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# The tangled cases of *Deinogalerix* (Late Miocene endemic erinaceid of Gargano) and Galericini (Eulipotyphla, Erinaceidae): a cladistic perspective

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## Abstract

The Late Miocene giant erinaceid *Deinogalerix* from Scontrone and Gargano (Italy) is associated with many other vertebrates in deposits of a past island, the "Abruzzo-Apulia Platform". At Gargano, *Deinogalerix* is accompanied by the moderately endemized Galericini *Apulogalerix*. This first extensive cladistic analysis is aimed at defining the relationships of *Deinogalerix* with characteristic members of the tribe Galericini. The analysis was performed on a matrix of 30 characters and 19 taxa and identified some smaller clades, nested within three major ones. The latter include: (i) a pentatomy of *Galerix* species, (ii) a polytomy of "transitional" *Galerix–Parasorex* species and (iii) a large clade with *Parasorex*, *Schizogalerix* and Gargano representatives. *Galerix* and *Parasorex* proved to be paraphyletic and *Schizogalerix* monophyletic. Based on the results of the analysis, *Deinogalerix* and *Apulogalerix* have distinct origins, which supports an asynchronous colonization of the island. The line of *Deinogalerix* possibly stemmed from some eastern species transitional between *Galerix* and *Parasorex* around Mammal Neogene (MN) zone 2. Conversely, the line of *Apulogalerix* originated from a primitive *Parasorex ibericus*, or a close relative, around MN 9–10. Another important result was detecting an impressive early Miocene (MN 2?) radiation of Galericini. Moreover, *Schizogalerix* and *Parasorex* originated from eastern Galericini morphologically transitional between *Galerix* and *Parasorex*.

The endemic, insular, giant galericine erinaceid *Deinogalerix* Freudenthal, 1972, with is one of the most amazing components of the renowned "Terre Rosse" faunal complex, otherwise known as the "*Mikrotia* fauna" (Freudenthal, 1971; Masini et al., 2010). This faunal assemblage was largely found in upper Miocene karst fissure fillings in Mesozoic limestones that are still actively quarried in the area between Apricena and Poggio Imperiale, near Foggia (Apulia, south-eastern Italy) (Savorelli and Masini, 2016; Savorelli et al., 2016; and references therein). *Deinogalerix* is one of the most staggering representatives of the Terre Rosse fauna, but it is not the only insectivore. The assemblage includes another galericine, *Apulogalerix pusillus*, less endemized than *Deinogalerix*, and comparable in size to the majority of the mainland counterparts (Masini and Fanfani, 2013).

More ancient representatives of *Deinogalerix* have also been recovered from lower Tortonian coastal tidal-flat layered calcarenites at Scontrone (Abruzzo, central Italy, Fig. 1; Savorelli et al., 2017). The Scontrone and Gargano fossil records thus prove the existence, at least during the late Miocene, of a land, known as the Apulia Platform, that had been repeatedly isolated from neighbouring mainland areas for long periods (De Giuli et al., 1987b; Patacca et al., 2008a,b, 2013).

*Deinogalerix* is a multispecific genus that was first described by Freudenthal (1972). Its type species is *Deinogalerix koenigswaldi* Freudenthal, 1972, which is the largest of the genus. Other species were added over

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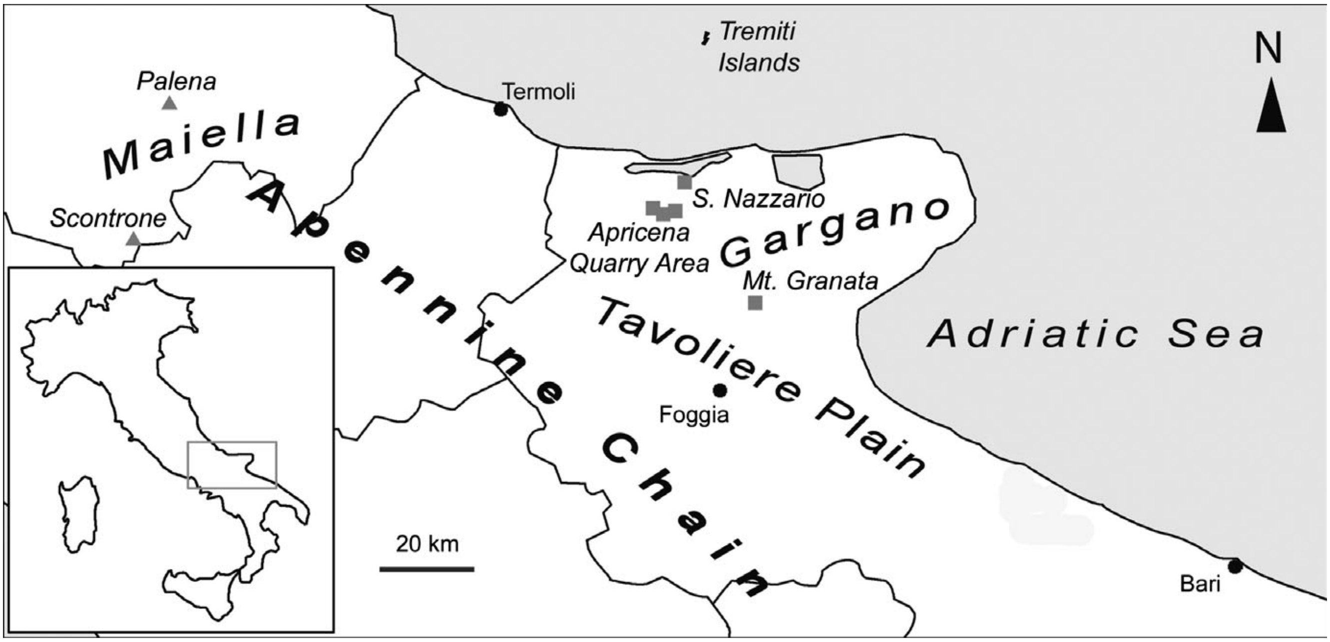

Fig. 1. Location map of localities that yielded the fossils of the Apulia Platform fauna. Modified from Savorelli et al. (2016).

the years: *D. brevirostris* Butler, 1980; *D. intermedius* Butler, 1980; *D. minor* Butler, 1980; *D. freudenthali* Butler, 1980; and *D. masinii* Villier et al., 2013; from Gargano and *D. samniticus* and *D.* sp. Savorelli et al., 2017; from Scontrone. *Deinogalerix masinii* comes from Gargano's most ancient fissure, M013 (Masini et al., 2013b; Villier et al., 2013), and *D. samniticus* and *D.* sp. from Scontrone are represented by scanty remains and constitute an independent phyletic line, separate from those from Gargano (Savorelli et al., 2017).

### *Origin of Deinogalerix*

The phylogenetic relationships and classification of *Deinogalerix* have been the topics of several studies (Butler, 1980; van den Hoek Ostende, 2001; Ziegler, 2005; Villier et al., 2013). In all these contributions *Deinogalerix* was included in the tribe Galericini.

This tribe includes only extinct taxa and was widespread in the Eurasian and African Miocene. It belongs in the subfamily Galericinae, which comprises all the living genera of gymnure and moonrats. Many Galericini had originally been classified as *Galerix* Pomel, 1848. Later on, several genera were introduced (e.g. *Pseudogalerix*, *Parasorex*). Currently, apart from the insular taxa, three genera are accepted besides *Galerix*, namely *Schizogalerix*, *Parasorex* and *Tetracus*. The former is clearly distinct from *Galerix*, while the latter is more difficult to discriminate, especially its earliest species (Savorelli et al., 2017; van den Hoek Ostende, 2001).

Butler (1980) supposed that *Deinogalerix* had originated from a still unknown Asian gymnure, and rejected that it could be related not only to any coeval European galericine, but also to *Lanthanotherium* Filhol, 1891, which, in his view, is rather linked to modern south Asian moonrats. Van den Hoek Ostende (2001) derived *Deinogalerix* from a middle to late Miocene "*Parasorex*-like" ancestor and demonstrated that *Deinogalerix* clusters with *Schizogalerix* Engesser, 1980, and *Parasorex* von Meyer, 1865, the latter including *P. socialis* von Meyer, 1865, *P. depereti* (Crochet, 1986) and *P. ibericus* (Mein and Martín-Suárez, 1993). For Ziegler (2005), *Deinogalerix* is the sister taxon to *Schizogalerix* and *Parasorex*. Villier et al. (2013) shared van den Hoek Ostende's (2001) opinion, but claimed an earlier forerunner than that supposed by van den Hoek Ostende (2001). Savorelli et al. (2017) agree with the latter hypothesis, proposing that *Deinogalerix* would have descended from a not better identified early to middle Miocene "*Parasorex*-like" galericine.

The relationship of *Deinogalerix* to *Apulogalerix* is still an open issue. It has received the attention of several researchers, but opinions range from those who think that both share a common ancestor (Freudenthal, 1972; van den Hoek Ostende, 2001; Freudenthal and Martín-Suárez, 2010; van den Hoek Ostende and de Vos in Villier et al., 2013, p. 74) to others who believe that the two lineages derived from independent ancestry (Savorelli et al., 2017).

### *Origin of the Apulia Platform fauna*

A hotly debated issue is whether immigration of the Apulia Platform fauna was the result of a single colonization event, or rather a palimpsest of multiple settlements. Freudenthal (1971, 1985), Freudenthal and Martín-Suárez (2006, 2010), van den Hoek Ostende et al. (2009) and Freudenthal et al. (2013) opt for a single colonizing event, or for several events very close in time. In contrast, Butler (1980), De Giuli et al. (1987a,b), Mazza et al. (1995, 2009), Abbazzi et al. (1996), Mazza and Rustioni (1996, 2008), Masini et al. (2002, 2008, 2010, 2013b), Rook et al. (2006), and Savorelli and Masini (2016) supposed multiple events of colonization, which Masini et al. (2002, 2008) indicated as a "polyphasic model". According to this hypothesis the fauna built up over time through a set of diachronous bio-events, with multiple (vicariant and/or dispersalist) mechanisms. Freudenthal (1985), van den Hoek Ostende et al. (2009), Freudenthal and Martín-Suárez (2010) and Freudenthal et al. (2013) dated the arrival of the forerunners of the Apulia Platform species to a time range spanning the Tortonian–Messinian. In particular, Freudenthal et al. (2013) dated the event to the late Tortonian, more precisely to MN 11 (zone 11 of the European Neogene Land Mammal Ages), based on the overlapping ranges of distribution of the putative ancestors of the Gargano taxa. This supposed time of colonization, however, is younger than the date of the Scontrone bonebed (Patacca et al., 2013). Based on stratigraphic and palaeontological considerations (Mazza and Rustioni, 1996, 2011; Patacca et al., 2008a,b, 2013; Savorelli et al., 2017), the Scontrone fauna is more ancient than the Gargano assemblages. Some of the supporters of the polyphasic model believe that the ancestors of the Apulia Platform fauna reached this land over time, through different waves of colonization that occurred during two time windows, one spanning the late Oligocene to early Miocene (Mazza and Rustioni, 1996, 2011; Mazza, 2013a,b), and the second an interval ranging from the late Tortonian to the Messinian (Masini et al., 2013b; Savorelli et al., 2016).

### *Aims*

Recently described material of *Deinogalerix* (Villier, 2012; Villier et al., 2013; Savorelli et al., 2017) imposes a reappraisal of the phylogenetic relationships of the genus. This improved knowledge helps to shed light on the origin as well as the interrelationships of this erinaceid.

Contributing to a more comprehensive knowledge of the phylogenetic relationships of *Deinogalerix* was the original intended goal of the present study. A cladistic analysis was conducted not only on this endemic erinaceid, but also on *Apulogalerix*, against a wide selection of other extinct members of Galericini, which were considered particularly helpful to the targets of the study. Addressing taxonomic issues and formally describing new taxa were beyond the scope of the analysis. The aim was finally extended to clarifying our basic understanding not only of the phylogenetic origin and relationships of *Deinogalerix*, but also of other Oligo-Pliocene species of the tribe.

Identifying possible source areas of the ancestors of *Deinogalerix* and *Apulogalerix*, which would require using specifically designed probabilistic modelling of geographical range evolution, is not the purpose of this paper. Nonetheless, some hints on the biogeography of Galericini are provided based on the information on the palaeogeographical distribution of the studied taxa included in this analysis.

## Material and methods

The list of species of Galericinae analysed in the present study is given in Table 1. The research is based both on literature data (Table 1) and direct observation. The material directly examined by us belongs to *Parasorex socialis* from La Grive (France), *Parasorex depereti* from Brisighella (Italy) and *Apulogalerix pusillus* from Gargano (Italy), all preserved in the Department of Earth Sciences of the University of Florence, and *Deinogalerix masinii*, also from Gargano, kept at the Department of Earth Sciences of the University of Turin.

Table 1
Selected taxa and main references

| Taxon | Reference(s) |
|---|---|
| *Zaraalestes minutus* | Ziegler et al. (2007) |
| *Eogalericius butleri* | Lopatin (2004, 2006) |
| *Eochenus sinensis* | Wang and Li (1990); Lopatin (2006) |
| *Galerix nanus* | Hugueney and Adrover (2003); Crochet (1974, 1995) |
| *Galerix saratji* | Van den Hoek Ostende (1992, 2001) |
| *Galerix aurelianensis* | Ziegler (1990); van den Hoek Ostende and Fejfar (2006) |
| *Galerix exilis* | Ziegler (1983) |
| *Galerix symeonidisi* | Doukas (1986); van den Hoek Ostende and Doukas (2003) |
| *Parasorex kostakii* | Doukas and van den Hoek Ostende (2006); Prieto et al. (2012) |
| *Galerix iliensis* | Kordikova (2000) |
| *Deinogalerix masinii* | Villier (2012); Villier et al. (2013) |
| *Parasorex socialis* | Engesser (1972); Prieto and Rummel (2009) |
| *Parasorex depereti* | Crochet (1986); Masini et al. (2013a) |
| *Parasorex ibericus* | Mein and Martín-Suárez (1993) |
| *Apulogalerix pusillus* | Masini and Fanfani (2013) |
| *Schizogalerix evae* | De Bruijn et al. (2006) |
| *Schizogalerix pasalarensis* | Engesser (1980) |
| *Schizogalerix anatolica* | Engesser (1980) |
| *Schizogalerix moedligensis* | Rabeder (1973); Rümke (1976) |

The study is largely focused on dental remains. Skull material is very rarely found and postcranials are little studied and rarely the subject of inquiry, because of their limited diagnostic value for extinct species. Complete mandibles are also infrequent. Moreover, many mandibular characters are not preserved and some, when present, such as those of the ascending ramus, have often been neglected in the literature. The characters used here were mostly drawn from the dental morphological features that are traditionally considered significant for establishing the taxonomy and phylogenetic relationships of Galericini, plus a set of diagnostic apomorphic traits possessed by the genus *Deinogalerix* (e.g. Butler, 1980; Engesser, 1980; van den Hoek Ostende, 2001; Ziegler, 2005; Villier et al., 2013; Savorelli et al., 2017; see also Table 1). The characters and character states are reported in Table 2 and discussed in the section "*Characters*".

Basic dental definitions and terminology (Fig. 2) used in this paper conform with those adopted by Savorelli et al. (2017). Capital letters indicate upper cheek teeth, while lower case letters represent lower teeth.

### *Informal nomenclature*

In the present study an informal nomenclature has been adopted. Galericini *sensu lato* (Galericini *s.l.*) indicates all Galericini, including the primitive genera *Eochenus* and *Eogalericius* (Lopatin, 2004, 2006), and Galericini *sensu stricto* (Galericini *s.s.*) all Galericini except *Eochenus* and *Eogalericius* (see Selection of the taxa for more details). *Galerix* and *Parasorex* are difficult to define because of the evolutionary mosaic of their characters. To facilitate their identification, informal names have been introduced to designate taxa that exhibit the whole set of features that are classically used to discriminate the two genera. *Galerix s.s.* and *Parasorex s.s.* include species with the typical characteristics of the two genera (see *Characters*).

### *Selection of the taxa*

The endemic fossil taxa analysed for this study are *Deinogalerix masinii* and *Apulogalerix pusillus*. Because of its primitiveness and of the richness of its fossil record, the former was selected to represent all the species of its genus, which is assumed to be monophyletic (e.g., Butler, 1980). *Apulogalerix pusillus* was included not only because it belongs to the second genus of Galericini known from Gargano, but also because some authors considered it a sister taxon (Freudenthal, 1972; van den Hoek Ostende and de Vos in Villier et al., 2013) or even ancestor (van den Hoek Ostende, 2001; Freudenthal and Martín-Suárez, 2010) of *Deinogalerix*.

In an early phase of our study, all available information on the extinct tribe Galericini was imported into He et al.'s (2012) matrix, which included only extant Erinaceidae (A. Borrani, unpublished). The cladogram obtained from this showed that Galericini group together in a distinct clade and form an unresolved polytomy. We also found, similarly to Corbet (1988), Frost et al. (1991), Gould (1995), Jenkins and Robinson (2002), Grenyer and Purvis (2003), He et al. (2012) and Bannikova et al. (2014), that the extant genera *Echinosorex* and *Hylomys* are the closest, phylogenetically, to Galericini. In a successive round of analysis, we therefore used *Echinosorex gymnura* as an outgroup, because the genus *Echinosorex* allowed for more complete coding than *Hylomys megalotis* (Jenkins and Robinson, 2002). The resulting cladogram appeared in stark contrast to the known evolution and stratigraphic distribution of Galericini, because of the high number of apomorphies in *Echinosorex*. We finally used the Tupaiodontinae *Zaraalestes* from the Oligocene of Mongolia as outgroup given its many plesiomorphic traits.

The other taxa of Galericini used for the present study were primarily chosen for the richness of their fossil record, but also for being particularly representative of the geographical and stratigraphic distribution of Galericini *s.l.* The taxonomy of the 19 taxa involved in the analysis follows that of the most recent literature. The taxa are listed below.

*Zaraalestes minutus (outgroup).* After accurate scrutiny of several candidate taxa the choice fell on *Zaraalestes minutus*, from the Oligo-Miocene deposits of the Valley of Lakes, Mongolia (Ziegler et al., 2007). This species belongs to the extinct subfamily Tupaiodontinae, which is one of the most ancient and primitive, morphologically, in Erinaceidae (Lopatin, 2006). *Zaraalestes minutus* is represented by a rich fossil record. What makes it an ideal outgroup for our cladistic analysis is that alongside a few derived features (e.g. the morphology of M3), the species shows an array of primitive traits, such as M1s and M2s particularly shortened mesio-distally and widened bucco-lingually, and carrying a small hypocone, and m3s with a well-developed hypoconulid.

*Eogalericius butleri and Eochenus sinensis.* We included these two archaic species of the Middle Eocene of Mongolia in our ingroup. Lopatin (2006) considers them as belonging in Galericini *s.l.*, because of their plesiomorphic traits compared to Galericini *s.s.* Similarly to *Zaraalestes*, both species possess a combination of primitive and derived traits. The plesiomorphies are the same as for *Zaraalestes*, i.e. a small hypocone on M1–2 (especially in *Eochenus*) and the hypoconulid on m3. *Eochenus* and *Eogalericius*

Table 2
Characters and character state coding

| Number | Character | Character state 0 | 1 | 2 | 3 |
|---|---|---|---|---|---|
| 0 | P3 hypocone | Absent | Present | | |
| 1 | M1–2 metaconule distal arm | Absent | Directed distally and connected or not to distal cingulum | Extended to the posterolabial corner of the tooth | |
| 2 | M1–2 mesostyle | Absent or usually undivided | Invariably divided | | |
| 3 | Relative breadth of M1–2 | Not widened | Widened | | |
| 4 | Protocone–hypocone–metaconule connections on M1 | Protocone only connected with metaconule | Protocone only connected with hypocone | Triple connection | |
| 5 | Distal arm of hypocone on M1 | Absent | Not connected with distal cingulum | Connected with distal cingulum | |
| 6 | Oblique mesolingual-distolabial elongation of M1 | Not elongated | Elongated | | |
| 7 | Protocone–hypocone–metaconule connections on M2 | Protocone only connected with metaconule | Protocone only connected with hypocone | Triple connection | |
| 8 | Distal arm of hypocone on M2 | Absent | Not connected with distal cingulum | Connected with distal cingulum | |
| 9 | Shape of M3 | Triangular M3 | Non-triangular (because of well-developed metastylar crest) M3 | | |
| 10 | Size of M3 | Large M3 (compared with Galericini *s.s.*) | Small M3 | | |
| 11 | i3 | Present | Absent | | |
| 12 | Relative size of p2/p3 | p2 < p3 | p2 ≥ p3 | | |
| 13 | Number of roots in p2 | two-rooted | fused roots | one-rooted | |
| 14 | Paraconid–protoconid connection on p4 | paraconid not connected with protoconid | paraconid connected with protoconid | | |
| 15 | Precingulid on p4 | present | absent | | |
| 16 | Degree of development of metaconid on p4 | strong and prominent | weak | absent | |
| 17 | Hypoconulid on m3 | present | absent | | |
| 18 | Position of the mental foramen | one mental foramen beneath p2 | one mental foramen beneath p3 | one mental foramen beneath p3/4 or beneath anterior root of p4 | two mental foramina, one beneath p2 and one beneath p3 |
| 19 | Relative size of the m1 trigonid | non-elongated | elongated | | |
| 20 | Relative size of P3 and P4 | non-enlarged | enlarged | | |
| 21 | Relative size of p3 and p4 | non-enlarged | enlarged | | |
| 22 | Morphology of P3/p3 and P4/p4 | slender and sharp | bulbous | | |
| 23 | Cuspids of p4 | pointed | blunt | | |
| 24 | Morphology of metastylid in m1 | sharp | bulbous | | |
| 25 | Preprotocristid in p4 | sharp | blunt | | |
| 26 | Crown of i1 | non-bilobed | bilobed | | |
| 27 | Coronoid process | high and robust | low and slender | | |
| 28 | Height of condyle above toothrow | high | low | | |
| 29 | Height of ascending ramus | high | low | | |

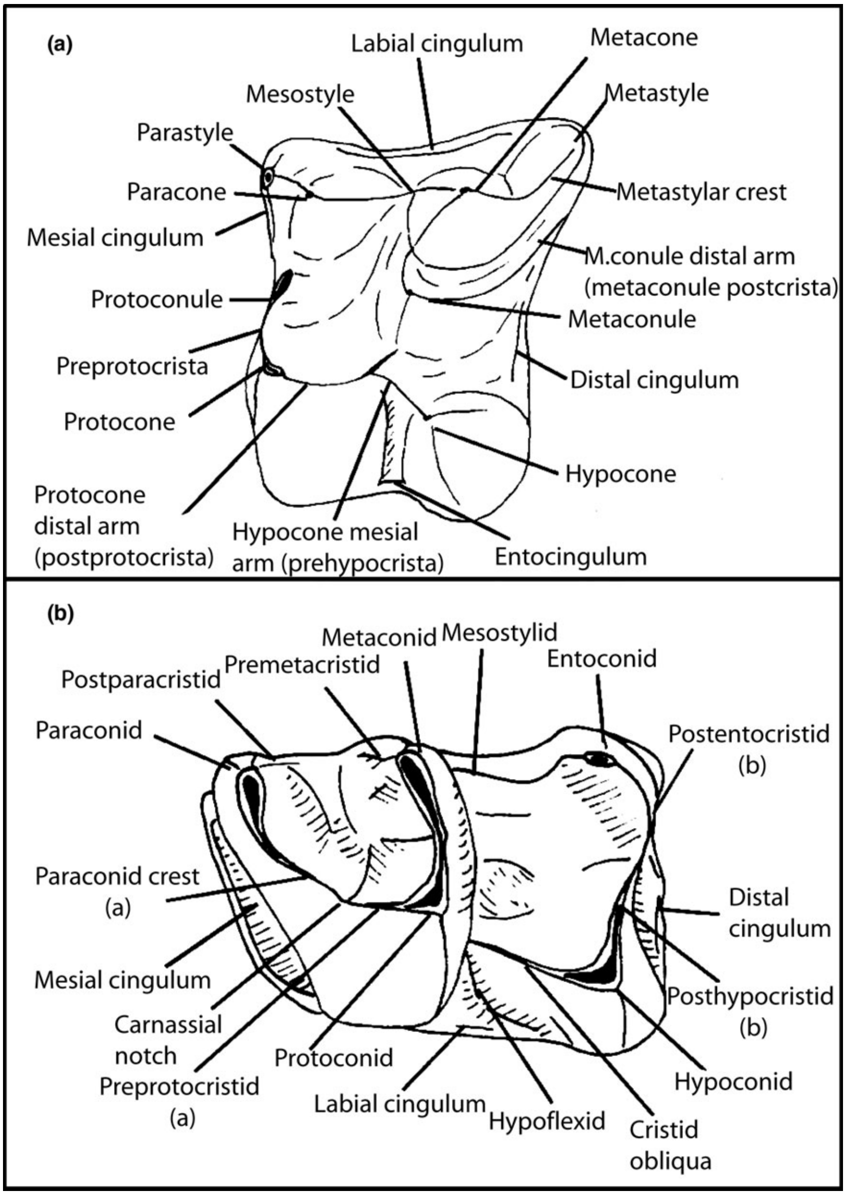

Fig. 2. Dental morphology terms adopted in this paper, from Engesser (1980), Gould (1995), Lopatin (2006) modified by Masini and Fanfani (2013): A, upper molar; B, lower molar; (a) paralophid (paracristid) = paraconid crest + preprotocristid *sensu* Lopatin (2006); (b) postcristid (hypolophid) = postentocristid + posthypocristid *sensu* Lopatin (2006). Modified from Savorelli et al. (2017).

add large M3s (in *Eogalericius* this can be inferred from the alveoli). *Eochenus* has large, conical, carnivore-like canines, i.e. non-procumbent, but rather upright and bent backwards. Moreover, *Eochenus* has very large p4s (much larger than p2 and p3), as well as p2s slightly smaller than p3s. Unlike *Eochenus*, *Eogalericius* has lower premolars that grow gradually smaller from p4 to p2 (Lopatin, 2004).

*Galerix spp.* The members of the genus *Galerix* should be characterized by having p2 as large as or larger than p3, a single lingual cusp (protocone) on P3, no or a very weak paraconid–protoconid connection on p4, the rear arm of the metaconule not reaching the distal cingulum on M1–2, and the protocone often connected with the metaconule on M1–2 (van den Hoek Ostende, 2001). *Galerix nanus* was selected because it is considered the most ancient member of the genus (van den Hoek Ostende, 2001). The species had a contentious nomenclatural history. For a long time it had been attributed to a distinct genus, *Tetracus*. Nonetheless, the synonymy with *Galerix* proposed by van den Hoek Ostende (2001) is convincingly supported by typical *Galerix* traits.

*Galerix saratji* is the earliest Miocene species of the genus and is documented by a rich fossil record. Moreover, van den Hoek Ostende (1992, 2001) considered it at the base of the radiation of the Miocene species of *Galerix*. *Galerix aurelianensis* is described in detail and is deemed a possible descendant of *Galerix saratji* (van den Hoek Ostende, 1992). It has also been regarded as the putative ancestor of *Galerix exilis* (Ziegler, 1990). *Galerix aurelianensis* was also selected to provide a more complete cover of the stratigraphic range of the genus. *Galerix exilis* is the type species of the genus (van den Hoek Ostende, 2001). It was described in detail by Ziegler (1983). This widespread European species is one of the best known members of *Galerix*.

*Parasorex spp*. The members of the genus *Parasorex* should be characterized by having a hypocone-bearing P3, the rear arm of the metaconule reaching the postero-labial corner of M1 and M2, the tendency to have protocone and hypocone connected on M1–2, p2 smaller than p3, a very robust connection between paraconid and protoconid on p4, and a strong metaconid on p4 (van den Hoek Ostende, 2001). Nonetheless, the early species *P. kostakii* constitutes an exception to this generalization (see below). *Parasorex socialis* was chosen because it is the type species and the best known member of the genus (van den Hoek Ostende, 2001). It is also the most ancient representative of our informal taxon *Parasorex s.s.* It is widespread throughout Europe. *Parasorex ibericus* is close to, but more advanced than, *Parasorex socialis*. It replaces the latter species in the Iberian Peninsula, where it is well documented from several MN localities on. *Parasorex depereti* is the youngest species of the genus. It is imperfectly known from France. It has recently been reported also from Italy (Brisighella, Emilia-Romagna, MN 13, Masini et al., 2013a; Mandriola, Sardinia, early Pliocene, Furió and Angelone, 2010). At the moment, alongside *Parasorex kostakii*, the three species *P. ibericus*, *P. socialis* and *P. depereti* are the only known species of the genus.

*Schizogalerix spp*. This genus shares several traits in common with *Parasorex*: p2 smaller than p3, hypocone-bearing P3, strong connection between paraconid and protoconid on p4, rear arm of the metaconule stretched to the postero-labial corner of M1 and M2, and well-developed metaconid on p4. *Schizogalerix* adds the tendency to have a divided mesostyle on M1–2, protocone and metaconule not connected to one another on M1–2, M1–2 short mesio-distally and broad bucco-lingually, M1 elongated obliquely in a mesiolingual–distolabial direction and the rear arm of the hypocone connected with the posterior cingulum in M1–2. All these traits, which are typical of the most derived species, are less marked in the most archaic representatives of the genus (e.g. *S. pasalarensis* has an imperfectly divided mesostyle). *Schizogalerix* is widespread both geographically and through geological time. It is markedly different from the other members of Galericini. To avoid inflating the number of taxa used for our study, we excluded the most derived species from North Africa, Greece, Turkey and Austria (e.g. *S. sinapensis*, *S. zapfei* and *S. macedonica*). In fact, it is most unlikely that these extremely advanced species share a last common ancestor with *Deinogalerix*. Although imperfectly known, *Schizogalerix evae* was included in the present analysis because it is the most ancient Anatolian species of the genus (De Bruijn et al., 2006). *Schizogalerix pasalarensis* and *S. anatolica* were selected because they belong to the most ancient line of Anatolian *Schizogalerix*. Finally, the moderately advanced, European species *Schizogalerix moedligensis* was chosen to represent the derived members of the genus.

*Transitional species*. To complete the list of the species used for this study, we also included *Parasorex kostakii*, *Galerix iliensis* and *G. symeonidisi,* which display a mosaic of morphological traits typical of members of the genera *Parasorex* and *Galerix*, but not of *Schizogalerix*, and are therefore here considered transitional species. Because isolated p2s and p3s are virtually impossible to discriminate from one another, so also is their mutual size relationship (Doukas and van den Hoek Ostende, 2006; Masini and Fanfani, 2013). Identifications at the genus level of some species based only on isolated premolars may therefore be arbitrary. *Parasorex kostakii*, for instance, had originally been attributed to the genus *Galerix* (Doukas and van den Hoek Ostende, 2006), although the relative proportion of its p2s and p3s is unknown. This species was later accommodated in *Parasorex* by Prieto et al. (2012) based on its having P3s with a hypocone and the rear arm of the metaconule extended to the postero-labial corner of the tooth. On the other hand, *P. kostakii* has the protocone connected with the metaconule on M2, and does not possess a preprotocristid on p4, which are common traits for the genus *Galerix*. Moreover, the metaconid on p4 is of variable size and may even be absent, whereas in *Parasorex* the cuspid is constantly well-developed. Unfortunately, the relative proportion of the p2s and p3s of *P. kostakii*, which is a discriminating feature between *Parasorex* and *Galerix*, is unknown.

Another problematic taxonomic position is that of *Galerix iliensis*. This gymnure was moved from "*Schizogalerix*", wherein it had originally been placed by Kordikova (2000), to *Galerix* by Doukas and van den Hoek Ostende (2006). Nonetheless, the p2s and p3s of this species are unknown. Without knowing the relative size of these two premolars the species cannot be accommodated easily in either of these genera. *Galerix iliensis* shares several traits in common with *Parasorex*, e.g. hypocone-bearing P3, p4 with large metaconid and well-developed protoconid, mesostylar area not clearly partitioned as in *Schizogalerix*, constant presence of the protocone–hypocone connection on upper molars, and absence of the connection between protocone and metaconule. The posterior arm of the metaconule on M1–2 varies and may reach the rear cingulum, whereas the preprotocristid is always absent on p4. These are the only traits not typical for *Parasorex s.s.* members. The latter are typified by tending to have the posterior arm of the metaconule extended to the disto-labial corner of the tooth and by possessing a preprotocristid connected with the paralophid. Nonetheless, based on the features described so far, *G. iliensis* seems somewhat closer to *Parasorex* than to *Galerix*.

Also *Galerix symeonidisi* exhibits a distinctive combination of features. The larger p2 than p3 is like in *Galerix*, and yet *G. symeonidisi* possesses a hypocone-bearing P3 similarly to *Parasorex*. A variety of morphotypes have been observed in the p4s of this species: metaconid of variable size (sometimes even absent), large and tubercular paraconid not connected with the protoconid, or paraconid connected to protoconid by a longitudinal crest.

The high variability generates contradictory morphological combinations even in species of agreed generic status. For example, *Galerix exilis* from Goldberg (southern Germany, MN 6: Ziegler, 1983), which displays most of the typical features of its genus, may or may not possess a hypocone on P3.

*Deinogalerix masinii.* This is the best represented of the most ancient species of the genus. It has many endemic apomorphies induced by evolution in insular settings: large size, swollen tooth morphologies, blunt cusps(ids), very enlarged premolars, enlarged trigonid on m1, elongated muzzle and thus long diastemas. Some traits are shared with *Parasorex* and *Schizogalerix*: p2 smaller than p3, robust metaconid on p4, hypocone-bearing P3, tendency to have protocone and metaconule disconnected on M1–2.

*Apulogalerix pusillus.* This species also possesses endemic autapomorphies, but less numerous than *Deinogalerix*: long premolar row compared to the molars, metaconid absent on p4 and premolars generally swollen, especially P4/p4. Also, this species shares common traits with mainland counterparts: p2 smaller than p3, hypocone-bearing P3 (with tendency to lose it over time), rear arm of the metaconule stretched to the postero-labial edge of M1 and M2, protocone constantly connected with hypocone on M1–2.

### *Stratigraphic and geographical distribution of the selected taxa*

From a stratigraphic and geographical perspective, *Zaraalestes minutus* comes from the Oligo-Miocene deposits of the Valley of Lakes, Mongolia (Ziegler et al., 2007), whereas *Eogalericius butleri* (Lopatin, 2004) and *Eochenus sinensis* (Wang and Li, 1990) are from the Middle Eocene of Mongolia.

The most ancient species of the genus *Galerix* is *G. nanus*, which dates back to the European Mammal Paleogene (MP) zone 21–26 (early to late Oligocene) of France. *Galerix saratji* comes from MN 1–2 sites of Turkey, *G. symeonidisi* from MN 4–5 localities scattered from Europe to Turkey and *G. iliensis* from the early Miocene of Kazakhstan (Kordikova, 2000). *Galerix aurelianensis* comes from MN 3–5 localities of central and eastern Europe (Ziegler, 1990; van den Hoek Ostende and Fejfar, 2006), whereas *G. exilis* is one of the most widely distributed species, both stratigraphically (MN 5–8) and geographically, in Europe.

The best known species of *Parasorex*, *P. socialis*, is distributed widely in Europe during the MN 6–8 time span, and perhaps persisted until the MN 9–10 time period. *Parasorex depereti* comes from MN 13–15 sites of France and Italy and is therefore the youngest species of the genus. *Parasorex ibericus* is reported from several MN 10–14 localities in Spain. *Parasorex kostakii*, from MN 4 of Greece, is the most ancient species of the genus, according to Prieto et al. (2012).

The most ancient member of the genus *Schizogalerix* is *S. evae* from the MN 3 of Anatolia. Also, *S. pasalarensis* (MN 4–7) and *S. anatolica* (MN 5–8) come from Turkey, and *S. moedligensis* from MN 11 localities of central Europe (Austria).

*Deinogalerix masinii* comes from the karstic fissure filling M013, which is the most ancient in Gargano (ca. MN 13). *Apulogalerix pusillus* actually constitutes a chronospecies whose type specimens were collected from the rich fissure F32, which is the most recent in Gargano (MN 13).

### *Characters*

Numbering is like in the matrix, from 0 to 29:

0. *P3 hypocone*. 0: absent; 1: present. This cusp is possessed by *Parasorex* and *Schizogalerix*. van den Hoek Ostende (2001) considered it a diagnostic feature of these genera, although it can also be observed in species of the genus *Galerix* (Ziegler, 1983; Doukas, 1986; Kordikova, 2000; van den Hoek Ostende, 2001; Zijlstra and Flynn, 2015). Engesser (1980) was the first to signal the constant presence of this cusp in the genus *Schizogalerix*.

1. *Distal arm of the metaconule in M1–2*. 0: distal arm absent; 1: directed distally and connected or not to distal cingulum; 2: extended to the posterolabial corner of the tooth. The posterior arm extending to reach the posterolabial end of the tooth is considered typical of *Parasorex* and *Schizogalerix* by van den Hoek Ostende (2001). Nonetheless it can also be observed in other genera of Galericini (e.g. *Eogalericius, Galerix*).

2. *M1–2 mesostyle*. 0: absent, or usually undivided; 1: invariably divided. The mesostyle (also indicated as centrocrista when not in the form of a cusp: e.g., Lopatin, 2006) is differently shaped and continuous in all genera except *Schizogalerix*, where it appears interrupted (Engesser, 1980; van den Hoek Ostende, 2001).

3. *Relative breadth of M1–2*. 0: not widened; 1: widened. Character state 1 is diagnostic for *Schizogalerix* (Engesser, 1980; van den Hoek Ostende, 2001).

4. *Protocone–hypocone–metaconule connection on M1*. 0: protocone only connected with metaconule; 1: protocone only connected with hypocone; 2: triple connection. Character state 2 is highly variable. There are cases where protocone, hypocone and metaconule are connected to one another (triple connection) and the highest crest may be located either between protocone and metaconule, or between protocone and hypocone. According to van den Hoek Ostende (2001) in *Schizogalerix*, *Parasorex* and *Deinogalerix* the protocone is connected only with the hypocone. Villier et al. (2013) added that the protocone is rarely connected with the metaconule in *Deinogalerix*. Nonetheless, in *Deinogalerix masinii* the protocone is only connected with the hypocone, as in *Parasorex* and *Schizogalerix*.

5. *Distal arm of the hypocone on M1*. 0: absent; 1: not connected with distal cingulum; 2: connected with distal cingulum. The hypocone distal arm is usually connected in some of the most advanced species of *Parasorex* and *Schizogalerix*.

6. *Oblique mesiolingual–distolabial elongation of M1*. 0: not elongated; 1: elongated. The oblique widening and elongation of M1 are typical of the genus *Schizogalerix* (Engesser, 1980).

7. *Protocone–hypocone–metaconule connection on M2*. 0: protocone only connected with metaconule; 1: protocone only connected with hypocone; 2: triple connection. For the explanation see character 4.

8. *Distal arm of the hypocone on M2*. 0: absent; 1: not connected with the distal cingulum; 2: connected with the distal cingulum. For the explanation see Character 5.

9. *Shape of M3*. 0: triangular M3; 1: non-triangular M3 (because of well-developed metastylar crest). See following explanation of character 10.

10. *Size of M3*. 0: large M3 (compared with Galericini *s.s.*); 1: small M3. Galericini *s.s.* have a small, triangular-shaped M3, usually with small or no conules. In contrast, *Eochenus sinensis*, among Galericini *s.l.*, has a proportionally larger M3, with stronger paraconule and metaconule (Wang and Li, 1990). The M3 of *Eogalericius butleri* is not preserved, but judging from its dental alveoli, it was of large size (Lopatin, 2004). The M3 of *Deinogalerix* is characterized by a long, distolingually protruding metastylar crest. The outgroup *Zaraalestes* bears a small, triangular M3 in common with Galericini *s.s.*, which is probably a parallel, derived trait. A large M3 is actually typical of the most ancient species of Erinaceomorpha (e.g. *Macrocranion nitens*: Novacek et al., 1985).

11. *i3*. 0: present; 1: absent. i3 is present in primitive species of Galericini *s.l.*, as well as in Tupaiodontinae. It tends to grow smaller in more advanced representatives and it disappears in all the species of *Deinogalerix* except *D. masinii*. It is parallely lost also in *P. ibericus* as well as in *Apulogalerix pusillus*.

12. *Relative size of p2/p3*. 0: p2 < p3; 1: p2> = p3. This is considered a highly diagnostic character to separate *Galerix* from *Parasorex* and *Schizogalerix* (van den Hoek Ostende, 2001). Nonetheless, it cannot always be verified in the very fragmentary fossil record, as in the case of *Parasorex kostakii* and *Galerix iliensis*. p2 is smaller than p3 in *Schizogalerix* and *Parasorex*, as well as in *Eogalericius*, *Eochenus* and *Zaraalestes*. In contrast, *Galerix* is expected to possess a p2 of equivalent size, or even larger, than p3 (van den Hoek Ostende, 2001).

13. *Number of roots in p2*. 0: two-rooted; 1: fused roots; 2: one-rooted. Galericini *s.l.* generally have a two-rooted p2, which can therefore be interpreted as a plesiomorphic character state. From this it follows that the fusion of the two roots or the loss of one of them are derived conditions, possibly subject to parallel evolution (e.g. the outgroup genus *Zaraalestes* possesses either single- or double-rooted p2s). A two-rooted p2 can still be found in ancient populations of *Parasorex ibericus*, whereas in younger ones the tooth has fused roots, or is single-rooted (Mein and Martín-Suárez, 1993).

14. *Paraconid–protoconid connection on p4*. 0: paraconid not connected with protoconid; 1: paraconid connected with protoconid. This character is considered particularly diagnostic by several authors (Ziegler, 1990; van den Hoek Ostende, 1992, 2001; Doukas and van den Hoek Ostende, 2006; Prieto et al., 2012; Masini and Fanfani, 2013). A crest-like connection between paraconid and protoconid is constantly present in *Parasorex* and *Schizogalerix*. The paraconid itself tends to be crest-shaped in these genera. In the other species studied here the paraconid is of variable size, more tubercular-shaped, and can be either isolated from the protoconid or more weakly connected with it than in *Parasorex* [e.g. *Galerix iliensis* has a very developed and crest-like paraconid (plate 1, fig. 10 in Kordikova, 2000), but the preprotocristid is absent]. In *Deinogalerix*, probably because of the swelling of p4, the two cuspids are linked by a blunt ridge, which has no equivalent in other Galericini (Savorelli et al., 2017). Van den Hoek Ostende (2001) considers this crest homologous to those of *Parasorex* and *Schizogalerix*.

15. *Precingulid on p4*. 0: present; 1: absent. The precingulid is possessed by the most ancient representatives of Erinaceidae (e.g. *Entomolestes grangeri* and *Litolestes ignotus*, Novacek et al., 1985). It occurs also in the Tupaiodontinae *Zaraalestes* and in the oldest Galericini *s.l.*, i.e. *Eogalericius*, *Eochenus* and *Microgalericulus* (Middle Eocene, Lopatin, 2006; not considered in our analysis owing to the very scanty record), whereas it is absent in Galericini *s.s.* The presence of this cingulid thus seems a plesiomorphic trait.

16. *Degree of development of metaconid on p4*. 0: strong and prominent; 1: weak; 2: absent. This character is also highly valuable (e.g., van den Hoek Ostende, 2001; Masini and Fanfani, 2013). Members of Galericini *s.s.* are characterized by

having a generally high and robust metaconid. However, the cuspid is quite variable: in some species (e.g. *Galerix nanus*, *G. aurelianensis* and *Parasorex kostakii*) it is small, or may be totally missing. *Apulogalerix pusillus* is one of the species lacking the metaconid, which was possibly lost secondarily and independently from other taxa (Masini and Fanfani, 2013). In the Galericini *s.l. Eogalericius* and *Eochenus* the metaconid is weak. *Zaraalestes*, on the other hand, possesses a robust metaconid.

17. *Hypoconulid on m3*. 0: present; 1: absent. The hypoconulid is present in primitive genera such as *Eogalericius* and *Zaraalestes*, whereas all Galericini *s.s.* lack it. Hence, the occurrence of the hypoconulid is unquestionably a plesiomorphic feature, because it is possessed by many primitive Eulipotyphla (Lopatin, 2006). In contrast, its absence is apomorphic in the Galericini tribe. This conule is large and isolated in *Zaraalestes*, and on the way to be connected with the entoconid in *Eogalericius* and *Eochenus*. In Galericini *s.s.* the conule disappears, replaced by a mere ridge linking hypoconid to entoconid.

18. *Position of the mental foramen*. The mental foramen may be either single or double. 0: one mental foramen beneath p2; 1: one mental foramen beneath p3; 2: one mental foramen beneath p3/p4, or beneath anterior root of p4; 3: two mental foramina, one beneath p2 and one beneath p3. These characters are seldom used for systematic purposes, although, in spite of their variability, they may be taxonomically significant (Lopatin, 2004, 2006; Savorelli et al., 2017).

19. *Relative size of the m1 trigonid*. 0: non-elongated; 1: elongated. Mainland Galericini possess m1s with trigonid proportionally as long as, or slightly shorter than, the talonid. *Deinogalerix* has very long trigonid relative to the talonid (Butler, 1980; Villier et al., 2013).

20. *Relative size of P3 and P4*. 0: non-enlarged; 1: enlarged. Mainland Galericini have a P4 comparable in size to, and a P3 smaller than, M1. In *Deinogalerix* both premolars, but especially P4, are larger than M1 (Butler, 1980; Villier et al., 2013).

21. *Relative size of p3 and p4*. 0: non-enlarged; 1: enlarged. In mainland Galericini lower premolar rows are shorter than molar rows. In *Deinogalerix* these premolars are much longer, with p4 almost reaching the size of the first lower molar (Butler, 1980; Villier et al., 2013).

22. *Morphology of P3/p3 and P4/p4*. 0: slender and sharp; 1: bulbous. In mainland Galericini posterior premolars are slender and sharp, whereas in *Deinogalerix* these teeth are swollen (Butler, 1980; Villier et al., 2013).

23. *Cuspids of p4*. 0: pointed; 1: blunt. Mainland Galericini generally have fourth premolars with more pointed cuspids, whereas a distinctive feature of *Deinogalerix* is possessing fourth lower premolars with characteristically blunt cuspids (Butler, 1980; Villier et al., 2013).

24. *Morphology of metastylid ("mesostylid" in Masini and Fanfani, 2013; and in Savorelli* et al.*, 2017) in m1*. 0: sharp; 1: bulbous. Mainland Galericini have a sharp crest between the metaconid and entoconid. The same crest is markedly bulbous in *Deinogalerix*.

25. *Preprotocristid in p4*. 0: sharp; 1: blunt. When present, the preprotocristid on p4s of mainland Galericini is sharp. The preprotocristid is constantly present and blunt on the p4s of *Deinogalerix* (Butler, 1980; Villier et al., 2013).

26. *Crown of i1*. 0: non-bilobed; 1: bilobed. In *Deinogalerix* the first lower incisor is distinctly bilobed, and never so in all other Galericini (Butler, 1980; Villier et al., 2013).

27. *Coronoid process*. 0: high and robust; 1: low and slender. Unlike mainland Galericini, the mandibles of *Deinogalerix* are equipped with coronoid process low and slender at the base (Butler, 1980; Villier et al., 2013).

28. *Height of condyle above toothrow*. 0: high; 1: low. The mandibular condyle is placed high above the cheek teeth in mainland Galericini *s.s.* and *Apulogalerix*, and lower in *Deinogalerix* and *Eochenus* (Butler, 1980; Wang and Li, 1990; Villier et al., 2013).

29. *Height of ascending ramus*. 0: high; 1: low. Mainland Galericini have mandibles with higher ascending ramus than *Deinogalerix* (Butler, 1980; Villier et al., 2013).

### *Phylogenentic analysis*

The phylogenetic analysis was performed using TNT 1.5 (Goloboff and Catalano, 2015), based on a character–taxon matrix. The taxa are those included in Table 1. The array of unordered character states consists primarily of the dental morphological characters listed above. The works of Frost et al. (1991), Gould (1995), van den Hoek Ostende (2001) and Ziegler (2005) form the background knowledge to the analysis. These papers provided also the necessary feedback to the discussion of the results of the study.

Because the study aims at establishing the phylogenetic relationships among exclusively extinct representatives of the tribe Galericini, and because morphological characters were the only option for estimating these phylogenies, a traditional, parsimony-based cladistic approach was used, where maximum parsimony is the sole optimality criterion (Wiley et al., 1991; Spencer and Wilberg, 2013). Heuristic searches were performed using 2000 random addition replicates, Tree Bisection Reconnection (TBR) branch-swapping algorithm, and default collapse all zero length branches ("rule 1") options. A restricted consensus tree was calculated using temporary collapse of the branches unsupported by synapomorphies, which results in a less-resolved topology, but also in more reliable nodes. Absolute Bremer supports were calculated using TBR branch swapping, retaining suboptimal trees by 30 steps. The program Mesquite 3.2 (build 801) was used to obtain tree lengths (L), consistency index (Ci) and retention index (Ri).

## Results

### *Topology of the cladogram*

The heuristic cladistic analysis based on the character–taxon matrix of 30 features and 19 extinct taxa produced only nine most parsimonious trees (MPTs)

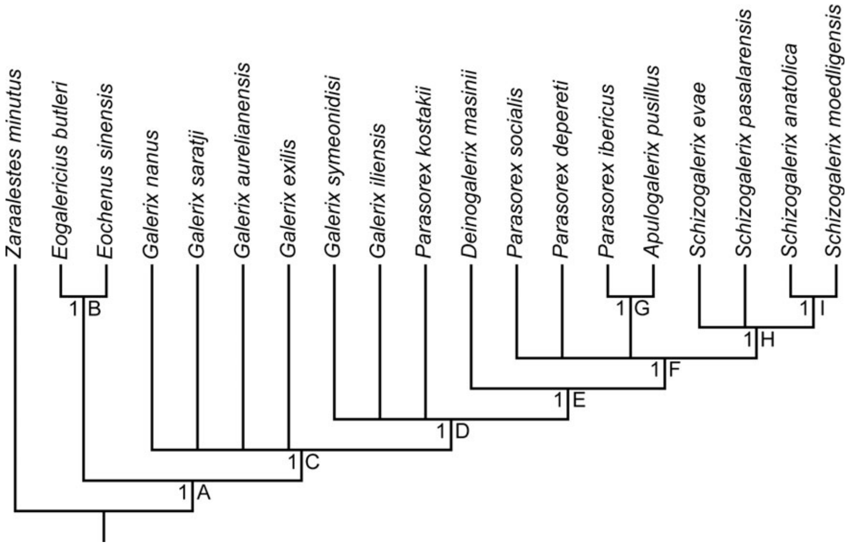

Fig. 3. Strict consensus tree generated from the nine MPTs. Nodes are indicated by capital letters. Labels left of nodes indicate absolute Bremer support.

from which a strict consensus tree (Fig. 3; L = 109, Ci = 0.8624, Ri = 0.7115) was generated. The resulting cladogram shown in Fig. 4 includes nine clades, their respective stems (indicated by numbers) and several polytomies. It also reveals the paraphyletic nature of the genera *Galerix* and *Parasorex*.

The rooted tree includes a hypothetical ancestor with the following traits: non-hypocone-bearing P3; distal arm of the metaconule present and either connected or not with the cingulum on M1–2; mesostyle absent or undivided on M1–2; non-widened M1–2; triple connection protocone–hypocone–metaconule on M1–2; distal arm of the hypocone absent or present and not connected with the distal cingulum on M1–2; M1 not elongated mesiolingually–distolabially; small, triangular M3; i3 present; p2 smaller than p3; single- or two-rooted p2; paraconid not connected with protoconid on p4; precingulid may be present on p4; metaconid present, either robust or weak, on p4; hypoconulid present on m3; one mental foramen beneath p3; non-elongated trigonid on m1; non-enlarged third and fourth upper and lower premolars; slender and sharp P3/p3 and P4/p4; pointed cuspids in p4; sharp metastylid in m1; sharp preprotocristid in p4; non-bilobed crown in i1; high coronoid process; condyle high or low; high ascending ramus.

The choice of *Zaaralestes* as outgroup imposed a small, triangular-shaped M3 to the common ancestor of all the taxa studied here, in place of the large, plesiomorphic M3 that it should be expected to possess (as already explained in *Characters*).

The tree exhibits a set of distinct groups, starting from the basal dichotomy (node A, Fig. 3) between the clade *Eogalericius butleri*–*Eochenus sinensis* (node B, Fig. 3) and Galericini *s.s.* (node C, Fig. 3). The latter contains a polytomy involving the most ancient and primitive *Galerix* and the ancestor of a large clade, which includes the most derived *Galerix*, *Parasorex*, *Schizogalerix* and the insular species (node D, Fig. 3). The large clade, in turn, consists of a polytomy, involving *Galerix symeonidisi*, *Parasorex kostakii* and *G. iliensis*, which is basal to a clade containing the insular taxa, *Parasorex s.s.* and *Schizogalerix*. The last large clade (node F, Fig. 3) is a pentatomy that includes advanced *Parasorex*, as well as *Schizogalerix* and *Apulogalerix pusillus*.

Node A (Fig. 3) has no synapomorphies (Table 3), but rather the following character changes: (1–2) the distal arm of the hypocone on M1–2, which changes from the double condition of being absent, or present and not connected, to being only present and not connected, (3) development of the metaconid on p4, which changes from being either strong or weak, to being only weak, and (4) p2, which changes from being single- or two-rooted, to being only two-rooted.

Node B (Fig. 3) represents the speciation that leads to the separation of *Eogalericius butleri* and *Eochenus sinensis*. It is defined by three character changes, one of which is a synapomorphy. The synapomorphy of possessing a large M3 is deduced by comparison with the outgroup's small, derived M3 (see *Characters*). The other two character changes are: (1) protocone–hypocone–metaconule connection on M1, which changes from being only triple, to the double character state of being either triple, or only consisting of the connection between protocone and metaconule; and (2) the mental foramen, which changes from being

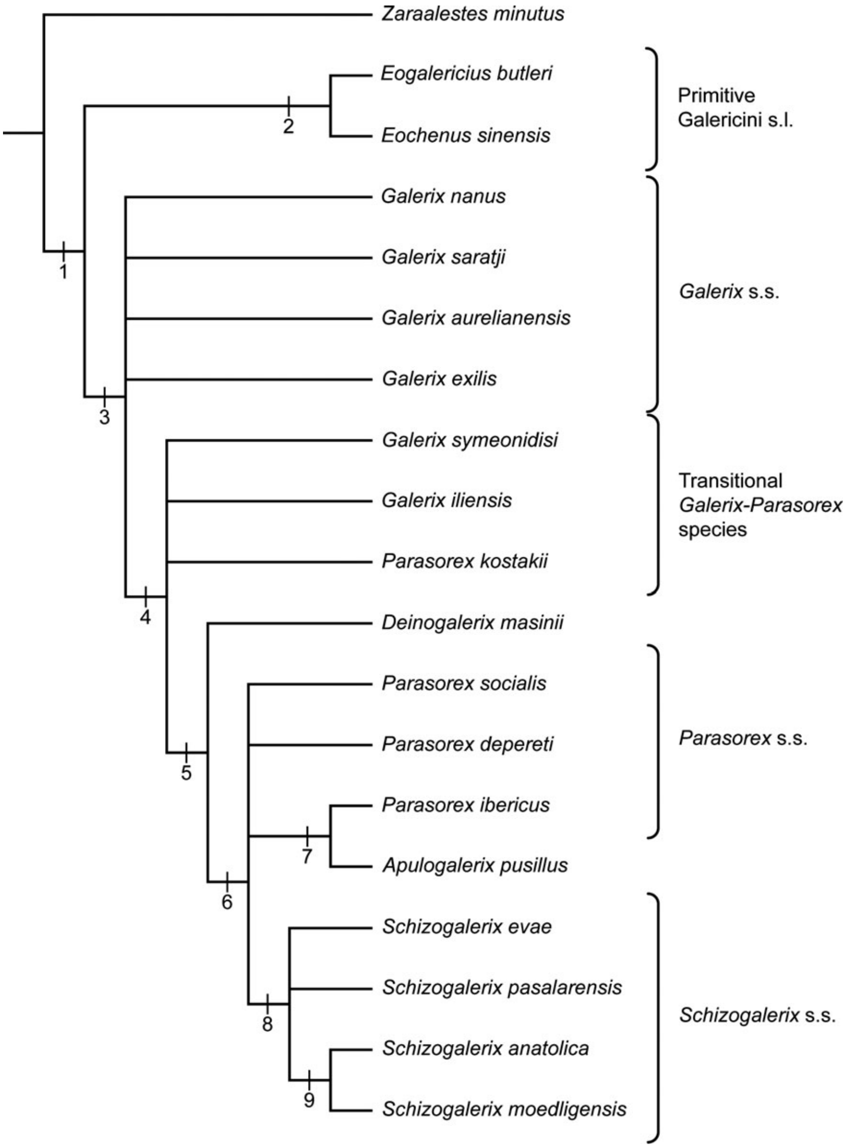

Figure 4. Strict consensus tree; numbers indicate the common ancestor of each clade. 1: ancestor of Galericini *s.l.*; 2: ancestor of primitive Galericini *s.l.*; 3: ancestor of Galericini *s.s.*; 4: ancestor of transitional *Galerix–Parasorex* species, *Deinogalerix*, *Parasorex s.s.*, *Apulogalerix* and *Schizogalerix*; 5: ancestor of *Deinogalerix*, *Parasorex s.s.*, *Apulogalerix* and *Schizogalerix*; 6: ancestor of *Parasorex s.s.*, *Apulogalerix* and *Schizogalerix*; 7: ancestor of *Apulogalerix* and *Parasorex ibericus*; 8: ancestor of *Schizogalerix*; 9: ancestor of advanced *Schizogalerix*.

single beneath p3, to being either single under p3 or double under p2 and p3.

Node C (Fig. 3) is defined by three synapomorphies: (1) p2 as large as, or larger than p3; (2) disappearance of the precingulid on p4; and (3) disappearance of the hypoconulid on m3.

Node D (Fig. 3) is a polytomy involving *G. symeonidisi*, *G. iliensis*, *P. kostakii*, the ancestor of the clade of the insular taxa, all the species of *Parasorex s.s.* and *Schizogalerix*. This node includes five character changes, four of which are synapomorphies. The latter are: (1) appearance of the hypocone on P3; (2) protocone–hypocone–metaconule connection on M1 and (3) M2, which changes from being only triple, to consisting only of the connection between protocone and hypocone; and (4) strong metaconid on p4. The non-synapomorphic character change involves the distal arm of the metaconule in M1–2, which may include the morphotype where the distal arm reaches the postero-labial edge of the tooth.

Node E (Fig. 3) places *Deinogalerix masinii* as the sister taxon of the *Parasorex–Schizogalerix* clade. It includes four character changes, two of which are synapomorphies. The two synapomorphic character changes are: (1) the connection between paraconid and protoconid on p4; and (2) relative size of p2, which

Table 3
Synapomorphies at each node in cladogram of Fig. 3

| Node | Synapomorphy |
|---|---|
| A | – |
| B | Character 10: 1 → 0 |
| C | Character 12: 0 → 1 |
|  | Character 15: 0 → 1 |
|  | Character 17: 0 → 1 |
| D | Character 0: 0 → 1 |
|  | Character 4: 2 → 1 |
|  | Character 7: 2 → 1 |
|  | Character 16: 1 → 0 |
| E | Character 12: 1 → 0 |
|  | Character 14: 0 → 1 |
| F | Character 18: 1 → 2 |
| G | Character 11: 0 → 1 |
| H | Character 3: 0 → 1 |
|  | Character 6: 0 → 1 |
| I | Character 2: 0 → 1 |

changes from being either as large as, or larger than p3, to the condition where it is smaller than p3. The two non-synapomorphic character changes are: (1) distal arm of the hypocone on M1 and (2) M2, which changes from being only not connected with the distal cingulum, to the double character state of being connected, or not. Of note are the many apomorphies of *Deinogalerix masinii*, among which is the well-developed metastylar crest on M3, which gives this tooth its peculiar shape.

Node F (Fig. 3) is a further polytomy, comprising the taxa *P. socialis* and *P. depereti*, and of the ancestors of the two clades *Schizogalerix* and *Apulogalerix pusillus* + *Parasorex ibericus*. This node is defined by four character changes, one of which is a synapomorphy. The synapomorphy consists of the rear positioning of the mental foramen, from beneath p3 to beneath p3/p4, or p4. The three non-synapomorphic character changes are: (1) the distal arm of the metaconule on M1–2 constantly extended to the postero-labial corner of the tooth; (2) distal arm of the hypocone on M1 constantly connected to the distal cingulum; and (3) condyle which changes from being variably elevated above the toothrow to being constantly high above the toothrow.

The *Apulogalerix* + *Parasorex ibericus* clade (node G, Fig. 3) is defined by the synapomorphic disappearance of i3. *Apulogalerix pusillus* shows two autapomorphies on p4: (1) the lack of connection between paraconid and protoconid; and (2) the lack of metaconid.

Node H (Fig. 3) is a polytomy that includes *Schizogalerix pasalarensis*, *S. evae* and the clade *S. moedligensis–S. anatolica*. This node is defined by three character changes, two of which synapomorphies. The latter are: (1) relative widening of M1–2; and (2) oblique elongation of M1. The character change consists of the distal arm of the hypocone on M2, which changes from being connected or not, to being always connected with the distal cingulum.

Node I (Fig. 3), the clade *S. moedligensis–S. anatolica* is characterized by the constantly divided mesostyle on M1–2.

## Discussion

### *Systematic implications*

This is the first cladistic analysis, performed on a wide and comprehensive character–taxon matrix, to focus on the insular genus *Deinogalerix*, as well as on extinct members of the tribe Galericini *s.l.* In line with Gould's (2001) predictions, the cladistic analysis of solely dental material, and in addition being incomplete (being fossil), presents difficulties. Despite these limitations, "a poor estimate of phylogenetic relationships may be preferable to no estimate of relationships at all" (Gould, 2001, p. 21).

The careful selection of dental features that are widely used in the systematics of Galericini gave quite convincing results. Although some unresolved polytomies do remain, the tree shown in Fig. 3 presents an interesting branching pattern, in which lies the strength of the analysis. Of note are the many apomorphies of *Deinogalerix masinii*, the affinities between *Deinogalerix* and early–middle Miocene taxa from Anatolia and eastern Europe, as well as the close phylogenetic relationships of this giant moonrat with *Parasorex*-like species. These results confirm the close and long-lasting palaeogeographical ties between the Apulia Platform and eastern domains already supposed by several scholars (De Giuli et al., 1986, 1987b; Mazza et al., 1995, 2015; Mazza and Rustioni, 2008; Patacca et al., 2008b, 2013; Masini et al., 2010; Masini and Fanfani, 2013; Mazza, 2013a,b; Savorelli and Masini, 2016), as well as the phylogenetic hypotheses formulated by Ziegler (2005) and Villier et al. (2013).

Moving on to a more detailed examination of the tree, and progressing up from its root (Fig. 3), the most primitive Galericini *s.l.* (*Eogalericius* and *Eochenus*) are included in a sister clade of Galericini *s.s.*, in agreement with Lopatin's (2004, 2006) phylogenetic interpretation, and *Galerix s.s.* appears basal to all the other Galericini. However, the analysis was not able to resolve the phylogenetic relationships among the different species of the genus *Galerix*. The latter form a polytomy, inclusive of the most ancient known species of the genus, *Galerix nanus*, but also of *G. saratji*, *G. aurelianensis* and *G. exilis*. *Galerix symeonidisi*, which was supposed to be the ancestor of *G. exilis* (Ziegler, 2000), is included by contrast in the following clade. This agrees with van den Hoek Ostende and

Doukas (2003) who excluded *G. symeonidisi* from the ancestry of *G. exilis*. *Galerix symeonidisi*, *G. iliensis* and *Parasorex kostakii* present a mosaic of features shared with both *Galerix s.s.* and *Parasorex s.s.* They are therefore placed in an intermediate position between the latter two genera.

The cladogram indicates that *Deinogalerix* possibly derived from a *Galerix–Parasorex* transitional species. Moreover, *Deinogalerix* is sister to a clade containing *Parasorex s.s.* and *Schizogalerix*. Node E, from which *Deinogalerix* and the ancestor of the clade *Parasorex s.s.* + *Schizogalerix* emerge, is characterized by two synapomorphies typical of *Parasorex s.s.* (paraconid connected with protoconid on p4 and p2 smaller than p3). Nonetheless, *Deinogalerix* is more primitive than *Parasorex s.s.* and *Schizogalerix* in the anterior location of the mental foramen (a feature discussed at length by Savorelli et al., 2017) as well as in the variable patterns of the posterior arm of the metaconule on M1–2 and of the hypocone on M1. Conversely, in *Parasorex s.s.* and *Schizogalerix*, the mental foramen tends to be located in a more rearward position than in *Deinogalerix* and the pattern of the aforementioned arms (distal arm of hypocone on M1 connected with the distal cingulum; distal arm of the metaconule in M1–2 extended to the posterolabial corner of the tooth) are stabilized by now.

Alongside other peculiar dental features, *Deinogalerix* possesses a subtriangular M3 with well-developed metastylar crest, quite similar to that of *Lantanotherium*, which is yet another extinct erinaceid genus, but not belonging to the tribe Galericini. *Deinogalerix* is believed to have evolved this morphology independently while in isolation on the Apulia Platform. Hence, it is here interpreted, in line with van den Hoek Ostende's (2001) opinion, as a convergence with *Lantanotherium*. Van den Hoek Ostende (2001) considers the strong metastylar crest on M3 a plesiomorphic trait also given its widespread presence in many modern Galericinae. Nonetheless, the sister group of Galericinae, i.e. Tupaiodontinae, includes species (one of them is the outgroup of the present analysis, *Zaraalestes minutus*) with triangular M3. Also, the M3s in the primitive Galericini *Eochenus* and *Eogalericius* are triangular, besides being large relative to M2s (Lopatin, 2006). These lines of evidence contrast with the assumption that M3 with a well-developed metastylar crest is plesiomorphic for Galericinae.

Also the clade including *Parasorex* and *Schizogalerix* forms an unresolved polytomy. Of note is the close phylogenetic relationship between *Apulogalerix pusillus* and *Parasorex ibericus*, already supposed by Masini and Fanfani (2013), based on the loss of i3. Masini and Fanfani's (2013) opinion was grounded on the assumption that the loss of this incisor should not be construed as a parallelism due to evolution on an island. Rather, it should be interpreted as a synapomorphy with *P. ibericus*.

The lack of i3 in *Deinogalerix* had been considered indicative of a close relationship to *Apulogalerix pusillus* (van den Hoek Ostende, 2001). The discovery of *Deinogalerix masinii*, which bears a small i3, suggests that the two genera originated from distinct ancestors, in agreement with the present phylogenetic hypothesis, and that the loss of i3 is an instance of parallel evolution. This feature adds to the other lines of evidence indicating a different origin of the two insular taxa from Gargano.

The clade of the members of the genus *Schizogalerix* forms yet another unresolved tritomy. Two Anatolian species occur at its base, *Schizogalerix pasalarensis* and *S. evae*, accompanied by the common ancestor of *S. moedligensis* and *S. anatolica*. *Schizogalerix pasalarensis* and *S. evae* differ from *S. moedligensis* and *S. anatolica* by possessing a primitive trait, i.e. a not always divided mesostyle in M1–2. The position of *Schizogalerix* in a polytomy with *Parasorex s.s.* is one of the most problematic issues of this cladogram. It will be addressed in the following section.

### *Palaeogeographical and stratigraphic implications*

Focusing on the insular taxa analysed in this study, the line leading to *Deinogalerix* emerged prior to the divergence of *Schizogalerix* from *Parasorex s.s.* To avoid unreasonably long ghost lineages, the first occurrences of these taxa are constrained within the early Miocene (MN 2). Based on the results of our analysis, the two insular genera *Deinogalerix* and *Apulogalerix* would arise from different ancestors and in different time periods, thus supporting an asynchronous mode of colonization (polyphasic model: Masini et al., 2002, 2008) of the Apulia Platform. *Deinogalerix* is in fact closer to the transitional *Galerix–Parasorex* species, which are dated stratigraphically to MN 4–5, whereas *Apulogalerix* is closer to more advanced Galericini, i.e. *Parasorex s.s.* (Fig. 4).

The issues connected with the close phylogenetic relationship between *Apulogalerix pusillus* and *Parasorex ibericus* have also been addressed by Masini and Fanfani (2013) from palaeogeographical and palaeontological standpoints. Our analysis indicates that the *Apulogalerix pusillus* and *Parasorex ibericus* speciations occurred prior to MN 10, in line with Masini and Fanfani's (2013) opinion. Based on palaeogeographical data (Patacca et al., 2008a,b, 2013) the Apulia Platform and the Balkans were isolated from one another, or intermittently connected during the period spanning the MN 7 and MN 11 zones. A rich literature exists (De Giuli et al., 1986, 1987b; Mazza et al., 1995, 2015; Mazza and Rustioni, 2008; Patacca et al., 2008b, 2013; Masini et al., 2010; Masini and Fanfani, 2013; Mazza, 2013a,b; Savorelli and Masini, 2016) to support the hypothesis that the Balkans are the most likely source area for the Apulia Platform fauna. Palaeogeographical reconstructions (Popov et al., 2004; Patacca et al., 2008b, 2013) show that during the Miocene a set of oceanic basins at the front of the eastward-moving Apennine chain formed a strong barrier for any potential western Mediterranean ancestor of the two species. Based on the absence or irregularity of connections with the Balkans (Patacca et al., 2008b, 2013), it seems unlikely that the ancestor of *Apulogalerix pusillus* reached the Apulia Platform during the middle to early late Miocene. Indeed, *Parasorex ibericus* is reported only from the Iberian peninsula. However, as suggested by Masini and Fanfani (2013), imperfect knowledge of the Balkan Miocene faunas prevents conclusive inferences regarding the origin of this small insular moonrat. Nonetheless, Marković and Milivojević (2010) reported the presence of Galericini (i.e. *Parasorex socialis*, *Galerix symeonidisi* and *G. exilis*) of central European affinity in the early and middle Miocene of Serbia. Hence, the European morphological links of *Apulogalerix pusillus* may suggest that although the ancestors of the Apulia Platform taxa probably arrived from the Balkans, they did not necessarily have Asian phylogenetic connections. Notable is the ‘reapperance’ of *Galerix exilis* recently reported by Prieto et al. (2011) from the middle/late Miocene transition in southern Germany. This shows how imperfect is our knowledge even of the central European Miocene faunas. Recent palaeontological findings from Moncucco, Piedmont (Colombero et al., 2017), reportedly from MN 13 layers bearing remains of *Parasorex* aff. *ibericus*, seem to attest to the occurrence of a European stock of *Parasorex* with *P. ibericus*-like traits, compatible with those of a potential ancestor of *A. pusillus*.

Zooming out to a broader palaeogeographical and stratigraphic perspective, the most ancient known species of *Galerix* is *G. nanus* from MP 21–26 zones of France. In the present analysis *Galerix nanus* is in polytomy with much younger representatives of the genus *Galerix*, which causes an extension of the ghost lineages of the other *Galerix s.s.* members, in particular that of *G. exilis*. Van den Hoek Ostende (2001) called attention to the absence, in Europe, of any fossil record of Galericini during the time straddling the Oligocene/Miocene boundary, prior to the first occurrence of *G. aurelianensis* (MN 3). The genus *Galerix* is actually represented only by *G. saratji* from MN 1–2 zones of Anatolia. The absence of this genus from Europe during this period suggests that *Galerix aurelianensis* and *G. exilis* may not have stemmed directly from *G. nanus*, in spite of their dental similarities. Van den Hoek Ostende (1992) claims that *Galerix aurelianensis* might have dispersed into Europe from East (Anatolia), which is in accordance with our results. An Anatolian origin has also been suggested for the only *Galerix* known from Africa, *G. africanus* (Ziegler, 2006). *Galerix symeonidisi*, *G. iliensis* and *Parasorex kostakii* are reported from a time span included between MN 4 and MN 5. *Galerix iliensis* comes from Kazakhstan (Kordikova, 2000) and *Parasorex kostakii* from Greece (Doukas and van den Hoek Ostende, 2006), whereas *G. symeonidisi* is widespread throughout Europe and is reported also from Anatolia (van den Hoek Ostende and Doukas, 2003). In the foregoing section (*Topology of the cladogram*), the three species were observed to show a mosaic of characters, which places them in an intermediate position between *Parasorex s.s.* and *Galerix s.s.* Hence, *Galerix iliensis* may be as close to *Parasorex* as *P. kostakii*, as already mentioned previously. In contrast, based on the relative proportions of p2 and p3, *Galerix symeonidisi* is closer to *Galerix*, but shares with *Parasorex s.s.* the constant occurrence of the hypocone on P3. *Galerix symeonidisi*, *G. iliensis* and *Parasorex kostakii* suggest that the members of the genus *Parasorex* may have derived from central Asian *Galerix*-like species, which had already manifested *Parasorex* evolutionary trends. Recent literature reports the existence of even more ancient central Asian species with transitional *Galerix*–*Parasorex* traits, such as *G. wesselsae* (MN 3–6) and *G. rutlandae* (MN 6–8), from the Potwar Plateau, Pakistan (Zijlstra and Flynn, 2015).

Typical *Parasorex* morphologies became stable in Europe after the MN 5/6 transition, when *P. socialis* appeared and dispersed throughout continental Europe. *Parasorex socialis* persisted at least till the MN 8–9 transition. Based on Furió (2007) the species seems to have disappeared elsewhere from its original areas of distribution, surviving only in Spain until MN 10. The fossil record of *Parasorex s.s.*, since MN 9, is confined to western Europe, represented by *P. ibericus* and *P. depereti*. The former is reported only from the Iberian Peninsula, and the latter from Italy, France and Spain. In Fig. 5 *Parasorex s.s.* exhibits long ghost lineages (that of *P. socialis*, for instance, lasts some 5 Myr), due to its coexistence, in polytomy, with the ancestor of the clade *Schizogalerix*, whose earliest member is *Schizogalerix evae* from the MN 3 zone of Anatolia. The topology of the cladogram implies that the succession of clades including the transitional genera, *Deinogalerix*, *Parasorex s.s.* and *Schizogalerix*, all originated from a pre-MN 3 radiation, which can parsimoniously be dated to MN 2 (Fig. 5).

Figure 5 shows that the earliest members of *Schizogalerix*, a genus which includes the most highly diversified and widely distributed members of Galericini, are known from Anatolia. Several more advanced species subsequently radiated from them (Furió et al., 2014), but only a few species of this genus, those of particular

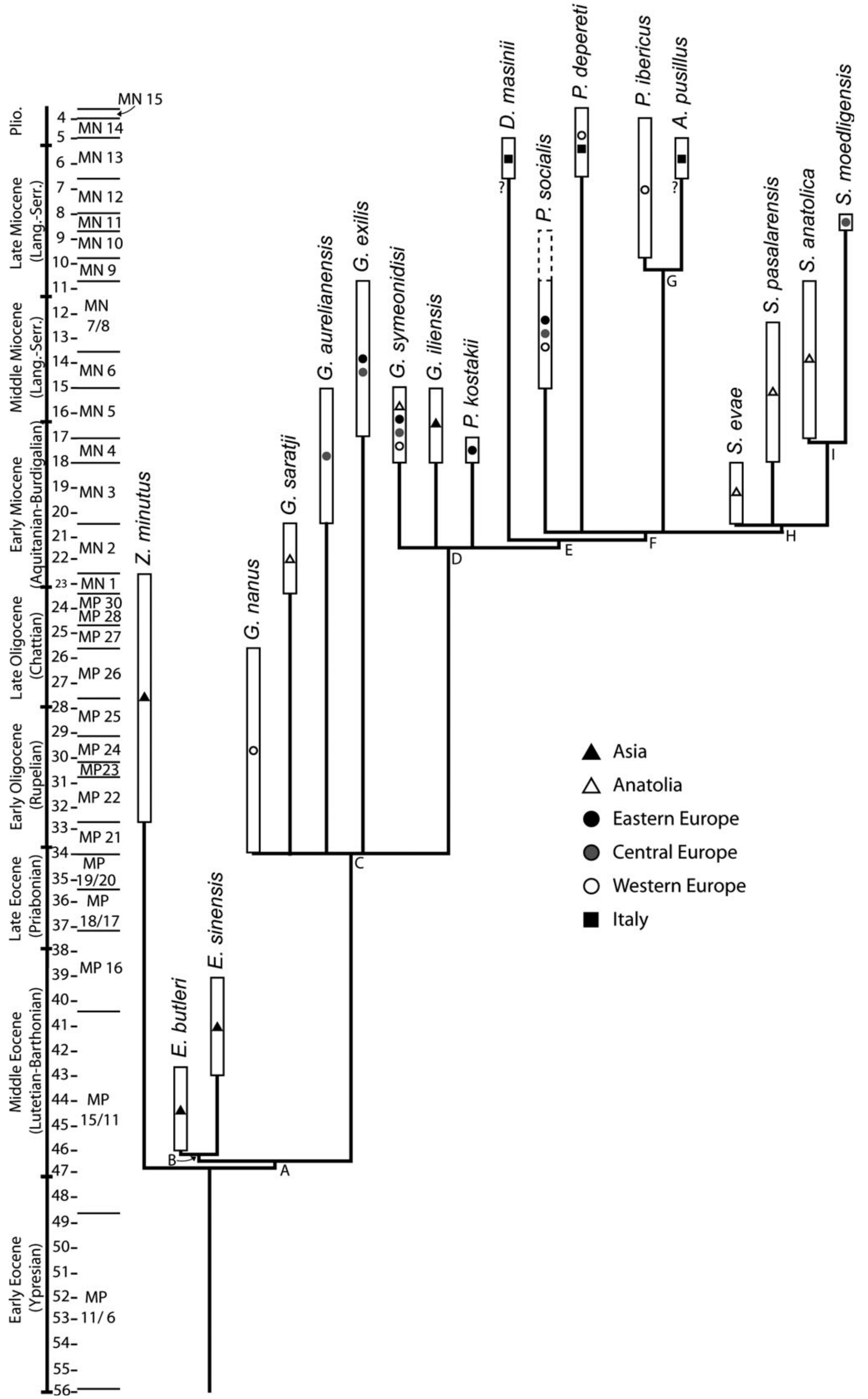

Figure 5. Consensus of MPTs in an integrated chronostratigraphic–biochronological framework. Symbols indicate the different geographical ranges of fossiliferous sites that yielded Galericini taxa. Question marks indicate the tentative chronological attribution of the Gargano taxa. Dashed line reports the possible occurrence of *Parasorex socialis* in zones MN 9 and 10 (Furió, 2007).

interest, were selected for this study. For this reason, *Schizogalerix* is not represented here in its entirety. The oldest *Schizogalerix* is *S. evae*, from MN 3 faunal contexts; it is followed through time by the MN 4–7 *S. pasalarensis* and then by the more advanced MN 5–8 *S. anatolica*. The Turkish clade finally became extinct in MN 13 (Engesser, 1980). From its birthplace in Anatolia, the genus dispersed to Asia (MN 6/7 Halamagai, China: *Schizogalerix duolebulejinensis*, Bi et al., 1999; Deng, 2006; MN 8/9 Siwalik, Pakistan: *Schizogalerix* sp. A, Zijlstra and Flynn, 2015), Africa (MN 7/8 Pataniak 6: *Schizogalerix* cf. *S. anatolica*, Engesser, 1980; MN 12 Amama II: *Schizogalerix* sp., Engesser, 1980), and eastern (e.g. MN 12 Pikermi, Greece: *S. zapfei*, Rümke, 1976; MN 13 Maramena, Greece: *S. macedonica*, Doukas et al., 1995) and central Europe (MN 10: Vösendorf, Austria: *S. voesendorfensis*, Engesser, 1980; MN 11: Eichkogel, Austria: *S. moedligensis*, Engesser, 1980; MN 11 Kohfidisch, Austria: *S. zapfei*, Bachmayer and Wilson, 1970). Although older stratigraphically, *Schizogalerix evae* is already morphologically more advanced than the members of *Parasorex s.s.* We can suppose that the ancestor of the genus *Schizogalerix* is an MN 2 taxon from areas east of Anatolia (Popov et al., 2004). The hypothetical ancestor would thus be a transitional *Galerix–Parasorex* species with advanced features also shared by *Schizogalerix*.

Two alternative options can be proposed regarding the origin of *Parasorex s.s.* One is that exhibited by our cladogram, where the taxon shares with *Schizogalerix* an MN 2 ancestor from eastern areas with transitional *Galerix–Parasorex* traits.

Although represented by very scanty remains, the recently recovered *Galerix wesselsae* accounts for the existence of Asian taxa with at least one *Parasorex* trait (typically a hypocone-bearing P3) already in MN 3 times. Transitional *Galerix–Parasorex* species probably already occurred in the east in earlier times (MN 2), but the assumption cannot be verified in the still imperfectly known Asian fossil record.

The second possibility regarding the appearance of *Parasorex s.s.* is that it derived from a species more recent than MN 2 and close to the transitional ones reported in the literature (e.g. *P. kostakii* or *G. iliensis*). In the latter case, *Parasorex s.s.* and *Schizogalerix* would have emerged independently from one another.

The appearance, in early Miocene times, of the Anatolian *Schizogalerix evae* accords positive weight to van den Hoek Ostende's (2001) opinion that the evolution of *Schizogalerix* in Anatolia precedes that of *Parasorex* in Europe. Both taxa share a set of basic traits, but nonetheless some derived features, such as the reduction of the set of teeth in front of the molars, and the constant fusion of the rear arm of the hypocone with the posterior cingulum on M1–2s, appear much later in *Parasorex* (e.g., late Miocene *P. ibericus*). The distinct evolutionary rate of the two genera generates the marked discrepancy between the phylogenetic pattern depicted in the cladogram and the stratigraphic distribution of the taxa delineated above. A parallel can be found in the evolution of the Cricetodontinae (e.g., *Deperetomys*) wherein advanced features (e.g., continuous ectolophs in the upper molars) appeared much earlier in Anatolia (MN 1) than in Europe (MN 7, De Bruijn et al., 1993). Members of *Schizogalerix* that reached eastern Europe during the late Miocene were even more evolved. If the common traits shared by *Parasorex* and *Schizogalerix* did not evolve in parallel starting first in Anatolia and later in Europe, *Parasorex* is not an indigenous European genus, but rather immigrated from other geographical areas. At the moment the most likely source area seems to be the latitudinal belt between central Asia (north of the Himalayan range) and eastern Europe. The so-called "transitional" species that evolved in this vast territory probably originated *Parasorex* more recently than the time imposed by the common ancestor indicated in our cladogram.

## Conclusions

This study is aimed at investigating the relationship of *Deinogalerix* within the tribe Galericini. Insular faunas are known to be exposed to strong endemic changes, which make it difficult to determine the phylogenetic links with their mainland counterparts on morphological grounds alone. The phylogenetic relationships of *Deinogalerix* have been the subject of many different contributions (Butler, 1980; van den Hoek Ostende, 2001; Ziegler, 2005; Villier et al., 2013; Savorelli et al., 2017), but none of these studies attempted a comprehensive cladistic analysis inclusive of the most representative Galericini members.

Our investigation on the Apulia Platform endemics provided significant new insights into the status and reciprocal phylogenetic relationships of numerous outstanding members of the tribe Galericini. It led to the identification of a total of nine clades of different size (Figs 3–5) with four polytomies, and showed the paraphyletic nature of the two genera *Galerix* and *Parasorex*. Besides a clade including the most ancient Galericini *s.l.*, *Eogalericius* and *Eochenus*, the analysis recognized a set of smaller clades, nested within three major clades. Of the latter, one is represented by a polytomy comprising five *Galerix s.s.* species. A second includes a polytomy of what we call here "transitional" *Galerix–Parasorex* species, namely species subjected to taxonomic instability in the recent literature, characterized by a mosaic of characters typical of *Galerix* and *Parasorex*. The third is the largest clade:

it includes the most advanced taxa, i.e. *Schizogalerix*, *Parasorex s.s.* and the insular Gargano representatives. *Schizogalerix* is monophyletic, and represents the only case here where the results of the cladistic analysis agree with those of more "traditional" taxonomic approaches. The two endemic species *Deinogalerix masinii* and *Apulogalerix pusillus* do not share common ancestry, thereby supporting the hypothesis of a diachronous dispersal of mainland taxa in the Apulia Platform.

The projection of our cladogram onto the geochronological and European Land Mammal Age time scales (Fig. 5) shows that the *Deinogalerix* line should have started around MN 2. On the other hand, *Apulogalerix* should have appeared during a wide time span, from MN 9 to MN 13, although its primitive, double-rooted p2 suggests that its ancestor should have stemmed from a species related to *Parasorex ibericus* (Masini and Fanfani, 2013). *Deinogalerix* shares common derived traits with *Parasorex s.s.* and *Schizogalerix*, and yet it also exhibits primitive features, suggesting an origin from species transitional between *Galerix* and *Parasorex* (Savorelli et al., 2017). Based on our results, *Deinogalerix* should have a putative eastern ancestor. In contrast, the analysis indicates that *Apulogalerix* is a species very close to *Parasorex ibericus*, as already proposed by Masini and Fanfani (2013).

Figure 5 indicates an imposing evolutionary radiation at the onset of the Miocene (MN 2?) whereby typical *Parasorex* and *Schizogalerix* traits appeared and spread. Our results exclude the possibility that *Schizogalerix* derived from some *Parasorex s.s.* species. The two genera may share a common ancestor of pre-MN 3 age, with transitional *Galerix–Parasorex* features and of eastern origin. Alternatively, *Parasorex* may have emerged successively deriving from a transitional and stratigraphically more recent species.

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