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Reappraisal of some species of the giant galericine *Deinogalerix* (Mammalia, Eulipotyphla, Erinaceomorpha, Erinaceidae) from the Miocene of south-eastern Italy, with a review of the genus

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Abstract

A revision of the remains of *Deinogalerix* from the Terre Rosse of Gargano, stored at the Department of Earth Sciences of Florence, improved our knowledge of the genus. The goals of this study are to clear the taxonomic status of the specimens and to tackle several issues connected with the evolutionary relationships of the different species. The sample of dental remains of *Deinogalerix freudenthali* provides new information, which confirms that this species belongs to the most primitive members of the genus, alongside *D. masinii*. It is now clear that *D. freudenthali* is very close to the hypothetical ancestor of all other Gargano species, except *D. masinii*. Nonetheless, the oldest fissures of the Gargano Terre Rosse contain also primitive species of unsettled taxonomic and phylogenetic position. The present analysis shows the systematic validity of *D. minor* and *D. intermedius*, whose status was debated. Moreover, the study verifies the consistency of the two phyletic lineages *Deinogalerix minor*–*D. brevirostris* and *Deinogalerix intermedius*–*D. koenigswaldi*, as well as the co-occurrence of members of the two lines at least in the most recent Terre Rosse fissures. The enhanced information contributes to our understanding of the genus *Deinogalerix* and especially of the most ancient phases of colonisation of the Apulia Platform. Nonetheless, the fossil record of the genus remains imperfect, with many gaps blurring the origins of its various evolutionary lines.

Keywords

Deinogalerix
Galericinae
Endemism
Late Miocene
Terre Rosse
Apulia Platform

Electronic supplementary material

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Introduction

Remains of the giant galericine erinaceid *Deinogalerix* are known from infillings (“Terre Rosse”) of a network of karstic fissures carved in limestones, which are still actively quarried in the Gargano Promontory (Apulia, south-eastern Italy), as well

as from stratified tidal flat calcarenites that crop out at Scontrone (Abruzzo, central Italy). In Gargano, *Deinogalerix* is associated with a variety of large and small vertebrate taxa which underwent various evolutionary changes in insular isolation (e.g. the artiodactyl *Hoplitomeryx*, the murid *Mikrotia*, the Anseriformes *Garganornis*). These assemblages are known either as the “Terre Rosse” faunal complex, or as the “*Mikrotia* fauna” (Freudenthal 1971, 2006; Masini et al. 2010; Savorelli and Masini 2016; Savorelli et al. 2016). This faunal complex includes also another galericine, *Apulogalerix pusillus*, comparable in size to the majority of the mainland counterparts and less modified than *Deinogalerix* (Masini and Fanfani 2013).

At Scontrone, the genus is accompanied by a highly endemic but far poorer faunal assemblage than at Gargano. The former fossiliferous site dates back to around 9 Ma (Patacca et al. 2013) and is considered stratigraphically older than the Gargano fissure fillings (see section “Age of Apulia Platform deposits”); unfortunately, however, up to now, no remains of small mammal (*Deinogalerix* grew too large to still be considered a small mammal) have ever been found at Scontrone (Rustioni et al. 1992; Mazza and Rustioni 2008; Patacca et al. 2013). Geological and palaeontological evidence indicates the existence of a land, called the Apulia Platform, which has been repeatedly isolated from neighbouring mainland areas for long periods of time (Freudenthal 1971, 1976; De Giuli et al. 1987a; b; Patacca et al. 2008a, 2008b, 2013; Masini et al. 2010, 2013).

Deinogalerix was first introduced by Freudenthal (1972), based on an almost complete skeleton from Terre Rosse sediments. It is the holotype of the largest species of the genus, *Deinogalerix koenigswaldi*. Butler (1980) described four more species: *D. brevirostris*, *D. intermedius*, *D. minor*, and *D. freudenthali*, and adopted Freudenthal’s (1976) chronological ordering of the karstic fissure fillings (which is based on the biochronology of the murid *Mikrotia* as well as on the cricetids from Gargano). Against that framework, he reconstructed the phylogeny of the genus, indicating its smallest species *Deinogalerix freudenthali* as a possible common ancestor to all the other species. Based on Butler’s (1980) scheme, two lineages emerged from *D. freudenthali*: one leading to the larger-sized and most advanced *D. koenigswaldi*, passing through the transitional *D. intermedius*; the other ending up with *D. brevirostris* (which is coeval with, but smaller than, *D. koenigswaldi*) and passing through *D. minor*. Body sizes increase considerably along both lineages.

Several years later, Villier (2012) lowered the status of *D. freudenthali* and *D. minor*, considering them merely two different morphotypes of *Deinogalerix*

koenigswaldi, and described a new species, *Deinogalerix masinii* Villier, 2013 (in Villier et al. 2013) based on remains from the fissure infilling M013, which was discovered in 2009 by a team from the University of Turin and was then found to be the Terre Rosse's most ancient deposit (Masini et al. 2013). While calling attention to its morphological primitiveness, Villier et al. (2013) excluded *Deinogalerix masinii* from the direct ancestry of the four species described by Butler (1980). Villier et al. (2013, p. 74) considered Butler's (1980) species as a "...more modern [than *D. masinii*] group of *Deinogalerix* represented by *D. koenigswaldi* and *D. freudenthali* at the extreme"; Villier and Carnevale (2013, p. 902) supported this opinion, stressing "[...] that only two former species [besides *D. masinii*] can be interpreted as valid: *D. koenigswaldi*, the largest, most derived, and most variable in size; and the smaller and less derived, *D. freudenthali*." Moreover, Villier (2010, 2012) and Villier and Carnevale (2013) described an additional, nearly complete skeleton from the fissure *Mikrotia* 010 (= M010) at Cava dell'Erba (Gargano). Villier (2010) referred it to *Deinogalerix brevirostris*, whereas Villier (2012) and Villier and Carnevale (2013) attributed it to *D. koenigswaldi*.

Working on the first remains of *Deinogalerix* ever found at Scontrone, Mazza and Rustioni (2008) reported the occurrence of *D. freudenthali*. This erroneous attribution was rectified by Savorelli et al. (2017), based also on a few new specimens found at Scontrone over the last 20 years. The latter authors introduced two new species: a larger one, formally called *Deinogalerix samniticus*, and a smaller one, generically indicated as *Deinogalerix* sp. Savorelli et al. (2017) reassigned the remains that had previously been attributed to *Deinogalerix freudenthali* now to *D. samniticus*. Peculiar dental proportions and morphological traits distinguish the Scontrone representatives from the Gargano ones and rule out the former from the direct ancestry of the latter (Savorelli et al. 2017; Borrani et al. 2017).

Many questions relative to the taxonomy of *Deinogalerix* are still open. Savorelli et al. (2017) find that the taxonomic revision proposed by Villier et al. (2013) and Villier and Carnevale (2013) still needs further insight. Remains of *Deinogalerix* from Gargano stored at the Department of Earth Sciences of Florence, which had been preliminarily studied by Villier (2012), have therefore been carefully re-examined in order to shed new light on *Deinogalerix freudenthali*, but also on the genus as a whole.

Biochronology of the Terre Rosse fissure fillings

The lack of vertical successions of superimposed layers, which is common to these karstic infillings, imposed a biochronological ordering of the Gargano fissure deposits based on the composition and degree of evolution of their faunal content. Both makeup and endemic features of the taxa vary considerably throughout the successive fissures. The Terre Rosse faunal assemblages changed quite uniformly through time, both from the evolutionary viewpoint and in their composition. For this reason, reworked fossil material is deemed negligible (Masini et al. 2010) or is fairly easily detectable, as occurs in fissures M013 (Masini et al. 2013) and F21c (Savorelli 2013).

The criteria adopted by Freudenthal's (1976) pioneer paper were of fundamental importance to all the subsequent research on the biochronology of the Terre Rosse deposits. Freudenthal (1976) ordered the fossiliferous fissures biochronologically based mainly on the increase in size and in the number of molar crests of the endemic murids of the genus *Mikrotia* (Freudenthal 1976: Table 1 and fig. 4, pp. 10–13). For further corroboration, Freudenthal (1976) cross-compared his succession with that obtained based on the evolution of the endemic cricetids of the genus *Hattomys*.

Table 1

List of specimens analysed for the present study

AQ1

Species	Deposit	Inventory	Description
Original material of the Florence Collection			
<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	F15-039	Fragmental left jaw with m1, m3

Species	F15 Deposit	F15-041 Inventory	Isolated right P4 Description
	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	F15-050	Fragmental isolated right P4
<i>D. cf. freudenthali</i>	F15	F15-047	Isolated right P2
	F15	F15-049	Isolated right I1
	F15	F15-052	Fragmental isolated left M2
<i>D. minor</i>	F9	F9-001	Isolated left i1
	F9	F9-014	Fragmental skull with left C, both P1s, P3s, P4s, M2s and M3s
	F9	F9-018	Isolated left M1
<i>D. cf. minor</i>	F1	F1-002	Fragmental right jaw with p1
	F1	F1-004	Isolated right P2
	F1	F1-009	Isolated left m2
<i>D. intermedius</i>	F21c	F21-002	Isolated right p4
	P81D	P81D-001	Fragmental left jaw without teeth
	P81D	P81D-003	Fragmental right jaw without teeth
	P81D	P81D-005	Isolated right c
	P81D	P81D-006	Isolated right c
	P81D	P81D-007	Isolated left c
	P81D	P81D-008	Isolated right c
	P81D	P81D-009	Isolated left m1, broken
	P81D	P81D-010	Isolated right I1
	P81D	P81D-011	Isolated right P3, broken
	P81D	P81D-012	Isolated right i1
	P81D	P81D-013	Fragmental right jaw without teeth
	P81D	P81D-014	Fragmental left maxillary without teeth

Species	P81D Deposit	P81D-015 Inventory	Fragmental right jaw without teeth Description	
<i>D. intermedius</i>	P81D	P81D-016	Fragmental left jaw without teeth	
	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	
	NBS	NBS-001	Isolated left p4	
	F1	F1-001	Isolated left i1	
	F1	F1-006	Isolated left P4	
	F1	F1-007	Isolated left P4	
	F8	F8-001	Isolated right i1	
	F8	F8-002	Isolated left p2	
	F8	F8-040	Left jaw with c, p3–m3 (broken m1)	
	F9	F9-002	Isolated left I1	
	F9	F9-003	Isolated left c	
	F9	F9-017	Fragmental left maxillary with P1–P2, P4	
	F9	F9-022	Fragmental right jaw with p4	
	<i>Deinogalerix</i> sp. 1	F15	F15-038	Fragmental left maxillary with P3–M2
		F15	F15-046	Isolated right p3
F15		F15-048	Isolated right i1	
<i>Deinogalerix</i> sp. 2	P81D	P81D-002	Fragmental left jaw without teeth	
	P81D	P81D-004	Fragmental left jaw with m2–m3	
Casts of Naturalis specimens				
<i>D. minor</i>	Fina H	RGM 178184 (h) cast	Fragmental right jaw with p2–m3	
	Gervasio 1	RGM 179174 (p)	Fragmental left jaw with p3–m3	

Species	Deposit	cast Inventory	Description
<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. breviostris</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

Around a decade after this, De Giuli et al. (1987a) proposed a chronological arrangement of the Gargano deposits focused primarily on the morphological changes, more than on size variations, of the teeth of *Mikrotia* and *Prolagus* from seven fissure infillings that had been sampled by a University of Florence team. In order to obtain the most parsimonious chronological succession, De Giuli et al. (1987a) minimised possible conflicts (e.g. evolutionary inversions in size and morphology) by assuming the minimum number of bioevents (extinctions, originations/migrations), while working on the largest possible amount of taxa. Using all the available biochronological information, De Giuli et al. (1987a) originally identified three phases of faunal settlement within the ordered succession of fissures; *Deinogalerix* is not present in the last of these phases. After several

decades of research (Masini et al. 2008, Masini et al. 2010, Masini et al. 2013; Rinaldi and Masini 2009; Maul et al. 2014), five faunal settlement phases have been recognised.

Rinaldi and Masini (2009) cross-compared Freudenthal's (1976) and De Giuli et al.'s (1987a) biochronological schemes and underlined the difficulty of using different approaches for the biochronological arrangement of the Gargano fossiliferous deposits, and especially of the imperfectly described fossil assemblages. Based on the information yielded by the newly discovered fissure M013, but also on the contribution of the endemic glirids from Gargano, Masini et al. (2013) presented a revised version of the biochronology of the most ancient Terre Rosse fissures.

Age of Apulia Platform deposits

The ages of the various Gargano karstic fissures are still debated (Masini et al. 2013; Freudenthal et al. 2013; Savorelli et al. 2016). Several attempts have been made to date the time when the latest ancestors of the various Gargano taxa first arrived in the Apulia Platform: opinions ranged from the late Tortonian–Early Messinian (MN 11–12 zone of the Neogene Mammalian Biochronology; Freudenthal and Martín-Suárez 2010; Freudenthal et al. 2013) to the Messinian (MN 12–13, De Giuli et al. 1987a; Freudenthal 1985), or even early Pliocene (MN 14, De Giuli et al. 1987a). Recently, Savorelli et al. (2016) dated the latest faunal dispersion to Gargano to MN 13. The Scontrone fossiliferous site is stratigraphically dated, with reasonable confidence, to about 9 Ma (MN 11; Patacca et al. 2013) and is therefore considered somewhat more ancient than the whole complex of Gargano fissure fillings (see also Savorelli et al. 2017).

Material and methods

Material

The material from Gargano stored at the Department of Earth Sciences of Florence (DSTF) and examined for this study is listed in Table 1. It has been compared with: (1) remains of *Deinogalerix* retrieved from Gargano over the last decades and now housed both in the National Museum of Natural History (Naturalis) of Leiden (Netherlands) and in the Italian Department of Earth Sciences of the University of Turin (DSTT); (2) the specimens from Scontrone, which are kept at the Centro di Documentazione Paleontologica “*Hoplitomeryx*” of Scontrone; and (3) uncatalogued specimens of *Parasorex socialis* and *Galerix stehlini* from La Grive

Saint Alban and of *Apulogalerix* from the Gargano fissures F1 and F32, all preserved at the DSTF.

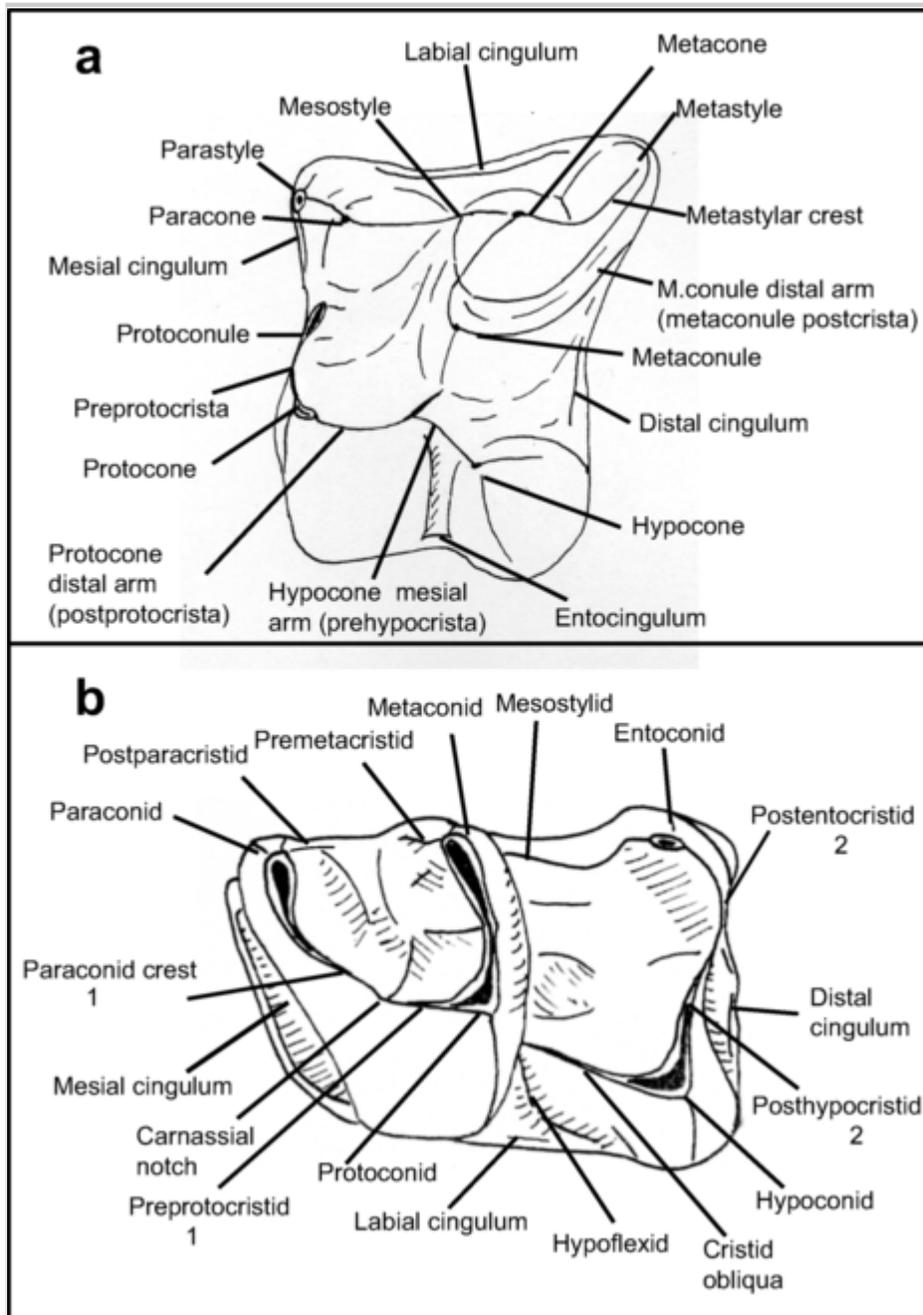
Comparisons were performed on casts of Butler's (1980) type specimens made by the Naturalis staff and now stored in the laboratories of the Archaeological Superintendency of Abruzzo in Chieti (Table 1), supplemented by literature information. Comparisons with *Deinogalerix masinii* from the fissure *Mikrotia* 013 (= M013), and with the *Deinogalerix* species from the fissure M010 (specimen PU 100044), preserved at the DSTT, are based on direct observation but also on data from the literature (Villier 2012; Villier et al. 2013; Villier and Carnevale 2013).

Methods

Capital letters (e.g. M1, M2, M3) are used to indicate upper teeth, and lower case letters for lower ones (e.g. m1, m2, m3). Figure 1 shows the tooth nomenclature used in this paper. In the upper molars, the mesial cuspule between protocone and paracone, sometimes called paraconule, is here indicated as protoconule (Engesser 1980). The metastylar crest designates the distal arm of the metastyle (metastylar spur in Gould 1995). The disto-lingual extension of the paracone in p4–m1–3 is called postparacristid, following Savorelli et al. (2017).

Fig. 1

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



A Mitutoyo Dial Caliper was used for measurements (in millimetres). Size measurements are reported in Table 2 and Table S1 and Figs. 2, 3 and 4. Length (L) and width (W) of the upper and lower teeth have been measured following Prieto et al. (2010). The measurements of the *Naturalis* and *DSTT* specimens were obtained from Butler (1980), Villier (2012) and Villier et al. (2013). The sizes of the teeth of *Deinogalerix koenigswaldi* were obtained from Villier (2012). A few dental measurements provided in the literature were outliers lying at abnormal distances from other values. These measurements were taken again by the writers for the present study. For the morphological analyses, a Wild Heerbrugg microscope type

308700 was used. Photographs were taken with a Canon Powershot S70 and with a Panasonic Lumix DMC-TZ20 digital cameras.

Table 2

Raw dental measurements of the lower and upper teeth of the DSTF. (a) Lower teeth; measured measurements in italics are inferred and those with (*) match *L* and *W* in Butler (1980), Villier W2; in P4, Wpa (tooth breadth at the paracone) matches Butler's (1980), Villier's (2012), Villi (2013) WpaP4; in M1–2, WA (anterior breadth) is Prieto et al.'s (2010) W2 and matches Butl minimum length from the mesial margin to the distal angle of the tooth, which is indicated as (2012), Villier et al.'s (2013) and Villier and Carnevale's (2013) *L*. Measurements are in millim

a		il		c			p1
		DAP	DT	DAP	DT	Hmax	<i>L</i>
<i>D. freudenthali</i>	F15-015						
	F15-016						
	F15-039						
	F15-043						
	F15-044						
	F15-045						
	F15-031						
	F15-034						
<i>D. cf. minor</i>	F1-002						4.6
	F9-001	3.5	5.5				
<i>D. intermedius</i>	F21c-002						
	P81D-005			6	6	7	
	P81D-006			6.9	5.5	11.8	
	P81D-007			7.5	6.2	13	
	P81D-008			6.9	5.8	10.9	
	P81D-009						
	P81D-012	4.8	6.7				

	F15-052										
<i>D. minor</i>	F9-014 right						5.7	2.8			9.9
	F9-014 left				5.4	3.2	5.2	2.8			9.9
	F9-018										
<i>D. cf. minor</i>	F1-004								7.4	3.7	
<i>D. intermedius</i>	P81D-010	6.6	6.4	12.1							
	P81D-011										/
	P81D-025										
	P81D-026										13.7
	F1-006										
	F1-007										
	F9-002	7.8	6.6	11.2							
	F9-017							5.3	3.2	7.9	4.1
<i>Deinogalerix</i> sp. 1	F15-038										11.3
	F21c-001										

Fig. 2Scatter diagrams of **a** P4 and **b** p4

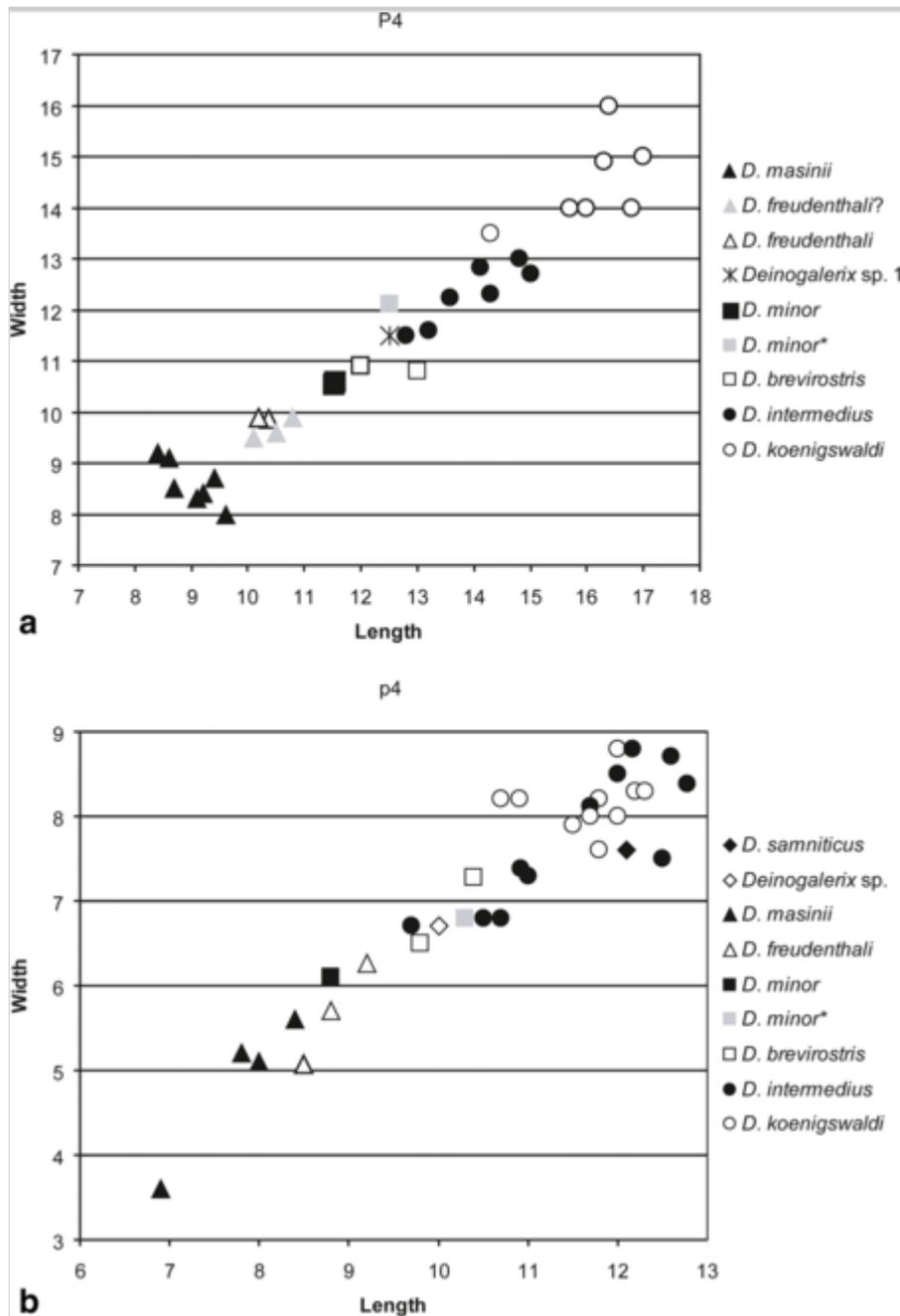


Fig. 3

Ratio diagrams comparing **a** the p3–m3 lengths (L) and **b** the P3–M3 lengths in different species of *Deinogalerix* (measurements in Table 3). The standard used for these analyses is *D. masinii*. *Deinogalerix minor** from M010 is called *D. koenigswaldi* by Villier and Carnevale (2013). Methodological details are included in the “Material and methods” section. The diagrams are commented in the Comparisons section

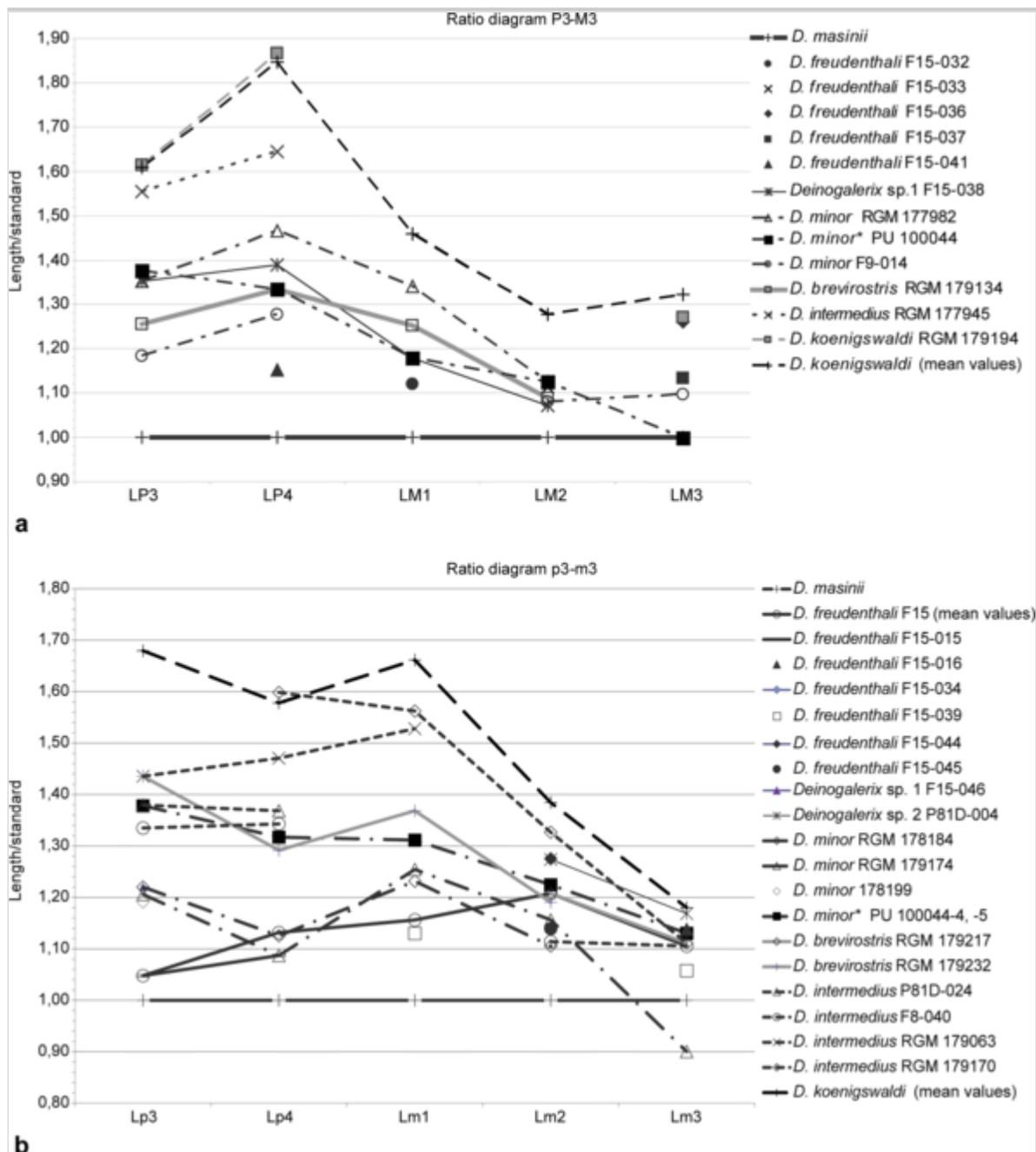
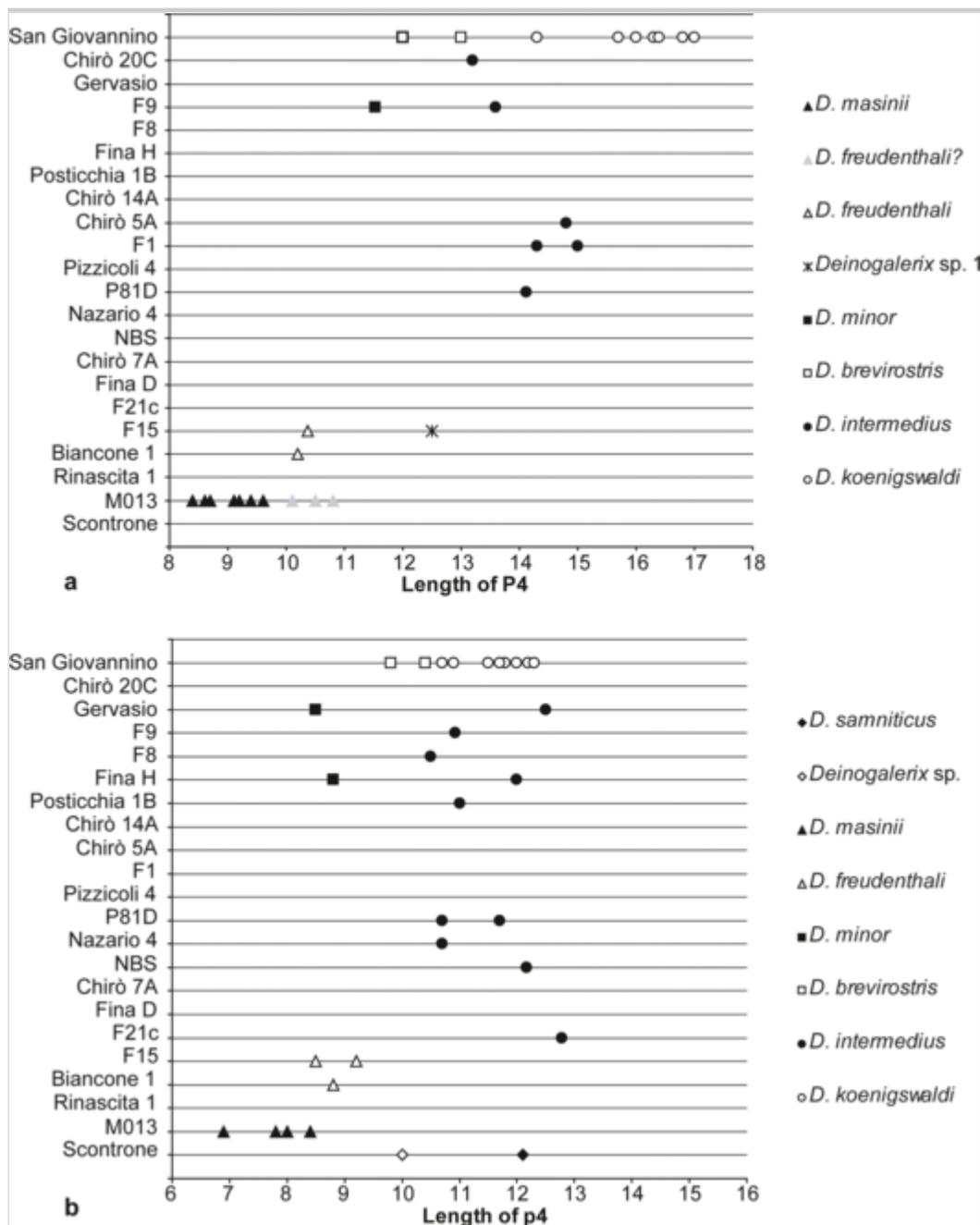


Fig. 4

Stratigraphic distribution of the variation in length of **a** P4 and **b** p4. Measurements are in millimetres. See Table 4 for the biochronological order of the fissures



Metric comparisons have been performed using scatter plots (length vs width, Fig. 2) and ratio-diagrams of the lengths of the p3–m3 and P3–M3 tooth rows (Fig. 3, Table 3). The measurements of p1 and p2 and P1 and P2 have been excluded due to the paucity of the data. Comparative odontometric measurements (Fig. 3) have been performed using a simplified, non-logarithmic version of the well-known “Simpson Log-Ratio Diagram” method (Simpson 1941; Masini and Fanfani 2013). The ratio diagrams were constructed to show the proportional relationships existing between the average dental lengths of the well-documented and primitive species *Deinogalerix masinii* (Villier et al. 2013), which was chosen as the standard, and the mean dental measurements of the most advanced species,

D. koenigswaldi (Butler, 1980), which represents the other extreme of comparison. The data of the other species have been plotted individually to avoid the introduction of patterns based on biased mean values obtained from too small or non-homogeneous samples.

Table 3

Data for Fig. 3; (a, c) raw data; (b, d) ratios using *D. masinii* as standard. *Deinogalerix minor** from M010 is called *D. koenigswaldi* by Villier and Carnevale (2013). *Deinogalerix minor** from Chirò 20C is called *D. intermedius* by Butler (1980). Measurements in italics are controlled by the writers

a			Length				
Species	Locality		P3	P4	M1	M2	M3
<i>D. masinii</i>	M013	Sample mean	8.36	9.00	6.79	5.60	4.41
<i>D. freudenthali</i>	F15	F15-041		10.37			
<i>D. freudenthali</i>	F15	F15-032			7.60		
<i>D. freudenthali</i>	F15	F15-033				6.24	

<i>D. freudenthali</i>	F15	F15-036					5.56
<i>D. freudenthali</i>	F15	F15-037					5.00
<i>Deinogalerix</i> sp. 1	F15	F15-038	11.31	12.50	8.00	6.00	
<i>D. minor</i>	F9	F9-014 (left hemimaxilla)	9.90	11.50		6.05	4.84
^a Values from Villier (2012)	M010	PU 100044 (left hemimaxilla)	11.50	12.00	8.00	6.30	4.40
^b Values inferred and measurements of m3 omitted because they were considered flawed							
<i>D. minor</i> *	Chirò	RGM 177 982	11.30	13.20	9.10	6.30	
^c Indicates inferred values							

<i>D. breviröstris</i> ^a	SG	RGM 179 134	10.50	12.00	Length	6.10	4.80
<i>D. Species intermedius</i>	Locality Chiro 5A	RGM 177 945	P3 13.00	P4 14.80	M1	M2	M3
<i>D. koenigswaldi</i>	SG and SG Low	Sample mean (Butler 1980)	13.45	16.62	9.90	7.15	5.83
<i>D. koenigswaldi</i>	SG	RGM 179 194	13.50 ^a	16.80 ^a			5.60 ^a
b			Length				
Species	Locality		P3	P4	M1	M2	M3
<i>D. masinii</i>	M013	Sample mean	1.00	1.00	1.00	1.00	1.00
<i>D. freudenthali</i>	F15	F15-041		1.15			
<i>D. freudenthali</i>	F15	F15-032			1.12		
<i>D. freudenthali</i>	F15	F15-033				1.11	
<i>D. freudenthali</i>	F15	F15-036					1.26

<i>D. freudenthali</i>	F15	F15-037					1.13
<i>Deinogalerix</i> sp. 1	F15	F15-038					
<i>D. minor</i>	F9	F9-014 (left hemimaxilla)	1.18	1.28		1.08	1.10
<i>D. minor</i> *	M010	PU 100044 (left hemimaxilla)	1.38	1.36	1.17	1.09	1.07
^a Values from Villerö (2012)	Chiro 20C	RGM 177 982	1.35	1.47	1.34	1.13	
^b Values inferred and measurements of m3 omitted because they were considered flawed							
<i>D. breviröstris</i>	SG	RGM 179 134	1.26	1.33	1.25	1.09	
^c Indicates inferred values							

<i>D. intermedius</i>	Chirò 5A	RGM 177 945	1.56	1.64	Length			
<i>D. Species</i>	Locality		P3	P4	M1	M2	M3	
<i>D. koenigswaldi</i>	SG and SG Low	Sample mean (Butler 1980)	1.61	1.85	1.46	1.28	1.32	
<i>D. koenigswaldi</i>	SG	RGM 179 194	1.61	1.87				1.27
c			Length					
Species	Locality		p3	p4	m1	m2	m3	
<i>D. masinii</i>	M013	Sample mean	6.97	7.82	8.77	5.88	5.22	
<i>D. freudenthali</i>	F15	Sample mean	7.3	8.85	10.14	7.1	5.77	
<i>D. freudenthali</i>	F15	F15-015	7.3	8.5				
<i>D. freudenthali</i>	F15	F15-039			9.91		5.52	
<i>D. freudenthali</i>	F15	F15-044				6.7		
<i>D. freudenthali</i>	F15	F15-045				7.5		

<i>D. freudenthali</i>	F15	F15-016					5.94	
<i>D. freudenthali</i>	F15	F15-034					5.85	
<i>Deinogalerix</i> sp. 1	F15	F15-046	8.5					
<i>Deinogalerix</i> sp. 2	P81D	P81D-004				7.49	6.1	
<i>D. minor</i> from Villor (2012)	Fina H	RGM 178 184	8.5	8.8	10.8	6.5		
<i>D. minor</i> inferred and measurements of m3 omitted because they were considered flawed	Fina H	RGM 178 199	8.3					
<i>D. minor</i> inferred values	Gervasio	RGM 179 174	8.4	8.5	11	6.8	4.7	

<i>D. breviostris</i>	SG Low	RGM 179 232	10	10.1	Length	7 ^b	/ ^b
<i>D. breviostris</i>	SG Low	RGM 179 217	P3	P4	M1	M2 7.1	M3 5.8
<i>D. minor</i> *	M010	PU 100044-4, -5 (right hemimandible)	9.6	10.3	11.5	7.2	5.9
<i>D. intermedius</i>	P81D	P81D-024	9.61	10.7			
<i>D. intermedius</i>	F8	F8-040	9.3	10.5	/	6.55 ^c	5.77 ^c
<i>D. intermedius</i>	Nazario 4	RGM 179 063	10	11.5	13.4		
<i>D. intermedius</i>	Gervasio	RGM 179 170		12.5	13.7	7.8	5.8
<i>D. koenigswaldi</i>	SG and SG Low	Sample mean (Butler 1980)	11.70	12.34	14.57	8.14	6.16
d			Length				
Species	Locality		p3	p4	m1	m2	m3
<i>D. masinii</i>	M013	Sample mean	1.00	1.00	1.00	1.00	1.00

<i>D. freudenthali</i>	F15	Sample mean	1.05	1.13	1.16	1.21	1.11
<i>D. freudenthali</i>	F15	F15-015	1.05	1.09			
<i>D. freudenthali</i>	F15	F15-039			1.13		1.06
<i>D. freudenthali</i>	F15	F15-044				1.28	
<i>D. freudenthali</i>	F15	F15-045				1.14	
^a Values from Villier (2012)							
^b Values inferred and measurements of m3 omitted because they were considered flawed							
<i>D. freudenthali</i>	F15	F15-016					1.14
^c Indicates inferred values							

<i>D. freudenthali</i>	F15	F15-034			Length			1.12
Species	Locality		P3	P4	M1	M2	M3	
<i>Deinogalerix</i> sp. 1	F15	F15-046	1.22					
<i>Deinogalerix</i> sp. 2	P81D	P81D-004				1.27	1.17	
<i>D. minor</i>	Fina H	RGM 178 184	1.22	1.13	1.23	1.11		
<i>D. minor</i>	Fina H	RGM 178 199	1.19					
<i>D. minor</i>	Gervasio	RGM 179 174	1.21	1.09	1.25	1.16	0.90	
<i>D. brevisrostris</i>	SG Low	RGM 179 232	1.44	1.29	1.29	1.19		
<i>D. brevisrostris</i>	SG Low	RGM 179 217				1.21	1.11	
<i>D. minor</i> *	M010	PU 100044-4, -5 (right hemimandible)	1.38	1.32	1.31	1.22	1.13	
<i>D. intermedius</i>	P81D	P81D-024	1.38	1.37				
<i>D. intermedius</i>	F8	F8-040	1.33	1.34		1.11	1.11	

<i>D. intermedius</i>	Nazario 4	RGM 179 063	1.44	1.47	1.53			
<i>D. intermedius</i>	Gervasio	RGM 179 170		1.60	1.56	1.33	1.11	
<i>D. koenigswaldi</i>	SG and SG Low	Sample mean (Butler 1980)	1.68	1.58	1.66	1.38	1.18	

^aValues from Villier (2012)

^bValues inferred and measurements of m3 omitted because they were considered flawed

^cIndicates inferred values

Criteria for taxonomic attribution

The different species of *Deinogalerix* are quite uniform, especially in the dental morphologically. Butler (1980) distinguished them based primarily on size, providing only a few taxonomically diagnostic morphological details for *Deinogalerix freudenthali*.

The DSTF collection of remains of *Deinogalerix* has been taxonomically identified using morphological and morphometric criteria, combined with biochronological constraints. Various species of *Deinogalerix* are morphologically similar and overlap in size. This greatly complicates the taxonomic identification of some specimens—especially isolated teeth—and some degree of uncertainty persists about their specific assignment. In particularly difficult cases, we followed biological naming conventions (International Code of Zoological Nomenclature, fourth edition, International Commission on Zoological Nomenclature 2017), using the “cf.” abbreviation for the specific attribution of some isolated, taxonomically non-diagnostic and/or badly preserved teeth (i.e. *Deinogalerix cf. freudenthali* and *Deinogalerix cf. minor*).

The diagnoses provided by Butler (1980) have been emended based on the direct observations by the writers. In fact, because of the paucity and poor state of preservation of some of the DSTF specimens examined for this contribution, the emended diagnoses are sometimes completed based on Butler’s (1980) original material.

Working on the DSTT remains of *Deinogalerix masinii* from M013, Villier et al. (2013) argued that the P4 PU128530 may be attributed to *Deinogalerix freudenthali*. The present authors share this opinion and believe that also to PU128515 and PU106927 can be moved from *D. masinii* to *D. freudenthali*. With the unsettled taxonomic status of these specimens, it has been found opportune not to include the sizes of these isolated teeth in the computation of the mean values of the P4 diametres of *Deinogalerix masinii*.

The writers suppose that the taxonomic status of other specimens from Naturalis (RGM 177945 and RGM 177982) and DSTT (PU 100044) should be reviewed. See below (“Diagnostic differences between the species represented in the DSTF collection” section).

Biochronological methods and adopted biochronological framework

Given its scope, the present biochronological scheme (Table 4) regards only the *Deinogalerix*-bearing deposits of the Apulia Platform and is an updated version of previous schemes presented by various authors (Rinaldi and Masini 2009; Masini et al. 2010; Masini et al. 2013; Savorelli 2010; Savorelli 2013; Maul et al. 2014). The information was drawn from Freudenthal (1976), Abbazzi et al. (1993), Masini et al. (2013) and Maul et al. (2014), but it includes also data collected under the supervision of C. De Giuli and partly published in De Giuli et al. (1987a). The different fissures are placed chronologically based primarily on the number of crests (NC) on the m1s of the resident line of *Mikrotia*, bearing in mind that the increasing number of crests expresses the evolutionary progress of this murid (Freudenthal 1976; Maul et al. 2014). In the calculation of NC values, paired crests are here counted as “1”, and single, unpaired ones as “0.5” (Table 4 includes average NC counts obtained from samples of variable “*n*” size collected from the different Gargano fissures).

Table 4

Clustering of the different Apulia Platform fossiliferous deposits in their corresponding phases of settlement. The relative sequencing of the deposits (relative order) is based on NC (number of crests in the rodent genus *Mikrotia*) and faunal assemblages in the different fossiliferous deposits (see text for explanation)

Phase	Deposits	Relative order	NC	<i>n</i> (size of the sample)	Source
3	San Giovannino	22	6.23	20 ^a	Freudenthal (1976)
	Chirò 20C	21	6.05	20 ^a	Freudenthal (1976)
	Gervasio ^b	20	5.96	15	Freudenthal (1976)
	F9	19	5.88	89	De Giuli unpublished
	F8	18	5.8	62	De Giuli unpublished
	Fina H	17	/ ^c	/ ^c	Freudenthal (1976)
	Posticchia 1B	16	5.65	10	Freudenthal (1976)
2	Chirò 14A	15	5.23	20 ^a	Freudenthal (1976)

Phase	Deposits	Relative order	NC	<i>n</i> (size of the sample)	Source
	Chirò 5A	14	5.13	20 ^a	Freudenthal (1976)
	F1	13	5.1	243 (unpublished)	Savorelli (2010)
	Pizzicoli 4	12	5.03	20 ^a	Freudenthal (1976)
	P81D	11	4.94	37	De Giuli unpublished
	Nazario 4	10	4.89	20 ^a	Freudenthal (1976)
	NBS	9	4.84	158 (unpublished)	Savorelli (2010)
	Chirò 7A	8	4.68	20 ^a	Freudenthal (1976)
	Fina D	7	4.58	20 ^a	Freudenthal (1976)
1b	F21c ^d	6	4.28 (F21b)	315 (F21b)	Masini et al. (2013)
	F15	5	3.99	178	Masini et al. (2013)
	Biancone 1	4	3.93	16	Masini et al. (2013)
1a	Rinascita 1	3	3.95	20 ^a	Masini et al. (2013)
0	M013	2	3.5	29	Masini et al. (2013)
	Scontrone	1	/	/	Savorelli et al. (2017)

^aFreudenthal (1976) set a maximum of 20 mls of *Mikrotia* in all the samples he examined

^bFreudenthal (1976) distinguished “Gervasio 1” from “Gervasio 2” and considered both older than San Giovannino. Butler (1980) mentioned a single “Gervasio”, which probably matches Freudenthal’s (1976) “Gervasio 1”. Based on the evolutionary degree of *Mikrotia* in the main line of evolution, “Gervasio 2” may even be younger than San Giovannino. Butler’s (1980) “Gervasio” contains more primitive specimens of *Deinogalerix* compared to San Giovannino and may therefore reasonably correspond to Freudenthal’s (1976) Gervasio 1

^cFreudenthal (1976, p. 15) defined the biochronologic position of Fina H without providing its morphological index, because of the possible co-occurrence of several species of *Mikrotia* with overlapping size ranges

Phase	Deposits	Relative order	NC	n (size of the sample)	Source
<p>^dFissures F21a, F21b and F21c come from different sections of the same megakarren; their position in the biochronologic scheme should thus be virtually the same. Nonetheless, based on the anomalous variability of <i>Mikrotia</i> (De Giuli et al. 1987a) and <i>Hattomys</i> (Savorelli 2010, 2013), it suggests that F21c (which was collected from the lowest part of the infilling) may likely be contaminated by fossil material from younger fissures. Fissure F21c is here given the NC value of fissure F21b</p>					

The biochronological ordering of the Gargano collections of Naturalis differs in some respects from Freudenthal's (1976): Posticchia 1B, for example, is here considered younger than Chirò 14A not only for its higher NC value, but also because it contains three advanced species of *Mikrotia* (small-sized, medium-sized/main lineage and *Mikrotia magna*). In fact, Chirò 14A is still included in the phase with a single advanced *Mikrotia* (Freudenthal 1976; De Giuli et al. 1987a).

For the sake of simplicity, in the biochronological succession used in the present study (Table 4), the fossiliferous deposits are spaced at constant intervals and numbered 1 to 22, from the oldest, Scontrone, to the youngest, San Giovannino. The numbering represents the reference against which plotting the sizes of the teeth of the different species of *Deinogalerix* (Fig. 4). Actually, the different fossiliferous deposits do not necessarily follow one another regularly through time: fissure F9, for example, follows F8 biochronologically, and yet both fissures belong to the same megakarren, have taxonomically similar faunas, albeit not exactly equivalent, and are thought to be virtually coeval.

Systematic palaeontology

Class Mammalia Linnaeus, 1758

Order Eulipotyphla Waddell, Okada and Hasegawa, 1999

Suborder Erinaceomorpha Gregory, 1910

Family Erinaceidae Fischer, 1814

Subfamily Galericinae Pomel, 1848

Tribe Galericini Pomel, 1848

Genus *Deinogalerix* Freudenthal, 1972

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

Included species: *Deinogalerix brevirostris*; *Deinogalerix freudenthali*; *Deinogalerix intermedius*; *Deinogalerix minor*; *Deinogalerix masinii*; *Deinogalerix samniticus*.

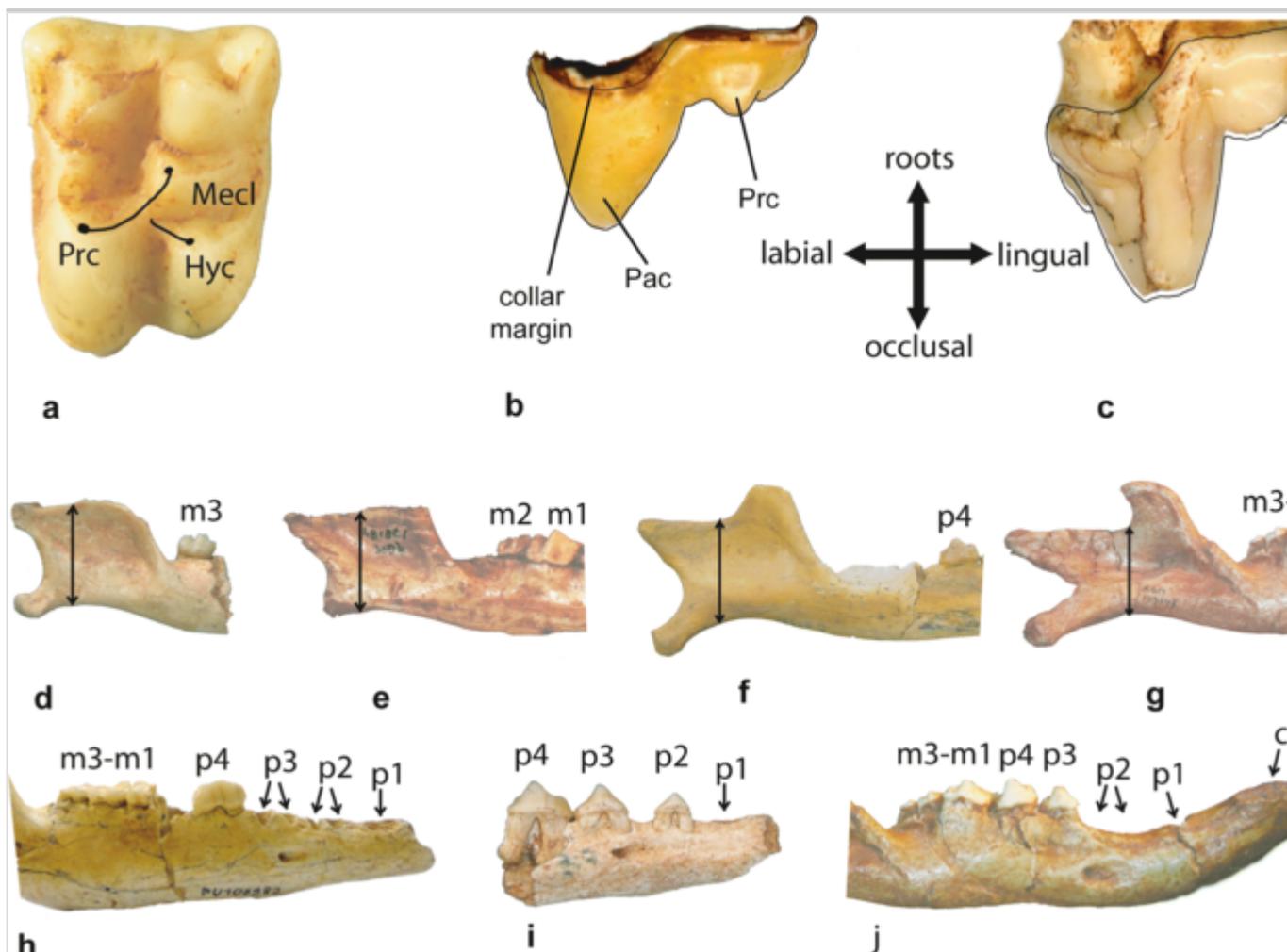
Distribution: Early Tortonian (early late Miocene) of Scontrone (Abruzzo, central Italy) to Messinian (late late Miocene) of Gargano (south-eastern Italy).

Original diagnosis. See Freudenthal (1972).

Revised diagnosis (partially from Villier et al.'s 2013 emended diagnosis and from Savorelli et al. 2017, slightly modified): Large Galericipini; 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 distinct trigonid, paralophid blunt and no carnassial notch, and with metaconid and distal cingulum joined by bulbous mesostylid; carnassial notch present on m2 and m3 and hardly visible or absent on m1; hypocone constantly present on P3; on M1 and M2 protocone and metaconule very rarely connected (Fig. 5a), bulging and undivided mesostyle and distal cingulum interrupted or continuous, sometimes distal arm of metaconule confluent with uninterrupted distal cingulum; metastylar crest well-developed and inflated on M3; supraorbital processes present and formed by frontal bone; mandible with small coronoid process, low condyle, and mental foramen under mesial root, or between roots on p3.

Fig. 5

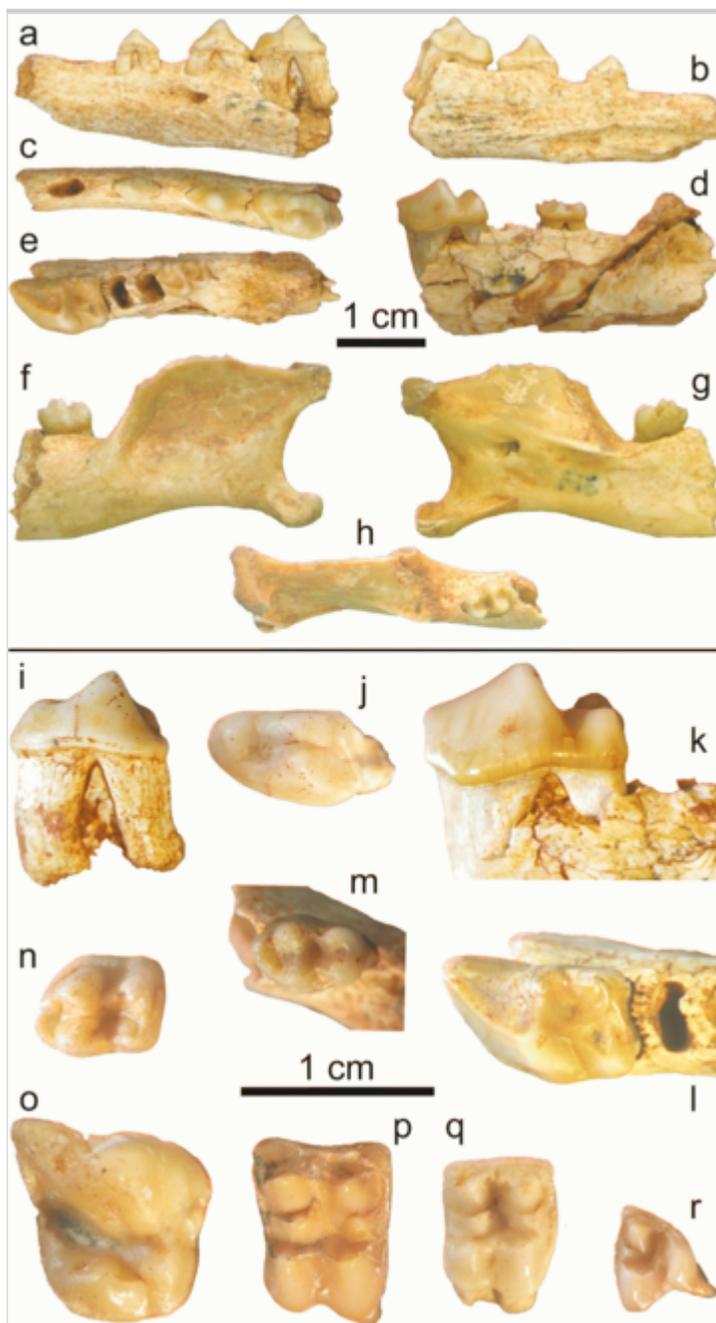
a Left M1 (F9-018), *Deinogalerix minor* from fissure F9, occlusal view. Rare example of the protocone–metaconule connection. Figure not to scale. **b, c** Outlines of P4 in mesial view. Variations in the collar profile in *D. freudenthali* (**b**) and *D. intermedius* (**c**). **d–g** Outlines of the lateral views of the ascending mandibular rami. Comparisons of the heights in *D. freudenthali* (**d**), *D. minor* (**e**), *D. intermedius* (**f**) and *D. koenigswaldi* (**g**). **h–j** Rostral tapering of the horizontal ramus in *Deinogalerix masinii* (**h**) and *D. freudenthali* (**i**), compared to the mandible of *D. koenigswaldi* (**j**). Figures **d–j** are depicted in the same size and not to scale to make morphological and proportional differences readily apparent. Hyc = Hypocone, Mecl = Metaconule, Pac = Paracone, Prc = Protocone



Deinogalerix freudenthali (Fig. 6)

Fig. 6

Deinogalerix freudenthali, fragmental left mandible F15-015: **a** lateral view; **b** medial view; **c** occlusal view. *Deinogalerix freudenthali*, fragmental left mandible F15-039: **d** lateral view; **e** occlusal view. *Deinogalerix freudenthali*, fragmental left mandible F15-016: **f** lateral view; **g** medial view; **h** occlusal view. *Deinogalerix freudenthali*, left p4 F15-015: **i** labial view; **j** occlusal view. *Deinogalerix freudenthali*, m1 on fragmental left mandible F15-039: **k** labial view; **l** occlusal view. *Deinogalerix freudenthali*, m3 on fragmental left mandible F15-016: **m** occlusal view. *Deinogalerix freudenthali*, right m2 F15-045: **n** occlusal view. *Deinogalerix freudenthali*, right P4 F15-041: **o** occlusal view. *Deinogalerix freudenthali*, right M1 F15-032: **p** occlusal view. *Deinogalerix freudenthali*, right M2 F15-033: **q** occlusal view. *Deinogalerix freudenthali*, left M3 F15-036: **r** occlusal view



Emended diagnosis: Small-sized *Deinogalerix*, slightly larger than *D. masinii*, but with similar dental proportions. Relatively low-crowned teeth; m2s and m3s with relatively large talonids; hypoconid particularly developed on m3; compared to other species (except *D. masinii*) P4 proportionally shorter than M1 and with undivided hypocone; posterior arm of the metaconule on M1 and M2 either barely connected with uninterrupted distal cingulum or interrupts distal cingulum. Compared to other species, M3 relatively larger than M1. Mandible: in aboral view, angular process aligned with rest of ascending ramus; in medial view, ridge delimiting ventral border of the fossa for the insertion of temporalis muscle straight

and running above mandibular foramen; relatively high ascending ramus (from base to sigmoid notch); masseteric fossa confined posteriorly by thick, prominent border.

Material: See Table 1. All the remains attributed to *Deinogalerix freudenthali* come from the fissure filling F15.

Measurements: See Table 2.

Descriptions

Teeth

p2: The sample from the fissure filling F15 includes only the unworn specimen still preserved on the fragmental left mandible F15-015. This single-cusped (protoconid?) tooth has two large roots. The cusp is low and rather blunt, asymmetrically triangular in lateral view, steeper mesially and more gently sloping distally. The tooth has a narrow (narrower than p3), oval outline, without a distinct talonid.

p3: The unworn specimen, preserved on the fragmental left mandible F15-015, is similar to p2 but much larger and higher. Labially, the protoconid is relatively swollen at the base. The tooth bears two large, slightly divergent roots, a straighter distal one and a more oblique mesial one. In occlusal view, the crown has a sub-oval outline. The distal margin of the talonid is concave and asymmetric, with a marked disto-lingual protrusion.

p4: Two different-sized specimens are present in the sample from F15, a smaller, relatively less worn one, preserved on the fragmental left mandible F15-015, and a larger, more worn, isolated one, F15-031. The teeth are larger and wider than p3. Both appear sub-oval occlusally, slightly larger distally, and with a slightly concave and disto-labially asymmetric distal margin. The trigonid includes three fairly low and blunt cuspids. The protoconid is dominant, and the metaconid is smaller and slightly lower. A well-marked cleft is clearly visible between protoconid and metaconid on the distal face of F15-015; wear obliterated it on F15-031. The paraconid is more robust and quite lower than the metaconid. A very reduced, blunt, smooth and low crest-like paralophid runs from the anterolabial side of protoconid to the labial side of the paraconid (the carnassial notch is absent). The distal portion of the paralophid (=blunt preprotocristid) slopes gently downwards from the protoconid. The tooth bears a small cusplule near its disto-lingual corner and the distal cingulum appears quite inclined outwards and backwards linguo-

labially. At the disto-lingual margin of the metaconid, a bulbous metastylid merges with the cingulum. The trigonid basin is roundish and very shallow, and well-delimited lingually on F15-031, and quite less so on F15-015. The collar is more uplifted in the inter-root area in F15-031 than in F15-015.

m1: Two teeth of similar size are present in the F15 collection, one preserved on the fragmental left mandible F15-039, the other isolated, F15-043. The former is moderately worn, the latter just slightly so. The trigonid is particularly long, which is typical for the genus. Its lingual wall is high and continuous. The paralophid is a high, prominent, continuous, blade-like structure, resulting from the fusion of the paraconid crest with the preprotocristid. The carnassial notch is weak on F15-043 and is absent on F15-039. It is located halfway between the paraconid and protoconid. The metaconid is much smaller and lower than the protoconid. The two cuspids appear aligned transversally in occlusal view and separated by a sharp notch, which is completely obliterated by wear on F15-039. A metastylid occurs on the distal wall of the metaconid. The hypoconid is low and connected mesially with the protoconid by the cristid obliqua and lingually with the entoconid by the postcristid. The talonid is narrower and much lower than the trigonid. The entoconid is slightly higher than the hypoconid. The hypoconulid is absent. In F15-043, the labial cingulum is absent, whereas in F15-039, a faint trace of it is present in the mesial part of the tooth and next to the hypoflexid. The distal cingulum is weak and short and not connected with the distal arm of the entoconid (in F15-039 the cingulum connects as a consequence of wear). The enamel is much thinner in the trigonid than in the talonid. The mesial root is much larger than the distal one.

m2: Two right, unworn, isolated m2s come from F15, a larger one, F15-044, and a smaller one, F15-045. The teeth are quite smaller and less specialised than m1s by having a proportionally smaller trigonid. The carnassial notch separates the preprotocristid from a long and low, labially directed paraconid crest. The paraconid is crest-like and the postparacristid, which prolongs distally and lingually, does not reach the base of metaconid (on F15-045 this crest is longer than it is on F15-044). The metaconid is positioned somewhat more mesially than the protoconid and separated from it by a deep, V-shaped notch. The two cuspids are approximately the same height. The talonid is much narrower than in m2s of mainland species. The entoconid is slightly lower than the meta- and protoconid, and the hypoconid is the lowest cuspid. The mesostylid is well-developed and dips downward, separated from the entoconid by a deep notch (clearly marked by a groove on the lingual wall of the tooth). In F15-044, the postcristid is divided into a posthypocristid and postentocristid by a deep, V-shaped notch, which is aligned

sagittally with that separating the metaconid from the protoconid. In F15-045, the postcrisid is more complete. The distal cingulum is short, located at the base of the hypoconid, and not fused to the post-entocristid. A complete and robust mesio-labial cingulum is present on F15-045; in contrast, on F15-044, the mesial and labial cingula are weak and separated from one another, and the latter is restricted only to the outlet of the hypoflexid.

m3: There are 3 m3s from F15: two left ones, F15-039 and F15-016, still preserved on the mandibles, and an isolated right one, F15-034. F15-039 is very worn, the others are moderately worn and F15-034 was somewhat corroded during laboratory preparation. These teeth are essentially small replicas of the m2s, but with proportionally much narrower talonids. The ento- and hypoconid are aligned to one another latero-medially. The hypoconid is positioned more distally, compared to the m3s of continental counterparts. The distal cingulum is absent and the labial cingulum is weak. F15-016 has a mesio-labial cingulum that curves upwards at its mesial and distal ends.

P4: Two P4s come from fissure F15: a dental gem, F15-041, and a labial fragment of an isolated specimen, F15-050. P4s have trapezoidal outline, with a dominant large, high and pointed paracone, which occupies a large part of the labial side of the crown, as occurs in P3s. The postparacrista (=Lopatin's 2006, anterior portion of the centrocrista; Villier and Carnevale's 2013, central crest) originates from the tip of the paracone, dips down to the carnassial notch and then runs almost horizontally merging with the metastylar crest (Lopatin's 2006, postcrista), which extends backwards and somewhat labially. The parastyle on F15-041 is weak, low, split and bears an accessory lingual cuspule.

No anterior cingulum is visible on F15-041. The protocone is located mesio-labially, very close to the paracone; it is connected by a crest to the base of the paracone in both specimens. The valley between the paracone and hypocone widens distally towards the disto-lingual corner of the tooth. The furrow between the protocone and hypocone is fairly shallow, whereas the valley between the paracone and hypocone is deep. The hypocone is lower than the protocone and is blunt, swollen, elongated and slopes distally. It is not divided. The distal cingulum bears a weak style at the base of the hypocone.

M1: The sample from F15 includes an isolated and unworn right M1, F15-032. The tooth bears six, rather low cusps; the metacone is the highest and the hypocone the lowest, whereas the protocone is slightly lower than the metacone and the most massive cusp. Occlusally, the tooth has a trapezoidal outline, wider mesially than

distally. The distal margin is oblique and the disto-labial corner of the tooth is not stretched disto-labially. The labial margin is slightly concave, and the mesial one almost straight. The lingual margin of the crown is oblique and concave because of the lingual prominence of the base of the protocone. The mesio-labial corner of the tooth is occupied by a bulging, “crest-like” parastyle, which is separated from the anterior arm of the paracone. A robust metastylar crest extends labially from the notch at the base of the metacone, and merges with a bulging metastyle. The latter is fused to a labially extended anterior arm of the metacone. A very small accessory crest extends labially from the mesostyle. The labial cingulum is moderately developed, and in labial view, its dorsal margin is convex and reaches almost the height of the mesostyle. The protoconule is well-developed and its mesial arm is barely connected with the anterior cingulum, whereas its posterior arm is absent. The protoconule is separated from the protocone by a V-shaped and deep notch. The metaconule is larger than the protoconule and triangular-shaped; its anterior arm leans against the base of the metacone without merging with it. A tiny accessory enamel crest connects the posterior arm of the metaconule with the distal cingulum, which is uninterrupted. The posterior arm of the protocone forms a continuous crest that merges with the mesial arm of the hypocone, and is not connected with the metaconule. The anterior arm of the protocone slopes and is separated from the base of the protoconule by a deep notch. The hypocone is a well-developed, sub-conical cusp; its posterior arm dips similarly to the anterior arm of the protocone and merges with the posterior cingulum. The trigon basin is deep and connected with a longitudinal valley that is delimited lingually by the protocone–hypocone complex. This valley opens mesially through the notch between protoconule and protocone. A short entocingulum occurs between the protocone and hypocone. The tooth has three roots: two sub-triangular labial ones and a larger lingual one, vertically separated by a very deep groove, and three accessory crests that converge towards the centre of the tooth.

M2: The specimen retrieved from fissure F15 is an isolated right m2, F15-033. The tooth is similar to, but smaller than M1; it also differs from the latter in having: (1) occlusally, a sub-rectangular outline, with a weakly convex mesial border; (2) less prominent disto-labial corner; (3) shorter metastyle; (4) posterior arm of the metaconule bent labially towards the disto-labial corner of the tooth; (5) distal cingulum interrupted.

The mesostylar region is occupied by an extension of the mesial arm of the metacone, which reaches the labial border of the tooth. The mesial arm of the protoconule bends labially connecting with the parastyle. The mesial cingulum is

short and interrupted and not connected with the mesial arm of the protoconule; the labial cingulum is absent.

The tooth bears two lingual roots fused together, two mesio-distally flattened lingual roots and three accessory crests that converge to form a central rootlet. The entocingulum is absent between the protocone and hypocone.

M3: Two M3s were recovered from fissure F15, F15-036 and F15-037. Both are much smaller than M2, occlusally sub-triangular and slightly broader than long. The mesial margin is almost straight, the disto-labial one markedly arched, and the lingual one slightly bilobed because of the protruding of the protocone and of the presence of the curved metastylar crest. The protocone is the largest cusp; its distal arm extends labially joining a small enamel pillar at the base of the metastylar crest in F15-036, whereas in F15-037 the posterior arm of the protocone bends lingually and the pillar is isolated. The protoconule is well-developed, its mesial arm bends labially connecting with the parastyle. The mesial cingulum is short, interrupted and not connected with the mesial arm of the protoconule. The latter is separated from the protocone by a deep, V-shaped notch. The parastyle is moderately developed. The labial cingulum is absent in F15-037, whereas F15-036 bears a short cingulum on the mesial portion of its disto-labial margin. The mesostyle is short, crest-shaped and labially directed on F15-036, and is a hardly visible swell on F15-037. The angle between the mesial and labial margins of the crown is acute. The metacone is strongly shifted disto-lingually compared to M1s and M2s. In the disto-labial region of tooth the posterior arm of paracone is fused to the metacone forming a continuous, arched crest that terminates into a swollen metastylar crest, separated from the posterior arm of the protocone. The trigon valley is deep and opened lingually, but also mesially through the notch between the protocone and protoconule. The lingual outlet of the valley is deeper in F15-036 than in F15-037 and is bordered by a very short endocingulum, which is absent in F15-037. The tooth bears three roots: the mesio-lingual one is the largest, the second in size is the disto-lingual one, which is flattened mesio-distally and bent to follow the distal profile of the tooth, and the smallest root, which is located under the paracone, is long and conical.

Mandibles

There are four fragments of mandible, three left ones, F15-015, F15-016, F15-039, and a right fragment, F15-042. The three left ones include the rostral portion of the horizontal ramus from the alveoli of p1 to p4, F15-015, still preserving the p2–p4 premolar row; two aboral portions, one, severely crushed, F15-039, with m1 and

m3 and the rostral portion of the base of the ascending ramus; the other, F15-016, with the rear portion of the alveolus of m2, m3 still preserved and the ascending ramus, which still bears the condyle and the angular process, but not the coronoid process.

F15-015 shows two diastemas approximately of the same length, between p1 and p2, and p2 and p3. The ramus is slender; the mental foramen opens under the rostral root of p3. The scar of the symphysis extends distally to the anterior root of p3.

The rostral border of the ascending ramus of F15-016 is inclined backwards. In medial view, the ventral margin of the fossa for the insertion of temporalis muscle shows a strong, but thin, ridge running straight from the alveolus of m3 to just above the mandibular foramen (character clearly visible also in F15-042). The angular process is elongated and enlarges medially with a markedly concave dorsal surface and a crest-like medial margin for the insertion of the internal pterygoideus muscle. In aboral view, the angular process appears aligned with the horizontal ramus and coronoid process. The masseter fossa is very deep. F15-016 shows an incomplete ossification of the condyle, which indicates that it belongs to a young adult. The profile of the condyle is slightly raised above the base of the sigmoid incisure. The condyle is sub-cylindrical and widened transversely, more medially than laterally. Its articular surface is slightly flattened dorsally and extends asymmetrically downwards, more laterally than medially. The rostral margin of the condylar process is well marked. In front of the medial part of the condylar process, there is a small, fairly deep fossette.

F15-042 is another aboral portion of the horizontal ramus without teeth, and with the m1–3 alveoli and the rostral portion of the base of the ascending ramus. The alveolus of m3 is wide enough to suggest that the tooth was erupting. The bone wall of this specimen is more porous than in F15-016; F15-042 is therefore younger ontogenetically than F15-016, whose m3 is at initial wear. In turn, F15-016 is younger than F15-039, whose m3 is quite worn.

Deinogalerix cf. freudenthali

Material: See Table 1.

Measurements: See Table 2.

Descriptions

The following specimens, tentatively attributed to *Deinogalerix cf. freudenthali*, are isolated, taxonomically non-diagnostic teeth.

Teeth

I1: Only one right first upper incisor, F15-049, is included in the F15 sample. Half the root is missing. The specimen is somewhat damaged on the distal side and was a bit corroded during laboratory preparation.

I1 is the largest of the three incisors. It is a robust, “canine-like” tooth, somewhat backwardly curved, with a tapering crown that is sub-triangular in cross-section, flattened distally, and slightly convex labially and concave lingually. It implants vertically in the premaxillary with a long, strong root, which is moderately flattened mesio-distally. As wear progresses, a flat distal wear surface forms extending from the tip virtually to the base of the crown.

P2: Only one isolated right P2, F15-047, was recovered from F15. Following Butler’s (1980, p. 3 and 7) criteria, the tooth is believed to be a second upper premolar, because of its pointed crown and well-developed posterior shoulder. It is attributed to *Deinogalerix cf. freudenthali* based on its size. This single-cusped, two-rooted tooth has a crown with sub-triangular outline in side view and is asymmetrically sub-oval in occlusal view, slightly flatter lingually and somewhat more convex labially. The crown extends posteriorly in a low talon. The tip of the cusp is not aligned on the vertical of the divergence of the two roots, but shifted a bit forwards. The posterior margin of the crown is smooth. It has two large, sub-equal roots, which diverge from one another.

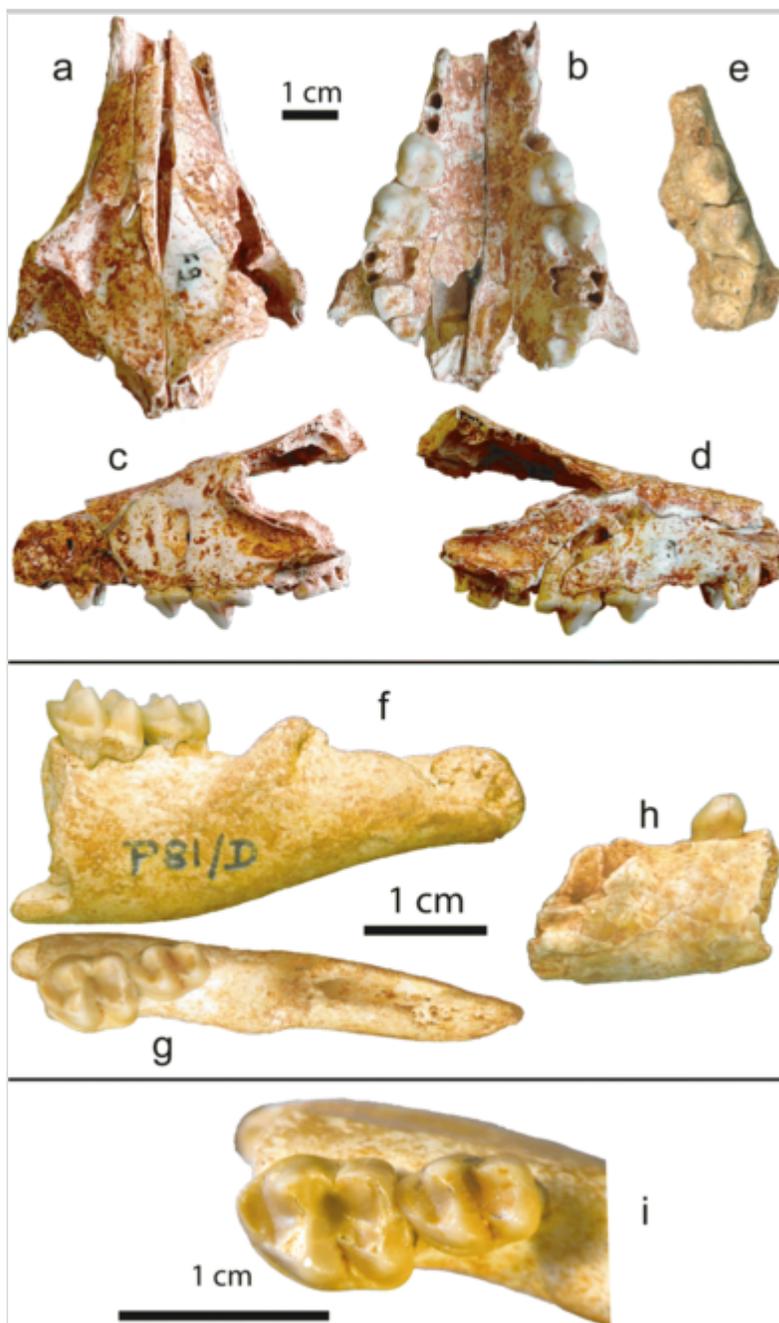
M2: The tooth is represented by the labial fragment of an isolated left M2, F15-052. The posterior arm of the metaconule is barely joined with the distal cingulum. A weak crest connects the mesostyle with the labial cingulum. The labial cingulum is present.

Deinogalerix minor (Fig. 7a–d)

Fig. 7

Deinogalerix minor, fragmental skull F9-014: **a** dorsal view; **b** palatal view; **c** left lateral view; **d** right lateral view. *Deinogalerix* sp. 1, fragmental maxillary F15-038: **e** occlusal view. *Deinogalerix* sp. 2, fragmental left mandible P81D-004: **f** lateral view; **g** dorsal view. *Deinogalerix cf. minor*, fragmental right mandible with p1 F1-002: **h**

lateral view. *Deinogalerix* sp. 2, magnification of m2 and m3 on fragmental left mandible P81D-004: i occlusal view



Emended diagnosis: Small- to medium-sized *Deinogalerix*, but larger than *D. freudenthali*. Teeth larger than *D. masinii*, especially m1. Teeth relatively high-crowned compared with *D. samniticus*, *D. masinii* and *D. freudenthali*, and morphologically similar to those of *D. intermedius* and *D. koenigswaldi*; m2s and m3s with rounded outline due to reduced talonids; hypoconid not labially prominent on m3; P4 with divided or undivided hypocone; distal cingulum uninterrupted on M1. M3 with anterolabial corner squarish and less prominent labially. Mandible

morphologically close to those of *D. freudenthali*: in aboral view, angular process aligned with rest of ascending ramus; in medial view, ridge delimiting ventral border of the fossa for the insertion of temporalis muscle straight or somewhat more arched with dorsal concavity and running above mandibular foramen; relatively high ascending ramus (from base to sigmoid incisure); masseteric fossa confined posteriorly by thick, prominent border.

Material: See Table 1.

Measurements: See Table 2.

Descriptions

Teeth

il: The tooth is represented by an isolated, unworn, left incisor from F9, F9-001. The tooth is compressed labio-lingually and has bilobed crown: the mesial lobe is larger and rounded lingually, the distal one is smaller and convex lingually. The root is long, robust and compressed mesio-distally.

C: The fragmental skull F9-014 preserves its left canine, and both P1s, P3s, P4s, M2s and M3s. The canine is a premolariform, two-rooted tooth, triangular in lateral view, somewhat similar in shape to P1. The crown consists of a single, slender, high and pointed conical cusp, with a slightly concave rear side. It is higher than the first premolar. The roots are long, with a longitudinal groove on the posterior face of the anterior root, and on the anterior face of the posterior one, and diverge antero-posteriorly from one another moving ventrally. The anterior root is arched with rostral convexity.

P1: The P1s on the skull F9-014 are moderately worn. Morphologically, the teeth are very similar to the canine, but with a relatively less pointed tip and more divergent roots. Moving from the roots upwards along the crown, the tooth is slightly concave lingually.

P3: Two P3s come from fissure F9, belonging to the skull F9-014. These teeth are bulbous, with a distinct trapezoidal outline in occlusal view. The crowns are low and blunt, dominated by a large, high, labially prominent paracone. A shallow depression separates the paracone from a small, distally prominent metastyle (metacone in Villier and Carnevale 2013). The teeth are moderately elongated mesially by shoulder-shaped parastyle. The protocone is slightly higher than the

hypocone; both cusps are imperfectly divided by a shallow groove, which does not reach the lingual wall of the crown. The hypocone is bulbous, elongated and declines gently towards distal margin of the tooth and reaches the metastyle. The lingual root has a shallow furrow, aligned with the groove between the protocone and hypocone.

P4: The DSTF collection counts two moderately worn P4s on the skull F9-014 from F9. The teeth are characterised by a squarish outline because of the relatively wide postero-lingual margin. Both specimens have a swollen parastyle and faint anterior cingulum. The crest connecting the protocone to the base of the paracone is always absent. The protocone is separated from the hypocone by a furrow, which prolongs labially merging with the valley between paracone and hypocone. On the F9-014 P4s, a faint bulge is located at the mesio-lingual outlet of the furrow. The valley between the paracone and hypocone widens distally towards the disto-lingual corner of the tooth. The hypocone is worn out on both P4s. Despite wear, the hypocone seems vaguely split although no incisure can be observed on the lingual wall. The distal cingulum is well-developed.

M1: The tooth is represented by a single isolated, left M1, F9-018, from fissure F9.

The general outline and morphology are similar to those described for *D. freudenthali*.

The mesostylar region is occupied by a bulging mesostyle, which is connected with the posterior arm of the paracone. The labial cingulum is absent. The mesial arm of the protoconule is barely connected with the anterior cingulum, which is partially broken. The posterior arm of the protoconule is absent.

The protoconule is separated from the protocone by a deep, V-shaped notch. The posterior arm of the metaconule is weakly connected, through a tiny accessory enamel crest, with the uninterrupted distal cingulum. This connection is even weaker than on F15-032 of *D. freudenthali*. The anterior arm of the hypocone is very low, in touch with the posterior arm of the protocone; the latter is connected with the base of the metaconule. Similar to the anterior arm of the protocone, the posterior arm of the hypocone slopes down steeply (more than on F15-032 of *D. freudenthali*) and merges with the posterior cingulum. The basin is distally closed by the protocone–metaconule connection. The tooth has three roots: the largest, which is lingual, is missing on F9-018. The enamel is very thick, but its thickness actually varies in the different parts of the tooth.

M2: The two specimens of the DSTF are the two M2s of the skull F9-014. Both the F9-014 teeth are so heavily worn that only little detail of the main cusps of the protoconule and of the parastyle is discernible, together with some enamel of the labial side of the crown and of the mesial (in the proximity of the paracone) and distal cingula. The labial cingulum is absent.

M3: The morphological details of the two M3s of the skull F9-014 are obliterated by wear. The occlusal outlines of these teeth show less acute (approximately right) mesio-labial angles relatively to *D. freudenthali*, thereby suggesting that the parastyle was not very extended mesio-labially. The lingual side of the tooth is faintly bilobed by the protrusion of the protocone and the arching of the metastylar crest. The teeth, quite small, bear a large, triangular root in lingual position, under the protocone, a flattened disto-labial one under the metastylar crest, and a small, triangular mesio-labial one under the paracone-parastyle.

Skull and maxillaries

The frontal bones of F9-014 are broken at the convergence of the two temporal lines, where the bones are pierced by a few irregular foramina. The foremost part of the orbital rim forms a right angle at the lacrimal foramen, which opens inside the orbital cavity and is not visible externally. The ventral rim of the orbit does not extend beyond the half of the infraorbital foramen. The nasals are long and slender; their posterior ends wedge between the frontals up to slightly beyond the anterior orbital rim.

The maxilla of F9-014 shows a subhorizontal, narrow, deep, elongated fossa for the anterior portion of the masseter muscles, enclosed between the orbital rim, located dorsally, and the ventral crest-like anterior end of the zygomatic arch. Rostrally, a flat surface extends between the anterior end of the masseter fossa and the infraorbital foramen; its rear margin is located over the anterior root of P4. It is placed low, close to the cheek teeth, with the ventral margin levelled with the ventral anterior crest of the zygomatic arch. The palatal flange of the maxillary suggests a very concave palate, which is typical of Eulipotyphla. The maximum width of the maxilla is across the parastyle of M1. The maxilla and the lacrimal are fused. The base of the zygomatic process of the maxilla extends from the middle of M1 to the distal end of M2 and is very low, close to the cheek teeth alveoli. The antorbital fossa is absent. In the nasal cavity, a sharp horizontal crest ends against the medial border of the lacrimal duct, which ends rostrally next to the maxilloturbinal ridge.

A very short diastema is present between P1 and P2 (1.6 mm). A somewhat wider diastema occurs between C and P1 (4.5 mm).

Deinogalerix cf. minor (Fig. 7h)

Material: See Table 1.

Measurements: See Table 2.

Descriptions

As in the case of *Deinogalerix cf. freudenthali* mentioned above, the following specimens, tentatively attributed to *Deinogalerix cf. minor*, are isolated, taxonomically non-diagnostic teeth.

Teeth

p1: The only specimen present in the DSTF collection, F1-002, is preserved on a fragmental right mandible. This single-cusped (protoconid?) tooth has a single, very large root, elongated mesio-distally in cross-section. The tooth is inserted somewhat inclined forwards. In lateral view, the crown shows an asymmetric outline with a steep and convex anterior margin and a more gently sloping rear profile. The collar margin is slightly festooned on the lingual side, somewhat uplifted at the mesial root. In occlusal view, the crown is sub-oval, with the lingual side that is almost straight. The crown is very low and rather blunt, and its tip is slightly worn.

m2: The only specimen is an isolated, unworn, left dental gem from F1, F1-009.

The general morphology is similar to that of the m2s of *D. freudenthali*. The carnassial notch that separates the preprotocristid from the long and low paraconid crest is shallower in F1-009 than in *D. freudenthali*. The distal cingulum is connected with the post-entocristid by a short, sub-vertical enamel ridge. The two structures are more strongly connected with one another on F1-009. The mesio-labial cingulum is divided on F1-009 into a strong mesial portion and a continuous labial one.

P2: An isolated right P2 from fissure F1, F1-004, is present in collection. The tooth is morphologically similar to, but somewhat larger than, the P2 of *D. freudenthali*. The tip of the cusp is aligned with the point of divergence of the two roots. The terminal part of the mesial root bends backwards.

Deinogalerix intermedius (Fig. 8)**Fig. 8**

Deinogalerix intermedius, fragmental left mandible P81D-023: **a** lateral view; **b** dorsal view. *Deinogalerix intermedius*, fragmental left mandible P81D-024: **c** lateral view; **d** medial view; **e** dorsal view. *Deinogalerix intermedius*, fragmental left mandible F8-040: **f** lateral view; **g** dorsal view. *Deinogalerix intermedius*, fragmental right mandible F9-022: **h** lateral view; **i** dorsal view. *Deinogalerix intermedius*, left P3 P81D-026: **j** occlusal view; **k** lingual view. *Deinogalerix intermedius*, left P4 F1-007: **l** occlusal view. *Deinogalerix intermedius*, magnification of p3 and p4 on fragmental left mandible P81D-024: **m** lateral view. *Deinogalerix intermedius*, right p4 F21c-002: **n** occlusal view. *Deinogalerix intermedius*, left p4 NBS-001: **o** labial view; **p** occlusal view



Emended diagnosis: Medium- to large-sized *Deinogalerix*. Teeth relatively high-crowned and morphologically similar to those of *D. minor* and *D. koenigswaldi*; m1 with more elongated trigonid than in *D. masinii* and *D. freudenthali*; rounded outline in m2 and m3, because of reduced talonids; relatively small-sized hypoconid on m3; P3 with protocone more clearly divided than in *D. freudenthali* and *D. minor* and with comparatively more elongated parastyle; P4 with divided or undivided hypocone; posterior arm of protocone rarely connected with metaconule on M1–M2. Mandible: mandibular condyles flat, elongated rostrally upon the condylar process and with imperfectly delineated anterior margin; angular process inclined downwards and curved laterally; ridge delimiting the ventral border of the

fossa for the temporalis muscle widely arched, positioned slightly lower relative to the mandibular foramen, and thickened rostrally; ascending ramus lower and more backward-stretched than in *D. masinii*, *D. freudenthali* and *D. minor*; masseteric fossa shallow and open posteriorly.

Material: See Table 1.

Measurements: See Table 2.

Descriptions

Teeth

i1: Three i1s, P81D-012, F1-001 and F8-001, come from three different fissures, P81D, F1 and F8, respectively. F8-001 is quite worn. The teeth have a characteristically bilobed (with larger and lingually rounded mesial lobe, and smaller and lingually convex distal lobe) and labio-lingually compressed. The teeth bear long, robust and mesio-distally compressed roots.

c: Six lower canines were retrieved from three different fissures: four isolated ones, P81D-008, P81D-005, P81D-007 and P81D-006, come from P81D; one, on the mandible F8-040, which also preserves the cheek tooth row p3–m3, from F8; and an isolated one, F9-003, from F9. The canine is a conical, pointed, single-rooted tooth, with the tip of the crown pointed upward. A faint ridge runs longitudinally along its dorsal (convex) side and ends at the base of the crown in a shoulder, which is generally hardly visible, although sometimes it may be slightly more pronounced (e.g. P81D-008). The height of the crown ranges from about one-fourth (P81D-005, P81D-007) to about one-third (P81D-006, F9-003) the mesio-distal length of the tooth. The collar is slightly raised upwards ventro-mesially. The root is somewhat curved mesio-distally, with dorsal concavity, and bent labially; its lingual side is flattened. Its section is roundish close to the crown and tapers distally with slight linguo-labial compression. The root is grooved labially on P81D-006.

p2: The isolated, unworn, left p2, F8-002, probably belongs to the mandible F8-040. The single-cusped tooth is broken longitudinally and preserves only its large anterior root. The cusp, low and rather blunt, is triangular in lateral view and has a rather prominent talonid, which gives it a concave posterior profile.

p3: Four p3s come from P81D and F8. Two of them are preserved on mandibles: P81D-024, which also holds p4, and P81D-023; the third, P81D-027, is isolated.

The specimen from F8 belongs to the mandible F8-040. These teeth are morphologically similar to the p3s of *D. freudenthali* and *D. minor*. F8-040 has a somewhat more pointed crown than the specimens from P81D. F8-040 bears a disto-lingual cuspule. P81D-024 has a somewhat narrower crown than other p3s (P81D-023, P81D-027). P81D-027 is more swollen than the other specimens. The collar of p3 is raised in the inter-root area, and somewhat straighter in F8-040.

p4: It is represented by six specimens from five different fissure fillings: the isolated F21c-002, from F21c; one from the mandible P81D-024 and the isolated P81D-028, from P81D; the isolated NBS-001, from Nazario Bivio Sinistra; one from the mandible F8-040, from F8; and the sixth from the mandible F9-022 without other teeth, from F9. The general morphology of these teeth is similar to the two p4s attributed to *D. freudenthali*. The labial outline is generally quite convex, except in the specimens P81D-024 and F8-040 where it is straighter. Mesially, the paraconid is well-defined and has a steep anterior wall. The trigonid portion occupied by the paraconid is relatively short. On some specimens (e.g. F9-022), this portion is somewhat longer than on other ones (e.g. F21c-002). The blunt preprotocristid is very steep. The trigonid basin is shallow. The lingual side of the trigonid is characterised by a marked notch between the paraconid and metaconid; the notch is connected with a weak cleft on the lingual wall of the crown. In three specimens, the trigonid basin is squeezed to form a groove that prolongs into the lingual cleft of the crown (P81D-024, NBS-001, F8-040). The distal cingulum is very inclined labially and bears a small cuspule positioned roughly in line with the cleft between protoconid and metaconid. The size of the accessory cuspule is slightly variable. The tooth has two long roots, the mesial one is slightly more elongated mesio-distally than the posterior one.

m1: This quite significant tooth is represented only by two fragmental, very worn left specimens, one on the mandible F8-040 and the other the isolated P81D-009. The metastylid of these teeth is very bulbous.

m3: A single and very worn specimen is inserted on the left mandible F8-040. Its general morphology is similar to those of the m3s attributed to *D. freudenthali* and *D. minor*, but with a more roundish outline due to a reduced talonid as well as to the hypoconid that does not protrude labially. On F8-040, the mesio-labial cingulum is obliterated by wear.

I1: Two isolated specimens, P81D-010 and F9-002, are practically larger replicas of the I1 of *Deinogalerix cf. freudenthali* described above.

P1: The large left hemimaxillary F9-017 preserves its P1, P2 and P4. P1 is morphologically similar to that borne by the skull F9-014 attributed to *D. minor*.

P2: F9-017 is morphologically similar to the P2 of *D. minor*, but somewhat larger-sized.

Like on *D. minor*, the tip of the cusp is aligned with the point of divergence of the two roots. The dorsal end of the mesial root is not bent backwards.

P3: Two isolated specimens, P81D-026 and P81D-011, represent this tooth in the DSTF collection. P81D-026 is a large, complete left tooth; P81D-011 is a smaller, fragmental, right specimen. Both are morphologically similar to those attributed to *D. minor*. On P81D-011, a shallow depression separates the paracone from a small, distally prominent metastyle, whereas P81D-026 is a bulging metastylar crest which ends into the metastyle. The protocone and hypocone are separated by a marked groove, which extends to the collar. P81D-026 has a very small protocone. Both specimens bear a bulbous, elongated hypocone, which slopes gently towards the distal margin of the tooth.

P4: Four specimens: two of them, F1-006 and F1-007, are isolated; one is mounted on the hemimaxillary F9-017; the fourth, P81D-025, is preserved on a right hemimaxillary, with no other tooth. The teeth are similar to the P4s attributed to *D. freudenthali* and *D. minor*. The postparacrista is directed backwards and quite labially. F1-006, F1-007 and F9-017 have a low, bulging parastyle at their mesio-labial corner. The protocone is located mesio-labially and is connected by a crest with the base of the paracone on P81D-025, whereas there is no crest connecting the protocone with the paracone on F1-006, F1-007 and F9-017.

The mesio-lingual outlet of the protocone–hypocone valley is occupied by a crest; on P81D-025 the crest holds a weak accessory cusplule, which is substituted by a faint bulge on F1-006, F1-007 and F9-017. In rostral view, considering the tooth held in the alveolus, the collar appears markedly stepped, with the base of the protocone raised dorsally. The hypocone is elongated and slopes distally; it is lower than the protocone and extends into a well-defined distal cingulum on F1-006, F1-007 and F9-017. The hypocone is split on F1-006 and F9-017 and undivided on F1-007; in P81D-025, wear obliterates the possible presence of a weak partition. The palatal side of the lingual root is carved by a main groove and by several smaller secondary ones.

Mandibles

The mandibles attributed to this species come from three fissure fillings: P81D, F8 and F9. There are nine specimens: five left ones, P81D-023, P81D-024, P81D-001, P81D-016 and F8-040, and four right ones, P81D-003, P81D-013, P81D-015 and F9-022. P81D-023, P81D-024, F8-040 and F9-022 are more informative than the other specimens. F8-040 and F9-022 are more gracile and slender than P81D-023 and P81D-024. P81D-023 preserves p3, large part of the horizontal ramus and the basal parts of the ascending ramus; P81D-024 its p3 and p4, the condyle, the angular process and most of the horizontal ramus and of the coronoid process; P81D-001 conserves the m3 alveoli, the posterior alveoli of m2 and part of the coronoid process (only the tip is missing); P81D-016 the alveoli of m3 and anterior alveolus of m2; F8-040 c, p3, p4, the talonid of m1, m2 and m3, most of the horizontal ramus, the condyle, but not the coronoid process. P81D-003 preserves the m3–m1 alveoli; the toothless, polished specimen P81D-013 the m3 alveoli and anterior alveoli of m2; the toothless rostral fragment P81D-015 part of the alveolus of p1, the alveoli of p2 and the anterior alveolus of p3; the fragmental specimen F9-022, which is broken at the posterior alveolus of p3, conserves p4 and the alveoli of m1–m3, virtually all the coronoid process, with only the tip slightly abraded.

P81D-024, P81D-023 and F8-040 have long p1–p2 diastemas (10.1, 10.6 and 8.7 mm, respectively), and no diastema between p2 and p3. The mental foramen is larger in P81D-024 and P81D-023 than in F8-040. It opens under the rostral root of p3 in P81D-024 and F8-040 and more backwards, between the two roots of p3, in P81D-023. The symphyseal scar extends distally to the anterior root of p3 in P81D-024, to the mid-length of p3, i.e. somewhat more backwards than the mental foramen, in both P81D-023 and F8-040. In all three P81D-023, P81D-024 and F8-040, in contrast to F15-015 and *D. masinii*, the symphyseal region curves upwards rostrally. The molars on F8-040 are more worn than the premolars; the extent of wear is such to cause the exposure of part of the roots.

In all four P81D-023, P81D-024, F8-040 and F9-022, the rostral border of the ascending ramus is inclined backwards. In medial view, the fossa for the insertion of temporalis muscle is deeper than in *D. freudenthali* (F15-016); the ventral margin of the fossa is bordered by a prominent, wide, U-shaped, crest-like ridge, which extends, thickening progressively, from the mandibular foramen to the alveolus of m3. In F8-040 and F9-022, the ridge is somewhat weaker than in P81D-023 and P81D-024. The angular process is more elongated than *D. freudenthali* and bends ventrally and laterally; in P81D-024, it is flat dorsally and has a very blunt medial margin. In F8-040, the angular process is grooved dorsally, somewhat like in

D. freudenthali, and with fairly sharp lateral and medial margins. All four P81D-023, P81D-024, F8-040 and F9-022 have a deep masseter fossa bordered by a smooth rostral margin.

In P81D-023, P81D-024 and F8-040, the condyle and the condylar process are projected backwards and levelled off with the base of sigmoid incisure. The condyle of P81D-024 is slightly broken at the lateral and medial ends; it is sub-cylindrical aborally, flattened dorsally, and its articular surface extends rostrally, for a moderate extent, over the flat dorsal surface of the thickened and triangular-shaped condylar process. The flattening of the condylar process causes the disappearance of the small fossette that occurs in *D. freudenthali*.

In F8-040, the condyle is well-preserved, complete, slightly asymmetric, and more prominent medially than laterally; the lateral part of the condyle is slightly uplifted, giving a concave profile to the joint in aboral view. The condylar articular surface extends somewhat rostrally, over the dorsal surface of the condylar process.

The coronoid process of P81D-024 is fairly straight. The anterior margin of the ascending ramus is gently inclined backwards. In F9-022, the coronoid process is more slender than that of P81D-024; it inclines slightly more aborally than the ascending ramus. The rostral border of the sigmoid incisure is arched.

Maxillaries

The maxillaries assigned to this species were retrieved from two fissure fillings: P81D and F9. There are three specimens: two left ones, i.e. the very polished P81D-014 and F9-017, and a larger-sized right one, P81D-025. P81D-025 bears P4; it is broken rostrally at the anterior root of P3 and distally at the anterior root of M2. P81D-014 preserves the alveoli of P3–P4 and part of those of P2. F9-017 still conserves P1, P2, alveoli of P3 and P4; it is broken in front of P1 and behind P4.

P81D-025 and F9-017 preserve a small portion of the palate, with a flange that suggests a very concave palate. All three maxillaries possess a wide infraorbital foramen with rear margin over the mesial root of P4 and placed low, close to the cheek teeth. In the nasal cavity of F9-017, a sharp horizontal crest extends dorsally to the border of the lacrimal duct. A comparatively notable diastema is present between P1 and P2 (4.8 mm).

Deinogalerix sp. 1 (Fig. 7e)

Material: See Table 1.

Measurements: See Table 2.

Descriptions

Based on their anomalous sizes, the following specimens could not be accommodated into any known species. For this reason, they are referred to as *Deinogalerix* sp. 1.

Teeth

i1: A rootless right dental gem, F15-048, from F15, is morphologically similar to the i1 of *D. minor*.

p3: One isolated specimen, F15-046, comes from fissure F15. Morphologically, the tooth is roughly similar to F15-015, which is described above and attributed to *D. freudenthali*, but it is much larger, swollen and higher-crowned.

P3: A left P3 is preserved on the fragmental maxillary F15-038, which also conserves the P4–M2 tooth row. The specimen was corroded during laboratory preparation and shows an unusual circular damage pattern at its centre.

The tooth is similar to that of *Deinogalerix minor*; the only significant difference is that protocone and hypocone are imperfectly divided by a shallow groove, which is fairly visible occlusally and lingually.

P4: The P4 preserved on the fragmental left maxillary F15-038 is moderately worn. It has a slightly more squarish outline than the P4 of *Deinogalerix minor* from F9 because of its wider postero-lingual margin. The protocone is separated from the hypocone by a deep furrow, which prolongs labially merging with the valley between the paracone and hypocone. A small accessory cuspule is located at the mesio-lingual outlet of the furrow. The hypocone consists of an accessory mesial cuspule and of a longer cusp unequally sub-divided by a groove into a shorter anterior portion and a longer posterior one. The latter slopes gently towards the distal cingulum.

M1: Two left specimens from different fissures, F15 and F21c, are present in the DSTF collection; one is preserved on the maxillary F15-038; the other, F21c-001, is an isolated tooth. The general outline of the two teeth is similar to that described

for the M1 of *Deinogalerix freudenthali*. F15-038 is heavily worn and its morphological traits are largely obliterated; it is inserted obliquely on the maxilla and the protocone is thus placed more mesially than the paracone.

F21c-001 is also fairly worn. Its mesostylar region is occupied by a bulged mesostyle, the labial cingulum is reduced to two separate portions, a mesial one next to the parastylar region and a distal one near the metastylar region. The mesial arm of the worn protoconule runs parallel to the anterior cingulum. The posterior arm of the protoconule is absent on both specimens. The protoconule is separated from the protocone by a deep, V-shaped notch, which is widened by wear on the labial side of the protocone. Although quite worn, the posterior arm of the metaconule seems relatively short and not extended to the disto-labial corner of the crown. Moreover, the uninterrupted condition of the distal cingulum indicates that the latter is not reached by the posterior arm of the metaconule. The posterior arm of the protocone forms an uninterrupted crest with the mesial arm of the hypocone; the posterior arm of the protocone is separated from the metaconule. Moreover, remnants of the heavily worn anterior arm of the protocone suggest that the structure sloped down fusing to the base of the protoconule, with a deep notch in between. The trigon basin is deep; it extends into a longitudinal valley delimited lingually by the wall of the protocone–hypocone complex. Between the protocone and hypocone, there is a short entocingulum. The tooth has three roots: two sub-triangular labial roots, a larger lingual one, vertically sub-divided by a very deep groove, and three accessory crests that converge to the centre of the tooth.

M2: The outline of the tooth is similar to that of *Deinogalerix freudenthali* and *D. minor*. Heavy wear obliterated the morphological characters of this specimen.

Maxillary

The sample includes only a fragmental left specimen, F15-038, broken short rostrally from the roots of P2 to the very base of the zygomatic arch, and still preserving the tooth row from P3 to M2, and a small portion of the palate. The palatal flange of the maxillary suggests a very concave palate, which is typical of Eulipotyphla. The remain has a very wide infraorbital foramen, with the rear margin on a line between the roots of P4, and the rostral border of the zygomatic arch overlying M1.

A flat surface seems to extend between the anterior end of the masseter fossa and the infraorbital foramen. The latter is narrower than that of F9-014 of *Deinogalerix*

minor and its rear margin is located over the area included between the two roots of P4.

Deinogalerix sp. 2 (Fig. 7f–i)

Material: See Table 1.

Measurements: See Table 2.

Descriptions

As in the case of *Deinogalerix* sp. 1, the following fragmental mandibles are intermediate in size between *Deinogalerix freudenthali* and *D. intermedius*. For this reason, they are referred to as *Deinogalerix* sp. 2.

Teeth

m2: The fragmental left mandible P81D-004 from P81D preserves its m2 and m3. The second lower molar is slightly worn, but with a heavily worn protoconid.

The general morphology is similar to that of the m2s of *D. freudenthali*. The distal cingulum is connected with the post-entocristid by a short, sub-vertical enamel ridge.

The mesio-labial cingulum on P81D-004 is interrupted; the labial portion is weak and divided into two parts by an enamel protrusion in the hypoflexid.

m3: The single tooth on the fragmental left mandible, P81D-004, has an overall morphology similar to those of the above described m3s F15-039 and F15-016, here attributed to *D. freudenthali*. Somewhat like in F15-016, on P81D-004, the distal end of the labial cingulum tends to curve upwards.

Mandibles

There are two fragmental left mandibles, P81D-002 and P81D-004. P81D-002 is a fragment with part of the ascending ramus including the coronoid process and part of the horizontal ramus with the posterior alveoli of m2, and the alveoli of m3. P81D-004 is a fragment of horizontal ramus preserving m2 and m3.

In P81D-002, the anterior border of the ascending ramus inclines slightly more rostrally than the coronoid process. In P81D-004, the remnant of the medial wall

suggests that the distal ridge of the temporal fossa was straight and not prominent.

Discussion

Diagnostic differences between the species represented in the DSTF collection

Teeth

Detailed dental morphological comparisons between the various species of the genus *Deinogalerix* have rarely been conducted. Butler (1980) distinguished his species from one another primarily on a dimensional basis rather than morphologically, with the only exception of *Deinogalerix freudenthali* for which Butler (1980, p. 38) provided four distinctive dental features: “hypocone of P4 not divided”, “posterobuccal corner of P4 less extended, so that the buccal edge of P4 is shorter relatively to M1”, “posterior cingulum in M1 and M2 interrupted in some specimens by the posterior crest of the metaconule” and “M3 less reduced in size in comparison with M1”.

The comparisons conducted for this study among the specimens of the DSTF and with specimens of the collections listed in the “Material and methods” section, revealed new, quite diagnostic dental and mandibular traits.

A general feature that can be observed comparing the teeth of the different species of the genus is a moderate increase in crown height. Based on this character, the various species might be clustered into two groups, one equipped with relatively low-crowned teeth (*Deinogalerix samniticus*, *D. masinii* and *D. freudenthali*), the other with somewhat higher ones (*D. minor*, *D. brevirostris*, *D. intermedius* and *D. koenigswaldi*).

The mesial wall of the paraconid is reclined on the p4s of *D. freudenthali* and is quite more vertical on the p4s of *D. minor* and *D. koenigswaldi* (type mandibles) and of *D. intermedius* (type and DSTF specimens). On the p4s and m1s of *Deinogalerix masinii* (Villier et al. 2013), *D. samniticus* (Savorelli et al. 2017), and *D. freudenthali*, the metaconid is proportionally larger, relative to the protoconid; it is somewhat smaller in *D. minor* and *D. intermedius* and much smaller in *D. koenigswaldi*.

One of the typical traits of *Deinogalerix* is the elongation of the trigonid of m1 in proportion to the total length of the tooth: the trigonid is shorter in *D. masinii* (55–60%) and somewhat longer in the other Gargano species (*D. freudenthali* 62 and

68%, *D. minor* 68 and 74%, *D. intermedius* 69%, *D. brevisrostris* 70%, *D. koenigswaldi* 68–74%). In contrast to this apparent trend, the stratigraphically ancient *Deinogalerix samniticus* has a relatively long trigonid (71%), similar to the advanced representatives of the genus.

Similar to the mainland counterparts and to the primitive *Deinogalerix masinii* (Villier et al. 2013) and *D. samniticus* (Savorelli et al. 2017), *D. freudenthali* from F15 and *Deinogalerix* sp. 2 from P81D have m2s and m3s with relatively large talonids. The hypoconid is particularly developed on both these teeth, and especially on m3, which has a wider talonid precisely because of this labially prominent cuspid. *Deinogalerix freudenthali* and *Deinogalerix* sp. 1 are both reported from F15. For the sake of parsimony, and based primarily on dimensional criteria, isolated m2s and m3s from this fissure have been attributed to the former species. However, we cannot exclude that some of these teeth actually belong to *Deinogalerix* sp. 1.

The sample analysed by Butler (1980) contained no mandibles nor isolated lower teeth of *Deinogalerix freudenthali*. The m2s, but especially m3s on the mandibles included in the type material of *Deinogalerix minor*, *D. brevisrostris*, *D. intermedius* and *D. koenigswaldi* studied by Butler (1980), as well as on the jawbone F8-040 of *D. intermedius*, appear roundish occlusally on account of their reduced talonids and weak hypoconids.

The parastylar region is fairly short on the P3s of *Deinogalerix minor* and *Deinogalerix* sp. 1 and quite more prominent on the third upper premolars of *D. intermedius* from P81D, *D. brevisrostris*, and *D. koenigswaldi*. Moreover, the protocone is imperfectly separated from the hypocone in *Deinogalerix minor* and *Deinogalerix* sp. 1 and quite more in *D. intermedius* from P81D, *D. brevisrostris*, and *D. koenigswaldi*. RGM 177982 was attributed by Butler (1980) to *Deinogalerix intermedius*. This specimen has cheek teeth similar morphologically (especially P3), but also dimensionally, to those of *D. minor* and *D. brevisrostris*.

The hypocone on the P4 F15-041 is not divided, similar to the P4 hypocones of *D. freudenthali* studied by Butler (1980). The same occurs to most of the P4 hypocones of *Deinogalerix masinii* from M013 analysed by Villier (2012); only a few of them display an initial, very shallow division. Also *Deinogalerix samniticus* has an undivided P4 hypocone (Savorelli et al. 2017). Imperfect signs of division are visible on the P4 hypocones of *Deinogalerix minor* from F9, whereas somewhat more divided are those of *Deinogalerix* sp. 1 from F15. Two P4 hypocones of *D. intermedius*, one from P81D and the other from F1, are undivided, whereas another

one from F1 is divided; in contrast, the P4 hypocones of the type specimens of *D. brevirostris* and especially of *D. koenigswaldi* studied by Butler (1980) are all split.

Comparing the P4s of the different species and observing them mesially and capsized, in the position they had originally in the skull, the collar profile appears straight in *Deinogalerix samniticus*, gently sloping dorso-ventrally moving in labio-lingual direction in *Deinogalerix freudenthali*, *D. masinii*, *D. minor* and *Deinogalerix* sp. 1, or step-shaped, connecting the lowered labial collar margin with the raised lingual one in *D. brevirostris*, *D. intermedius* and *D. koenigswaldi* (Fig. 5b, c).

On the M1–2s, the posterior arm of the metaconule can be disconnected or variably connected with the distal cingulum. On the M1s and M2s from F15 and F9, the cingulum is uninterrupted and barely connected with the posterior arm of the metaconule by a thin enamel crest. F15 yielded also a morphotype wherein the extended posterior arm of the metaconule interrupts the distal cingulum. The same occurs also on the M1s and M2s of *Deinogalerix masinii*. In contrast, in the type specimen of *Deinogalerix koenigswaldi* (RGM 177777), the distal cingulum is clearly uninterrupted and unreachd by the posterior arm of the metaconule.

The protocone is generally disjoint from the metaconule in the genus *Deinogalerix*. On F9-018 (*Deinogalerix minor*), however, the two structures are actually connected (Fig. 5a); a similar condition was also observed by Villier et al. (2013) on RGM 177975 (*D. intermedius*).

The M3s of *Deinogalerix freudenthali* (F15-036, F15-037) have a distinctive, acute, anterolabial corner, due to a particularly developed parastyle. The parastyle is also elongated on the M3s of *Deinogalerix masinii* and very robust and prominent labially on the third upper molars of *D. samniticus*. In contrast, in *Deinogalerix minor* (F9-014), but also in the type specimens of *D. brevirostris* and *D. koenigswaldi* described by Butler (1980), the anterolabial corner is squarish and less prominent labially. As observed by Butler (1980), *Deinogalerix freudenthali* has proportionally larger M3s, in comparison with M1s (but also with M2s—see Fig. 3a), than other species, included the F9 representatives of *D. minor*.

Mandibles

The condyles on the mandible F15-016 of *Deinogalerix freudenthali* and on RGM 178184 of *D. minor* are quite similar to one another; the latter differs only by lacking the fossette in front of the articular surface and on the medial side of the

condylar process. The shapes of the condylar processes of *Deinogalerix freudenthali* and *D. minor* are reminiscent of those of *Parasorex socialis*: the latter differ by being less triangular in dorsal view and by having an articular surface with better marked anterior margin.

The condyles on the jawbones F8-040, P81D-023 and P81D-024 and of the type specimen RGM 179063 of *Deinogalerix intermedius* are very similar to one another; F8-040 is only slightly more asymmetric. Compared with those of *Deinogalerix freudenthali* and *D. minor*, the mandibular condyles of *D. intermedius* are much flatter, lengthened rostrally upon the condylar process and have an imperfectly delineated anterior margin. Rostrally to the medial part of the condylar articulation, F8-040 and RGM 179063 have a barely visible fossette. This peculiar shape of the condylar articular surface of *Deinogalerix intermedius* recalls that of RGM 177777 (type specimen) and RGM 179147 of *Deinogalerix koenigswaldi*, which bear a flat articulation, very extended rostrally on the condylar neck and with an anterior margin virtually impossible to discern.

In aboral view, the angular process is aligned with the rest of the ascending ramus in F15-016 of *Deinogalerix freudenthali*, as well as in the type specimens of *D. minor*. Dorsally, in these species, the angular process is fairly deeply grooved and bordered on the two sides, laterally and medially, by two sharp crests. The angular process of *Parasorex socialis* shows similar morphologic features. The same applies to the angular processes of *Deinogalerix masinii*, which however are quite more robust dorso-ventrally. In P81D-024, F8-040 and RGM 179063 of *Deinogalerix intermedius*, and in RGM 177777 and RGM 179147 of *D. koenigswaldi*, the angular process is characteristically inclined downwards and bent laterally. Similar to *Deinogalerix freudenthali* and *D. minor*, the angular process in the mandibles of *Deinogalerix intermedius* is fairly deeply grooved and bounded on the two sides by a blunt labial crest and a sharp lingual one. In contrast, the dorsal groove and crests are less developed on the angular processes of *Deinogalerix koenigswaldi*.

In medial view, in the mandibles of *Deinogalerix masinii*, *D. freudenthali*, *Deinogalerix* sp. 2 (P81D-004) and RGM 179174 of *D. minor*, the ridge delimiting the ventral border of the fossa for the insertion of temporalis muscle is straight and runs above the mandibular foramen; such a condition is reminiscent of that visible in the jawbones of the mainland *Parasorex socialis*. In another jawbone of *Deinogalerix minor*, RGM 178184, the ridge is somewhat more arched with dorsal concavity. In five mandibles of *Deinogalerix intermedius*, F8-040, F9-022, P81D-

023, P81D-024 and RGM 179063, but also in two of *D. koenigswaldi*, RGM 177777 and RGM 179147, the ridge is widely arched, positioned slightly lower with respect to the mandibular foramen, and thickens rostrally.

Comparing the ascending rami in the mandibles of the different species of *Deinogalerix*, we notice a number of significant differences. The height of this structure (from the base to the sigmoid incisure) is greater in *Deinogalerix freudenthali*, and *D. minor*, somewhat lower in *D. intermedius* and quite more reduced in *D. koenigswaldi* (Fig. 5d–g). Moreover, the ascending ramus is more backward-stretched in *D. intermedius* and even more so in *D. koenigswaldi*; in connection with this, its anterior margin is more inclined backwards and the curvature of the rear margin (i.e. the portion between the condyle and the angular process) grows increasingly more acute. *Deinogalerix masinii* has a very high and slightly uplifted (i.e. base sensibly higher than the ventral profile of the horizontal ramus) ascending ramus and a rostrally tapering horizontal ramus (Fig. 5h–j).

Similar to the mainland *Parasorex socialis*, the masseteric fossa is deep and confined posteriorly by a thick, prominent border in *Deinogalerix freudenthali*, *D. masinii* and in the type specimens of *D. minor*. In *Deinogalerix intermedius* and *D. koenigswaldi*, this border is flat and the masseteric fossa is shallow and open posteriorly.

Ratio diagrams

Compared to the standard *Deinogalerix masinii*, in all the Gargano species of the genus, we notice a marked tendency to enlarge the p3–m1 tooth row; the two rear premolars have roughly the same proportions of m1 (Fig. 3b). In addition to this, the molars appear to grow progressively larger from m3 to m1. The maximum expression of these trends is reached in *Deinogalerix koenigswaldi*.

The third and fourth lower premolars of *Deinogalerix intermedius* are smaller, on average, than those of *D. koenigswaldi*, but the size ranges of these teeth in the two species partly overlap (Fig. 3b). F8-040 is the smallest *Deinogalerix intermedius* in the DSTF collection. It misses m1, but its other cheek teeth are similar in proportions to the cheek teeth of other members of the species.

Deinogalerix freudenthali bears larger cheek teeth than *D. masinii*, but the two species are close in dental proportions. Also *Deinogalerix brevirostris* has p4s and m1s proportionally similar to those of the standard. PU 100044 shares the dental

patterns of *Deinogalerix brevis*, and the same occurs also in *D. minor*, but the latter species has smaller p3s and p4s relative to m1 (Fig. 3b).

P81D-004 differs from all other species. It has morphologically primitive, large-sized m2s and m3s, borne by a slender, gracile mandible; for this reason, it has been attributed here to *Deinogalerix* sp. 2. The ratio diagram of the upper cheek teeth in Fig. 3b suggests a scenario similar to that observed for the lower dentitions, with the only notable difference that the relative growth in size, starting from M2, peaks at P4, instead of M1, consistently with the pattern of occlusion with the lower cheek teeth. Quite expectedly from what observed in the lower dentition, this trend peaks in *Deinogalerix koenigswaldi*. In contrast, in his diagnosis of *Deinogalerix freudenthali*, Butler (1980, p. 38) observed that the labial length of P4, relative to that of M1, is proportionally shorter than in the other Gargano species. This is also true for the DSTF specimens of *Deinogalerix freudenthali*, as it is for *D. masinii*.

RGM 177945 from Chirò 5A, which Butler (1980) attributed to *Deinogalerix intermedius*, preserves P3 and P4. These teeth are close in size to those of *Deinogalerix koenigswaldi*, but the P4 is proportionally similar to the same teeth of the other species (Fig. 3a). RGM 177982, which is attributed to *Deinogalerix intermedius* by Butler (1980), is similar, in relative dental sizes, to *D. minor*, *D. brevis* and PU 100044. The teeth of the latter two and of PU 100044 are similar in size and proportions; they are characterised by having a P4 not so enlarged as that of *Deinogalerix koenigswaldi* (Fig. 3a). Unfortunately, *Deinogalerix freudenthali* is represented only by isolated teeth. These appear to be close in proportions to those of *D. masinii*; only M3 is somewhat larger.

Cross-comparison of the remains of *Deinogalerix* from different Gargano fissure fillings in the DSTF collection

The remains of *Deinogalerix freudenthali* preserved at the DSTF offers the chance to bridge the gap of knowledge regarding *Deinogalerix minor*, mainly thanks to the skull fragment F9-014. The fossiliferous fissure filling P81D has produced the richest amount of remains of *Deinogalerix* of the DSTF collection. This material contributed to our knowledge of the most ancient representatives of *Deinogalerix intermedius*. All this, joined to the rest of the fossil material from the other Gargano fissure fillings (despite its paucity), improves our comprehension of the evolutionary history of the genus *Deinogalerix*. The general stratigraphic distribution of all the species of *Deinogalerix* is reported in Table 5.

<i>brevis</i>	<i>ix</i> sp.	<i>inii</i>	<i>thali</i>	<i>x</i> sp. 1	<i>x</i> sp. 2	<i>or</i>	<i>istris</i>	<i>idius</i>	<i>waldi</i>
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Phase	Deposits	<i>D. samnit</i>	<i>Deinogaleri</i>	<i>D. masi</i>	<i>D. freuder</i>	<i>Deinogaleri.</i>	<i>Deinogaleri.</i>	<i>D. min</i>	<i>D. breviro</i>	<i>D. interme</i>	<i>D. koenigs</i>
4	F32								†		†
3	San Giovannino								X		X
	Chirò 20C							X?		X	
	Gervasio							X		X	
	F9							X		X	
	F8									X	
	Fina H							X		X	
	Posticchia 1B									X	
2	Chirò 14A							X			
	Chirò 5A									X	
	F1							cf.		X	
	Pizzicoli 4									X	
	P81D					X				X	
	Nazario 4									X	
	NBS									X	
	Chirò 7A							X			
Fina D							X		X		
1b	F21c					X				X?	
	F15				X	X					
	Biancone 1				X						
1a	Rinascita 1				X						
0	M013			X	X?						
	Scontrone	X	X								

Table 5

Range chart of the species analysed for this study

X = actual occurrence; X? = doubtful attribution; in grey = possible phyletic lines

Deinogalerix freudenthali was hitherto known only from a small number of specimens (e.g. only eight teeth) described by Butler (1980). The material from fissure F15, especially the lower teeth, add up to Butler's (1980) sample and considerably improves our knowledge of *Deinogalerix freudenthali*. Nonetheless, many issues still need to be tackled.

The faunal assemblages from the earliest karstic fissures of Gargano are notoriously difficult to interpret because of the coexistence of taxa with primitive endemic

modifications, next to others that are not or only slightly modified. Even so, numerous taxa added to these early Gargano communities (by faunal interchange between islands or between different areas), while many others became extinct. Emblematic examples of archaic communities with the same degree of complication are displayed by *Mikrotia*: i.e. in F15, this endemic murid occurs with three different species, distinct in size, but often with partly overlapping size ranges; the largest members of these species are particularly difficult to discriminate (De Giuli et al. 1987a; Masini et al. 2013).

Also the fossil record of *Deinogalerix* from fissure F15 is not devoid of complication. Most of the remains display morphologies typical of *Deinogalerix freudenthali*; a small handful of specimens, however, are more difficult to assign to species. The morpho-dimensional analysis performed in this study indicates that *Deinogalerix freudenthali* shares primitive traits and small size with the better known *D. masinii* (Villier 2012; Villier et al. 2013). The pattern of the curves of the molars of *Deinogalerix freudenthali* and *D. masinii* (Fig. 3) recalls that of the mainland species, in which the relative sizes of the molars differ much less than they do in *D. koenigswaldi*.

Primitive features of *Deinogalerix freudenthali* that can be added to those described by Butler (1980) are the small size of m1 relative to those of the other teeth of the tooth row, the prominent hypoconid possessed by m3 and protruding anterolabial corner of M3. However, the fragmental maxillary F15-038 and the p3 F15-046, both from fissure F15, suggest the occurrence of a hitherto undetected species, here indicated as *Deinogalerix* sp. 1, whose size exceeds that of *Deinogalerix freudenthali*. Especially, F15-038 has size and morphologic traits (e.g. the low and blunt cuspids), nearing it to *Deinogalerix minor* from fissure F9.

Another fissure with faunal complications is P81D. It had been studied several years ago, but the results were never published (De Giuli et al., unpublished). The fissure belongs to the second phase of settlement (Masini et al. 2013; Table 4); it yielded scarce remains of small mammals, but numerous ones of *Deinogalerix*. Most of the specimens from P81D are attributed to *Deinogalerix intermedius*, based on dental and mandibular features, but also size, which is not far from that of *D. brevirostris* from San Giovannino. *Deinogalerix intermedius* from P81D possesses a P4 similar, in morphology and crown height, to that of *D. koenigswaldi*. Its teeth are smaller, on average, than those of Butler's (1980) holotype RGM 179063. Alongside *Deinogalerix intermedius*, P81D shows also the presence of another species, here called *Deinogalerix* sp. 2, indicated by a fragmental, small-sized

mandible with teeth dimensionally comparable to those of *Deinogalerix intermedius*. Notable is that this jawbone fragment preserves a primitive m3 (with well-developed talonid), quite similar to those of *Deinogalerix freudenthali*.

Fissure F1, which belongs to the same phase of settlement of P81D, gave scanty remains. It records the occurrence of *Deinogalerix intermedius*, accompanied by another smaller species, attested to only by a fragmental jawbone still preserving p1, approximately the size of the mandibles of *Deinogalerix minor*. This isolated specimen, equipped with a scarcely diagnostic tooth, is here ascribed to *Deinogalerix cf. minor*.

Fissure F9 belongs to the same phase of settlement of fissures Fina H and Gervasio (Table 4) from which *Deinogalerix minor* was first reported, accompanied by *D. intermedius* (Butler 1980). F9 is not particularly rich; it is anyhow notable for the co-occurrence of these two species. The two larger specimens fall in the morphologic and dimensional variability of *Deinogalerix intermedius*. The smaller species is present with a fragmental muzzle, F9-014, still preserving many of its teeth; it is attributed here to *Deinogalerix minor* in spite of the fact that the species was described by Butler (1980) only on mandibles and lower teeth. Although close, dimensionally, to *Deinogalerix brevirostris*, F9-014 has teeth comparatively less advanced than *Deinogalerix brevirostris* and comes from a fissure biochronologically older than San Giovannino, which justifies attributing it to *Deinogalerix minor*. Fissure F8 is virtually coeval with F9 (Table 4). It yielded a single, slender mandible attributed to *Deinogalerix intermedius*.

Fissure F21c belongs to the same archaic phase of settlement of F15. It provided two identifiable specimens; one is a first upper molar, which is attributed here to *Deinogalerix* sp. 1 from F15 based on its sized, but also on the biochronologic position of the fissure. The other specimen, a very large and morphologically advanced p4, is compatible morphologically and dimensionally with *Deinogalerix intermedius* and *D. koenigswaldi*. As explained in Table 4, note d, F21c may likely be contaminated; the specimen, therefore, could actually belong to *Deinogalerix intermedius* or *Deinogalerix koenigswaldi* and come from a more recent fissure filling. If not, the isolated fourth lower premolar would belong to an already advanced and large-sized *Deinogalerix intermedius*.

NBS also belongs in the same phase of settlement of P81D and F1. It yielded a single, large-sized and advanced p4, which may be the earliest occurrence of *Deinogalerix intermedius*.

Phylogenetic implications

The DSTF sample speaks in favour of the primitiveness of *Deinogalerix freudenthali* stated by Butler (1980) and Villier et al. (2013). This biochronologically very early species shares features in common with the most primitive and ancient species ever found in Gargano, *Deinogalerix masinii* from fissure M013 (Villier et al. 2013). Yet, as already stated by Villier et al. (2013), it is quite unlikely that *Deinogalerix masinii* is the direct ancestor of the Gargano species on account of its exclusive adaptations (Villier 2012). On the other hand, as already observed by Butler (1980), based on its morphologic traits, *Deinogalerix freudenthali* is close to, or can even be identified as, the ancestor of the other Gargano species except *D. masinii*.

The results of the present study indicate that *Deinogalerix freudenthali* is associated with *Deinogalerix masinii* in the fissure M013, as already assumed by Villier et al. (2013). Two species of *Deinogalerix* seem to be constantly present in the Gargano faunal assemblages. However, we cannot exclude that the remains of *Deinogalerix freudenthali* from fissure M013 may result from a contamination; this deposit actually contains a low number of younger remains, referable to the earliest phase of settlement recorded by the Terre Rosse (Masini et al. 2013).

The faunal consistency in fissure F15 seems ruling out the possibility that the remains of uncertain attribution referred here to *Deinogalerix* sp. 1 can be due to contamination. The specimens may belong to an extreme variant of *Deinogalerix freudenthali*, and its morphologic traits and size may fall in the variability of that species. However, the size and morphology of the fragmental maxilla F15-038 are also quite close to those of *Deinogalerix minor*; this raises the possibility that this species, or its ancestor, were already present during the earliest settlement in Gargano. Given the paucity of the available evidence, is not too parsimonious to assume that the line of *Deinogalerix minor* existed already since the time of fissure F15 and that it persisted all the way up to Gervasio (or San Giovannino). On account of these considerations, but especially of the paucity of remains, we therefore decided to call these F15 specimens *Deinogalerix* sp. 1. There can be another option, which is that these remains belong to a species not closely related either to *Deinogalerix freudenthali* nor to *D. minor*; this hypothetical taxon would then have become extinct without descent. This alternative, however, seems by far the less parsimonious of all.

Like in the case of *Deinogalerix* sp. 1, *Deinogalerix* sp. 2 from fissure P81D is difficult to place phylogenetically. It may either be a large-toothed descendant of

Deinogalerix freudenthali, or a primitive ancestor of *Deinogalerix minor*. A third, but less convincing alternative, is that it is an additional, primitive immigrant from a neighbouring area.

A high number of remains of *Deinogalerix intermedius* come from various Gargano fissures, i.e. NBS, F1, F8, F9, and especially P81D. The jawbone specimens from the latter fissure are very similar to the mandibles of *Deinogalerix koenigswaldi*, but have somewhat more primitive ascending rami. Dentally, *Deinogalerix intermedius* and *D. koenigswaldi* are virtually identical; the teeth of the former vary more widely in size and partly overlap with those of the latter. This indicates a close relationship between the two species, as already supposed by Butler (1980).

The origin of *Deinogalerix intermedius* is still shrouded with uncertainty. The species may be a local descendant of *Deinogalerix freudenthali*; otherwise, its sudden appearance with evolutionarily advanced members may reveal the entrance of a thoroughly new lineage from neighbouring areas. This possibility could be supported by the occurrence of the large-sized and advanced p4 NBS-001 from a fissure, Nazario Bivio Sinistra, somewhat older than P81D (Fig. 4).

Deinogalerix minor is here regarded as a valid species. It is smaller-sized and more slender than, and morphologically distinct from, *D. intermedius* and close to *D. brevirostris*. Some of its mandibular traits (e.g. the features of the ascending ramus) are primitive and shared with *Deinogalerix freudenthali*. In fissure F9, *D. minor* is represented for the first time ever by upper teeth. The species co-occurs with *Deinogalerix intermedius*, as already reported by Butler (1980), in relatively late deposits (third phase of settlement) and is most probably a primitive member of the line terminating in *D. brevirostris*.

Butler (1980) attributed specimen RGM 177982 from fissure Chirò 20C to *Deinogalerix intermedius*. It belongs to the third phase of settlement, which can be referred to a time span somewhat more ancient than San Giovannino. It is actually more consistent, morphologically and dimensionally, with *Deinogalerix minor* and *D. brevirostris*; the remain should therefore be moved to the *Deinogalerix minor–D. brevirostris* evolutionary line. Similar to RGM 177982, the writers also believe that the skeleton PU 100044, which Villier and Carnevale (2013) attributed to *Deinogalerix koenigswaldi*, should more appropriately be included in the *Deinogalerix minor–D. brevirostris* lineage (as suggested by Villier 2010), in spite of the lack of a precise stratigraphic location of the fissure that yielded the specimen.

The problems Butler (1980) had in reconstructing the origin of *Deinogalerix minor* could not be circumvented in the present study. The co-occurrence of the line of *Deinogalerix minor* with that of *Deinogalerix intermedius* is clearly observed only in more recent fissures, such as F9 and Fina H. Despite this, in F1, a single, small-sized specimen may represent the line of *Deinogalerix minor*. The morphological similarities linking *Deinogalerix minor* to *Deinogalerix freudenthali* support the hypothesis that *Deinogalerix freudenthali* is close to the common ancestor of the other species from Gargano described by Butler (1980).

San Giovannino yielded a high amount of remains of *Deinogalerix* and is therefore one of the most significant fissures of the Gargano area. In agreement with Butler (1980) and contrary to Villier et al. (2013), the writers find that, the divergence between *D. brevirostris* and *D. koenigswaldi* is well apparent, similar to *Deinogalerix minor* and *D. intermedius*. Nonetheless, some skulls and mandibles of *Deinogalerix koenigswaldi* from San Giovannino are actually problematic. Albeit apparently hypermorphic, several individuals are in fact impossible to differentiate from the others on both the dental sizes and proportions. Butler (1980) had supposed that *Deinogalerix koenigswaldi* from San Giovannino may exhibit a remarkably high degree of ontogenetic differentiation and sexual dimorphism; in fact, he attributed RGM 179194 to an adult male and RGM 177777 to a prime-age female.

Nonetheless, Butler's (1980) interpretation does not seem to find support. Based on the present literature, size differences like those displayed by *Deinogalerix koenigswaldi* have never been observed between living male and female Eulipotyphla (Lindenfors et al. 2007) and have never been attributed to sexual dimorphism in extinct taxa. The supposed size dimorphism in the San Giovannino *Deinogalerix* is never displayed by the representatives of more ancient fissures, not even by those of M013, which yielded a sample approximately the size of that provided by San Giovannino. The presumed dimorphism would therefore be apomorphic of the genus *Deinogalerix* and, in particular, of its most advanced species, *D. koenigswaldi*. Within an evolutionary lineage, increasing size dimorphism with increasing body size may occur where males exceed females in size, and decreasing size dimorphism with increasing average body size when females are the larger sex (Rensch's rule: Rensch 1950; Lindenfors et al. 2007; Zidarova 2015). A case where the former circumstance was actually observed was that of the late representatives of the early Pleistocene giant deer *Eucladoceros* (Azzaroli and Mazza 1992). Although the rule does not seem to apply to Eulipotyphla, in which size dimorphism is minimum or totally absent (Lindenfors

et al. 2007; Zidarova 2015), *Deinogalerix* is so highly modified and large-sized that we cannot exclude its allometry may have been consistent with the Rensch's rule. On the other hand, in the same way as for the recent species of *Mikrotia* (Maul et al. 2014), the complex faunal history of the Apulia Platform may also justify that RGM 179194 (an adult male of *D. koenigswaldi*, according to Butler 1980) is actually a third, newly immigrated species, possibly derived from a species similar to *Deinogalerix intermedius*.

Conclusions

The present study aims at clearing the taxonomic status of the DSTF specimens and the evolutionary relationships of the different species of the genus *Deinogalerix*. The analysis performed here broadly validates and strengthens the framework depicted by Butler (1980), while at the meantime it shows that the taxonomic revision proposed by Villier et al. (2013) and Villier and Carnevale (2013) is somewhat less convincing. The dental sample of *Deinogalerix freudenthali* is now richer than that examined by Butler (1980). Based on this additional information, the species enlists with the most primitive members of the genus, alongside *Deinogalerix masinii*. Nonetheless, *Deinogalerix freudenthali* is the closest to the hypothetical ancestor of the other Gargano species described by Butler (1980). Moreover, the present study corroborates (1) the validity of *Deinogalerix minor* and *D. intermedius*, (2) the reliability of the phyletic lineages *Deinogalerix minor*–*D. brevisrostris* and *D. intermedius*–*D. koenigswaldi* and (3) the co-occurrence of members of these two lines at least in the most recent Terre Rosse fissures. Two different species of *Deinogalerix* seem to be present constantly in the faunal assemblages of the Apulia Platform, ever since the earliest deposits (Scontrone, Savorelli et al. 2017). The most ancient phases of colonisation are now better detailed, but the improved information also further complicates the picture. The earliest fissures in fact contain primitive species of unclear taxonomic and phylogenetic status.

The DSTF collection certainly improved our knowledge of the genus *Deinogalerix*. Nonetheless, many issues still need to be addressed. The fossil record of the genus remains imperfect; the many gaps in it do not permit to utter a final word on the origins of the various lines that characterise its evolution.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Electronic supplementary material

Table S1

Raw dental measurements of the lower and upper teeth of the Naturalis, DSTT and Chieti Collections. *Deinogalerix minor** from M010 is called *D. koenigswaldi* by Villier and Carnevale (2013). Measurements in italics are controlled by the writers. ¹ values inferred. **(a)** Raw dental measurements of the lower teeth of the Naturalis, DSTT and Chieti Collections. ² values inferred and measurements of m3 omitted because considered flawed. References: a: Butler (1980); b: Villier (2012); c: this paper; d: Villier and Carnevale (2013); e: Villier et al. (2013); f: Savorelli et al. (2017). **(b)** Raw dental measurements of the upper teeth of the Naturalis, DSTT and Chieti Collections. References: a: Butler (1980); b: Villier (2012); c: Villier and Carnevale (2013); d: Villier et al. (2013); e: Savorelli et al. (2017). Measurements are in millimetres. (DOC 236 kb)

Table S2

(DOC 243 kb)

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