, Soricomorpha, Mammalia) from Karydia and Komotini (Thrace, Greece; MN 4/5). *Beitraege zur Palaeontologie*, 30:109-131.
- Engesser, B. 1980. Insectivora und Chiroptera (Mammalia) aus dem Neogen der Türkei. *Schweizerische Palaeontologische Abhandlungen*, 102:45-149.
- Fischer, G. 1814. *Zoognosia tabulis synopticis illustrata. Volumen tertium. Quadrupedum reliquorum. Cetorum et montrymatum descriptionem continens*. Nicolai Sergeidis Vsevolozky, Mosquae.
- Filhol, H. 1891. Etudes sur les mammifères fossiles de Sansan. *Annales des Sciences Géologiques*, 21:1-315.
- Freudenthal, M. 1971. Neogene vertebrates from the Gargano Peninsula, Italy. *Scripta Geologica*, 3:1-10.
- Freudenthal, M. 1972. *Deinogalerix koenigswaldi* nov. gen., nov. sp., a giant insectivore from the Neogene of Italy. *Scripta Geologica*, 14:1-19.
- Freudenthal, M. 1976. Rodent stratigraphy of some Miocene fissure fillings in Gargano (prov. Foggia, Italy). *Scripta Geologica*, 27:1-23.
- Freudenthal, M. 1985. Cricetidae (Rodentia) from the Neogene of Gargano (prov. Foggia, Italy). *Scripta Geologica*, 77:29-75.
- Freudenthal, M. and Martín-Suárez, E. 2006. Gliridae (Rodentia, Mammalia) from the late Miocene fissure filling Biancone 1 (Gargano, prov. Foggia, Italy). *Palaeontologia Electronica*, 9:1-23.
- Freudenthal, M. and Martín-Suárez, E. 2010. The age of immigration of the vertebrate faunas found at Gargano (Apulia, Italy) and Scontrone (l'Aquila, Italy). *Comptes Rendus Palevol*, 9:95-100. doi:10.1016/j.crpv.2009.12.004.
- Freudenthal, M., van den Hoek Ostende, L. and Martín-Suárez, E. 2013. When and how did the *Mikrotia* fauna reach Gargano (Apulia, Italy)? *Geobios*, 46:105-109. doi:10.1016/j.geobios.2012.10.004.
- Gould, G. 1995. Hedgehog Phylogeny (Mammalia, Erinaceidae)-the Reciprocal Illumination of the Quick and the Dead. *American Museum Novitates*, 3131:1-45.
- Kordikova, E. 2000. Insectivora (Mammalia) from the Lower Miocene of the Aktau Mountains, South-Eastern Kazakhstan. *Senckenbergiana lethaea*, 80:67-79. doi:10.1007/bf03043665.
- Linnaeus, C. 1758. *Systema Naturae*, 10th Edition; Volume 1. G. Engelmann, Leipzig.
- Lopatin, A. 2006. Early Paleogene insectivore mammals of Asia and establishment of the major groups of Insectivora. *Paleontological Journal* 40:S205-S405. doi:10.1134/s0031030106090012.
- Masini, F., Bonfiglio, L., Petruso, D., Marra, A.C., Abbazzi, L., Delfino, M., Fanfani, F., and Torre, D. 2002. The role of coastal areas in the Neogene-Quaternary mammal island populations of central Mediterranean. *Biogeographia*, 23:165-189.
- Masini, F. and Fanfani, F. 2013. *Apulogalerix pusillus* nov. gen., nov. sp., the small-sized Galericinae (Erinaceidae, Mammalia) from the "Terre Rosse" fissure filling of the Gargano (Foggia, South-Eastern Italy). *Geobios*, 46:89-104. doi:10.1016/j.geobios.2012.10.008.
- Masini, F., Petruso, D., Bonfiglio, L., and Mangano, G. 2008. Origination and extinction patterns of mammals in three central Western Mediterranean islands from the Late Miocene to Quaternary. *Quaternary International*, 182:63-79. doi:10.1016/j.quaint.2007.09.020.
- Masini, F., Rinaldi, P.M., Petruso, D., and Surdi, G. 2010. The Gargano Terre Rosse insular faunas: An overview. *Rivista Italiana di Paleontologia e Stratigrafia*, 116:421-435.
- Masini, F., Rinaldi, P., Savorelli, A., and Pavia, M. 2013. A new small mammal assemblage from the M013 Terre Rosse fissure filling (Gargano, South-Eastern Italy). *Geobios*, 46:49-61. doi:10.1016/j.geobios.2012.10.003.
- Mazza, P. 2013a. The systematic position of Hoplitomerycidae (Ruminantia) revisited. *Geobios*, 46:33-42.
- Mazza, P. 2013b. Hoplitomerycidae (Ruminantia; Late Miocene, Central-Southeastern Italy): Whom and where from? *Geobios*, 46:511-520. doi:10.1016/j.geobios.2013.08.001.
- Mazza, P., Delfino, M., van den Hoek Ostende, L.W., Masini, F., Pavia, M., Rinaldi, P.M., and Rustioni, M. 2009. How, when and where from of the Abruzzo-Apulian palaeofauna, p. 57-60. In Fanti, F. and Spalletta, C. (eds.), *International Conference of Vertebrate Palaeobiogeography*. Abstract Book, Bologna.
- Mazza, P., Rossi, M., and Agostini, S. 2014. Hoplitomerycidae (Late Miocene, Italy), an Example of Giantism in Insular Ruminants. *Journal of Mammalian Evolution*, 22:271-277. doi:10.1007/s10914-014-9277-2.
- Mazza, P. and Rustioni, M. 1996. The Turolian artiodactyls from Scontrone (Abruzzi, central Italy). *Bollettino Società Paleontologia Italiana*, 35:93-106.
- Mazza, P. and Rustioni, M. 2008. Processes of island colonization by Oligo-Miocene land mammals in the central Mediterranean: New data from Scontrone

- (Abruzzo, Central Italy) and Gargano (Apulia, Southern Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 267:208-215.
doi:10.1016/j.palaeo.2008.06.018.
- Mazza, P. and Rustioni, M. 2011. Five new species of *Hoplitomeryx* from the Neogene of Abruzzo and Apulia (central and southern Italy) with revision of the genus and of *Hoplitomeryx matthei* Leinders, 1983. *Zoological Journal of the Linnean Society*, 163:1304-1333.
doi:10.1111/j.1096-3642.2011.00737.x.
- Mazza, P., Rustioni, M., Aruta, G., and Di Carlo, E. 1995. A Messinian *Prolagus* from Capo di Fiume Quarry (Palena, Abruzzo, Central Italy). *Bollettino della Società Paleontologica Italiana*, 34:55-66.
- McKenna, M., Bell, S., and Simpson, G. 1997. *Classification of Mammals Above the Species Level*. Columbia University Press, New York.
- Mein, P. and Martín-Suárez, E. 1993. *Galerix iberica* sp. nov. (Erinaceidae, Insectivora, Mammalia) from the Late Miocene and Early Pliocene of the Iberian Peninsula. *Geobios*, 26:723-730.
doi:10.1016/s0016-6995(93)80055-v.
- Novacek, M.J. 1986. The skull of leptictid insectivorans and the higher-level classification of eutherian mammals. *Bulletin of the American Museum of Natural History*, 183:1-112.
- Patacca, E., Scandone, P., and Carnevale, G. 2013. The Miocene vertebrate-bearing deposits of Scontrone (Abruzzo, Central Italy): Stratigraphic and paleoenvironmental analysis. *Geobios*, 46:5-23.
doi:10.1016/j.geobios.2012.11.001.
- Patacca, E., Scandone, P., and Mazza, P. 2008a. The Miocene land-vertebrate fossil site of Scontrone (Central Apennines). *Bollettino della Società Geologica Italiana*, 127:51-73.
- Patacca, E., Scandone, P., and Mazza, P. 2008b. Oligocene migration path for Apulia macromammals: the Central-Adriatic bridge. *Bollettino della Società Geologica Italiana*, 127:337-355.
- Pavia, G., Bertok, C., Ciampo, G., Di Donato, V., Martire, L., Masini, F., Pavia, M., Santangelo, N., Taddei Ruggiero E., and Zunino, M. 2010. Tectono-sedimentary evolution of the Pliocene to Lower Pleistocene succession of the Apricena-Lesina-Poggio Imperiale quarrying district (western Gargano, southern Italy). *Italian Journal of Geosciences*, 129:132-155.
- Pomel, A.N. 1848. Etudes sur les carnassiers insectivores (extrait). Seconde partie, Classification des insectivores. *Archives des Sciences Physiques et Naturelles*, 9:244-251.
- Prieto, J., Gross, M., Böhmer, C., and Böhme, M. 2010. Insectivores and bat (Mammalia) from the late Middle Miocene of Gratkorn (Austria): biostratigraphic and ecologic implications. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 258:107-119.
doi:10.1127/0077-7749/2010/0088.
- Prieto, J., Hoek Ostende, L., and Hír, J. 2012. The Middle Miocene insectivores from Sámsonháza 3 (Hungary, Nógrád County): Biostratigraphical and palaeoenvironmental notes near to the Middle Miocene Cooling. *Bulletin of Geosciences*, 227-240.
doi:10.3140/bull.geosci.1296.
- Rook, L., Gallai, G., and Torre, D. 2006. Lands and endemic mammals in the Late Miocene of Italy: Constraints for paleogeographic outlines of Tyrrhenian area. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 238:263-269.
doi:10.1016/j.palaeo.2006.03.027.
- Savorelli, A., Colombero, S., and Masini, F. 2016. *Apatodemus degiulii* n. gen. et sp. (Rodentia, Muridae), a hitherto undescribed endemite from the Terre Rosse of Gargano (Late Miocene, Southeastern Italy). *Paläontographica Abteilung A*, 306:25-49.
- Savorelli, A. and Masini, F. 2016. *Mystemys giganteus* nov. gen. nov. sp.: an enigmatic and rare cricetid from the Terre Rosse M013 fissure filling (Gargano, Southeastern Italy). *Paläontographica Abteilung A*, 306:1-23.
- Valleri, G. 1984. New data on Planktonic Foraminifera biostratigraphy from the Neogene of the Gargano Peninsula (Foggia, Southern Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 90:375-406.
- van den Hoek Ostende, L. 2001. A revised generic classification of the Galericiini (Insectivora, Mammalia) with some remarks on their palaeobiogeography and phylogeny. *Geobios*, 34:681-695.
doi:10.1016/s0016-6995(01)80029-2.
- van den Hoek Ostende, L. and Fejfar, O. 2006. Erinaceidae and Talpidae (Erinaceomorpha, Soricomorpha, Mammalia) from the Lower Miocene of Merkur-Nord (Czech Republic, MN 3). *Beitraege zur Palaentologie*, 30:175-203.
- van den Hoek Ostende, L., Meijer, H., and van der Geer, A. 2009. A bridge too far. Comment on "Processes of island colonization by Oligo-Miocene land mammals in the central Mediterranean: New data from Scontrone (Abruzzo, Central Italy) and Gargano (Apulia, Southern Italy)" by P.P.A. Mazza and M. Rustioni [Palaeogeography, Palaeoclimatology, Palaeoecology 267 (2008) 208–215]. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 279:128-130.
doi:10.1016/j.palaeo.2009.02.029.
- Villier, B. 2012. *The anatomy of Deinogalerix and systematics of the Galericiini*. Unpublished PhD Thesis, University of Turin, Turin, Italy.
- Villier, B. and Carnevale, G. 2013. A new skeleton of the giant hedgehog *Deinogalerix* from the Miocene of Gargano, southern Italy. *Journal of Vertebrate Paleontology*, 33:902-923.
doi:10.1080/02724634.2013.743897.
- Villier, B., van Den Hoek Ostende, L., De Vos, J., and Pavia, M. 2013. New discoveries on the giant hedgehog *Deinogalerix* from the Miocene of Gargano (Apulia, Italy). *Geobios*, 46:63-75.
doi:10.1016/j.geobios.2012.10.001.

- Von Meyer, C.E.H. 1865. Briefe an den Herausgeber. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, 1865:215-221.
- Waddell, J., Okada, N., and Masami, P. 1999. Towards resolving the interordinal relationships of placental mammals. *Systematic Biology*, 48:1-5. doi:10.1080/106351599260391.
- Ziegler, R. 1983. *Odontologische und osteologische Untersuchungen an Galerix exilis (Blainville) (Mammalia, Erinaceidae) aus dem miozänen Ablagerungen von Steinberg und Goldberg im Nördlinger Ries (Süd-Deutschland)*. Unpublished PhD Thesis, Universität München, München, Germany.
- Ziegler, R. 1990. Didelphidae, Erinaceidae, Metacondontidae und Dimylidae (Mammalia) aus dem Oberoligozän und Untermiozän Süddeutschlands. *Stuttgarter Beiträge zur Naturkunde, B* 158:1-99.
- Ziegler, R. 2005. Erinaceidae and Dimylidae (Lipotyphla) from the Upper Middle Miocene of South Germany. *Senckenbergiana lethaea*, 85:131-152. doi:10.1007/bf03043423.
- Zijlstra, J. and Flynn, L. 2015. Hedgehogs (Erinaceidae, Lipotyphla) from the Miocene of Pakistan, with description of a new species of *Galerix*. *Palaeobiodiversity and Palaeoenvironments*, 95:477-495. doi:10.1007/s12549-015-0190-3.