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

Andrea Savorelli, Federico Masini, Paul P. A. Mazza, Maria Adelaide Rossi, and Silvano Agostini

**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 Erinaceidae 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.

Andrea Savorelli. Department of Earth Sciences, University of Florence, via La Pira 4, Florence 50121, Italy; andrea_savorelli@yahoo.it
Federico Masini. Department of Earth and Marine Sciences (DISTEM), University of Palermo, Via Archirafi 22, Palermo 90123, Italy; federico.masini@unipa.it
Paul P. A. Mazza. Department of Earth Sciences, University of Florence, via La Pira 4, Florence 50121, Italy; paul.mazza@unifi.it
Maria Adelaide Rossi. Archaeological Superintendency of Abruzzo, via degli Agostiniani 14, Chieti 66100, Italy; mariaadelaide.rossi@beniculturali.it
Silvano Agostini. Archaeological Superintendency of Abruzzo, via degli Agostiniani 14, Chieti 66100, Italy; silvano.agostini@beniculturali.it

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Savorelli, Andrea, Masini, Federico, Mazza, Paul P. A., Rossi, Maria Adelaide, and Agostini, Silvano. 2017. New species of *Deinogalerix* (Mammalia, Eulipotyphla) from the late Miocene of Scontrone (Abruzzo, central Italy). *Palaeontologia Electronica* 20.1.16A: 1-26
paleo-electronica.org/content/2017/1658-deinogalerix-from-scontrone
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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 endemism, 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. freudenthalii: 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. brevirostris, 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 freudenthalii 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. freudenthalii 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. freudenthalii." 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 Galericini. 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 galericines known at those times in Europe, or to Lanthanotherium 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. freudenthalii, 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 Giovaninno 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-
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 (Vallé, 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

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**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 calcarenite; 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 = coastal 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 calcarudites; 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).
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.
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...
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 PALAEONTOLOGY**

Class MAMMALIA Linnaeus, 1758
Superorder INSECTIVORA sensu Novacek, 1986
Order EULIPOTYPHLA Waddell, Okada, and Hasegawa, 1999
Family ERINACEIDAE Fischer, 1814
Subfamily GALERICINAE Pomel, 1848
Tribe GALERICINI Pomel, 1848
Genus DEINOGLERIX 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 brevirostris* Butler, 1980; *Deinogalerix freudenthali* Butler, 1980; *Deinogalerix intermedius* Butler, 1980; *Deinogalerix minor* Butler, 1980; *Deinogalerix masinii* Villier et al., 2013; *Deinogalerix samniticus* sp. nov.

| Species          | Deposit | Inventory | Description                      |
|------------------|---------|-----------|----------------------------------|
| *Deinogalerix* sp. | F21c    | F21-001   | isolated left M1                 |
|                  | F21c    | F21-002   | isolated right p4                |
| *Deinogalerix* 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                 |
| *Deinogalerix* sp. | NBS     | NBS-001   | isolated left p4                  |
| *Deinogalerix* sp. | F1      | F1-006    | isolated left P4                  |
|                  | F1      | F1-007    | isolated left P4                  |
|                  | F1      | F1-009    | isolated left m2                  |
| *Deinogalerix* sp. | F8      | F8-040    | left jaw with c, p3-m3 (broken m1)|
| *Deinogalerix* 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      |
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; supraorbital 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.

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

**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. samnitanus* 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 lingually; 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 buniondont 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,

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**TABLE 2.** Odontometrics of *Deinogalerix samniticus* sp. nov. and *Deinogalerix* sp. (SCT 243). 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 L W L W L W   |                |                |
| p3            | 8.8 5.0 12.1 7.6    | 12.25          | 6.5            |
| p4            | 7.1 3.5 10 6.7      | 10.3           | 6.5            |
| m1            | 12.1               | 8              |                |
| m2            | /                  | /              |                |
| m3            | /                  | /              |                |

|                | Mandible Measurements |                |                |
|----------------|-----------------------|----------------|----------------|
|                | aL aL aL aL H m1 W m1 H p2 |                |                |
| m1-m3         | 27.55                 | 32.7           | 21.1           |
| p2-p4         | 20.6                  | 18.5           | 14.5           |
| p4-p3         | >15                   |                |                |

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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, Mecd = Metaconid, Pac = Paracne, 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).
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 para style. 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 protocone. Protocone and metaconule separated. Enamel thick.

**M3.** Sub-triangular outline. Mesial margin almost straight, disto-labial margin markedly concave, 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 protocrista extended towards antero-lingual corner. Paracone connected with well-developed para-lingual crest. Parastyle projected mesiolabially and lingual 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 lingu ally. Very short entocingulum at outlet of the trigon valley. Short mesial cingulum. Protocone with flat wear surface. Enamel thick.

**Comparison.** The specimens from Scontone 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.
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 ligually 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, this enamel profile is continuous and straight. In D. masinii the mesiolingual bulge never dips downward and ligually 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 distolabial 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-
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.

**Material.** Left hemimandible SCT 243.

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**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; \( \sigma \) = standard deviations.* Inferred from diagrams and figures. Raw data for Figure 7.1.

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

### 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     | p3   | p4   | m1   | m2   | m3   |
|---------------|------------------|--------------|------|------|------|------|------|
| Deinogalerix  |                  |              |      |      |      |      |      |
| *D. masinii*  | Fissure M013     | 4.14         | 3.80 | 2.91 | 2.39 | 2.34 |
| *D. freudenthali* | Fissure F15   | 5.08         | 4.52 | 3.50 | 2.87 | 2.87 |
| *D. minor*    | Various fissures | 4.99         | 4.20 | 3.61 | 2.68 | 2.26 |
| *D. brevirostris* | Fissure SG Low | 5.94         | 4.91 | 3.98 | 2.87 | 2.79 |
| *D. samniticus* sp. nov. | SCT246 | 5.23         | 5.88 | 4.04 | 2.65 | 2.79 |
| *Deinogalerix* sp. | Scontrone   | 4.22         | 4.86 | 3.41 |
| *D. intermedius* | Various fissures | 6.08         | 5.61 | 4.35 | 3.07 | 2.79 |
| *D. koenigswaldi* | Fissures SG and SG Low | 6.95         | 5.99 | 4.83 | 3.32 | 2.97 |
| Parasorex     |                  |              |      |      |      |      |      |
| *P. socialis* | 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 |
|------------------|--------------|----------|-------------------------|-----|-----|
| *D. masinii*     | Fissure M013 | PU128502 | Villier et al., 2013    | 6.9 | 8.4 |
| *D. freudenthali*| Fissure F15  | F15-015  | This paper              | 7.3 | 8.5 |
| *D. minor*       | Fissure Gervasio | RGM178184 | Butler, 1980            | 8.5 | 8.8 |
| *D. intermedius* | Fissure Nazario 4 | RGM179063 | Butler, 1980            | 10.0| 10.7|
|                  | WG 354 294   | RGM178085/086 | Butler, 1980           | 8.9 | 9.7 |
| *D. brevirostris*| Fissure SG Low | RGM179232 | Butler, 1980            | 10.0| 10.1|
| *D. koenigswaldi*| 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|
|                  | Fissure SG Low | RGM179224 | Villier, 2012           | 11.5| 11.5|
| *D. samniticus* sp. nov. | Scontrone | SCT 246   | This paper              | 8.8 | 12.1|
|                  | Scontrone    | SCT 243   | This paper              | 7.1 | 10.0|
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. masini* and *D. freudenthali*): p4 with enclosed trigonid compared to more advanced

**FIGURE 9.** Left mandible (SCT 243), *Deinogalerix* sp. 1, lateral view; 2, dorsal view.
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. freudenthalii*) imposes a drop in the dimensions of p4, and the passage to the larger species (i.e., *D. intermedium* 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 hypothetical 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 already an 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
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. masini 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 Galericini, 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-metaconule connection in M1–2, p3 larger than p2, p4 with trigonid-like paraconid-protoconid-metaconid 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 Villier 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 supposedly 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 samngetic 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 Platform 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.

ACKNOWLEDGEMENTS

We thank the Superintendent of the Archaeological Superintendency of Abruzzo, A. Pessina, for the casts of the Gargano type specimens, as well as the laboratory technician of the same Superintendency, S. Caramiello, for the restoration of the Scontrone specimens. We are particularly indebted to L. van den Hoek Ostende and B. Villier for critically reviewing an early version of the manuscript and very much improving it. We also thank L. Rook (Florence University, Italy) who provided the facilities and the access to the lab. FFR 2012 (Palm erno University) and PAULMAZZARICATEN13 - Mazza P. Fondo Ateneo 2013 MIUR (the Italian Ministry of Education, University and Research) grants supported this study.

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