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INDAGINE DELLE RELAZIONI FILOGENETICHE INTERNE AI GALERICINAE (EULIPOTYPHLA: ERINACEOMORPHA: ERINACEIDAE), IN PARTICOLARE RIGUARDO AI GENERI ENDEMICI INSULARI ITALIANI *DEINOGALERIX* E *APULOGALERIX* RISPETTO AGLI ALTRI GALERICINAE CONTINENTALI.

PHYLOGENETIC RELATIONSHIPS OF GALERICINAE (EULIPOTYPHLA: ERINACEOMORPHA: ERINACEIDAE), WITH SPECIAL REGARD TO THOSE BETWEEN THE ITALIAN ENDEMIC INSULAR GENERA *DEINOGALERIX* AND *APULOGALERIX* AND MAINLAND GALERICINAE.

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A mia moglie, Silvia,

e a tutti coloro che hanno creduto in me in questi lunghi anni

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INTRODUCTION

Erinaceidae (Mammalia: Erinaceomorpha) are one of the most ancient groups of present-day mammals. The first members of the group known since the Middle Paleogene (*Cedrocherus* and *Litocherus* from the middle Tiffanian of North America; Gingerich, 1983). It belongs to Eulipotyphla *sensu* Waddell et al., 1999, a group of basal Laurasiatheria previously considered to include also golden moles and tenrecs (Afrosoricida; Stanhope, 1998), alongside solenodonts, moles and shrews.

Eulipotyphla is one of the best studied groups of small mammals over the last few years. It has repeatedly attracted the attention of scholars for its phylogenetic position, basal to the Laurasiatheria group tree (*inter alios* Asher et al. 2009; dos Reis et al., 2012; Foley et al., 2016; Nishihara et al., 2009; Springer et al., 2018; Upham et al., 2019) and for its high variability. Interest was revived by recent discoveries and new assessments (e.g., the removal of Chrysocloroidea and Tenrecoidea from Eulipotyphla; Waddell et al. 1999).

Erinaceids are probably related to the family Sespedectidae in the suborder Erinaceomropha (Gunnell et al., 2007). According to Lopatin (2006), Erinaceidae includes five subfamilies: Changlelestinae Tong and Wang, 1997, Tupaiodontinae Butler, 1988, Galericinae Pomel, 1848, Brachyericinae Butler, 1948 and Erinaceinae Fischer von Waldheim, 1817. Only two, Galericinae (with the moonrats and gymnures of the South-East Asia) and Erinaceinae (the “true hedgehogs), are still living today, with a total of 24 species (He et al., 2012; Ai et al., 2018). However, the relationships of these various subfamilies, in particular the extinct ones, are still not fully understood (Gould, 1995, 2001).

Van den Hoek Ostende (2001d) proposed the tribe Galericini for some Oligocene-Pliocene Galericinae (*Galerix*, *Parasorex*, *Schizogalerix* and *Deinogalerix*), based on dental features (e.g., M1-2 clearly wider than longer). *Apulogalerix* was added to this tribe by Masini and Fanfani (2013).

In Italy, three taxa of fossil Neogene Galericini have been described, *Apulogalerix*, *Parasorex depereti* and *Deinogalerix* (see Appendix I). The latter is one of the most impressive erinaceids never discovered: they were giant, Late Miocene insular erinaceids whose remains were originally retrieved from the "Terre Rosse" karstic infillings of the Gargano Promontory; members of this genus had peculiar adaptations and could reach the size of a medium-sized dog (Butler, 1980). The "Terre Rosse" fauna included a much smaller species of Galericinae, *Apulogalerix pusillus*. Nonetheless, the systematics of Galericinae, especially the extinct genera, has been subject of only a limited investigation (Gould, 1995; van den Hoek Ostende 2001d; Ziegler, 2005; Borrani et al., 2018).

The present work aims at exploring the taxonomic status and phylogenetic relationships, as well as the paleobiogegrophy of Galericini performing a heuristic phylogenetic analysis under maximum parsimony criteria. The study was carried out on a large dataset (41 taxon, 128 character dataset). In addition, the work particularly focuses on the phylogenetic relationships proper to *Apulogalerix* and *Deinogalerix*, which still needed to be clarified.

2 – Material and methods

MATERIAL

The present study is based on both direct observation and literature data. Literature references are listed in Table 1 (together with the species directly employed in the phylogenetic analysis). Other taxa used for comparisons and to define character polarities are reported in Appendix II. The material directly examined includes specimens of *Apulogalerix pusillus, Deinogalerix minor, D.* freudenthali, *D. intermedius*, *Galerix stehlini, Erinaceus europaeus* and *Parasorex socialis* stored at the Department of Earth Science of the University of Florence, specimens of *Parasorex depereti* kept at the Museo Civico di Scienze Naturali Malmerendi of Faenza, remains of *Deinogalerix masinii* and *D. minor* from the Department of Earth Sciences of the University of Turin, casts of the specimens of *D. brevirostris, D. freudenthali, D. intermedius, D. koenigswaldi* and *D. minor* of the National Museum of Natural History (Naturalis) of Leiden (Netherlands) and of *D. samniticus* from the Centro di Documentazione Paleontologica "*Hoplitomeryx*" of Scontrone. An uncatalogued skull of *Hemechinus auritus*, privately owned by the author, was also used.

Taxon	Age	Distribution	References
Eogalericius butleri	Middle Eocene (Irdinmhanan)	Khaychin-Ula 2 (Mongolia)	Lopatin (2004, 2006)
Microgalericulus esuriens	Middle Eocene (Irdinmhanan)	Khaychin-Ula 3 (Mongolia)	Lopatin (2006)
Zaraalestes minutus	Early Oligocene (MP 21) - Early Miocene (MN 2)	Various localities of Hsanda Gol and Loh Formations (Mongolia)	Lopatin (2003a, in Lopatin, 2006); Sulimski (1970, as *Ictopidium tatalgolensis*; see Lopatin, 2006); Ziegler et al. (2007)

Apulogalerix pusillus	Late Miocene/earliest Pliocene (MN 13)	Various phase 1-4 "Terre Rosse fauna" fissure infillings (Gargano, Apulia, Italy)	Masini and Fanfani (2013)
Deinogalerix brevirostris	Late Miocene/earliest Pliocene (MN 13)	Phase 3 (San Giovannino) "Terre Rosse fauna" fissure infilling (Gargano, Apulia (Italy)	Butler (1980); Savorelli et al. (2019)
Deinogalerix freudenthali	Late Miocene/earliest Pliocene (MN 13)	Phase 0?-1b (?M013, Rinascita 1, Biancone 1, F15) "Terre Rosse fauna" fissure infillings (Gargano, Apulia, Italy)	Butler (1980); Savorelli et al. (2019)
Deinogalerix intermedius	Late Miocene/earliest Pliocene (MN 13)	Various phase 2-3 "Terre Rosse fauna" fissure infillings (Gargano, Apulia, Italy)	Butler (1980); Savorelli et al. (2019)
Deinogalerix koenigswaldi	Late Miocene/earliest Pliocene (MN 13)	Phase 3 (San Giovannino) "Terre Rosse fauna" fissure infilling (Gargano, Apulia, Italy)	Butler (1980); Savorelli et al. (2019)
Deinogalerix masinii	Late Miocene/earliest Pliocene (MN 13)	Phase 0 (M013) "Terre Rosse fauna" fissure infilling (Gargano, Apulia, Italy)	Savorelli et al. (2019); Villier et al. (2010, 2013)
Deinogalerix minor	Late Miocene/earliest Pliocene (MN 13)	Various phase 2-3 "Terre Rosse fauna" fissure infillings (Gargano, Apulia, Italy)	Savorelli et al. (2019); Villier (2010); Villier and Carnevale (2013, as *Deinogalerix koenigswaldi*; see Savorelli et al., 2017)
Deinogalerix samniticus	Late Miocene (Tortonian)	Scontrone (Abruzzo, Italy)	Savorelli et al. (2017, 2019)
Galerix africanus	Early Miocene (MN 3)	Various localities (Koru Formation, Legetet Formation, Karurtay Agglomerates, Songhor, Hiwegi Formation) (Kenya); Napak (Uganda)	Butler (1956b, 1969 as *Lantanotherium* sp., 1984)
Galerix aurelianensis	Early Miocene (MN 3) - Middle Miocene (MN 5)	Erkertshofen 1+2; Petersbuch 2; 28; Stubersheim 3; Wintershof-West ; Obersdorf 3 and 4 (Germany)	Klietmann (2013); van den Hoek Ostende and Fejfar (2006); Ziegler (1990, 1994, 1998)
Galerix exilis	Middle Miocene (MN 5-6)	Sansan and Contres (France); Steinberg and Goldberg (Germany)	Engesser (2009); Gagnaison et al. (2006); Ziegler (1983)
Galerix iliensis	Early (MN 4) - Middle Miocene (MN 5)	Middle member of the Chul'adyr Formation (Kazakhstan)	Kordikova (2000)

Galerix remmerti	Early Miocene (MN 3)	Estrepouy (Gers, France); various Spanish localities	Hugueney and Bulot (2011); van den Hoek Ostende (2003a); van den Hoek Ostende et al. (2020)
Galerix rutlandae	Middle Miocene (MN 6-7/8)	Mae Moh Basin (Thailand); many Chinji Formation, Potwar Plateau and Sehwan localities (Pakistan)	Cailleux et al. (2020); Munthe and West (1980); Zijlstra and Flynn (2015)
Galerix saratji	Latest Oligocene - Early Miocene (MP 30 - MN 2)	Kargi, Kilcak and Harami (Turkey)	Corbet (1988, as *Hemiechinus daauricus*); Frost et al. (1991)
Galerix stehlini	Middle Miocene (MN 7-8)	La-Grive-Saint-Alban (France)	Butler (1948, 1980); Engesser (1980, as *Galerix exilis*); Gaillard (1929); Viret (1938, 1940); Ziegler (1983)
Galerix symeonidisi	Early Miocene (MN 4) transition) - Middle Miocene (MN 5)	Aliveri (island of Evia, Greece); Oberdorf 3 (Austria); many South Bavaria localities (Germany); many Spainish localities	Doukas (1986); Ziegler (1998); Ziegler and Fahlbusch (1986)
Galerix uenayae	Early Miocene (MN 2-3)	Keseköy, Sabuncubeli and Semsettin (Turkey)	De Bruijn et al. (2006); Sen et al. (1998, as *Galerix* sp. cf. *G. symeonidisi*; see van den Hoek Ostende and Doukas, 2006); van den Hoek Ostende (1992)
Galerix wesselsae	Early (MN 3) - Middle Miocene (MN 5)	Various localities from Sehwan, the Zinda Pir Dome, the Potwar Plateau and Banda Daud Shah (Pakistan)	Zijlstra and Flynn (2015)
Parasorex depereti	Late Miocene (MN 13) - Early Pliocene (MN 15)	Various Italian and France localities; Esbarrondadoiro (Alvalade Basin, Portugal)	Crochet (1986); Furió and Angelone (2010); Masini et al. (2019)
Parasorex ibericus	Late Miocene (MN 10) - Early Pliocene (MN 14)	Many Spanish localities across Madrid, Alicante, Teruel, Murcia, Granada, Albacede and Valencia	Álvarez-Sierra et al. (2017); Furió Bruno (2007); Furió and Augustí (2017); Gamonal et al. (2018); Mein and Martín-Suárez (1993); Minwer-Barakat Requena (2005); Sen et al. (2015)

Parasorex kostakii	Early Miocene (MN 4)	Karydia (Greece)	Doukas and van den Hoek Ostende (2006)
Parasorex pristinus	Middle Miocene (MN 5)	Mühlbach (Gaindorf Formation, Austria)	Ziegler (2003; see Prieto et al., 2012 for the allocation of *Galerix* cf. *aurelianensis* to *Parasorex pristinus*)
Parasorex socialis	Middle Miocene (MN 7-8)	La-Grive-Saint-Alban (France); Kleineisenbach, Giggenhausen, Petersbuch 6, 10, 18, 31, 35, 48 and Steinheim (Germany); Jamm (Austria)	Butler (1948, as *Galerix exilis*, 1980, 1984); Engesser (1980, 2009); Gaillard (1929, as *Galerix exilis*); Mein and Ginsburg (2002); Novacek et al. (1985); Prieto (2007); Ziegler (1983, 1999, 2005, 2006)
Riddleria atecensis	Early Miocene (MN 3)	Ateca III (Saragoza, Spain)	Van den Hoek Ostende (2003b)
Schizogalerix anatolicus	Middle Miocene (MN 7-8)	Eskhisar (Turkey); localities 64 and 65 (Sinap Formation, Turkey); Mátraszőlős (Hungary)	Engesser (1980); Gál et al. (1999); Sen (1990); Selänne (2003)
Schizogalerix duolebulejinensis	Middle Miocene (MN 6)	Duolebulejin (Fuhai Country, Suosuoquan Formation, China)	Bi et al. (1999)
Schizogalerix evae	Early Miocene (MN 3)	Sabuncubeli (Turkey)	De Bruijn et al. (2006)
Schizogalerix intermedius	Late Miocene (MN 7-8/9 transition - MN 9)	Localities 4 and 94 (Turkey)	Selänne (2003)
Schizogalerix macedonicus	Late Miocene (MN 13)	Maramena (Greece)	Doukas et al. (1995)
Schizogalerix moedlingensis	Late Miocene (MN 11-12)	Eickhogel (Austria); Pikermi (Greece)	Engesser (1980); Rabeder (1973); Ziegler (2006)
Schizogalerix pasalarensis	Middle Miocene (MN 5)	Paşalar (Turkey)	Engesser (1980)
Schizogalerix sarmaticum	Late Miocene (MN 9)	Bužor I (Moldavia)	Lungu (1981); Rzebik-Kowalska and Lungu (2009)
Schizogalerix sinapensis	Late Miocene (MN 9 - 12)	Hayranli 1 (Turkey); Düzyayla (Turkey); sites 1, 8 A, 120, 84, Inönü (Sinap Formation, Turkey)	Furió et al. (2014); Selänne (2003); Sen (1990)
Schizogalerix voesendorfensis	Late Middle Miocene - Late Miocene (MN 8-10)	Vösendorf (Austria); Gratkorn (Austria)	Engesser (1980); Prieto et al. (2010, 2014); Rabeder (1973)

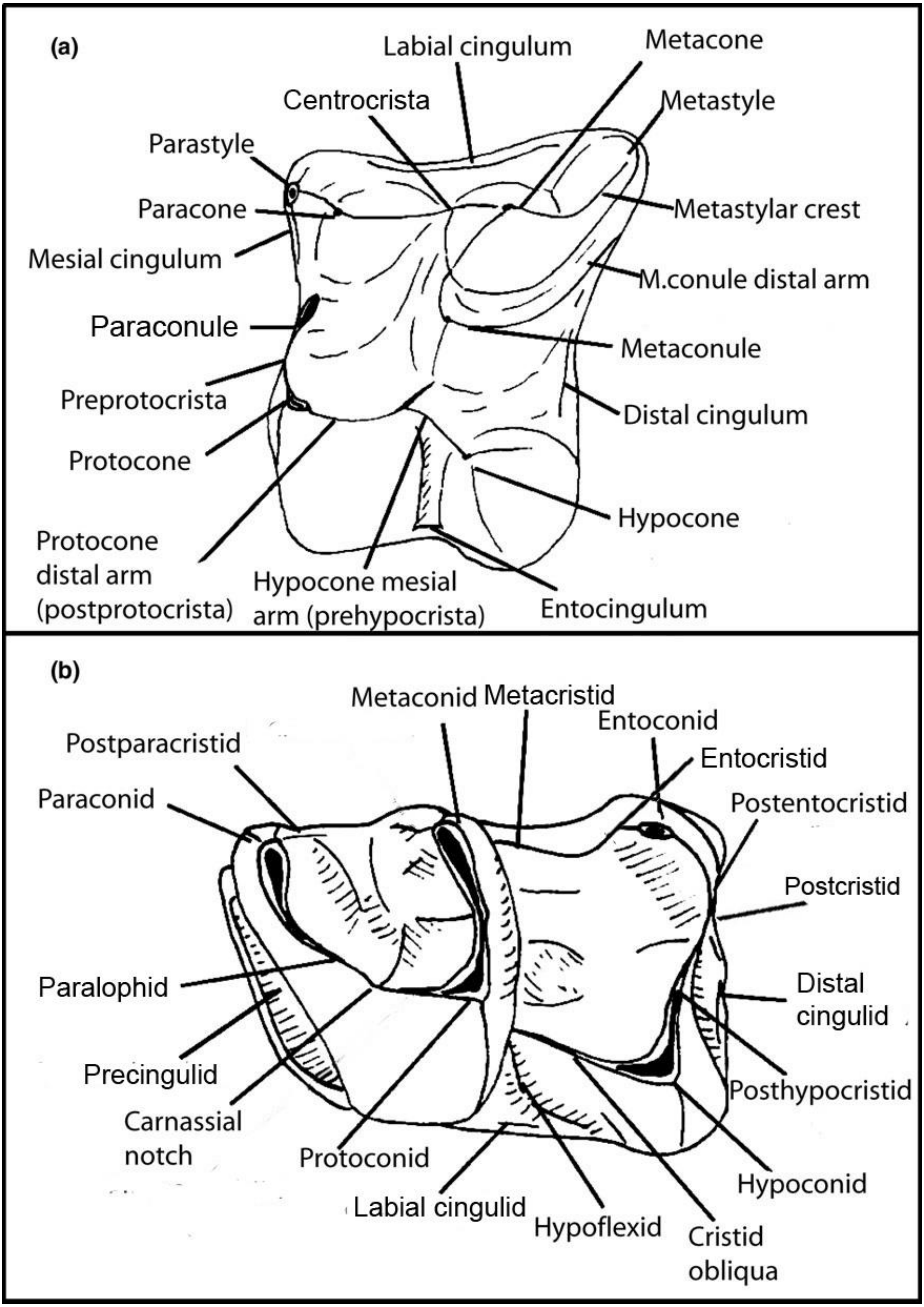
Schizogalerix zapfei	Late Miocene (MN 11-12)	Kohfidisch (southern Burgenland, Austria); Pikermi (Greece); Samos (Greece)	Bachmayer and Wilson (1970); Engesser (1980); Rabeder (1973)
Tetracus daamsi	Early Oligocene (MP 22-23)	Paguera 1 and 2 (Majorca Island, Spain)	Huguerney and Adrover (2003)
Tetracus nanus	Eocene/Oligocene boundary (?MP 20-21) - early Late Oligocene (MP 26)	Various localities of Quercy (France); Mas de Got (France); Ronzon (France); Montalban (Spain); Heimersheim (Germany); St. Martin de Castillion (Lione, France); Hoogbutsel (Belgio)	Crochet (1974, 1995); Hugueney and Adrover (2003); Lavocat (1951, in Gureev, 1979, as *Tetracus boutii*); Smith (2004)

Table 1 – List of taxa used in the phylogenetic analysis, with age, distribution and main references.

METHODS

The analysis was performed under maximum parsimony criteria using freeware TNT (v. 1.5), under the TBR (tree bisection reconnection) swapping algoritm, with 99999 replies. The data matrix (Appendix III) includes all the Galericinae species presently described (38), togheter with three outgroups (*Eogalericius butleri*, *Zaraalestes minutus* and *Microgalericulus esuriens*) and 128 characters (6 cranial, 17 mandibular, 6 inherents to dental ratios and diastema, and 99 dental); doubtful species, such as *Schizogalerx* (=*Galerix*) *paraexilis* (Gureev, 1979), were excluded (see Appendix IV for the complete list and extensive review of the characters). The information is partly unpublished and considered for the first time in this study, and partly drawn or modified from the literature. The nomenclature used for the dental elements is shown in Figure 1.

The ratio diagrams used for comparison are a simplified, non-logarithmic version of the "Simpson Log-ratio diagrams" (Simpson, 1941), as presented in Masini and Fanfani (2013). *Macrocranion tupaiodon* was chosen as reference standard for the diagrams concerning the lower teeth of


(a)
Labial cingulum
Metacone
Centrocrista
Metastyle
Parastyle
Paracone
Metastylar crest
Mesial cingulum
M.conule distal arm
Paraconule
Metaconule
Preprotocrista
Distal cingulum
Protocone
Hypocone
Protocone distal arm (postprotocrista)
Hypocone mesial arm (prehypocrista)
Entocingulum
(b)
Metaconid
Metacristid
Entoconid
Postparacristid
Entocristid
Paraconid
Postentocristid
Postcristid
Paralophid
Distal cingulid
Precingulid
Posthypocristid
Carnassial notch
Protoconid
Hypoconid
Labial cingulid
Hypoflexid
Cristid obliqua

← Figure 1 - Dental morphology terms adapted from Engesser (1980), Gould (1995), Lopatin (2006) and Masini and Fanfani (2013). Modified from Savorelli et al. (2017) and Borrani et al. (2018).

Tupaiodontinae (Fig. 4), since it is a well-known early species outside the group considered, for which measurements of practically all teeth are available (Tobien, 1962). Under the same criterion, *Eogalericius butleri* was chosen for the ratio diagrams of the lower teeth of the Galericinae and stem-Galericinae considered in this paper (see Appendix IV). Where possible, means and weighted means of dental measurements reported by the various authors were used.

The outgroups used for the analysis were chosen following Lopatin (2006) indications and Borrani et al. (2018); they are very similar, morphologically, to early Galericinae (e.g., *Tetracus nanus*), and posses many plesiomorphic traits (e.g., precingulid on p4, hypoconulid on m3, non-reduced M3 and dentition in *Eogalericius*) that still separate them from Galericinae *sensu stricto*. "Galericinae" (when not otherwise intended) is used to indicate the total group considered herein, "Galericinae *sensu lato*" includes the earlier species lacking some of the character of more-derived Galericinae, and "Galericinae *sensu stricto*" most derived species (see also Borrani et al., 2018).

Some species (e.g., *Galerix exilis*, *Parasorex socialis*) are better known and represented than others (e.g., *Parasorex pristinus*, *Schizogalerix duolebulejinensis*); the morphologies present of only up to 2% of the specimens are not scored in the matrix, both to avoid biases related to dental variability and possible ontogenetic variations.

Two analyses were performed, but the first using all the 41 taxa of the matrix and the second on 37 taxa; the taxa eliminated from the second are those less codified than the 50% (*Deinogalerix samniticus, Riddleria atecensis*, *Schizogalerix duolebulejinensis* and *S. evae*). The outgroups were the same for both analyses.

The most parsimonious trees (MPT) obtained from the analysis were used to obtain a strict consensus tree; its length (TL), consistency index (CI) and retention index (RI) were analyzed using Mesquite (v. 3.61, build 927). Bremer support (=decay index) and standard bootstrap frequencies

(99999 replicates) for each node were obtained directly through TNT. Comparisons were made between the two strict consensus trees obtained from the analysis, to identify common patterns and synapomorphies. The basic principles of cladism and the difficulties to the application of this methodology to the fossil record are reported in Appendix V.

3 - Relation between Galericinae, Hylomyinae and Tupaiodontinae

Tupaiodontinae is a group of primitive-looking Erinaceidae from the Middle Eocene – Early Miocene of Asia and North America, diagnosed by many primitive features (e.g., “more transverse upper molars, with small hypocones, and proportionately wider lower molars than in Galericinae”; Storch and Dashzeveg, 1997: p. 438). At present day, six species of four different genera are assigned to Tupaidontinae: *Anatolechinos huadianensis, A. neimongolensis, Ictopidium lechei, Tupaiodon morrisi, Zaraalestes minutus* and *Z. russelli*.

On the other hand, present-day gymnures (genera *Echinosorex*, *Hylomys*, *Neohylomys*, *Neotetracus*, *Otohylomys* (=*Hylomys*) and *Podogymnura*) from South-East Asia are usually ascribed to the subfamily Galericinae (Corbet, 1988; He et al., 2012). This subfamily also contains many extinct genera, i.e., *Apulogalerix Deinogalerix, Eochenus, Eogalericius, Galerix, Lantanotherium, Microgalericulus, Neurogymnurus, Oligochenus, Parasorex, Pseudoneurogymnurus, Riddleria, Schizogalerix*, *Tetracus*, *Thaiagymnura* and possibly the enigmatic early Oligocene American genus *Ocajila.* However, as already noticed by Lopatin (2006: fig. 59, p. 375), this classification may accommodate many species in a sort of “basket-taxon” (from a phylogenetic perspective) of primitive-looking gymnures. In addition, Bannikova et al. (2014) proposed to rank Galericinae and Erinaceinae as distinct families inside the suborder Erinaceomorpha. On the other hand, Frost et al. (1991) underlined that Galericinae is not the correct name for the subfamily, because the general name “Galerices” was used by Pomel (1848) for *Galerix* and its relatives and not latinized until 1948, whilst Butler used for the first time the term “Galericini” as the name of a tribe of Echinosoricinae (which was widely used, until van Valen, 1967, to indicate mainly present-day gymnures). Frost et al. (1991) proposed the use “Hylomyinae” to define the present-day Galericinae. Van den Hoek Ostende (2001d) diagnosed for the first time the tribe Galericini (in which he included *Galerix, Parasorex, Schizogalerix* and *Deinogalerix*) and concluded that it is a group of extinct Galericinae with peculiarly-shaped upper molars (M1-2 wider than loong, with posterior arm on the metaconule, and simple M3, usually without metastylar crest) and P3 (with well-developed lingual lobe and with at least the protocone). Van den Hoek Ostende (2001d), however, failed to provide the list of characters shared by Hylomyinae (*sensu* Frost et al., 1991) and Galericini; he only noted that the present-day *Echinosorex* has an additional cuspule on the metastylar crest.

DENTAL AND MANDIBULAR COMPARISONS BETWEEN TUPAI0DONTINAE AND OTHER PALEOGENE ERINACEOMORPHA

Most of the morphological traits that are considered diagnostic of Tupaiodontinae by Butler (1988) and Storch and Dashveg (1997) are actually plesiomorphic, for being in possessed by almost all Paleocene-Eocene erinaceids and, in some cases, even by Sespedectidae (Appendix VI). The list of species used for comparisons and the relative literature are listed in Appendix II.

Only the upper teeth (Fig. 2a) of *Tupaiodon morrisi*, have been figured and described in detail; therefore, only two characters of the revised diagnosis by Storch and Dashzeveg (1997) (“more transverse upper molars, with small hypocones”) can be checked with a certain degree of confidence. Transverse upper molars are present in many early basal hedgehogs (e.g., *Changlelestes, Litocherus, Oncocherus, Silvacola*; see Eberle et al., 2014; Gazin, 1956; Gingerich, 1983; Rankin, 2018; Scott, 2006; Tong and Wang, 1993) and a small, posteriorly elongated hypocone is a primitive trait, reminiscent of the disto-lingual cingulum from which this cusp probably arose (see Butler, 1990). The upper teeth of *Tupaiodon* shows other plesiomorphic characters: prominent P4 parastyle, connected with crests both to the paracone and to the mesio-labial cingulum (as in *Eogalericius, Litocherus* and *Litolestes*); P4 with very large paracone, as in other basal erinaceids (e.g., *Changlelestes, Eogalericius, Litolestes, Litocherus, Protogalericius*);

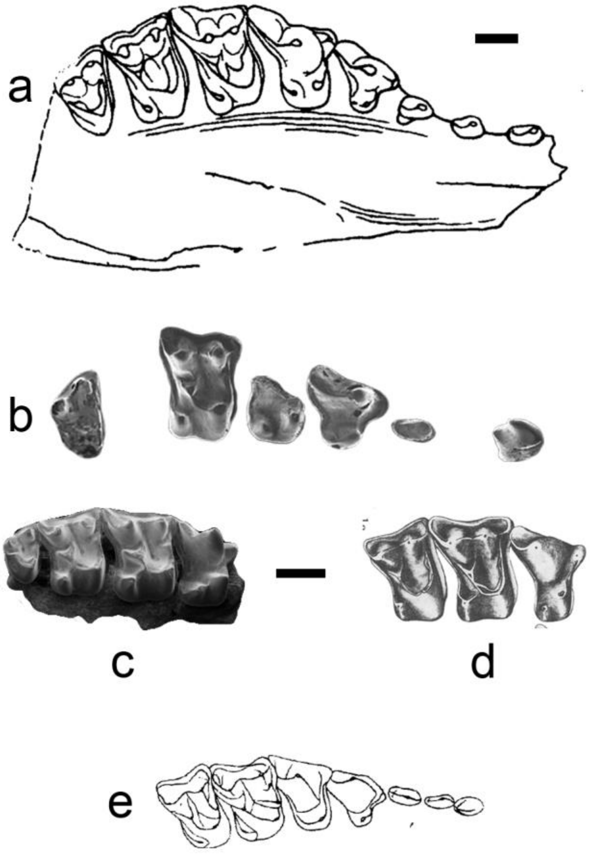


Figure 2 – Comparisons between upper tooth of some Tupaiodontinae and *Changlelestes dissetiformis*. a: *Tupaiodon morrisi*, maxillary with C-M3 (from Matthew and Granger, 1924). b*: Anatolechinos neimongolensis*, C, P2-M1 and M3 (modified from Wang, 2008). c: *Zaraalestes minutus*, P4-M3 (from Ziegler et al., 2007). d: *Zaraalestes russelli*, P4-M2 (from Storch and Dashzeveg, 1997). e: *Changlelestes dissetiformis*, C-M2 (from Tong and Wang, 1993). Scale bars=1 mm.; *Tupaiodon morrisi* has its own scale.

metaconule distal arm on M1-2 elongated to the postero-labial corner of the tooth; presence of metaconule and a well-developed labial cingulum on M3, which is a relatively large tooth, extended labio-lingually. However, the presence of an individualized (yet posteriorly-elongated) hypocone on P4 indicates that the species is relatively more derived than the earlier Paleogene erinaceomorphs (with the exception of *Silvacola*, which already has this cusp; Eberle et al., 2014), which is consistent with its Early Oligocene age. Only two characters of the lower molars described by

Storch and Dashzeveg (1997) are useful for taxonomical purposes, i.e., hypoconulid absent on m1-2 and (relatively?) reduced on m3. Both of these features are not strictly related to putative Tupaiodontinae (see below). On this basis, *Tupaiodon* cannot be reliably assigned to any subfamily of Erinaceidae.

The presence of one single mental foramen under p3, or between p3-4, is a derived character for early Erinaceidae, because in Sespedectidae there are two or three distinct mental foramina and in *Eogalericius*, *Litocherus*, *Litolestes* and *Oncocherus* there are still two mental foramina; one mental foramen is present in *Cedrocherus*, *Eochenus*, *Entomolestes*, *Microgalericulus* and *Oligochenus*. One characteristic of the mental foramen in Tupaiodontinae should be the presence of an antero-dorsal canal or its placement in a shallow fossa; however, an antero-dorsal canal can at least be observed in *Microgalericulus esuriens* and *Oligochenus grandis*, and in *Entomolestes grangeri* the mental foramen is located in a shallow fossa.

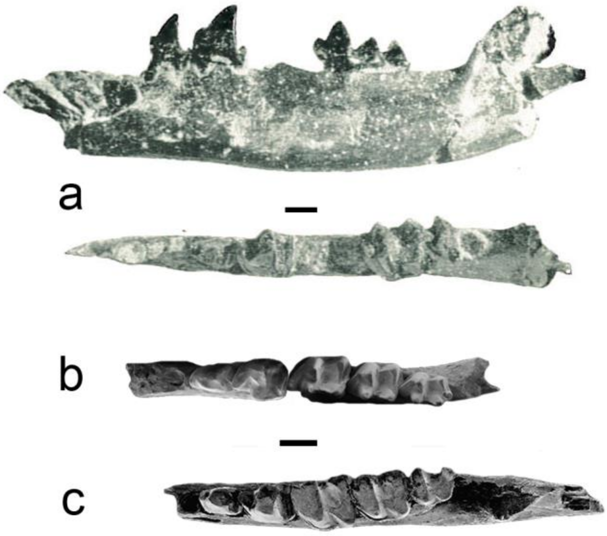


Figure 3 – Mandibular comparisons of some Tupaiodontinae. a: *Ictopidium leakey*, in labial (above) and occlusal (below) view (from Zdansky, 1930). b: *Zaraalestes minutus*, occlusal view (modified from Ziegler et al., 2007). c: *Anatolechinos neimongolensis*, occlusal view (from Wang, 2008). Scale bars= 1 mm; *Ictopidium* has its own scale bar.

A small, incisor-like lower canine, unmeasured by various scholars, can be observed in many Sespedectidae as well as in many subfamilies of early Erinaceidae (*Macrocranion*, *Changlelestes*, *Eogalericius, Entomolestes, Litolestes, Oncocherus* and *Oligochenus*) other than Tupaiodontinae, therefore it cannot be considered as a specialized or derived character for erinaceomorphs. The only exception in the time span considered is the very large, high-crowned canine of *Eochenus*.

A small, single-rooted p1 is shared by various early Erinaceidae. An important difference of this family from Sespedectidae (in particular *Macrocranion*, for which complete mandibles are known) is that Erinaceidae possesses a small p1, while in Sespedectidae p1 is the largest in the p1-3 premolar row. A one-rooted, small p2 is also shared by Sespedectidae and some Paleogene Erinaceidae alongside Tupaiodontinae (*Cedrocherus, Changlelestes, Entomolestes* and *Oligochenus*); therefore, it is possibly a plesiomorphic character for the family. Noteworthy is that *Entomolestes* has a p3 as large as or somewhat smaller or similar in size than p2, which recalls the proportionally very small p3 of *Macrocranion*.

In general, in Tupaiodontinae p3-4 have high, pointed and sharp main cuspids. In *Anatolechinos* the cupids are low and relatively blunt, and this distinguish them from any other early erinaceids. The presence of high, sharp cuspids is probably related to a more insectivorous diet, and is frequent among the Paleocene Erinaceomorpha; the only exceptions are *Cedrocherus, Oligochenus* and *Oncocherus*, which have high but relatively blunt cusps (especially the first two) and *Macrocranion*, which has a small p3 with relatively low and rounded cuspids.

In m1-2 a low *crista obliqua* that ends mesially against the protoconid is a derived character, because in other Paleogene Erinaceomorpha it is usually more diagonal, and ends between the metaconid and the protoconid (*Entomolestes, Litocherus, Litoleste,s Macrocranion, Oncocherus, Scenopagus*) or at the base of the metaconid (*Changlelestes*). However, this character is not unique of Tuapiodontinae, being present even in other early erinaceids (*Cedrocherus, Eochenus, Eogalericius, Microgalericulus* and *Oligochenus*).

The reduction or absence of the m1-2 hypoconulid can be observed in *Eochenus*, *Eogalericius*, *Microgalericius* and *Oligochenus*; therefore, it is rather typical of most derived erinaceids, which have the tendency to reduce or lose the hypoconulids on these teeth.

A wide m1-2 distal cingulid that descend to the base of the hypoconid is common in Tuapaiodontinae. Members of this subfamily also share other significant differences: in *Anatolechinos* and *Ictopidion* the distal cingulum is not connected to the postcristid, but ends against the base of the cristid, forming the so-called "erinaceid fold" (Klietmann, 2013), while in *Zaraalestes* it is connected to the postcristid in m1 but not in m2. In Sespedectidae, as well as in *Cedrocherus, Litocherus, Litolestes, Oncocherus* and possibly *Changlelestes,* the distal cingulum is absent, therefore its presence could be a derived character of Erinaceidae. In *Entomolestes grangeri,* it seems to be absent on m1 but present, though relatively narrow, on m2; the contrary occurs in *E. westgatei*. In *E. westgatei*, the distal cingulid extends to the base of the hypoconid like in Tupaiodontinae. In *Eogalericius* the m1-2 distal cingulid is well-developed, connected to the postcristid and extends to the base of the hypoconid. In other early "Galericinae", such as *Eochenus, Microgalericulus* and *Oligochenus* the distal cingulid is moderately-developed to weak, cand onnected to the postcristid (on m2s of *Eochenus*, *Oligochenus* and *Microgalericulus*) or not (on m1 of *Microgalericulus*) but it is always more or less extended to the base of the hypoconid.

A more or less transverse paralophid and a more mesio-distally compressed trigonid on m1, are commonly observed in primitive Erinaceidae; however, there are some differences between the various groups. In Sespedectidae, as well as in *Ictopidium, Cedrocherus, Changlelestes, Litocherus, Litolestes, Oncocherus, Oligochenus* and *Protogalericius*, the paraconid is crest-like, approximately transverse, making the trigonid appear very "closed"; this is probably a plesiomorphic condition for Erinaceomorpha. On the other hand, in *Anatolechinos* and *Zaraalestes,* as well as in the more derived Galericinae and in the m1 of *Entomolestes westgatei,* the paralophid is elongated more mesially and thus slightly oblique. Therefore, the lower molars of *Ictopidium* have a more primitive aspect, in contrast with those of *Anatolechinos* and *Zaraalestes.* The high paraconid (or paralophid) on m1 is a character shared with other Paleogene Erinaceidae (i.e., *Cedrocherus, Changlelestes, Eogalericius, Microgalericulus, Oligochenus* and *Protogalericius*; in the latter it is particularly high), but it is not present in all Tupaiodontinae: in *Anatolechinos huadianensis* the m1 paraconid is relatively low, and in *A. neimongolensis* all the cuspids are low and relatively blunt.

A well-developed m3 hypoconulid is a plesiomorphic trait, shared with other early Paleocene erinaceids (i.e., *Eogalericius, Eochenus, Litocherus, Litolestes, Oncocherus*) and already present in Paleogene Sespedectidae (e.g., *Scenopagus* and *Macrocranion*). This cuspulid is variously developed in the different members of Tupaidontinae: in *Zaraalestes,* the hypoconulid is well-developed and placed mesio-lingually (as in some specimens of *Macrocranion*, *Cedrocherus, Eochenus*, *Litocherus* and *Litolestes*). Therefore, a well-developed hypoconulid is probably the plesiomorphic state of character for Erinaceidae. On the other hand, *Anatolechinos* and possibly *Tupaiodon* have a small m3 hypoconulid, as have *Eogalericius* and *Entomolestes*: this probably more derived state of character indicates the progressive reduction and disappearance of this cuspulid in the main groups of derived Galericinae (Brachyericinae, Erinaceinae and Galericinae).

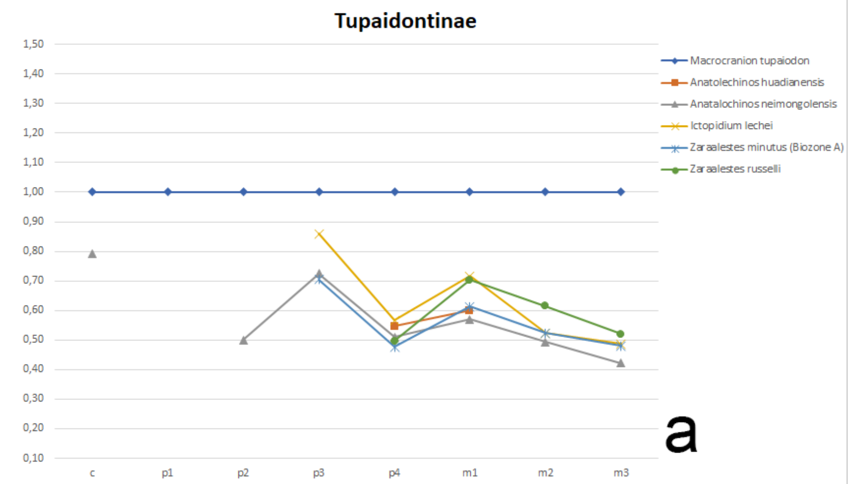
RATIO DIAGRAMS

In terms of lower dental proportions, the ratio diagrams (Fig. 4) show that Tupaiodontinae is not clearly distinguished from other Paleogene erinaceids as a whole. Dental measurements are reported in Appendix VII.

One of the diagnostic characters of the premolars, i.e., the reduced p1-2 compared to p3-4, is shared with other early Erinaceidae, especially the Galericinae *Oligochenus grandis* (in which the reduction of p2 is even more pronounced than in *Ictopidium lechei*), *Eochenus sinensis, Eogalericius butleri* and *Microgalericulus esuriens;* fig. 4d). The measurements of the teeth anterior to p3 are available only for *Changlelestes, Litocherus, Litolestes* and *Oncocherus* among Paleocene-Early Eocene Erinaceidae. In *Changlelestes,* in particular, the relative proportions of p1-2 and of p3-4 are similar to those of *Anatolechinos neimongolensis* (fig. 4c); the preservation of small, single-rooted p1s and p2s is a plesiomorphic character for erinaceids, as is also having a small canine (like in the stem-Galericinae *Eogalericius*; fig. 4d). These features cannot be considered diagnostic of a subfamily of this group of mammals. Moreover, the proportion between canine and p1 in *Ictopidium* and *Anatolechinos neimongolensis* is similar to those in *Changlelestes* and *Litolestes* (fig. 4c), because the lower canine is not particularly reduced. Cases in which p1 is absent are not homologous to reduced p1-2: *Oligochenus*, for example, has a very small p2 and has lost p1 absent, and therefore has a shortened premolar series. At the same time, at least some Tupaiodontinae (some specimens of the earliest *Zaraalestes minutus* from Biozone A of Hsanda Gol and also *Ictopidium lechei*) retain the p1, in contrast to *Zaraalestes russelli* and possibly *Anatolechinos*.

Anatolechinos neimongolensis retains a p4 proportionally large compared to m1, similarly to Sespedectidae, *Changlelestes* and *Eochenus*; the p4 is proportionally smaller in *Zaraalestes* as it is in other Paleogene Erinaceidae, such as *Entomolestes*, *Eogalericius* and *Microgalericulus* (but in contrast with *Litocherus*, *Litolestes* and *Oncocherus*, in which it is proportionally larger).

→ Figure 4 - Ratio diagrams comparing Tupaiodontinae and other Paleogene erinaceids. a: Ratio diagram including only Tupaiodontinae. b: Ratio diagram comparing Tupaiodontinae and Sespedectidae (*Macrocranion nitens* and *Scenopagus edensis*). c: Ratio diagram comparing Tupaiodontinae and basal Paleogene erinaceids (*Cedrocherus aceratus, Cedrocherus ryani, Changlelestes dissetiformis, Entomolestes westgatei, Litocherus notissimus, Litolestes ignotus* and *Oncocherus krishtalkai*). d: Ratio diagram comparing Tupaiodontinae and early "Galericinae" (*Eochenus sinensis, Eogalericius butleri, Microgalericulus esuriens* and *Oligochenus grandis*). The chosen standard is *Macrocranion tupaiodon*, because its complete and well-known remains.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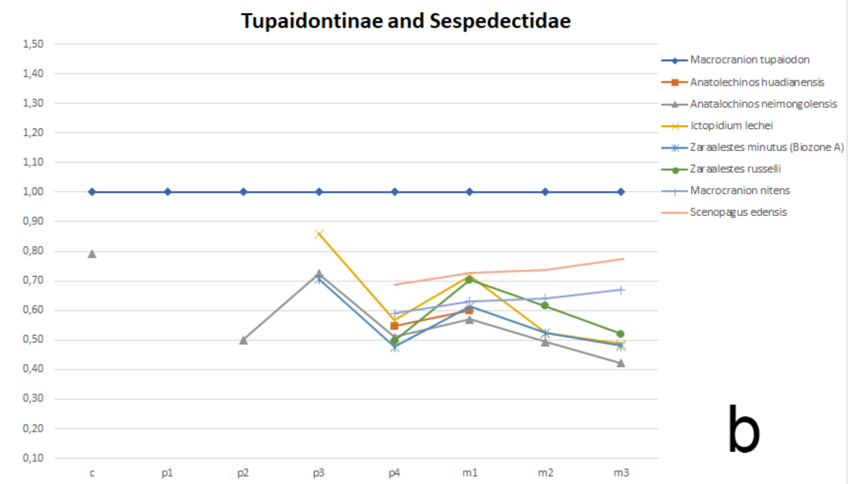
Macrocranion tupaiodon
Anatolechinos huadianensis
Anatalochinos neimongolensis
Ictopidium lechei
Zaraalestes minutus (Biozone A)
Zaraalestes russelli
a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Macrocranion tupaiodon
Anatolechinos huadianensis
Anatalochinos neimongolensis
Ictopidium lechei
Zaraalestes minutus (Biozone A)
Zaraalestes russelli
Macrocranion nitens
Scenopagus edensis
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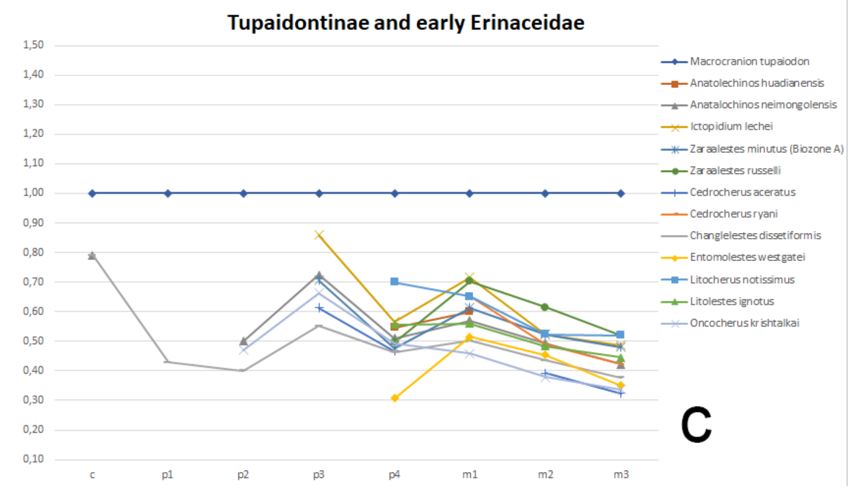
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Macrocranion tupaiodon
Anatolechinos huadianensis
Anatalochinos neimongolensis
Ictopidium lechei
Zaraalestes minutus (Biozone A)
Zaraalestes russelli
Cedrocherus aceratus
Cedrocherus ryani
Changlelestes dissetiformis
Entomolestes westgatei
Litocherus notissimus
Litolestes ignotus
Oncocherus krishtalkai
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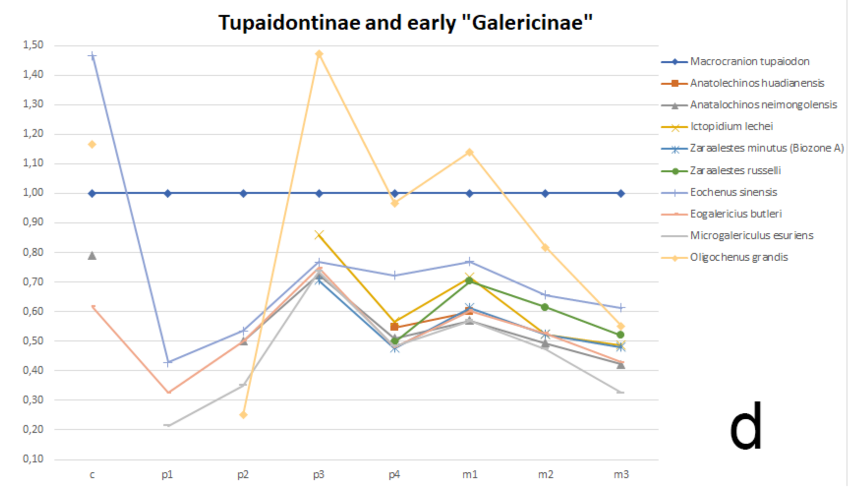
Tupaidontinae and early "Galericinae"
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Macrocranion tupaiodon
Anatolechinos huadianensis
Anatalochinos neimongolensis
Ictopidium lechei
Zaraalestes minutus (Biozone A)
Zaraalestes russelli
Eochenus sinensis
Eogalericius butleri
Microgalericulus esuriens
Oligochenus grandis
d

COMPARISON BETWEEN EXTANT AND EXTINCT SPECIES OF GALERICINAE AND OTHER PALEOGENE EULIPOTYPHLA

Frost et al. (1991, p. 23) list the following 28 diagnostic characters for the Hylomyinae: “(1) rostrum long, greater than 42% of skull length; (2) anterior palatine foramina do not include middle palatine foramina; (3) lacrimal foramen hidden in lateral view by well-developed antorbital flange; (4) jugal does not reach posteroventral process of zygoma; (5) anterior process of alisphenoid absent; (6) suboptic foramen anterior to sphenorbital fissure; (7) sphenopalatine foramen anterodorsal or slightly posterodorsal to the palatine transverse torus; (8) zygomatic process of squamosal not elevated posteriorly; (9) postglenoid foramen posterior to glenoid fossa; (10) suprameatal fossa absent; (11) nasopharyngeal pocket of basisphenoid absent; (12) ectotympanic slender and ring-shaped; (13) stapedial foramen posterior to squamosal/alisphenoid suture and posterior to postglenoid foramen; (14) epitympanic recess formed by squamosal; (15) paroccipital process small; (16) occipital condyle emarginated, giving it a slightly lobed appearance; (17) condylar foramen of basioccipital anterior to ventral lip of condyle; (18) i1 present; (19) i2 subequal to other incisors; (20) I2 greater than I3; (21) p3 present; (22) M3 hypocone and metacone well developed; (23) posteroventral keel present on axis; (24) metacromion process of scapula elongated, fusiform; (25) sacral vertebral not fused into a longitudinal plate; (26) greatly elongated posteroventral process of pubis; (27) strongly developed lateral flange on anterosuperior margin of tibia; (28) pelage not composed of stout spines.” Obviously, only the first 27 characters can be used, because the 28th refers to soft tissues. Seventeen out of 27 are cranium characters; however, there are relatively few species of Paleogene-Neogene erinaceids in which the cranium is known in an acceptable manner. For this reason, Paleogene-Neogene erinaceids have also been compared with Leptictidae (*Leptictis* and *Megaleptictis*) and Sespedectidae (*Macrocranion*) to understand which state of characters are plesiomorphic or derived.

1) *Rostrum than 42% the length of the skull*: Unfortunately, only a few partial or more or less complete crania of extinct Galericinae are known at present, and only for a handful of species (*Deinogalerix brevirostris, D. minor, D. koenigswaldi*, *Galerix exilis, Parasorex ibericus* and *Schizogalerix voesendorfensis*). Frost et al. (1991) stated that an elongated muzzle is plesiomorphic for Erinaceidae, by comparison with the cranial morphology of *Leptictis* by Novacek (1986). However, comparisons with *Macronion* (Maier, 1977, 1979) show that in Sespedectidae, which is strictly related to Erinaceidae within Erinaceomorpha (see Gunnell et al., 2007), the snout is relatively short compared to the total length of the cranium. At the same time, *Galerix exilis* and *Parasorex ibericus* (and possibly also *Schizogalerix voesendorfensis*) have a relatively short rostrum. In *Deinogalerix*, the snout is noticeably elongated, in particular in the advanced species *D. koenigswaldi*; however, this endemic insular genus is relatively derived compared to *Galerix* and *Parasorex,* for its possessing relatively enlarged premolar series as well as for the presence of long diastemas (especially in the derived *D. intermedius* and *D. koenigswaldi*), which are not present in other early erinaceids (*Eochenus, Eogalericius, Microgalericulus*). Therefore, an elongated rostrum is a derived character for Erinaceidae, while the presence of a complete dental formula (but without enlarged premolars) and the absence of or very short diastemas should be considered a primitive character. The elongated snout in present-day Galericinae, as well as in the extinct *Deinogalerix*, is a derived character, probably achieved independently.

2) *Anterior palatine foramen without middle palatine foramina*: The presence of a very large anterior palatine foramina is typical of Erinaceinae. However, the anterior palatina foramen not extended to include middle palatine foramina (= *foramen palatinum minus* in Ziegler, 1983) that can be observed in Galericinae is also present in the Brachyericinae; therefore, this is probably a plesiomorphic character, which is also present in *Leptictis* (Novacek, 1986) and *Megaleptictis* (Meehan and Martin, 2012). In some Erinaceinae specimens

figured in Frost et al. (1991) the anterior palatine foramen is still more or less divided from the middle palatine foramina; therefore, their complete inclusion is possibly an ontogenetic outcome and/or is the result of individual variation.

3) *Lacrimal foramen hidden in lateral view by a well-developed lateral flange*: In present-day Galericinae the lacrimal foramen is usually hidden by a lateral flange (Butler, 1948, 1956b; Frost et al., 1991); this feature is also present in *Deinogalerix, Lantanotherium* and *Parasorex* (Butler, 1980). *Macrocranion tupaiodon* has a “delicate bony ridge, covering the tiny entrance of the nasolacrimal canal” (Maier, 1979: p. 43). This character, therefore, is probably primitive for Erinaceidae, because, as reported by Lopatin (2003), the lacrimal foramen visible in lateral view is typical only of *Proterix*, Brachyericinae and Erinaceinae. Even in *Neurogymnurus* the lacrimal foramen seems to be hidden by the lateral flange (Butler, 1948: p. 471, fig. 21). One exception is the skull of *D. minor* PU1000-44, in which an incompletely developed lateral flange leaves the lacrimal foramen visible laterally (Villier and Carnevale, 2013).

4) *Jugal not in reach of posteroventral process of zygoma*: Villier and Carnevale (2013) observed that in *Deinogalerix*, *Galerix* and *Parasorex* the jugal is relatively extended compared to present-day Galericinae, and that this state of character is probably plesiomorphic, because it is small and reduced even in the early Erinaceinae *Scymnerix* (Lopatin, 2003b) and *Gymnurechinus* (Butler, 1956b). This is also confirmed by *Leptictis* (Butler, 1956a, as *Ictops;* Novacek, 1986), in which the jugal is similarly extended.

5) *Absence of anterior process of alisphenoid*: According to Frost et al. (1991), the presence of the anterior process of the alisphenoid is related to the position of the sphenopalatine foramen. In *Deinogalerix* the anterior process of the alisphenoid is absent (Villier and Carnevale, 2013), as well as in present-day Galericinae. The sphenopalatine foramen is

placed in the same position also in *Galerix* as well (Ziegler, 1983); therefore, it is possible that this is a shared derived character.

6) *Suboptic foramen anterior to sphenorbital fissure*: In *Leptictis* the suboptic foramen opens in the medial wall of the sphenorbital fissure (Butler, 1956a; Novacek, 1986). Novacek (1986) also argued that this is probably the primitive condition for eutherians. The suboptic foramen is placed more anteriorly in modern "Echinosoricini", as it is also in *Neurogymnurus* (Butler, 1948: p. 453, fig. 7) and *Deinogalerix* (Butler, 1980; Villier and Carnevale, 2013). Butler (1980, p. 12) also reported that the orbital foramen in *Deinogalerix* "[…] is immediately dorsal to the suboptic foramen, as in *Neurogymnurus* and *Lantanotherium*". A similar placement of the suboptic foramen is also observed in *Galerix exilis* (Ziegler, 1983: p. 159, fig. 141c) and *Brachyerix* (Rich and Rich, 1971). In *Proterix*, as well as in the early Erinaceinae *Gymnurechinus* (Butler, 1956b), the suboptic foramen is clearly placed anteriorly to the sphenorbital fissure (Gawne, 1968: p. 14, fig. 8), An anteriorly-placed suboptic foramen is possibly a derived character shared by many erinaceids such as Galericinae, Brachyericinae, *Gymnurechinus*, *Proterix* and *Neurogymnurus*, but it is not exclusive of the first one.

7) *Sphenopalatine foramen anterodorsal or slightly posterodorsal to the palatine transverse torus*: In Leptictidae, the sphenopalatine is slightly posterodorsal (cf. fig. 1 and 10 in Novacek, 1986: p. 17 and 34) or it is approximately anterodorsal (Butler, 1956a, as orbitonasal foramen) to the palatine transverse torus. This character is also shared by *Deinogalerix* (Villier and Carnevale, 2013) as well as present-day "Echinosoricini", but not Erinaceinae (Butler, 1948, 1980; Frost et al., 1991; Lopatin, 2003b) or Brachyericinae (Rich and Rich, 1971). Therefore, it is possibly a plesiomorphic character for Erinaceidae.

8) *Zygomatic process of squamosal not elevated posteriorly*: Leptictidae differs from Erinaceidae in having a well-developed jugal component of the zygomatic arch; however,

the zygomatic process of the squamosal is not elevated posteriorly and the zygomatic arch itself is straight (Butler, 1956a; Novacek, 1986). Posteriorly-elevated zygomatic processes are typical of *Brachyerix* and Erinaceinae (Rich and Rich, 1971; Frost et al., 1991), but it is not present in *Scymnerix*, in which it is at the level of the M1 (Lopatin, 2003b), as well as in *Gymnurechinus*, *Neurogymnurus* and *Amphechinus* (see Butler, 1956b). Therefore, *Deinogalerix* (Villier and Carnevale, 2013), present-day "Echinosoricini" and possibly *Galerix exilis* still retain this plesiomorphic state of character, as already recognized by Frost et al. (1991).

9) *Postglenoid foramen posterior to glenoid fossa*: A well-developed postglenoid foramen located slightly distally to the glenoid fossa is already present in *Leptictis* (Novacek, 1986). The presence of a postglenoid foramen not confluent with the glenoid fossa is also shared by *Deinogalerix* (Villier and Carnevale, 2013), present-day Galericinae (Frost et al., 1991) and possibly *Galerix exilis* (Ziegler, 1983, as "foramen retroarticulare"), but not extant Erinaceinae. However, in *Scymnerix tartareus* it is separated from the glenoid fossa by the entoglenoid process (Lopatin, 2003b), as well in *Amphechinus, Gymnurechinus* (Butler, 1956b) and *Brachyerix* (Rich and Rich, 1971). Possibly, it is another plesiomorphic state of character for the group.

10) *Suprameatal fossa absent*: As recognized by Frost et al. (1991), the homology between the suprameatal fossa present in Leptictidae and some Erinaceidae is difficult to assess. A suprameata fossa is present in *Deinogalerix* (Villier and Carnevale, 2013), in Erinaceinae (Frost et al., 1991; Lopatin, 2003b) and apparently also in *Brachyerix*. However, the absence of the suprameatal fossa is a diagnostic character of present-day "Echinosoricini"; therefore, the presence of this character in *Deinogalerix* is problematic, as already recognized by Villier and Carnevale (2013).

11) *Nasopharyngeal pocket of basisphenoid absent:* The presence of a nasopharyngeal pocket is a derived character shared by many Erinaceinae (Frost et al., 1991), but it is absent in *Scymnerix* (Lopatin, 2003b), in *Deinogalerix* (Villier and Carnevale, 2013), as well as in *Brachyerix,* Leptictidae, Amphechinini erinaceines (Lopatin, 2003b) and *Galerix exilis*. For this reason, its shared absence in Galericini and "Echinosoricini" should be considered as a symplesiomorphic trait and not a synapomorphy.

12) *Ectotympanic slender and ring-shaped*: A slender and ring-shaped ectotympanic process can already be found in *Leptictis* (Novacek, 1986) and *Macrocranion tupaiodon* (Maier, 1979); on the contrary, a well-developed ectotympanic is present both in present-day Erinaceinae and *Brachyerix* (Rich and Rich, 1971). However, in *Scymnerix* and Amphechininae (Lopatin, 2003b and references therein), *Deinogalerix* (Villier and Carnevale, 2013) and present-day "Echinosoricini" the ectotympanic is still a ring-shaped structure; for this reason, this character cannot be considered as a synapomorphy between Galericini and "Echinosoricini", but a primitive character for the group.

13) *Stapedial foramen posterior to squamosal/alisphenoid suture and posterior to postglenoid foramen*: In Leptictida the stapedial foramen is placed posteriorly both to the squamosal/alisphenoid suture and to the postglenoid foramen, as in present-day Galericinae and *Brachyerix* (see Rich and Rich, 1971: p. 36, fig. 17). In *Deinogalerix* the stapedial foramen is placed posteriorly to the squamosal/alisphenoid suture slightly anterior to the postglenoid foramen (Villier and Carnevale, 2013). This condition seems to be intermediate to that of Galericinae and Erinaceinae, in which the stapedial foramen is near to the postglenoid foramen but also to the squamosal-alispenoid suture. In *Neurogymnurus* the postglenoid is located at the squamosal/alisphenoid suture, near the postglenoid foramen (see Butler, 1948: p. 455, fig. 9), as it is in Erinaceinae.

14) *Epitympanic recess formed by squamosal*: In present-day Galericinae, as well as in *Deinogalerix* (Villier and Carnevale, 2013), the lateral wall of the epitympanic recess is formed mainly by squamosal bone; this condition is possibly plesiomorphic, because the same state of character can be found in Leptictidae (Novacek, 1986). In *Macrocranion*, however, the epitympanic recess is possibly absent (Maier, 1979), and in Erinaceinae it is formed completely by petrosal (Frost et al., 1991). In *Brachyerix*, the epitympanic recess is possibly at least partially made by squamosal (see Rich and Rich, 1971: p. 38). Therefore, it is possible that this character is plesiomorphic, in contrast with the state present in Erinaceinae.

15) *Small paroccipital process*: *Leptictis* has a very weak paroccipital process (Butler, 1956a; Novacek, 1986); in *Megaleptictis* the structure is more developed, however it is still relatively smaller compared to Erinaceinae (see Meehan and Martin, 2012: p. 511, fig. A3-4). On the other hand, *Macrocranion tupaiodon* seems to have a well-developed paroccipital process (see Maier, 1979: p. 41, fig. 2). In *Deinogalerix*, as well as probably in *Galerix* ("processus paracondylaris" in Ziegler, 1983), the paroccipital process is small (Butler, 1980; Villier and Carnevale, 2013), as it is in present-day Galericinae. On the other hand, *Neurogymnurus cayluxi* (Butler, 1948: p. 471, fig. 21), extant Erinaceinae and also *Brachyerix* have a well-developed and broad process. In Amphechinini and *Scymnerix* the paroccipital process is reduced (Lopatin, 2003b); this might imply, as supposed by Novacek (1986), that the loss (and probably also the larger size) of this process probably occurred recurrently during the evolution of the various groups.

16) *Occipital condyle emarginated and somewhat lobed*: As reported by Butler (1956a: p. 464) "the occipital condyle in *Ictops* [=*Leptictis*] resembles that of *Echinosorex, Neurogymnurus* an *Gymnurechinus*". It seems also emarginated in *Proterix* (Gawne, 1968: p. 14, fig. 8C), *Deinogalerix* (Villier and Carnevale, 2013), and *Galerix* (Ziegler, 1983), together with

present-day “Echinosoricini”: therefore, it is possibly a symplesiomorphy, while the derived “occipital condyle not emarginated” condition is present in Erinaceinae already from *Scymnerix* (Lopatin, 2003b) and *Gymnurechinus* (Butler, 1956b).

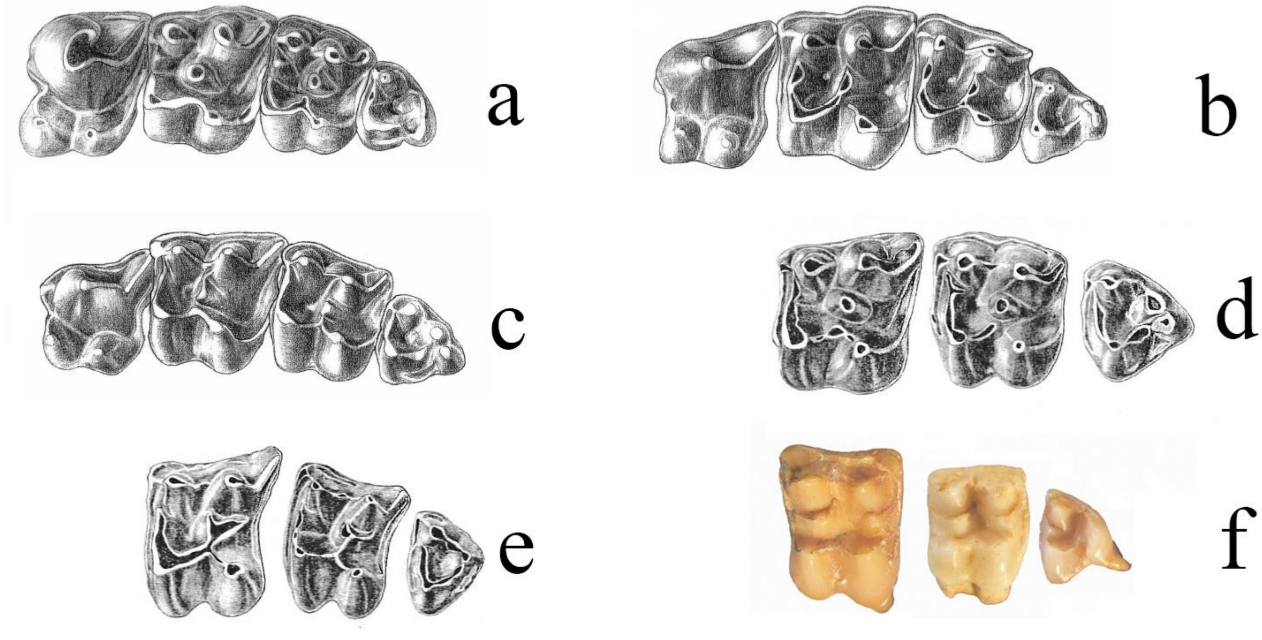
17) *Condylar foramen of basioccipital anterior to ventral lip of condyle*: As reported by Butler (1948: p. 456), “in the Echinosoricinae the condylar foramen is placed in an emargination of the condyle, which is thus divided into two lobes”; however, in *Scymnerix* the condylar foramen is placed near the condyle which, however, is not emarginated (Lopatin, 2003b), like in *Brachyerix* (Rich and Rich, 1971: p. 34). This kind of placement of the condylar foramen is shared also by *Leptictis* (Butler, 1956a), *Deinogalerix* (Villier and Carnevale, 2013) and *Gymnurechinus* (Butler, 1956b), but not by other Erinaceinae.

18) *Presence of i1*: This character is clearly plesiomorphic for Erinaceidae: in fact, it is present in Brachyericinae, Galericinae, early erinaceids (*Eochenus, Eogalericius, Litolestes, Oligochenus*), Leptictidae and Sespedectidae. Its absence is a synapomorphy of Erinaceinae.

19) *i2 subequal to other incisors*: The presence of subequal incisors seems to be a plesiomorphic character, being present in *Megaleptictis*, *Macrocranion* and also in some early Erinaceidae in which this character can be checked (*Changlelestes, Litolestes*). In *Eochenus*, i2 is larger than i3, as well as in *Oligochenus* (in which it is smaller than i3); the decreasing size of the lower incisors can be commonly observed in Galericini, with the exception of *Tetracus nanus* in which i2 is reported to be subequal to the other incisors (Crochet, 1995). In some Galericini the i3 is very small (*Deinogalerix masinii,* many species of *Parasorex, Schizogalerix*) or even absent (*Apulogalerix,* other species of the genus *Deinogalerix, Parasorex ibericus*). Between the primitive Galericinae only in *Eogalericius* the i2 is approximately as large as i1, and both are larger than i3; this is probably a condition reminiscent of the plesiomorphic condition.

20) *I2 greater than I3*: The upper incisors are poorly preserved in early Erinaceomorpha and, in most “insectivores”; however, they are known in a handful of species. In *Leptictis* I3 is slightly larger than I2; however, in *Macrocranion tupaiodon* the I2 is larger than both I1 and I3; therefore, the plesiomorphic state of character is difficult to establish in Erinaceidae. In Brachyericinae, I2 is subequal or smaller than I3. In Erinaceinae I3 is much larger than I2, which in fact is very reduced. In *Deinogalerix*, I3 is slightly larger than I2, as it is also in *Parasorex ibericus,* which has a relatively short muzzle. In *Apulogalerix,* I3 is the smallest tooth between the upper incisors; unfortunately, the size of I2 compared to I3 is not known in other species of Galericini. In present-day Galericinae, however, I2 is larger than I3, as it is in *Lantanotherium*, with the exception of *Podogymnura*, in which the two incisors are approximately subequal.

21) *Presence of p3*: This character is similar to character 18 (“Presence of i1”): in Erinaceidae the p3 is usually present, except in Brachyericinae and Erinaceinae (but not *Scymnerix*, in which it is still present but very reduced; Lopatin, 2003b), as well as in Sespedectidae and Leptictidae (in the latter p3 is particularly well-developed; see Meehan and Martin: p. 512, fig. 2). Therefore, its presence is a plesiomorphic character.



← Figure 5 – Comparison of the upper teeth of extant and extinct Galericinae. a: left P4-M3 of *Neotetracus sinensis*. b: left P4-M3 of *Hylomys suillus suillus*; c: left P4-M3 *Neohylomys hainanesis*; d: left M1-3 of *Lantanotherium sansaniense*; e: left M1-3 of *Galerix exilis*; f: right M1-2 and left M3 of *Deinogalerix freudenthali*. Pictures a, b, c from Engesser and Jiang (2011); d, e from Engesser (2009); f from Savorelli et al. (2020). Teeth are depicted to approximately to the same size and not to scale to underlines morphological and proportional differences.

22) *M3 hypocone and metacone well developed* (Fig.5): Together with the general shape of the upper molars, this is the greatest difference between present-day and extinct Galericinae. Present-day Galericinae, including *Lantanotherium* and *Thayagymnura*, have a metastylar crest on M3, sometimes developed into a hypocone-like cusp (e.g., *Lantanotherium sansaniense*; Engesser, 1979, 2009); a similar crest is a diagnostic character of *Deinogalerix*. There are four possible explanations to this:

I. *Deinogalerix* and Hylomyinae inherited the metastylar crest from a common ancestor. This is unlikely, because *Deinogalerix* is a Galericinae (present study) and it is therefore closer related to *Galerix, Parasorex* and *Schizogalerix* than to Hylomyinae (present study), as also shown by other molar and skull features. In addition, also the earlier Galericinae *Tetracus* and *Galerix* have no metastylar crest.

II. The metastylar crest evolved in *Deinogalerix* and Hylomyinae by parallelism, deriving from a primitive, labially elongated third molar, relatively similar, morphologically, to a second molar, as that of some early Erinaceomorpha (e.g., *Macrocranion* and *Changlelestes*). This hypothesis implies that all the other dental morphologies shown by *Deinogalerix* have been derived by parallelism with other Galericinae. This option implies an excess of parallel evolution that seems not realistic.

III. The character evolved in parallel in the two clades, as proposed by the second option, but with a notable difference: the M3 in *Lantanotherium* as well as in other Hylomyinae derives from a primitive, short and wide third molar, without metastylar crest, and

Deinogalerix derived it from an advanced, very reduced and triangular Galericinae-like M3.

IV. Both groups developed a metastylar crest by parallelism from a derived third molar and then a cusp, named hypocone by some authors (e.g., Butler, 1948; Frost et al., 1991), evolved from this structure in *Lantanotherium* and other Hylomyinae.

Cross-comparisons between *Deinogalerix* (considering the early species *D. freudenthali* and *D. masini*), *Hylomys*, *Echinosorex*, *Lantanotherium*, *Neohylomys*, *Neotetracus* and *Thaiagymnura* have shown that in *Lantanotherium* as well as in present-day species the metastylar crest is formed by two cusps or by a crest (metacone) and a cusp, or even by a crest split into two parts (in *Lantanotherium sawini* and *Neotetracus sinensis*). In *Neotetracus sinensis* the crest derives from the fusion of two cones. Therefore, in Hylomyinae the postero-lingual elongation of the tooth derives from the development of an additional cone, like in *Hylomys engesseri*. In the morphologically primitive *Thaiagymnura* the M3 is relatively short and the tooth bears a cone in its disto-lingual corner and a crest running to the paracone. The crest shows a bulge in place of a reduced metacone. The presence of a disto-labial cusp connected to a crest running along the disto-labial margin of the tooth can also be observed in *Lantanotherium sanmigueli*. Therefore, in Hylomyinae the metastylar crest seems to derive from the fusion, more or less complete, of two distinct structures, i.e., the metacone and an additional metastylar neo-cusp (see Engesser, 1979). On the other hand, in *Deinogalerix* the metastylar crest is formed by a single element, and there are no signs, even in the earlier species, of the co-presence of two structures. Therefore, the similarity between the two groups is the likely result of homoplasy, and the so-called “metastylar crest” in Hylomyinae should be considered a different character, because it is not the homologue of that of *Deinogalerix*.

23) *Presence of posteroventral keel on axis*: The presence of a posteroventral kneel on axis is a character shared by present-day Galericinae. However, as can be observed in Frost et al. (1991: p. 12, fig. 5), there are some differences between *Echinosorex* and *Neohylomys* (in which this process is rather slender and straight) and other “Echinosoricini” (in which it is stronger and arched dorsally). On the other hand, this process is absent in Erinaceinae; however, in *Gymnurechinus* the axis is similar to that in *Echinosorex* (Butler, 1956b). Unfortunately, this character cannot be evaluated in extinct Galericini, because only fragments of axis are known in *Deinogalerix* (Butler, 1980).

24) *Long, fusiform metacromion process of scapula*: How the metacromion could look like in early “insectivores” is difficult to say, because in many cases this character has not been described. However, it seems to be short or hook-shaped in *Macrocranion* (see Maier, 1979: p. 40, fig. 2; Rose, 2012: fig. 6) and *Leptictis* (see Rose, 2006: p. 43, text-fig.4). In *Echinosorex* and *Podogymnura*, as shown in Frost et al. (1991: p. 13) and Ziegler (1983: p-185-186), the metacromion is actually hook-shaped and relatively shorter than in *Hylomys*, *Neohylomys* and *Neotetracus*. In Erinaceinae, on the other hand, it is very short and strong; however, Butler (1956a) reports that in *Gymnurechinus* the metacromion is well-developed. Complete scapulas of Galericini are usually not known: the only exception is that of *Galerix exilis* (Ziegler, 1983: p. 181-182, fig. 156-157), which has a long, fusiform metacromion like occurs in present-day “Echinosoricini” (except *Echinosorex* and *Podogymnura*).

25) *Sacral vertebral not fused in a longitudinal plate*: The fusion of the sacral vertebrae is characteristic of Galericinae (see Frost et al., 1991: p. 14, fig. 7B-E). In *Deinogalerix*, the first neural spine of the first sacral is much smaller compared to those of *Echinosorex* (Butler, 1980), but the exact morphology of the sacral vertebrae is unknown. Unfortunately, this character is very difficult to check in fossil species.

26) *Very elongated posteroventral process of pubis*: In *Deinogalerix* the posteroventral process of pubis is not elongated (Butler, 1980: p. 29, fig. 13 A-B), unlike present-day Galericinae and also *Parasorex socialis* (Ziegler, 1983: p. 206, fig. 171), which share this feature. In modern Erinaceinae this structure is reduced; therefore, the elongation of the posteroventral process of the pubis is probably an apomorphy of Galericinae. Also, in *Leptictis* the posteroventral process of the pubis is not elongated (Rose et al., 2006). Frost et al. (1991) considered this character a derived condition of living Galericinae.

27) *Strongly developed lateral flange on anterosuperior margin of tibia*: According to Frost et al. (1991), the presence of a well-developed anterior crest is a derived character shared by present-day Galericinae. It is nonetheless present also in *Macrocranion tupaiodon* (Maier, 1979), *Leptictis* (Rose, 2006; Rose, 2012: fig. 7A) *Gymnurechinus* (Butler, 1956b), *Deinogalerix* (Butler, 1980; Villier and Carnevale, 2013), *Galerix exilis* and *Parasorex socialis* (Ziegler, 1983). In modern Erinaceinae this process is strongly reduced (see Frost et al., 1991: p. 15, fig. 8A).

Lopatin (2006: p. 282) also provided a diagnosis of Galericinae based mainly on dental characters: “Unspecialized erinaceids with dental formula I3/3–2C1/1P4–2/4–2M3/3. Rostrum and antemolar row relatively long. P4–M2 subsquare in outline, with large hypocone. M3 subtriangular in outline, with well-developed metacone, three-rooted. i1 present, i2 approximately equal in size to i1. p3 present. Lower molars gradually decreasing in size from M1 to M3; hypoconulid absent or extremely reduced, or, occasionally, well-developed on m3. m3 double-rooted, with well-developed talonid; similar in structure to m2”. As discussed above, most of these characters are plesiomorphic or not exclusive of Galericinae, such as the presence of i1 and p3, the i2 subequal to i1, the presence of a (small) hypoconulid on m3. Moreover, Galericini and “Echinosoricini” have differently shaped M1-2s (Fig. 5): in Galericini, M1-2s are longer labially than lingually, thus the teeth are more or less sub-rectangular shape. On the other hand, in Echinosoricini (see Engesser, 1979: p. 49, pl. 1) the upper molars are almost squarish, like in Erinaceinae, except in *Ocajila*, which still has a sub-rectangular M1, possibly like Galericini or more ancient erinaceids.

FINAL CONSIDERATIONS

No derived unequivocally identifies Tupaiodontinae from other Paleogene erinaceids. Some of the characters considered as typical of this group of primitive hedgehogs (i.e., short and wide upper molars, relatively small and one-rooted c-p2, m1-2 trigonid compressed mesio-disally, well-developed m3 hypoconulid) are plesiomorphic for the entire family, and cannot be taken into account to establish a subfamily. The remaining characters are derived for primitive hedgehogs, but not exclusive of Tupaiodontinae, as they are present in other Paleogene representatives.

Moreove, living gymnures do not seem to be closely related to Galericini: only two characters, the absence of the anterior process of the alisphenoid and maybe the very elongated posteroventral process of the pubis, could be regarded as synapomorphies. Present-day gymnures and *Lantanotherium* (see Engesser, 1980; Korth and Evander, 2016; Cailleux et al., 2020) differ from extinct Galericini in the shape of the upper molars, having neo-formed metastylar cusps and a very reduced, or even absent, lingual lobe on P3. Present-day gymnures (including *Thaiagymnura* and *Lantanotherium*) are therefore included here in a different subfamily, Hylomyinae (as proposed by Frost et al., 1991), and Galericini is elevated to a different subfamily, Galericinae.

4 – Results of the phylogenetic analysis

The full-taxa dataset provided 34 MPTs and one strict consensus tree (Fig. 6). The states of characters of the root are listed in Appendix VIII; they are the same for both trees.

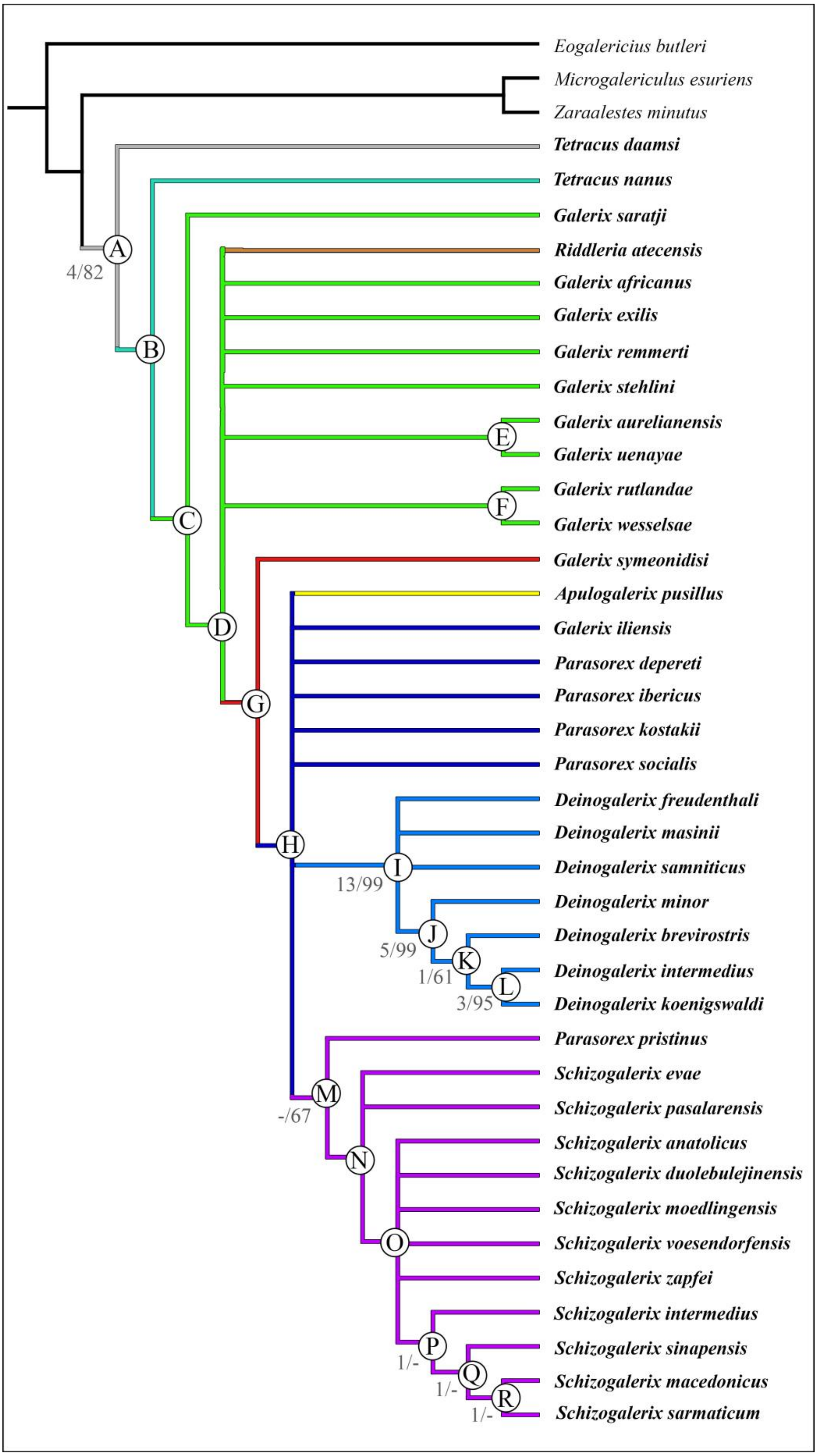
The clade Galericinae (node A) is identified by ten synapomorphies: (1) p3 reduced compared to p4 (less than 75% of the latter tooth); (2) cuspulid-size p4 metaconid on lingual side of protoconid; (3) low p4 paraconid connected with protoconid by low and rather straight crest; (4) tubercle-like m1 paraconid; (5) sharp m1 metacristid divided from entocristid by notch; (6) m3 talonid with continuous postcristid and nopostcingulid; (7) m3 hypoconulid absent; (8) P4 hypocone connected with protocone by low mesial arm of hypocone (=prehypocrista); (9) well-developed, long, wide P4 lingual lobe; (10) sub-rectangular M1, proportionally more elongated and narrower molars compared to Galericinae *sensu lato*. Node A is one of the most stable, with R.I.= 4 and bootstrap=82.

Node B includes the vast majority of Galericinae, but not *Tetracus daamsi*. It is based on 4 synapomorphies: (1) p4 without precingulid; (2) m1 paralophid oblique, developed more anteriorly; (3) m2 talonid with continuous postcristid and postcingulid not connected with postcristid; (4) P4 parastyle connected with mesial arm of paracone.

Node C includes all Galericinae but *Tetracus*. It is identified by 4 synapomorphies: (1) p4 without posterior cuspulid; (2) p4 paraconid and protoconid not connected; (3) P4 protocone approximately as high as hypocone; (4) M1 paraconule without distal arm.

Node D is a polytomy that includes *Riddleria,* all species of *Galerix* (except *G. saratji*), *Parasorex, Deinogalerix, Apulogalerix* and *Schizogalerix*. It is identified by 2 synapomorphies: (1) p2 with paraconid; (2) P4 hypocone not connected with protocone.

Two species of *Galerix, Galerix aurelianensis* and *G. uenayae*, show sister-taxon relationship and represent node E. It is supported by 3 synapomorphies: (1) m2 with postparacristid not reaching


Eogalericius butleri
Microgalericulus esuriens
Zaraalestes minutus
Tetracus daamsi
Tetracus nanus
Galerix saratji
A
4/82
Riddleria atecensis
Galerix africanus
Galerix exilis
B
Galerix remmerti
Galerix stehlini
Galerix aurelianensis
E
Galerix uenayae
Galerix rutlandae
F
Galerix wesselsae
C
Galerix symeonidisi
Apulogalerix pusillus
D
Galerix iliensis
Parasorex depereti
G
Parasorex ibericus
Parasorex kostakii
Parasorex socialis
Deinogalerix freudenthali
Deinogalerix masinii
H
Deinogalerix samniticus
I
13/99
Deinogalerix minor
J
5/99
Deinogalerix brevirostris
K
1/61
Deinogalerix intermedius
L
3/95
Deinogalerix koenigswaldi
Parasorex pristinus
Schizogalerix evae
M
-/67
Schizogalerix pasalarensis
Schizogalerix anatolicus
N
Schizogalerix duolebulejinensis
Schizogalerix moedlingensis
O
Schizogalerix voesendorfensis
Schizogalerix zapfei
Schizogalerix intermedius
P
1/-
Schizogalerix sinapensis
Q
1/-
Schizogalerix macedonicus
R
1/-
Schizogalerix sarmaticum

← Figure 6 - Strict consensus tree of the full-taxa matrix. Each node is indicated by a capital letter. Label's left node (in grey) indicates absolute Bremer supports (left) and bootstraps (right), when applicable.

metaconid; (2) P4 protocone higher than hypocone; (3) M1 distal arm not connected with distal cingulum.

Node F is a clade that includes two species of *Galerix*, *G. rutlandae* and *G. wesselsae.* It is based on 4 synapomorphies: (1) two-rooted p1; (2) p2 with distal cingulid; (3) m2 hypoconid approximately aligned with entoconid; (4) M1 triple protocone-hypocone-metaconule connection, through crests of equivalent height or through a high crest between protocone and hypocone.

Node G includes *Galerix symeonidisi* and all the most derived taxa of Galericinae, namely *Parasorex*, *Apulogalerix*, *Deinogalerix*, and *Schizogalerix.* It is identified by 9 synapomorphies: (1) p3 smaller than p4 (approximately between 75% and 90% of p4); (2) p1 with distal cuspid; (3) p4 paraconid relatively higher compared to protoconid; (4) p4 with discontinuous paralophid, interrupted by carnassial notch; (5) talonid as large as trigonid; (6) m3 entoconid placed distally to hypoconid; (7) P3 with strong hypocone; (8) distal arm of M2 hypocone not connected with distal cingulum; (9) well-developed M3 parastyle

The node H includes *Parasorex, Galerix iliensis, Apulogalerix, Deinogalerix,*and *Schizogalerix* on the basis of 9 synapomorphies: (1) p2 smaller than p3; (2) m1 labial cingulid poorly developed and not continuous, sometimes with precingulid; (3) distal margin of m1 talonid with continuous postcristid, postcingulid not connected with postcristid; (4) m1 with sharp metacristid united with entocristid; (5) crest-like P3 parastyle; (6) distal arm of metaconule extended to disto-labial corner of M1; (7) M1 with continuous, winding centrocrista, without distinct mesostyle; (8) distal arm of M1 hypocone not connected with distal cingulum; (9) M2 continuous, sinuous centrocrista, without distinct mesostyle.

The genus *Deinogalerix* (node I) displays the highest number of synapomorphies (43) between all nodes; it has also the highest R.I. score (13) of the entire tree, and a bootstrap of 99. The shared derived characters are: (1) anterior opening of infraorbital foramen above P4; (2) low condyle above toothrow; (3) angular process almost straight and oriented more or less disto-ventrally; (4) high horizontal rami under molars; (5) m1 approximately 115%-125% the size of p4 but more than 140% that of m2; (6) large P4, 130%-139% the size of M1; (7) bilobed i1-2 crown; (8) single-cusped, pointed lower canine, (9) higher than p3; (10) p1 with two fused roots; (11) p1 without disto-lingual cuspulid; (12) p2 without paraconid nor (13) distal cuspid; (14) p3 without paraconid; (15) mesial wall of p4 paraconid inclined distally; (16) blunt p4 paralophid; (17) tubercle-like p4 paraconid; (18) p4 talonid closed lingually by blunt cristid; (19) crest-like m1 paraconid; (20) inflated, steep m1 postparacristid; (21) m1 talonid narrower than trigonid; (22) m1 paralophid very elongated anteriorly; (23) m1 metaconid situated mesially to protoconid; (24) blunt m1 metacristid, divided from entocristid by notch; (25) m2 talonid narrower than trigonid; (26) m3 entoconid approximately aligned to hypoconid; (27) I2 as large as, or smaller, than I3; (28) bulging P3 protocone joined with hypocone; (29) shoulder-shaped P3 parastyle; (30) tubercle-like P4 parastyle, (31) not connected with paracone nor protocone; (32) P4 with paraconule; (33) well-developed and elongated P4 lingual lobe, narrow and squat tooth with relatively rounded lingual lobe; (34) M1-2 preprotocrista well separated from paraconule by groove; (35) M1 without centrocrista and with single mesostyle; (36) distal arm of M1 hypocone connected with distal cingulum; (37) M2 without labial cingulum; (38) M2 without centrocrista and with single mesostyle; (39) M2 hypocone with distal arm connected with distal cingulum; (40) poorly-developed M3 parastyle; (41) distal arm of M3 protocone not connected with metacone; (42) M3 paraconule without distal arm and with mesial arm connected with anterior cingulum; (43) M3 crest-like metacone extended like metastylar crest.

Node J includes the most derived species of *Deinogalerix*, i.e., *D. minor, D. brevirostris, D. intermedius* and *D. koenigswaldi.* It is identified by 13 synapomorphies: (1) nasals approximately in line with antorbital rim; (2) base of zygomatic arch extended over M1 to between M2-3; (3) poorly-developed antero-medial fossette of mandibular condyle; (4) p3 90%-100% the size of p4; (5) large P4, 140%-145% the size of M1; (6) i3 absent; (7) mesial wall of p4 paraconid secondarily uplifted; (8) p4 posterior cuspulid placed in median position or lingually; (9) m1 metaconid situated somewhat distally to protoconid; (10) m2 postparacristid connected with metaconid; (11) well divided P4 hypocone; (12) discontinuous M1 labial cingulum due to labial displacement of mesostyle; (13) short, poorly developed M3 parastyle, with squarish mesio-labial corner of crown. Also, node J has high R.I. (5) and very high bootstrap scores (99).

Deinogalerix brevirostris, *D. intermedius* and *D. koenigswaldi* are grouped together (node K) on the basis of only 1 synapomorphy: (1) P4 stepped outline of collar margin in mesial view. This node has R.I. score of 1 and bootstrap score 61.

Deinogalerix intermedius and *D. koenigswald* are placed in sister-taxon relationship (node L). The couple is identified by 3 synapomorphies: (1) ascending rami very inclined backwards; (2) long C - P2 and c - p4 diastemas; (3) lower canine much higher than p3. This clade is very supported, having R.I.=3 and bootstrap=95.

Parasorex pristinus and all species of *Schizogalerix* are grouped together in node M, which is identified by 6 synapomorphies: (1) m1 150% larger than p4 and 105%-120% than m2; (2) p4 metaconid located more mesially than protoconid; (3) m2 trigonid very compressed; (4) m2 metaconid situated far more mesially in relation to trigonid; (5) M1-2 elongated mesiolabially-distolingually; (6) M2 labial cingulum only mesially to metacone. Node M has bootstrap score 66.

Core-*Schizogalerix* cluster in node N, which is identified by 4 synapomorphies: (1) sharp m1 metacristid, divided by notch from entocristid; (2) discontinuous M1 labial cingulum; (3) M2 with sinuous and partially divided centrocrista and without mesostyle; (4) M3 relatively narrower lingually, not too compressed mesio-distally.

The majority of species of *Schizogalerix*, except early ones as *S. evae* and S. *pasalarensis* are included in node O which is identified by 8 synapomorphies: (1) p4 with complete paralophid; (2)

m1 hypoconid placed distally to entoconid; m1 (3) and m2 (4) continuous postcristid, connected with postcingulid; (5) P4 parastyle not connected with paracone nor protocone; (6) M1 without centrocrista and with double mesostyle; (7) M2 labial cingulum vestigial or absent; (8) M3 without distal cingulum.

The most derived species of *Schizogalerix*, namely *S. intermedius*, *S. sinapensis*, *S. sarmaticum* and *S. macedonicus* (node P) also share 8 synapomorphies: (1) one mental foramen below p3-p4 transition; (2) high horizontal rami under molars; (3) m1 with posthypocristid variously bent distally and also with postentocristid turned distally and fused with postcingulid; (4) m1 metaconid situated mesially to protoconid; (5) m1 anterolabial cingulid not extended distally to protoconid; (6) M1 without labial cingulum; (7) straight M2 labial margin; (8) M2 without centrocrista and with double mesostyle.

Schizogalerix sinapensis, *S. sarmaticum* and *S. macedonicus* belong to a clade (node Q) identified by 3 synapomorphies: (1) m2 posthypocristid variously bent mesially, with postentocristid strongly curved, bent distally and fused with postcingulid, the latter with accessory cuspulid; (2) P3 without parastyle; (3) P4 with disto-labial cuspule.

Finally, there is support of 2 synapomorphies for the sister-taxon relationship of *Schizogalerix sarmaticum* and S. *macedonicus* (node R): (1) m1 with posthypocristid variously bent mesially, and with postentocristid strongly curved distally and fused with postcingulid, the latter with accessory cuspulid and (2) P4 parastyle connected with paracone by short crests but not with protocone.

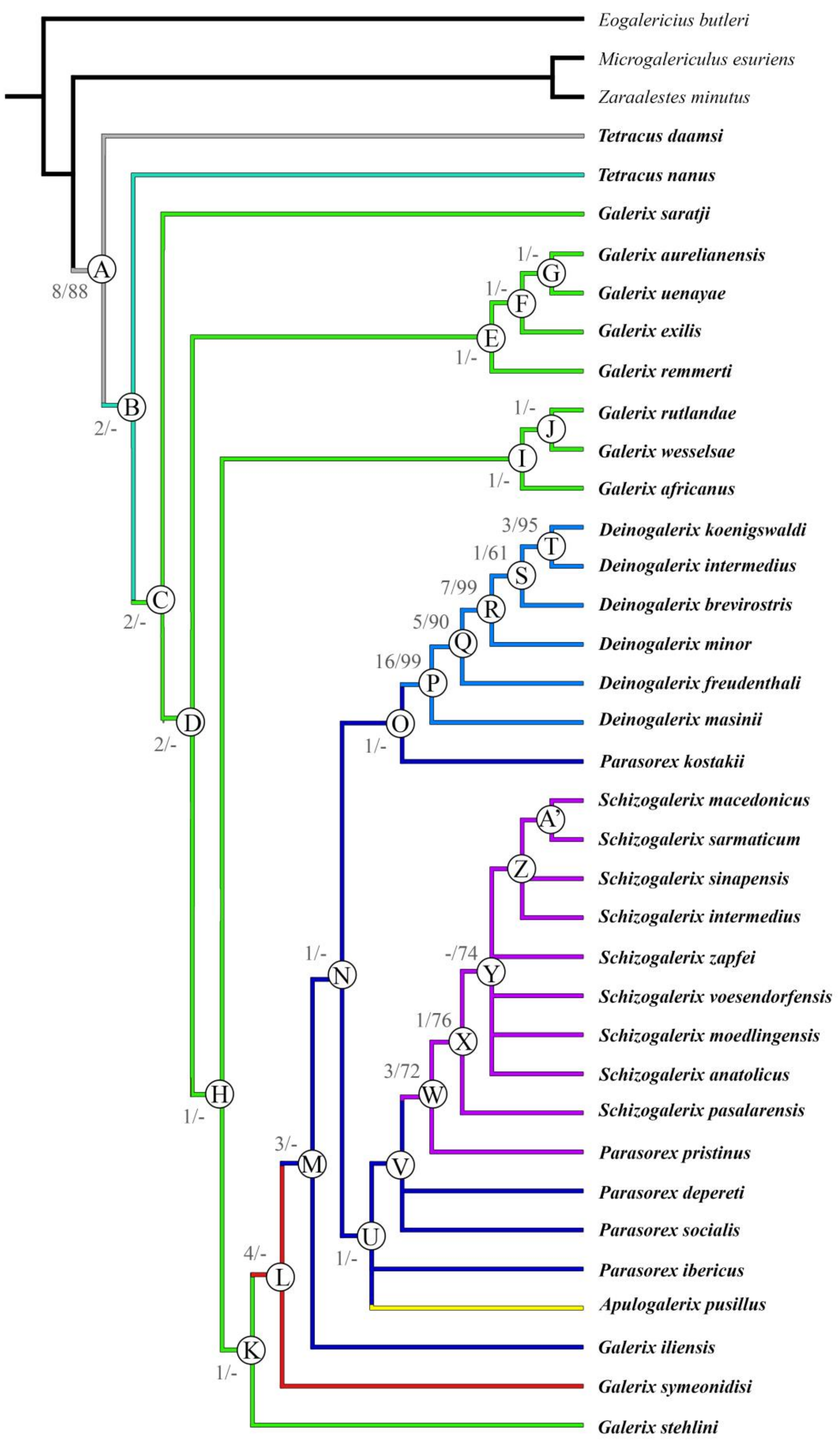
Repeating the analysis after exclusion of four “wildcard” taxa (*Deinogalerix samniticus*, *Riddleria atecensis*, *Schizogalerix duolebulejinensis* and *S. evae*) with a low number of coded characters (less than 50%) provided only 12 MPTs, from which the strict consensus tree (Fig. 7) was calculated.

Node A is the second-strongest node on the entire tree, with R.I. = 8 and bootstrap = 88. It includes all Galericinae, and is based on 10 synapomorphies: (1) p3 much smaller than p4 (less than 75% the size of p4); (2) p4 metaconid reduced to cuspulid next to protoconid; (3) p4 paraconid connected with protoconid by low and fairly straight crest; (4) tubercle-like m1 paraconid ; (5) sharp m1 metacristid, divided by notch from entocristid; (6) m3 with continuous postcristid and without distal cingulid; (7) m3 without hypoconulid; (8) P4 hypocone connected with protocone by prehypocrista and distal arm of protocone; (9) P4 poorly elongated and with lingual lobe expanded lingually; (10) sub-rectangular, elongated and narrow M1 compared to Galericinae *sensu lato*.

All Galericinae but *Tetracus daamsi* cluster in node B, which is identified by 4 synapomorphies: (1) p4 without precingulid; (2) oblique m1 paralophid, stretched anteriorly; (3) m2 with continuous postcristid and postcingulid not connected with postcristid; (4) P4 parastyle connected with mesial arm of protocone. The node is well-supported with R.I. = 2.

Node C, includes *Galerix saratji* and all the other Galericinae but *Tetracus*. It is characterized by 4 synapomorphies: 1) p2 without posterior cuspulid; (2) p4 with paraconid and protoconid not connected; (3) moderately protruding P4 parastyle; (4) M2 with paraconule and without distal arm. This node has R.I. = 2.

Node D gives origin to two clades, one including some species of *Galerix* (*Galerix remmerti, G.exilis, G. aurelianensis* and *G. uenayae*) and the other all the other species of *Galerix*(except *Galerix saratji*), *Parasorex, Deinogalerix, Apulogalerix,* and *Schizogalerix.* The clades are grouped sharing 2 synapomorphies: that is (1) p2 with anterior cuspule; (2) parastyle on P4 connected by crests with labial cingulum and paracrista. The retention index of this node is 2.


Eogalericius butleri
Microgalericulus esuriens
Zaraalestes minutus
Tetracus daamsi
Tetracus nanus
Galerix saratji
Galerix aurelianensis
Galerix uenayae
Galerix exilis
Galerix remmerti
Galerix rutlandae
Galerix wesselsae
Galerix africanus
Deinogalerix koenigswaldi
Deinogalerix intermedius
Deinogalerix brevirostris
Deinogalerix minor
Deinogalerix freudenthali
Deinogalerix masinii
Parasorex kostakii
Schizogalerix macedonicus
Schizogalerix sarmaticum
Schizogalerix sinapensis
Schizogalerix intermedius
Schizogalerix zapfei
Schizogalerix voesendorfensis
Schizogalerix moedlingensis
Schizogalerix anatolicus
Schizogalerix pasalarensis
Parasorex pristinus
Parasorex depereti
Parasorex socialis
Parasorex ibericus
Apulogalerix pusillus
Galerix iliensis
Galerix symeonidisi
Galerix stehlini
A
8/88
B
2/-
C
2/-
D
2/-
E
1/-
F
1/-
G
1/-
H
1/-
I
1/-
J
1/-
K
1/-
L
4/-
M
3/-
N
1/-
O
1/-
P
16/99
Q
5/90
R
7/99
S
1/61
T
3/95
U
1/-
V
W
3/72
X
1/76
Y
-/74
Z
A'

← Figure 7 - Strict consensus tree of the full-taxa matrix. Each node is indicated by a capital letter. Label's left node (in grey) indicates absolute Bremer supports (left) and bootstraps (right), when applicable.

Four species of *Galerix* (*Galerix aurelianensis, G. exilis, G. remmerti* and *G. uenayae*) are grouped together in a clade (node E) on the basis of 2 synapomorphies: (1) p4 talonid opened lingually; (2) crest-like P3 parastyle.

Node F includes *Galerix aurelianensis*, *G. exilis* and *G. uenayae.* It is based on only 2 synapomorphies, (1) p1 with disto-lingual cuspulid; (2) M2 distal arm of hypocone not connected with distal cingulum.

Finally, there is support of only 1 synapomorphy for the sister-taxon relationship of *Galerix aurelianensis* and *G. uenayae* (node G), (1) very protruding P4 parastyle.

The next clade (node H) includes all other Galericinae not listed until now; it is based on 4 synapomorphies: (1) base of zygomatic arch extended from above metastyle of M1 to whole M2; (2) high horizontal rami of mandible; (3) canine higher than p3; (4) P2 without distal cuspule.

Node I is a clade of three species of *Galerix* (*G. africanus, G. wesselsae* and *G. rutlandae*), which are grouped together by 1 synapomorphy, (1) m1 approximately 145%-150% the size of p4 and 110%-115% that of m2.

There is support of 3 synapomorphies for the sister-group relationship of *Galerix rutlandae* and *G. wesselsae* (node J): (1) p1 with two roots fused; (2) m2 hypoconid approximately aligned to protoconid; (3) M1 hypocone-protocone-metaconule triple connection, with crests of approximately same height or with higher crest between protocone and hypocone.

All other taxa of Galericinae, including, three species of *Galerix* (*G. iliensis*, *G. stehlini* and *G. symeonidisi*), *Parasorex, Deinogalerix*, *Apulogalerix* and *Schizogalerix*, are grouped together by 3 synapomorphies in a group (node K). The synapomorphies are (1) aboral extension of mandibular symphysis under p3; (1) p3 talonid with distal cingulid and central cuspulid, without *crista mediana*; (3) m2 talonid as large as trigonid.

Galerix symeonidisi branches off from the base of a clade (node L) based on 6 synapomorphies: (1) p4 with paraconid relatively higher than protoconid; (2) p4 with discontinuous paralophid, interrupted by carnassial notch; (3) m3 entoconid placed distally to hypoconid; (4) strong P3 hypocone; (5) M2 distal arm of hypocone not connected with distal cingulum; (6) M3 parastyle well-developed. This node is fairly well based, with R.I.=4.

Galerix iliensis is intermediate between *G. symeonidisi* and *Parasorex, Deinogalerix, Apulogalerix* and *Schizogalerix* (node M), based on 4 synapomorphies: (1) p3 talonid with distal cingulid and with disto-lingual cuspulid; (2) P3 parastyle shoulder-shaped; M1 (3) and M2 (4) continuous, winding centrocrista , without distinct mesostyle.

The next node (N) includes only representatives of the genera *Apulogalerix, Deinogalerix, Parasorex* and *Schizogalerix*. It is based on 3 synapomorphies: (1) p4 distal cuspulid present and displaced disto-lingually; (2) m1 with continuous postcristid and postcingulid not connected with the postcristid; (3) distal arm of metaconule extended to disto-labial corner of M1.

Parasorex kostakii and *Deinogalerix* cluster in Node O, on the basis of 3 synapomorphies: (1) m2 trigonid larger than talonid; (2) P4 parastyle tubercle-like and (3) not connected with paracone nor with protocone.

Deinogalerix is a very well-established clade (R.I.=16, bootstrap= 99), based on the highest number of synapomorphies (18) in all the tree (node P): (1) m1 approximately 115%-125% the size of p4 and over 140% that of m2; (2) large P4, 130% to 136%-139% the size of M1; (3) p4 with blunt paralophid; (4) p4 talonid closed by blunt crest; (5) m1 with inflated, steep postparacristid ; (6) m1 talonid narrower than trigonid; (7) m1 paralophid very elongated anteriorly; (8) blunt m1 metacristid, divided from entocristid by notch; (9) m1 entoconid situated approximately next to hypoconid; (10) bulging P3 protocone present, joined to hypocone; (11) p4 with paraconule; (12) narrow and squat P4 with well-developed and elongated lingual lobe, and with relatively rounded lingual lobe; (13) M1-2 preprotocrista well separated from paraconule by groove; M1 with (14) and

M2 without (15) centrocrista, both with single mesostyle; (16) poorly-developed M3 parastyle; (17) distal arm of M3 protocone not connected to metacone; (18) crest-like M3 metacone, extended as metastylar crest.

Five synapomorphies group together all the species of *Deinogalerix* but *D. masinii* in node Q: (1) angular process relatively thin dorso-ventrally; (2) low ascending rami; (3) reduced C - P2 and c - p4 diastemas; (4) m1 without precingulid, with only hint of labial cingulid between protoconid and hypoconid; (5) m3 talonid narrower than trigonid. This node is also well-established, with R.I.=5 and bootstrap=90.

The most derived species of *Deinogalerix* (*D. minor, D. brevirostris, D. intermedius* and *D. koenigswaldi*) are grouped by 10 synapomorphies (node R): (1) poorly developed antero-medial fossettes of mandibular condyles; (2) p3 about the size of p4 (90%-100% that of p3); (3) large P4, 140%-145% the size of M1; (4) secondarily uplifted mesial wall of p4 paraconid ; (5) p4 distal cuspulid displaced to median position of tooth or lingually; (6) m1 metaconid situated slightly distal to protoconid; (7) m2 postparacristid connected with metaconid; (8) P4 hypocone well divided; (9) discontinuous M1 labial cingulum due to labial displacement of mesostyle; (10) short, poorly developed M3 parastyle, with squarish outline of mesio-labial corner of crown. This node is very well established, with R.I.=7 and bootstrap=99.

Deinogalerix brevirostris, *D. intermedius* and *D. koenigswaldi* are placed together in a clade (node S) by only 1 synapomorphy, (1) P4 with stepped outline of collar margin P4 in mesial view. The bootstrap for this node is 61.

Finally, there is support of 3 synapomorphies for the sister-taxa relationship of *Deinogalerix intermedius* and *D. koenigswaldi* (node T): (1) ascending rami very inclined backwards; (2) elongated C - P2 and c - p4 diastemas; (3) lower canine much higher than p3. The retention index for this node is 3 and the bootrstap 95, which make it a rather well-based node.

Node U comprises *Apulogalerix, Schizogalerix* and all the remaining species of *Parasorex*; it is based on 6 synapomorphies: (1) one mental foramen under p3-p4 transition; (2) lower canine approximately as high as p3; (3) p1 with disto-lingual cuspulid; (4) m2 metacristid united to entocristid; (5) crest-like P3 parastyle; (6) weakly concave M2 labial margin, maximum concavity between metacone and paracone.

Node V includes *Parasorex socialis, P. depereti, P. pristinus* and *Schizogalerix*. It is based on 3 synapomorphies: (1) low horizontal rami under molars; (2) p4 distal cingulid with weak *crista mediana*; (3) one-rooted P1.

Node W groups *Parasorex pristinus* and *Schizogalerix*. It includes 6 synapomorphies: (1) p4 metaconid located more mesially with respect to protoconid; (2) m2 trigonid very compressed; (3) m2 metaconid situated very mesially to protoconid; (4) m2 metacristid divided by notch from entocristid; (5) M1-2 elongated mesiolingually-distolabially; (6) M2 with labial cingulum only mesially to metacone. This fairly well-supported node has a R.I. score of 3 and bootstrap score of 72.

The species of *Schizogalerix* (node X) are clustered by 4 synapomorphies: (1) sharp m1 metacristid, divided by notch from entocristid; (2) discontinuous M1 labial cingulum; (3) M2 centrocrista present, sinuous and partially divided, without mesostyle; (4) M3 relatively narrow lingually, not very compressed mesio-distally. The bootstrap is 76.

Except for the early *Schizogalerix pasalarensis*, the majority of the most derived species of *Schizogalerix* (node Y) and the common ancestor of *S. intermedius, S. sinapensis, S. sarmaticum* and *S. macedonicus* are grouped in a polytomy by 6 synapomorphies: (1) continuous p4 paralophid; (2) m1 hypoconid placed distally to entoconid; (3) m1 talonid with continuous postcristid and with postcingulid connected with postcristid, or posthypocristid variously bent mesially, with postentocristid bent distally and fused with postcingulid; (4) M1 without centrocristaand with double mesostyle; (5) M2 labial cingulum vestigial or absent; (6) M3 without distal cingulum. The bootstrap is 74.

Node Z includes the most advanced species of *Schizogalerix* (*S. intermedius*, *S. sinapensis*, *S. macedonicus* and *S. sarmaticum*); the node is supported by 7 synapomorphies: (1) one mental foramen situated under p4; (2) high horizontal rami under molars; (3) m1 metaconid very mesial to protoconid; (4) m2 anterolabial cingulid not extended distally to protoconid; (5) M1 without labial cingulum; (6) M2 labial margin straight; (7) M2 without centrocrista, with double mesostyle.

Finally, there is the support of 2 synapomorphies for the sister-taxa relationship of *Schisogalerix macedonicus* and *S. sarmaticum* (node A'): (1) distal margin of m1 talonid with posthypocristid variously bent mesially, with postentocristid strongly curved, bent distally and fused with postcingulid associated with accessory cuspulid; (2) m1 with accessory cuspid of hypoconid.

5 – Discussion

This systematic review is not only based on the results of the present analysis, but also on the patterns revealed by previous papers and on data from the literature (van den Hoek Ostende, 2001d; Ziegler, 2005; Borrani et al., 2018) to propose the most stable taxonomy for the analyzed taxa. The revised systematics is summarized in Table2.

Butler (1948)	Van Valen (1967)	Ziegler (1983)	McKenna and Bell (1997)	Van den Hoek Ostende (2001d)	Borrani et al. (2018)	This work
Galerix	*Galerix*	*Galerix*	*Galerix*	*Galerix*	*Galerix*	*Eotetracus* gen. nov.
?*Pseudogalerix*	*Pseudogalerix*	*Schizogalerix*	*Eochenus*	*Parasorex*	*Parasorex*	*Tetracus*
?*Tetracus*			*Tetracus*	*Schizogalerix*	*Apulogalerix*	*Galerix*
Tupaiodon			*Ocajila*	*Deinogalerix*	*Schizogalerix*	*Epigalerix* gen. nov
			Pseudogalerix		*Deinogalerix*	*Parasorex*
			Lantanotherium			*Apulogalerix*
			Echinosorex			*Schizogalerix*
			Schizogalerix			*Deinogalerix*
			Hylomys			
			Podogymnura			

Table 2 – The classification of Galericinae according to various authors (as from van den Hoek Ostende, 2001d).

SYSTEMATIC IMPLICATIONS

Tetracus

The genus includes two formally described species, *Tetracus nanus* (Aymard, 1846) and *Tetracus daamsi* Hugueney and Adrover, 2003. *Tetracus nanus* is known from the Early-Late Oligocene (MP 20/21-26) of Belgium, France and Spain (Crochet, 1975, 1995; Hugueney and Adrover, 2003; Remy et al., 1987; Smith, 2003, 2004), whilst *Tetracus daamsi* is an endemic Early Oligocene species of Paguera 1 and 2 (MP 22-23 of Majorca, Spain; Adrover et al., 1978; Hugueney, 1997; Hugueney and Adrover, 1982, 2003). Therefore, both the species are the earliest known Galericinae *sensu stricto*.

Borrani et al. (2018) considered *Tetracus nanus* as belonging to the genus *Galerix*; however, as noticed by van den Hoek Ostende (2018) and also on the basis of the present analysis, this species belongs to a genus of its own. Hugueney and Adrover (2003) listed the characters diagnostic for the genus, i.e., (1) p2 larger than p3 (as in *Galerix*); (2) p4 with more or less developed paralophid, (3) and with metaconid (in reduction through the evolution of the genus) connected to protoconid; (4) P3 without hypocone and with low protocone; upper molars with (5) well-developed paraconule connected to parastyle, (6) poorly developed metaconule distal arm and (7) straight lingual margin, (8) with cingulum; (9) M3 with large metacone not joined to distal cingulum, (10) small metaconule and (11) posterolingually opened trigon. However, in *Tetracus nanus* the metaconule on M3 can be very reduced or absent (Crochet, 1995). The well-developed p4 paralophid in *Tetracus daamsi* is also absent in *Tetracus nanus*, replaced by an almost straight, somewhat interrupted crest connecting the paraconid to the protoconid. *Tetracus daamsi* shows many characters that are plesiomorphic for Galericinae (i.e., presence of a well-developed precingulid on p4; short paralophid on m1, placed almost trasversally; continuous postcristid on m1; m2 distal cingulid not connected with postcristid and P4 parastyle connected with mesial arm of protocone). On the other hand, *Tetracus nanus* seems much more derived (e.g., the precingulid on p4 is absent, as in other Galericinae); for these reasons, *Tetracus daamsi* should be considered as a more primitive species, not directly related to *T. nanus*. It is highly probable that *Tetracus nanus* is more closely related to the Mio-Pliocene Galericinae than is *T. daamsi*; for these reasons, the latter species has been assigned to a genus of its own, *Eotetracus* gen. nov.

Riddleria

Riddleria is a monospecific genus that includes only *Riddleria atecensis* van den Hoek Ostende (2003b), known fromscanty remains from a single Early Miocene locality (Ateca III) of Spain. As reported by van den Hoek Ostende (2003b), this species is without doubt rather unusual, with a sub-quadrate M1 (with the labial margin only slightly larger than the lingual one) with concave margins. In the present analysis, *Riddleria* is identified by 16 synapomorphies, which are: (1) m1 only with precingulid; (2) m1 postparacristid present but notin reach of metaconid; (3) very anteriorly elongated, almost diagonal paralophid on m1; (4) metaconid placed very mesially compared to protoconid on m1; (5) m1 metacristid absent; (6) m2 metaconid placed very mesially than protoconid; (7) labial cingulid on m2 not extended posteriorly to protoconid; (8) talonid larger than trigonid on m2; (9) m3 distal cingulid and postcristid absent; (10) crest-like parastyle on P4; (11) M1-2 approximately subquadrate, with concave margins; (12) M1 centrocrista , continuous and winding, without mesostyle; (13) concave labial margin on M2, with maximum concavity between protocone and metacone; (14) M2 labial cingulum absent; (15) protocone connected both to hypocone and metaconule, high crest between protocone and hypocone; (16) M3 parastyle prominent antero-labially. Van den Hoek Ostende (2003b) considered *Galerix* as a possible ancestor of *Riddleria*, mainly on the basis of its stratigraphic position and the shape of P3, with an expanded lingual lobe with only one cusp (protocone). The only M3 tentatively assigned to *Riddleria* is virtually indistinguishable from those of *Galerix*. *Riddleria* could be considered an endemic, very peculiar sub-genus of *Galerix*. However, it should be noted that the analysis (node D, Fig. 6) is unable to resolve its phylogenetic position inside *Galerix*, and the too scanty remains prevents to include it in the 37-taxa analysis. Therefore, there are 3 possible different placements of *Riddleria* in the Galericinae sub-family tree:

1) *Riddleria* can be considered an intermediate between *Galerix saratji* and other Galericinae, endemic of Spain and immigrated from East Europe or even Anatolia at the beginning of the Miocene.

2) *Riddleria* could be a very peculiar, endemic *Galerix*. *Riddleria* would thus be closely related to other early members of *Galerix*, but with very unusual adaptations, especially regarding the shape of upper molars.
3) *Riddleria* is a transitional genus between *Galerix* and *Epigalerix symeonidisi*, more related to *Parasorex*-like taxa than to *Galerix* itself. This is the weakest hypothesis, because *Riddleria* lacks all the derived traits associated with *Epigalerix* and other *Parasorex*-like taxa (e.g., it has a unicuspidate lingual lobe on P3, without even a small hypocone-like cuspule).

For these reasons, the affinities of *Riddleria* with other *Galerix*-like Galericinae are still unclear; further studies and new future finds will probably clarify its affinities.

Galerix

Galerix has been considered widespread in Europe, Asia and Africa, from the latest Oligocene (*Galerix saratji*; van den Hoek Ostende, 2001a, b) to the Middle/Late Miocene transition (*Galerix* cf. *exilis*; Prieto et al., 2011). Presently, 11 species have been assigned to the genus: *Galerix africanus* Butler, 1956a; *G. aurelianensis* Ziegler, 1990, *G. exilis* (de Blainville, 1839), *G. iliensis* (Kordikova, 2000), *G. remmerti* van den Hoek Ostende, 2003, *G. rutlandae* Munthe and West, 1980, *G. saratji* van den Joek Ostende 1992, *G. stehlini* (Gaillard, 1929), *G. symeonidisi* Doukas, 1986, *G. uenayae* van den Hoek Ostende, 1992 and *G. wesselsae* Zijlstra and Flynn, 2015. Nonetheless, there are so many differences between the various species assigned to this genus than it is easier to define what is not *Galerix* than what it is. This is also the reason why *Tetracus nanus*, an earlier species rather similar to *Galerix* and near the origin of the species that are attributed to latter genus, has been assigned to *Galerix* by some authors (van den Hoek Ostende, 2001d; Borrani et al., 2018). in his revision of *Galerix*, van den Hoek Ostende (2001d) provided 4 distinctive characters, apart from size: (1) p3 smaller or as large as p2; (2) P3 usually without hypocone; (3) protocone-metaconule connection present in at least some specimens of M1-2; and (4) continuous distal cingulum on M1-2 in at least some specimens. However, these characters are not exclusive of the latter genus.

A p3 smaller or as large as p2 is also present in *Tetracus*; it is possibly a primitive condition for Galericinae, but a synapomorphy compared to earlier Galericinae *sensu lato* (i.e., *Eogalericius, Microgalericulus* and *Zaraalestes).* This character is the most frequent within *Galerix* and *Tetracus*, except for *G. rutlandae*, which has a distinctly smaller p2 than p3 (Zijlstra and Flynn, 2015) as in earlier species or in *Deinogalerix, Parasorex* and *Schizogalerix*. As shown by the analysis, it is possibly a character achieved independently by *Galerix rutlandae*, which does not share a common ancestor with the more derived, *Parasorex*-like species.

The presence or absence of a small hypocone on P3 is shared by various members of *Galerix*. In some species, such as *G. aurelianensis, G. rutlandae* and *G. stehlini*, as well as in Galericinae *sensu lato* and *Tetracus*, P3 has no hypocone, whereas in all the other species P3 may show a small hypocone. There are also 3 species, i.e., *G. iliensis, G. symeonidisi* and *G. wesselsae*, in which the hypocone is very developed as it is in *Deinogalerix, Parasorex* and *Schizogalerix*,.

The protocone-metaconule connection on M1-2 should be considered a primitive character rather than a derived character: for instance, in *Tetracus*, as well as in *Eogalericius* and *Zaraalestes*, protocone and metaconule are always connected, while the contemporary presence of a lower connection between hypocone and protocone (“triple connection”) is variable. This connection is also not exclusive of the genus *Galerix*: in some specimens of at least two species of *Parasorex, P. depereti* and *P. kostakii*, there is a triple connection, with higher crest between protocone and metaconule, (e.g., around 20% of M2s in *P. depereti* and 26% in *P. kostakii*; Masini et al., 2019); therefore, this character cannot be considered diagnostic for *Galerix*.

Finally, the distal cingulum not interrupted by the distal arm of the metaconule on upper molars is not an exclusive character of *Galerix*, but also occurs in *Tetracus*, *Riddleria* and at least in some specimens of *Zaraalestes* and *Deinogalerix*. This is yet another synapomorphy of earlier Galericinae, because in earlier Eocene species (e.g., *Eogalericius*) the metaconule distal arm is extended to the postero-labial corner of the tooth, but it is not a character that clearly identifies *Galerix* from other groups, because some species of the latter genus (e.g., *G. exilis*, *G. saratji*) have an extended distal arm of the metaconule that interrupts the distal cingulum.

From the analysis, some species of *Galerix* resulted having different placements along the trees: *G. saratji* is the basal-most species, intermediate between *Tetracus* and other Galericinae, in both topologies; this is in agreement with its relatively early age (MP30-MN 1). The synapomorphies that identifies this node (node C, Fig. 6; node C, Fig. 7) are the same between trees: (1) absence of postero-lingual cuspid on p4; (2) no connection between paraconid and protoconid on p4; (3) less developed parastyle on P4 compared to earlier species and (4) M2 paraconule without distal arm; it also differs from following nodes for two characters in both topologies of tree, i.e., (1) no anterior cuspulid on p2; (2) protocone connected with hypocone on P4 with both prehypocrista and postprotocrista. More in detail, the latter two characters are present only in a limited number of other species: the p2 anterior cuspulid is absent in all other Galericinae but *Tetracus* and two species of *Galerix* (*G. wesselsae* and *G. rutlandae*), whilst only *Tetracus* and *Schizogalerix evae* show the P4 protocone and hypocone on P4 connected to one another with prehypocrista and postprotocrista (in *S. evae* this character is possibly the result of a parallelism with earlier species). In both trees, the presence of an anterior cuspulid on p2 is also a synapomorphy shared by *G. rutlandae* and *G. wesselsae*; it can therefore be a character that possibly evolved twice, mimicking the plesiomorphic condition for this group, rather being a real plesiomorphy. For all these reasons, *Galerix saratji* is a mix of relatively derived and plesiomorphic characters, possibly reflecting an intermediate phylogenetic position between *Tetracus* and *Galerix*; however, the low number of synapomorphies of the next node makes to consider more parsimonious still consider *Galerix saratji* tentatively as a member of *Galerix.*

In the full-taxa analysis (Fig. 6), *Galerix africanus, G. exilis, G. remmerti, G. stehlini, Riddleria atecensis,* the common ancestors of *G. aurelianensis-G. uenayae, G. rutlandae-G. wesselsae* clades and that of more derived *Parasorex*-like Galericinae are placed together in a major polytomy (node D). Conversely, in the 37-taxa analysis (Fig. 7), they are scattered more widely: a basal clade of "true" *Galerix,* including *G. remmerti, G.exilis, G.uenayae* and *G. aurelianensis* (node E), which shares two characters: (1) talonid basin of p4 opened lingually, and (2) crest-like parastyle on P4. The other species of *Galerix* might form a paraphyletic group, closer to *Parasorex*-like species. Some species of *Galerix* may be more related to *Parasorex* than to *G. exilis*; however, for the sake of simplicity and because the nodes are not particularly well-based, all the other species of *Galerix* (excluding *G. symeonidisi* and *G. iliensis*) are maintained in the genus.

The imperfectly known *Riddleria* is still considered a separated genus (see above). However, both analyses provide two clades of *Galerix*: one of Pakistani species (*Galerix wesselsae* and *G. rutlandae*) and the another including *Galerix aurelianensis* and *G. uenayae* (nodes E and F, Fig. 6; J and G, Fig. 7). Zijlstra and Flynn (2015) claimed it is unlikely that *Galerix rutlandae* is a descendant of the earlier *Galerix wesselsae,* with which it sometimes coexists; however, their placement in the same clade suggests the existence of an Asian group of *Galerix*. This clade is identified by 3 synapomorphies in both tree topologies: (1) p1 costantly double-rooted; (2) m2 hypoconid always approximately aligned with the entoconid and (3) M1 protocone always connected with hypocone and metaconule by equally strong crests, or with a stronger connection between protocone and hypocone. Furthermore, in the 37-taxa analysis an additional character was provided (i.e., p1 without distal cingulid), not present in any other *Galerix*. As suggested by the 37-taxa topology, *Galerix africanus*, *G. rutlandae* and *G. wesselsae* may be somewhat related (node I, Fig. 7), on the basis of the relatively enlarged m1 compared to p4 (see Fig. 10 in Appendix IV).

However, it is more plausible that *Galerix africanus* immigrated in Africa from Asia during the Early Miocene rather than the opposite, as suggested by the occurrence of early *Galerix* species in Central Asia and Near East. In particular, by some authors (van den Hoek Ostende et al., 2015; van den Hoek Ostende, 2018) proposed *Galerix wesselsae* as possible ancestor of *Galerix symeonidisi*; this opinion is supported by the present analysis. In fact, despite the presence of some characters typical of Parasoricini (e.g., well-developed P3 hypocone and M3 parastyle prominent anterolabialally), a whole series of important characters concerning p4 (e.g., p4 with paralophid and well-developed protoconid) that could link it with this group are missing.

Galerix aurelianensis and *G. uenayae* are sister-taxa in both tree topologies (node E, Fig. 6; node G, Fig. 7); but based on only one synapomorphy, i.e., P4 parastyle very extended mesially. The 37-taxa analysis provided two additional synapomorphies: (1) m2 postparacristid constantly in reach of metaconid; (2) M1 hypocone not connected to distal cingulum. The latter character is present also in *G. exilis*, which however probably seems more closely related to *G. aurelianensis* (Ziegler, 1990). The other two characters are shared by *Galerix aurelianensis* and *G. uenayae*; this would implies a closer relationship between these two species than to *Galerix saratji*, contrary to what was argued by van den Hoek Ostende (1992). In the more resolved tree *Galerix aurelianensis* and *G. uenayae* result being the most advanced species of “true” *Galerix*, in spite their earlier stratigraphic position than *G. exilis*. The very high variability observed in *Galerix exilis* may have “reversed” the polarity of some characters, making the older species *G. aurelianensis* and *G. uenayae* seem more advanced than the younger *G. exilis*. Therefore, *Galerix uenayae* and *Galerix aurelianensis* may be more closely related to *Galerix remmerti* and *Galerix exilis* than to other taxa; alternatively, *G. uenayae* may be is one of the basal-most members of the group, that possibly immigrated and flourished in Europe from Anatolia.

In both tree topologies, as also recognized by Borrani et al. (2018), *Galerix symeonidisi*, but especially *G. iliensis*, are not members of the group of “true” *Galerix*. As already noticed by

Borrani et al. (2018), *Galerix iliensis* shares many typical traits with *Parasorex*, except the presence of a p4 preprotocristid and of a M1-2 metaconule distal arm not extended postero-labially. Both these traits are plesiomorphic for the genus, and anyway *Galerix iliensis*is nested in a major polytomic *Parasorex*-like group (including *Apulogalerix*; node H, Fig. 6), or is the sister taxon of a clade that includes *Parasorex*, *Apulogalerix*, *Deinogalerix* and *Schizogalerix* (node M, Fig. 7). However, because other characters considered diagnostic are missing (e.g., the relative size between p2 and p3), and because the next nodes are poorly based (R.I.=1) in the 37-taxa tree (Fig. 7), to consider *Galerix iliensis* as a member of *Parasorex* would be more parsimonious than founding an entirely new genus on it.

On the other hand, *Galerix symeonidisi* seems to be a “true” transitional species between *Galerix* and *Parasorex*. In both tree topologies, it is the sister taxon of the clade including *Galerix iliensis*, *Parasorex*, *Deinogalerix, Apulogalerix* and *Schizogalerix* (node G, Fig. 6; node L, Fig. 7). It shares a combination of primitive and derived characters: like more derived *Parasorex*-like species, it has a relatively high p4 paraconid, may have a crest connecting the paraconid to the protoconid that is probably ancestral to the “true” paralophid of many *Parasorex*, *Deinogalerix* and *Schizogalerix* species, the entoconid is placed distally to the hypoconid on m3, the P3 hypocone is always present and strong, the M2 hypocone distal arm not connected to the distal cingulum, and the M3 parastyle is prominent antero-labially. On the other hand, *Galerix symeonidisi* still retains a continuous M1-2 centrocrista, more or less parallel to the labial margin of the tooth and without mesostyle, as well as p2 and p3 relatively sized like earlier *Galerix* and *Tetracus* species. For these reasons, in spite of its being clearly a more advanced species compared to “true” *Galerix G. symeonidisi* lacks a pair of characters typical of more derived *Parasorex*-like species, i.e., a well-developed paralophid on p4 and p2 clearly smaller than p3. For these reasons, a new genus is proposed for *Galerix symeonidisii, Epigalerix* gen. nov.

Deinogalerix

Its gigantic size and many synapomorphies (e.g., bunodont P3 and p4, mandible with small coronoid process and low condyle) make *Deinogalerix* one of the most peculiar members not only of Galericinae, but also of the entire order Eulipotyphla. The genus was described by Freudenthal (1972).

Deinogalerix includes six species from Gargano, Apulia (*Deinogalerix brevirostris* Butler, 1980; *Deinogalerix freudenthali* Butler, 1980; *Deinogalerix intermedis* Butler, 1980; *Deinogalerix koenigswaldi* Freudenthal, 1972, *Deinogalerix masinii* Villier et al., 2013; *Deinogalerix minor* Butler, 1980) and one from Scontrone, Abruzzo (*Deinogalerix samniticus* Savorelli et al., 2017). The two areas belonged to a paleoisland, called the Apulia Platform (Patacca et al., 2013).*Deinogalerix samniticus* is Tortonian (MN 10) in age and thus the earliest representative of the genus (Patacca et al., 2013; Savorelli et al., 2017). The Gargano species are probably of Messinian age (Savorelli et al., 2016, 2019). In the full-taxa analysis, node I is not resolved because *Deinogalerix samniticus* is imperfectly known and the most primitive of the species from the Gargano "Terre Rosse", *Deinogalerix masinii,* is placed in a polytomy. This opens to two possible scenarios:

I. *Deinogalerix samniticus* is the most primitive of all the species assigned to *Deinogalerix*. In fact, the species is distinct from any other member of the genus by having straight profile of the collar on P4, unusual dental proportions (p3 75% smaller than p4; m1 around 170% longer than m2) and absence of M2 hypocone distal arm. It is also larger than the earliest "Terre Rosse" species *D. masinii* and *D. freudenthali* and approximates the size of the stratigraphically younger *Deinogalerix intermedius*. This would imply a later origin of the Gargano clade, possibly independent of that from which emerged *D. samniticus*.

II. *Deinogalerix samniticus* is more derived than *Deinogalerix masinii*, and placed phylogenetically between the latter and the other Gargano species. Under this perspective, the “Terre Rosse” clade would have originated at a time earlier than MN 10. Several lines of evidence contrast this conclusion: the Gargano members of *Deinogalerix* show an evolutionary trend of increase in size over time, from the small-sized early species (*D. masinii, D. minor* and *D. freudenthali*) to the much larger late representatives (*D. brevirostris*, *D. intermedius* and *D. koenigswaldi*). Nonetheless, we cannot exclude that *Deinogalerix samniticus* achieved its dental characteristics and larger size by rapidly evolving in total isolation from the other early members of *Deinogalerix* distributed on the Gargano part of the Abruzzo-Apulia Platform. *Deinogalerix masinii* would therefore have remained smaller and more primitive than *D. samniticus*, maintaining the m2 talonid as large as the trigonid (while *D. samniticus* reduced the m2 talonid, as occurred, later on, in the other, more advanced species of the genus).

Interestingly, in the 37-taxa topology *Deinogalerix masinii* (node P, Fig. 7) has only one autapomorphy, i.e., P4 protocone approximately as high as hypocone, similarly to *D. samniticus*. In contrast, in the full-taxa topology (node I, Fig. 6) *D. masinii* has two more autapomorphies, i.e., m2 talonid approximately as large as the trigonid and discontinuous M2 labial cingulum. At least the first two characters might be related to its primitiveness; if so, *Deinogalerix masinii* would be very close to the ancestor of all the other Gargano species, and maybe (if *D. samniticus* were somewhat more derived) to that of the whole genus *Deinogalerix*.

In both trees *Deinogalerix freudenthali* (node I, Fig. 6; node Q, Fig. 7) exhibits no autapomorphies. Unlike *Deinogalerix masinii*, the species may be the direct ancestor of all the other Gargano species (as proposed by Butler, 1980), or that at least very close to it.

In both trees *Deinogalerix minor* is placed at the base of a clade including the advanced *D. brevirostris*, *D. intermedius* and *D. koenigswaldi*. Similarly to *D. freudenthali*, in both trees *Deinogalerix minor* shows no autapomorphies and is therefore the likely ancestor of the most derived Gargano species (if it is already present in fissure F15; see Savorelli et al., 2019 for a complete discussion) or the closest to it.

On the other hand, in both trees (node K, Fig. 6; node S, Fig. 7) the clade is based on only one synapomorphy, that is the step-shaped labial collar on P4. We cannot exclude that this may be the result of parallelism between *D. brevirostris*, *D. intermedius* and *D. koenigswaldi*. At the same time, the only other character distinguishing *D. brevirostris* from *D. minor* in both trees is the absence of the M3 distal cingulum in the former species. In sum, *Deinogalerix minor* and *D. brevirostris* may represent end members of the same evolutionary lineage, as suggested by Butler (1980) and Savorelli et al. (2019).

The two largest species of the genus, *Deinogalerix intermedius* and *D. koenigswaldi*, are included in a clade with well-supported sister-group relationship in both trees (node L, Fig. 6; node T, Fig. 7). As in the case of *Deinogalerix minor* and *Deinogalerix brevirostris*, there are minimum differences between *D. intermedius* and *D. koenigswaldi*: *Deinogalerix intermedius* is not only smaller than *Deinogalerix koenigswaldi* (although the size ranges of p3 and p4 of the two species partially overlap; see Savorelli et al., 2019), but it also differs by having a smaller, and possibly plesiomorphic p3; furthermore, *Deinogalerix koenigswaldi* has a shallower dorsal groove on the angular process and a very low coronoid process. Also these characters may suggest that both *Deinogalerix intermedius* and *D. koenigswaldi* are the extremes of the same phyletic lineage.

As stressed by some authors (*inter alios* Borrani et al., 2018; Butler, 1980; Villier et al., 2013), the presence of a metastylar crest on M3 is one of the most peculiar features of *Deinogalerix*, apparently shared with Hylomyinae. However, as reported in “Relation between Galericinae, Hylomyinae, and Tupaiodontinae” (see section ” Comparisons between extant and extinct

Galericinae and other Paleogene Eulipotyphla), the metastylar crest is not homologous to the structures occurring in present-day taxa; therefore, it is a synapomorphy of *Deinogalerix* itself among Galericinae.

Deinogalerix has been proposed to be a scavenger (Freudenthal, 1972), a predator (Butler, 1980; van den Hoek Ostende, 2001) or even an herbivore that occasionally fed on invertebrates and carrions (Villier, 2012). The peculiar morphologies of this genus are indeed difficult to be related to a specific diet; however, a hypothesis can be made from comparisons with living mammals. Indeed, the most peculiar characteristics of *Deinogalerix* are 1) the gigantic size, much larger, even in the smaller, earlier species (i.e., *Deinogalerix freudenthali* and *D. masinii*), than any other living or extinct Erinaceidae; 2) I1 much larger compared to other incisors; 3) lower canine very high and pointed, higher than p3 (in particular in *Deinogalerix intermedius* and *D. koenigswaldi*); 4) very large P4 compared to M1 and, in particular, M2-3; 5) elongated trigonid on m1; 6) the bunodont premolars, in particular P3 and p4; 7) well-developed and elongated angular process, more or less displaced labially; 8) elongated snout, often with diastemas; 9) low coronoid process; 10) very low condyle and (11) well-developed sagittal and nuchal crests (at least in the most derived species).

As reported by Butler (1980, and references therein), erinaceids are usually opportunistic feeders, which usually feed on mollusks, arthropods and annelids; however, *Echinosorex* can even feed on fishes, and *Erinaceus* may catch mice. On the basis of cranial and skeletal morphologies, Butler (1980) proposed a relatively slow-moving, predatory animal, which mainly sought prey in the litter with its elongated snout; the low coronoid process, very suited for wide gape, and the particularly well-developed temporal musculature suggest fast-closing mandibles, particularly adapted to catch small animals. Villier (2012), on the other hand, proposed that *Deinogalerix* was mainly a vegetarian mammal, occasionally feeding on small animals and carrions, mainly because the absence of sharp teeth and the presence of a well-developed, bulging P3 hypocone. The presence of a P3 hypocone in Galericinae has been considered a hint of a more herbivorous diet by van den

Hoek Ostende (2001). However, it should be noticed that, even if not particularly sharp, the elongated postparacristid on m1 is a shearing surface, that occluded with the paracone-parastyle on P4. Of course, the relatively short limbs of *Deinogalerix* (as already noticed by Butler, 1980) compared to other carnivore mammals rule out the hypothesis of an active chasing predator.

Deinogalerix is in some respects very similar to the giant tenrec (*Tenrec ecaudatus* Schreber, 1778) among living taxa: the relatively large size, the low coronoid process, the elongated jaws with many diastemas, the high-crowned and pointed canines (in particular the lower ones), the well-developed cranial crests (especially the nuchal one) are all shared traits by both *Deinogalerix* and *Tenrec*. *Tenrec ecaudatus* is an omnivorous species, that feeds mainly on invertebrates and small vertebrates, which it catches probing fissures and litters with the elongated muzzle (Oron and Crompton, 1985; Stephenson et al., 2016). We can speculate that *Deinogalerix* had similar food procurement and feeding habits. Yet, the more developed sagittal crests and angular processes of *Deinogalerix* (especially of the largest, more derived species *Deinogalerix koenigswaldi*) indicate a particularly well-developed *musculum temporalis* and *m. pterigoideus internus* (see Villier, 2012), which indicate a particularly fast bite and powerful grinding action of the molars, respectevely (Butler, 1980). Butler (1980) argued that the labially divergent angular process in *Deinogalerix intermedius* and *D. koenigswaldi* may imply very wide mouth gaping. Villier (2012) noticed that the horizontal elongation of the ascending rami in *Deinogalerix* is associated to an augmented efficiency of the premolar series; however, he stated that the absence of retroarticular processes to stabilize the mandibular condyle in the glenoid fossa decreases the speed with which the jaws can be closed. Butler (1980) also underlined that the proportions of the forelimb, which is relatively elongated and with a relatively larger hand compared to other erinaceids, could be useful for "parting vegetation and turning stones during the searching of foods" (Butler, 1980: p. 55). All these lines of evidence and the absence of predator mammals in the "Terre Rosse" fauna (except for the marine otter *Paralutra garganensis;* Masini et al., 2010) suggests that *Deinogalerix* played at least partially the ecological role of small, mainly insectivore carnivores, as jackals or coatis. Due to the shorter muzzles, the less developed sagittal, nuchal crests and lower canine and the higher ascending rami, the smaller species of *Deinogalerix* (i.e., *Deinogalerix brevirostris, D. freudenthali, D. masinii, D. minor* and possibly *D. samniticus*) were probably more omnivorous than the larger and more derived ones *D. intermedius* and *D. koenigswaldi.* In general, the giant galericines of the Apulia Platform were probably relatively carnivorous, and fed mainly on hard-shelled prey, such as crayfishes, crabs, large beetles and snails, crushing their shells with the premolars and the elongated, blunt paralophid of m1, and using the molars to grinding action (Masini, pers. comm.). We cannot exclude that they also occasionally fed on small vertebrates (such as snakes, lizards, frogs and maybe even small tortoises; see *inter alios* Delfino, 2012 for a complete list of the "Terre Rosse" herpetofauna) as well as on fruit, seeds and eggs. In particular, the largest and most derived species of *Deinogalerix* may have more or less frequently preyed upon the small mammals of the "Terre Rosse" fauna (possibly the smaller species of the rodent genera *Mikrotia*, *Stertomys* and *Hattomys* and also *Apulogalerix*; see Masini et al., 2010). Of course, this does not rule out the possibility of occasional scavenging of larger carrions, such those of the artiodactyl *Hoplitomeryx*. Nonetheless, the overall skeletal morphology of *Deinogalerix* suggests a not very active, pursuing or ambushing predator, which hunted preys roughly its size. More likely, it probably probed leaf litter and holes with its snout as do living tenrecs, pulling out relatively small prey from lairs.

There are perhaps other three species of extinct erinaceids with adaptations similar to those of *Deinogalerix*: the Middle Eocene species *Eochenus sinensis*, the Early Miocene *Galerix africanus* and the Middle Miocene *G. stehlini*. However, only *Eochenus sinensis* has a mandibular morphology comparable to that of a small-sized, early species of *Deinogalerix*, with a relatively low condyle, high and unicuspidate lower canine and diastema between lower canine and p1, as can be found in long-muzzled mammals (Wang and Li, 1990). *Eochenus*, probably has distant relationships with "true" Galericinae. It has a 2.36 mm-long m1, in average, almost 4 times smaller than an average m1 of the smallest *Deinogalerix* species, *D. masinii* (8.77 mm; see Savorelli et al., 2019). This suggests that *Eochenus* was mainly a carnivore that fed on a variety small food items, such as terrestrial arthropods, mollusks and small vertebrates, like lizards and amphibians, without particular specialization to predation. Similar adaptations may be assumed for *Galerix stehlini* and especially *G. africanus*; the latter is a very large *Galerix* species (m1 mean length= 3.75 mm. in mean; see Butler, 1984), with a relatively strong mandibular ramus (compared to *Eochenus*). Altough the lower canines of *Galerix africanus* and *G.stehlini* are unicuspidated and higher than p3, they are anyhow relatively lower than the canines of *Deinogalerix* and *Eochenus*, whereby we can assume that the two species possibly had more omnivorous diet.

Parasorex

As for *Galerix*, it is simpler define what is not a *Parasorex* than what it actually is. Presently, 5 European Early Miocene (MN 4) to Early Pliocene (MN 14-15) species have been assigned to this genus: *Parasorex depereti* (Crochet, 1986), *Parasorex ibericus* (Mein and Martín-Suárez, 1993), *Parasorex kostakii* (Doukas and van den Hoek Ostende, 2006), *Parasorex pristinus* (Ziegler, 2003) and *Parasorex socialis* von Meyer, 1865. As discussed above, at least *Galerix iliensis* might belong to the genus, while *Parasorex pristinus* could be assigned to *Schizogalerix* (as it was in the original diagnosis by Ziegler, 2003)

Van den Hoek Ostende (2001d) reported that *Parasorex* is characterized by having p2 smaller than p3, p4 with well-developed paralophid and metaconid, no protocone-metaconule connection on M1-2, metaconule distal arm extended to the disto-labial corner of M1-2s and P3 always provided with hypocone. Nonetheless, some species do not fit this definition.

A p2 smaller than p3, for example, is a character also shared with *Apulogalerix, Deinogalerix* and *Schizogalerix*; probably, it is a parallelism with earlier Galericinae *sensu lato*, and evolved from a

Galerix/Tetracus-like condition with p2 larger than p3, as shown by *Epigalerix symeonidisi*. This character is shared with all the species considered, except for *Parasorex kostakii* and *P. pristinus* whose premolars are unknown.

Similarly, a well-developed paralophid, with or without carnassial notch, is not a character typical only of *Parasorex* but also of *Deinogalerix* and *Schizogalerix*; in some specimens of *P. kostakii* it is absent. Also a well-developed metaconid is yet another character shared by all these genera. Only in *Parasorex kostakii* the metaconid on p4 might be reduced or even absent, like in earlier *Galerix*-like species.

The absence of a connection between protocone and metaconule on M1-2 is the character that less stands to the test of time: today we know that at least in *Parasorex depereti* and *P. kostakii* a significant percentage of these teeth, in particular M2 (see Masini et al., 2019) have a well-developed connection between protocone and metaconule. Ziegler (2005) reported the presence of very few, aberrant upper molars of *Parasorex socialis* from Petersbuch (Germany) with this characteristic, whic is probably plesiomorphic for the genus. Moreover, the metaconule distal arm on M1-2 stretched to the disto-labial corner of M1-2s is a character shared by all the species assigned to *Parasorex*, but is also shared with *Apulogalerix*, *Schizogalerix* as well as some specimens of *Deinogalerix*; therefore, it is probably a primitive character shared by these genera.

The presence of a well-developed P3 lingual lobe with two cusps is shared by all the species of this genus. In some specimens of *Parasorex depereti* however the protocone may be reduced or even absent (it is probably a sign of relative primitiveness, but a result of convergence; see Masini et al., 2019), while in *Apulogalerix* the hypocone may be secondarily reduced or even absent (Masini and Fanfani, 2013), mimicking earlier Galericinae, such as *Tetracus* and *Galerix*, and anyway the presence of a well-developed P3 hypocone is also shared with *Epigalerix symeonidisi, Galerix iliensis, Deinogalerix* and *Schizogalerix*.

The more resolved tree topology (node U and V, Fig. 7), shows that *Parasorex* may include species more closely related to *Schizogalerix* and *Deinogalerix* than to *Galerix symeonidisi* and *G. iliensis*, with *Parasorex kostakii* that stems at the base of the *Deinogalerix* clade and *Parasorex socialis, P. ibericus* and *P. pristinus* (together with *Apulogalerix*) that are located in the lineage that leads to *Schizogalerix*. However, although this interpretation recalls van den Hoek Ostende's (2001d), in which *Schizogalerix* is essentially a genus very close morphologically to *Parasorex*, the nodes are poorly supported, except that of *Parasorex pristinus* + *Schizogalerix* one. For these reasons, and for the sake of simplicity, the relationships of *Parasorex pristinus* are simpler to analyze from polytomy in the less resolved tree (Fig. 6, node H). *Parasorex ibericus* is similar, for some respects, to *Schizogalerix* in the relatively reduced antemolar series, as already noticed by Ziegler (2005); also the upper molars with more or less divided centrocrista are features typically shown by *Schizogalerix*. On the other hand, there are many other characters (e.g., mesiolabially-distolingually elongation of upper molars) that *Parasorex ibericus* does not share with *Schizogalerix*.

As discussed above, based on the results of this analysis and according to Borrani et al. (2018), *Galerix iliensis* should be assigned to *Parasorex* rather than to *Galerix*. *I*n both the most and less resolved analysis (Fig. 6 and 7) *Apulogalerix* is nested in the clade of *Parasorex* (see below) and is therefore probably closely related to this genus. In fact, as observed by Masini and Fanfani (2013), *Apulogalerix* probably derives from a species close to *Parasorex ibericus*, which shares with it the absence of i3 and variability of the mesostylar region on upper molars. *Apulogalerix* shares typical *Parasorex* patterns (i.e., p2 smaller than p3, metaconule distal arm extended to the postero-labial corner of M1-2, no connection between protocone and metaconule on M1-2, m1 postcristid continuous and not connected with distal cingulid); however, the very derived and peculiar features related to the evolution in insular conditions (e.g., premolar series elongated compared to the molar row, p4 with bulging metaconid fused with protoconid and without paralophid, m1 with short paralophid, poorly developed anteriorly, hypocone on P3 reduced, often absent in the most derived populations) makes *Apulogalerix* clearly distinguishable from the various of *Parasorex* species, as well as from other genera of Galericinae. For these reasons, *Apulogalerix* can be tentatively considered a distinct genus, as proposed by Masini and Fanfani (2013).

Parasorex kostakii seems more closely related to *Deinogalerix* than to *Galerix iliensis* and other *Parasorex* in the 37-taxa topology (node O, Fig. 7), on the basis of three synapomorphies: (1) m2 talonid approximately as large as trigonid, (2) P4 tubercle-like parastyle, (3) not connected to protocone nor to paracone. However, the low retention index (=1) and low number of synapomorphies make the strict affinities between these two genera doubtful; for this reason, it is more parsimonious to keep including *Parasorex kostakii* in the genus *Parasorex,* rather than assigning it to a new genus or to *Deinogalerix* due the lack of most features of the latter genus (e.g., the very large size, the bulbous P3-4 and p3-4 and the more or less divided hypocone on P4).

On the other hand, *Parasorex pristinus* seems more related to *Schizogalerix* rather than to *Parasorex* itself: in fact, in both tree topologies (node M in the full-taxa tree, Fig. 6; node W in the 37-taxa tree, Fig. 7), the species is at the base of the *Schizogalerix* clade, as it results being the sister-taxon of all the other species of *Schizogalerix*, on the basis of 5 synapomorphies shared between both tree topologies: 1) metaconid placed more mesially compared to the protoconid on p4; m2 with 2) very compressed trigonid and 3) metaconid located more mesially than protoconid; 4) M1-2 elongated mesiolingually-distolabially and 5) reduced labial cingulum on M2 located only anteriorly to metacone. Furthermore, the full-taxa tree includes yet another character in the node (m1 larger than 150% of p4 and between 105 and 120% of m2) as a synapomorphy of this clade, while in the 37-taxa tree there is another synapomorphy (metacristid divided from the entocristid by a notch on m2) to support the *Parasorex pristinus* + *Schizogalerix* clade. Ziegler (2003) already described this species as *Schizogalerix pristina* (sic); later, Doukas and van den Hoek Ostende (2006) considered it as a member of *Parasorex*, mainly on the basis of a stratigraphical earlier (MN 3) but more derived *Schizogalerix* species in Anatolia, *Schizogalerix evae* De Brujin et al., 2006.

However, *Parasorex pristinus* shows all the characters of primitive *Schizogalerix* that are listed above (including the relative sizes of m1, common to all *Schizogalerix* but *S. moedlingensis* and *S. pasalarensis*) and not those of *Parasorex*; for these reasons, it is re-assigned to *Schizogalerix.*

Apulogalerix

Apulogalerix is a monospecific genus that includes only *Apulogalerix pusillus* Masini and Fanfani, 2013, from the Late Miocene "Terre Rosse" fauna of the Apulia Platform. Some authors (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) considered it more or less strictly related to the other endemic genus of Gargano Galericinae, *Deinogalerix*, and others scholars (Borrani et al., 2018; Savorelli et al., 2017) relate it to similar sized mainland species of the genus *Parasorexx*. *Apulogalerix* and *Deinogalerix* share various characters, as the bulbous shape of p3, or the loss of i3 (Masini and Fanfani, 2013; Borrani et al., 2018); but these few characters are not sufficient to related the two genera to one another. *Deinogalerix masinii* is the best known early species of *Deinogalerix* to date; it still retains a small third lower incisor. A small i3 can also be observed in mainland *Parasorex* (Masini et al., 2019), while *Parasorex ibericus* lost it. Masini and Fanfani (2013) and Borrani et al. (2018) postulated a close relationship of *P. ibericus* with *Apulogalerix*, also on account of the variable shape of the mesostylar region of the upper molars of both species. In the best resolved analysis (node U, Fig. 7), *Apulogalerix pusillus* and *Parasorex ibericus* are placed in a polytomy with the common ancestor of other species of *Parasorex* and *Schizogalerix*. Borrani et al. (2018) showed a convincing sister-group relationship between the two species. Nonetheless, both species appear to be more closely related to other species of *Parasorex* than to *Deinogalerix* in both trees (node H, Fig. 6; node U, Fig. 7). This might suggests to ascribe *Apulogalerix* to *Parasorex*; however, the presence of 10 autapomorphies shared by both tree topologies, not present in any other *Parasorex* (i.e., mandibular symphysis extended aborally to under p4; m1 approximately between 120 and 135% the length of p4 but over 140% that of m2; swollen p4 metaconid fused to protoconid; no p4 paralophid; relatively short m1 paralophid; bulbous m1 metacristid, fused with entocristid; secondarily reduced or no P3 hypocone; variably shaped M1 labial cingulum, sometimes discontinuous, vestigial or even absent; no M2 labial cingulum), and that probably resulted from an adaptation of the genus to insular conditions impose to keep *Apulogalerix* distinct at the genus level, to stress its differences from mainland species.

The peculiar dental morphologies of *Apulogalerix*, in particular p4, m1 and P3, compared to other Galericinae, can reflect particular dietary adaptations. More specifically, the evolutionary reduction of the P3 hypocone (Masini and Fanfani, 2013) is noteworthy: according to van den Hoek Ostende (2001d), the development of the P3 hypocone and p4 trigonid in *Parasorex*-like species is related to herbivorous diet; their loss in *Apulogalerix* might indicate the return to a more carnivorous diet. However, the overall small size, the reduced canines (not adapted to holding struggling prey), the bulbous shape of p3, p4, P3, P4 and the blunt m1 metacristid might be related to a specific diet mainly composed of small slow-moving animals with hard shells, such as snails (as suggested by Masini and Fanfani, 2013), arthropods as woodlice and small insects, integrated with berries, seeds and fruits.

Schizogalerix

Schizogalerix is the most diversified and widespread genus of Galericinae, known from Early Miocene (MN 3) to the earliest Pliocene (MN 14) of Europe, Asia and North Africa, with at least 11 species: *Schizogalerix anatolicus* Engesser, 1980; *Schizogalerix duolebulejinensis* Bi et al., 1999; *Schizogalerix evae* de Bruijn et al., 2006; *Schizogalerix intermedius* Selänne, 2003; *Schizogalerix macedonicus* Doukas et al., 1995; *Schizogalerix moedlingensis* (Rabeder, 1973); *Schizogalerix pasalarensis* Engesser, 1980; *Schizogalerix sarmaticum* (Lungu, 1981); *Schizogalerix sinapensis*

Sen, 1990; *Schizogalerix voesendorfensis* (Rabeder, 1973) and *Schizogalerix zapfei* (Bachmayer and Wilson, 1970). *Galerix paraexilis* Gureev, 1979, from the Late Miocene of Kazakhstan, may also possibly belongs to this genus (Zijlstra and Flynn, 2015).

The most basal species of *Schizogalerix* in both topologies is *Parasorex pristinus* (node M in the full-taxa tree, Fig. 6; node W in the 37-taxon tree, Fig. 7). As discussed in the paragraph "*Parasorex*" (see above), the original attribution of the species to *Schizogalerix* by Ziegler (2003) was probably correct, as indicated by the presence of 5 *Schizogalerix* synapomorphies (e.g., m2 with very compressed trigonid and metaconid located distinctively more mesially than protoconid and M1-2 elongated mesiolingually-distolabially). For this, following Ziegler (2003), *P. pristinus* is here assigned again to *Schizogalerix*. Ziegler (2003) believed that the presence of the morphologically most primitive *Schizogalerix* in Europe (MN 5 of Austria) indicates that poorly-known basal species of *Schizogalerix* species were already in both Europe and Asia (at the time he considered *Galerix iliensis* as a member of *Schizogalerix*, following Kordikova, 2000). The origin of *Schizogalerix* is still unknown: it may have originated from an yet unknown early *Parasorex*-like species. More derived species of *Schizogalerix* (including the primitive species *Schizogalerix evae* and *S. pasalarensis*) then diversified in Anatolia (as suggested by van den Hoek Ostende, 2001) between MN 3 and MN 5 from *Schizogalerix pristinus*-like species. Probably, the earliest *Schizogalerix* became extinct in Europe between the late MN 5 and MN 6, then the genus dispersed again westward with *Schizogalerix voesendorfensis* during the Serravallian (MN 7-8).

Interestingly, both analyses converge on a group of 4 most advanced species of *Schizogalerix* from Greece, East Europe and Anatolia (*Schizogalerix intermedius, S. sinapensis, S. sarmaticum* and *S. macedonicus*) (node P, Fig. 6; node Z, Fig. 7). These species date to between MN 7+8/9 limit and MN 13 and are thus Late Miocene in age. They cluster together on the basis of 7 shared synapomorphies shared by both tree topologies: 1) strong horizontal ramus, 2) with one mental foramen placed under p4; 3) m1 metaconid placed very anteriorly to the protoconid; 4) antero-labial cingulid not extended posteriorly to protoconid on m2; 5) labial cingulum absent on M1; 6) M2 with straight labial margin and 7) without centrocrista, with double mesostyle. The division of the centrocrista on M2, the development of a divided mesostyle, and the reduction of the labial cingulum on M1 are evolutionary trends of the genus: in *Schizogalerix pristinus*, the labial cingulum on M1 is continuous, while in other species of *Schizogalerix* it is usually discontinuous or even vestigial, and is completely lost in the more-derived Eastern clade. At the same time, the centrocrista on M2 becomes progressively disocntinuous through time: in *Schizogalerix pristinus*, the centrocrista on M2 is still *Parasorex*-like, undivided and winding, and has no mesostyle. In the early but more derived *Schizogalerix pasalarensis* the centrocrista is still winding and still has no distinct mesostyle, but it is already imperfectly divided; in later species, the centrocrista is always divided, wither with or without mesostyles; this trend reaches its extreme in the Oriental clade, with the disappearance of a true centrocrista but with a double mesostyle.

Selänne (2003) considered *Schizogalerix anatolicus* the first member of a chronospecies that ends with *S. sinapensis* passing through *S. intermedius*. Both topologies cannot confirm nor deny this scenario, however *S. intermedius* is placed in a polytomy with *S. sinapensis* in the 37-taxa tree (node P, Fig. 7) or at the base of the clade, while *S. sinapensis* is intermediate between *Schizogalerix intermedius*, *S. sarmaticum* and *S. macedonicus* (node Q, Fig. 6), which implies a close relationship between *Schizogalerix intermedius* and *S. sinapensis*. The two most derived species of *Schizogalerix*, *S. sarmaticum* (MN 9-10 of Moldavia; Rzebik-Kowalska and Lungu, 2009) and *S. macedonicus* (MN 13 of Greece; Doukas et al., 1995) are grouped together in both trees (node R, Fig. 6; node T, Fig. 7), forming a South-East Europe clade. The shared synapomorphy in both trees is the structure of the m1 talonid, with an hypoconid lingual arm more or less directed labially and with the labial arm of the entoconid (=postentocristid) very bent distally and fused with the distal cingulid, on which there is an additional cuspulid. In the full-taxa topology there is also another synapomorphy, i.e., the presence of an additional cuspulid of the m1 hypoconid. The 37-taxa topology reveals yet another synapomorphy, the P4 parastyle connected with the paracone by a short crest and not with the anterior arm of the protocone. This character is also found in other two European species, *Schizogalerix moedlingensis* and *S. voesendorfensis*.

REVISED SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Eulipotyphla Waddell et al., 1999

Suborder Erinaceomorpha Gregory, 1910

Family Erinaceidae Fischer, 1814

Subfamily Galericinae Pomel, 1848

Stratigraphic range: Eocene-Oligocene boundary/earliest Oligocene (MP 20/21)- Early Pliocene (MN 15).

Genera included: *Apulogalerix* Masini and Fanfani, 2013; *Deinogalerix* Freudenthal, 1972; *Eotetracus* gen. nov.; *Epigalerix* gen. nov.; *Galerix* Pomel, 1848; *Parasorex* von Meyer, 1865; *Schizogalerix* Engesser, 1980; *Tetracus* Aymard, 1850.

Definition: The least inclusive clade including *Apulogalerix pusillus, Deinogalerix koenigwaldi*, *Epigalerix symeonidisi*, *Eotetracus daamsi*, *Galerix exilis, Parasorex socialis, Riddleria atecensis*, *Schizogalerix anatolicus, Tetracus nanus*, their last common ancestor and all its descendants, but not *Eogalericius butleri, Microgalericulus esuriens* and *Zaraalestes minutus.*

Revised diagnosis (modified from “tribe Galericini” by van den Hoek Ostende, 2001d): Small to very large-sized Erinaceidae. Dental formula I3/3-2 C1/1 P4/4-3 M3/3. p3 smaller or approximately as large as p4, usually less than 75% of the latter tooth. Metaconid on p4 sometimes reduced or absent; paraconid sometimes connected to the metaconid by a crest. Metacristid on m1 usually present, connected or not with the entocristid. Hypoconulid on m1-3 absent. Lingual lobe always present on P3, bearing at least one cusp. P4 with well-developed, long and wide lingual lobe, always with well-developed hypocone and protocone. M1-2 most often sub-rectangular, wider than longer. M3 relatively small, without metastylar neo-cusp, sometimes with metacone elongated in a metastylar crest.

Eotetracus gen. nov.

Type species: *Tetracus daamsi* Hugueney and Adrover, 2003.

Stratigraphic range: Early Oligocene (MP 22-23).

Included species: *Tetracus daamsi* Hugueney and Adrover, 2003.

Derivatio nominis: “*Eotetracus”* mean “early *Tetracus*” (from the Greek word “ἕως”, dawn), in relationship to its primitive dentary characteristics compared to *Tetracus*.

Definition: The clade including all the species more related to *Eotetracus daamsi* than to *Eogalericius butleri*, *Microgalericulus esuriens*, *Zaraalestes minutus*, *Galerix exilis* and *Epigalerix symeonidisi*.

Diagnosis (modified from Hugueney and Adrover, 2003, as *Tetracus daamsi*): Medium-sized Galericinae with m1 approximately between 120 and 130% of p4 and 125 and 135% of m2; p2 larger than p3; p2 without distal cuspid; talonid on p3 with *crista mediana*, without accessory cuspids; p4 with well-developed cingulids (including precingulid); p4 with weak *crista mediana* on the distal cingulid; metaconid sub-aligned with protoconid on m1; P4 labial cingulum reduced, present only distally; concave labial margin of M2, with maximum concavity between paraconid and metaconid; M2 without metaconule distal arm; protocone distal arm on M3 ending “free”, it does not reach the metacone.

Tetracus Aymard, 1850

Type species: *Erinaceus nanus* Aymard, 1846.

Stratigraphic range: Eocene-Oligocene boundary/earliest Oligocene (MP ?20/21) – early Late Oligocene (MP 26).

Included species: *Erinaceus nanus* Aymard, 1846.

Revised diagnosis (modified after Hugueney and Adrover, 2003): p3 smaller than p2. Lower incisors subequal between them. p4 paraconid connected to the protoconid by a low crest; metaconid in reduction, might be absent. m2 without postparacristid and without metacristid, talonid closed only by the entocristid. P3 without hypocone. M3 with metacone not connected to the distal cingulum and trigon opened lingually; the metaconule might be present.

Riddleria van den Hoek Ostende, 2003b

Type species: *Riddleria atecensis* van den Hoek Ostende, 2003b.

Stratigraphic range: Early Miocene (MN 3).

Included species: *Riddleria atecensis* van den Hoek Ostende, 2003b.

Definition: The clade including all the species more related to *Riddleria atecensis* than to *Eotetracus daamsi, Epigalerix symeonidisi, Galerix exilis* and *Tetracus nanus.*

Diagnosis: see van den Hoek Ostende, 2003b.

Galerix Pomel, 1848

Type species: *Viverra exilis* de Blainville, 1839.

Stratigraphic range: latest Oligocene (MP 30) – late Middle Miocene (transition between Serravallian and Tortonian, MN 8; see Prieto et al., 2011).

Species included in *Galerix*: *Viverra exilis* de Blainville, 1839; *Pseudogalerix stehlini* Gaillard, 1929; *Galerix africanus* Butler, 1956a; *Galerix rutlandae* Munthe and West, 1980; Galerix *aurelianensis* Ziegler, 1990; *Galerix uenayae* van den Hoek Ostende, 1992; *Galerix remmerti* van den Hoek Ostende, 2003a; *Galerix saratji* van den Hoek Ostende, 1992; *Galerix wesselsae* Zijlstra and Flynn, 2015.

Definition: The clade including all the species more related to *Galerix exilis* than to *Deinogalerix koenigswaldi*, *Eotetracus daamsi*, *Tetracus nanus*, *Epigalerix symeonidisi*, *Apulogalerix pusillus*, *Parasorex socialis*, *Protogalerix saratji* and *Schizogalerix anatolicus*.

Revised diagnosis (modified from van den Hoek Ostende, 2001): Small to large-sized Galericinae. p2 larger than p3. Protocone-metaconule connection present in at least part of the M1 and M2. P3 very often with hypocone small or absent. The distal cingulum is often not interrupted by the metaconule distal arm on M1-2.

Parasoricini, new tribe

Type genus: *Parasorex* von Meyer, 1865.

Stratigraphic range: Early Miocene (MN 3) – Early Pliocene (MN 15).

Derivatio nomins: From the type genus, *Parasorex*.

Definition: The clade including all the species more related to *Deinogalerix koenigswaldi*, *Epigalerix symeonidisi*, *Parasorex socialis* and *Schizogalerix anatolicus* than to *Eotetracus daamsi*, *Galerix exilis*, *Riddleria atecensis* and *Tetracus nanus*.

Included genera: *Parasorex* von Meyer, 1865; *Deinogalerix* Freudenthal, 1972; *Schizogalerix* Engesser, 1980; *Epigalerix* gen. nov.

Diagnosis: Tribe of small to very large-sized Galericinae. Paraconid on p4 relatively high compared to metaconid, not much lower than the latter cusp, with paralophid usually well-developed and present in at least some specimens, with or without carnassial notch. Entoconid often placed distally to hypoconid on m3. Hypocone on P3 very often present, well developed and strong; sometimes can be secondly reduced or absent. M3 parastyle usually well-developed, antero-labially prominent.

Epigalerix gen. nov.

Type species: *Galerix symeonidisi* Doukas, 1986

Stratigraphic range: Early-Middle Miocene (MN 4-5)

Included species: *Galerix symeonidisi* Doukas, 1986

Derivatio nominis: from the Greek ἑπί, “above”, “more”, and *Galerix*, in relationship to its relatively more derived morphological characters compared to *Galerix*.

Diagnosis (modified from Doukas, 1986): Parasoricini with p2 larger than p3, as in *Galerix*. Entoconid placed distally to hypoconid on m3. P3 with distinctively emarginated distal margin, hypocone always present, well developed and strong. M3 always with well-developed parastyle.

Deinogalerix Freudenthal, 1972

Type species: *Deinogalerix koenigswaldi* Freudenthal, 1972.

Stratigraphic range: Late Miocene (MN 10-13).

Definition: the clade including all the species more related to *Deinogalerix koenigswaldi* than to *Epigalerix symeonidisi, Parasorex socialis* and *Schizogalerix anatolicus.*

Included species: *Deinogalerix koenigswaldi* Freudenthal, 1972; *Deinogalerix freudenthali* Butler, 1980; *Deinogalerix minor* Butler, 1980; *Deinogalerix brevirostris* Butler, 1980; *Deinogalerix intermedius* Butler, 1980; *Deinogalerix masinii* Villier et al., 2013; *Deinogalerix samniticus* Savorelli et al., 2017.

Revised diagnosis (modified after Savorelli et al., 2019): Large-sized Parasoricini. I1 much larger than I2 and I3. P3, P4 (large approximately the 120% of M1 or more), p3, p4, and trigonid of m1 enlarged, with paralophid very elongated anteriorly. Posterior molars reduced, with m1 approximately as large as the p4 or larger (until 125-130%), but longer over the 140% of m2. P3 and p4 bunodont. p4 with distinct trigonid, paralophid blunt and no carnassial notch, and with metaconid and distal cingulum joined by a bulbous, inflated cristid. Postparactistid on m1 present, inflated and steep. Talonid on m1 narrower than the trigonid; metacristid blunt, divided from the entocristid by a notch. Hypocone constantly present on P3; protocone bulging, more or less joined to it. P4 with well-developed and elongated lingual lobe, narrow and squat tooth with relatively rounded lingual lobe, with paraconule. On M1 and M2 protocone and metaconule very rarely connected, bulging and undivided mesostyle without centrocrista and distal cingulum interrupted or continuous, sometimes distal arm of metaconule confluent with uninterrupted distal cingulum, preprotocrista well separated from paraconule by a groove. Metastylar crest well-developed and inflated on M3; parastylar crest often poorly developed, relatively shorter compared to other Parasoricini, determining a squarish outline of the mesio-labial corner of the crown; distal arm of protocone not connected to the metacone. 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.

Parasorex von Meyer, 1865

Type species: *Parasorex socialis* von Meyer, 1865.

Stratigraphic range: late Early Miocene (MN 4) – Early Pliocene (MN 15).

Included species: *Parasorex socialis* von Meyer, 1865; *Galerix depereti* Crochet, 1986; *Galerix ibericus* Mein and Martín-Suárez, 1993; *Galerix iliensis* Kordikova, 2000; *Galerix kostakii* Doukas and van den Hoek Ostende, 2006; *Apulogalerix pusillus* Masini and Fanfani, 2013.

Revised diagnosis (modified from van den Hoek Ostende, 2001): Middle to large-sized Galericinae. p2 smaller than p3. p4 paralophid present in at least some specimens. Postcristid continuous on m1, with distal cingulid not connected to it. Connection between protocone and metaconule on M1-2 usually absent. Metaconule distal arm extended to the postero-labial corner of the tooth on M1-2.

Apulogalerix Masini and Fanfani, 2013

Type species: *Apulogalerix pusillus* Masini and Fanfani, 2013.

Stratigraphic range: Late Miocene (MN 13).

Included species: *Apulogalerix pusillus* Masini and Fanfani, 2013.

Diagnosis: see Masini and Fanfani, 2013.

Schizogalerix Engesser, 1980

Type species: *Schizogalerix anatolicus* Engesser, 1980

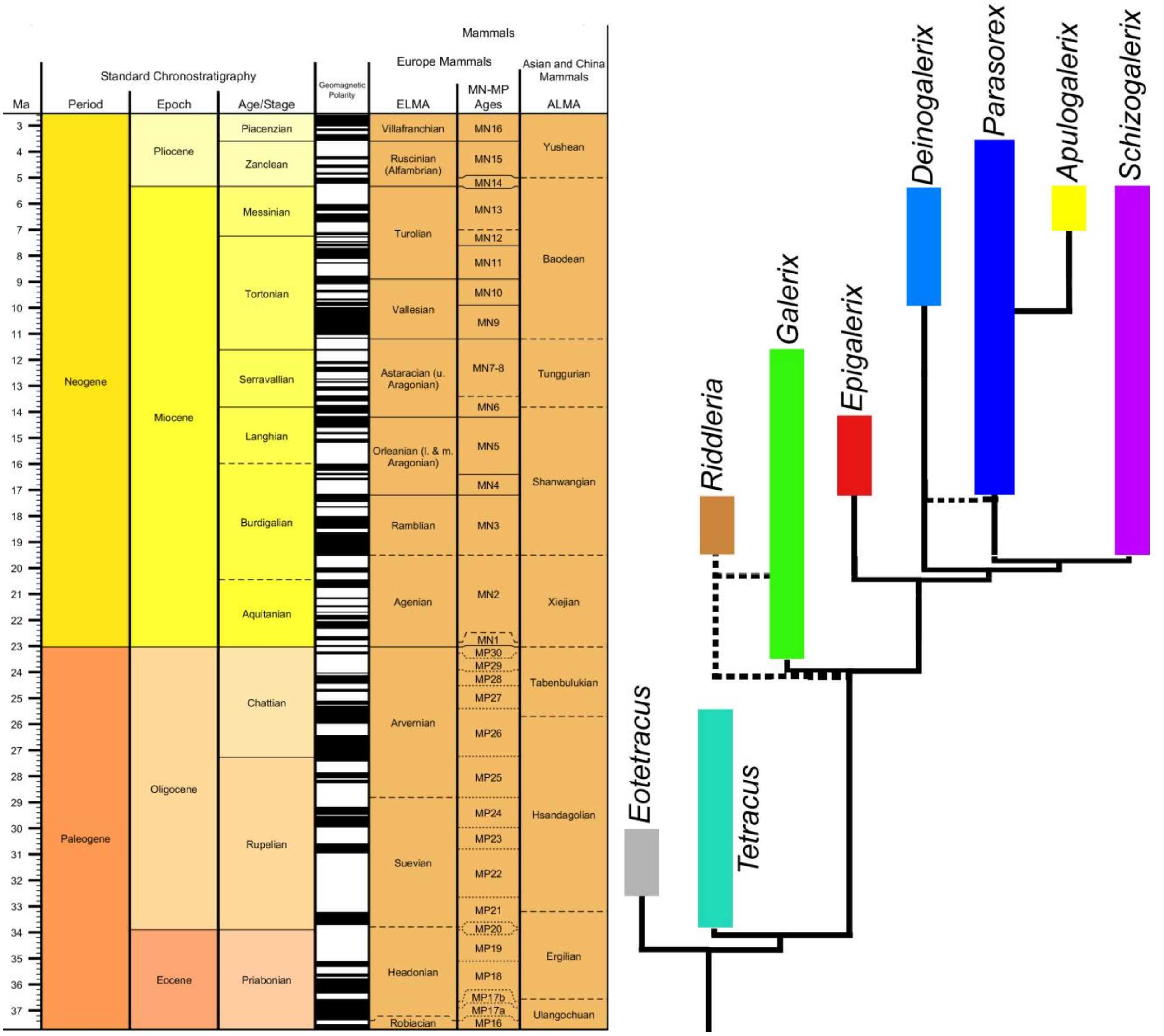
Stratigraphic range: Early Miocene (MN 3) – Early Pliocene (MN 14).

Included species: *Galerix zapfei* Bachmayer and Wilson, 1970; *Galerix sarmaticum* Lungu, 1971; *Galerix moedlingensis* Rabeder, 1973; *Galerix voesendorfensis* Rabeder, 1973; *Schizogalerix anatolicus* Engesser, 1980; *Schizogalerix pasalarensis* Engesser, 1980; *Schizogalerix sinapensis* Sen, 1990; *Schizogalerix macedonicus* Doukas et al., 1995; *Schizogalerix duolebulejinensis* Bi et al., 1999; *Schizogalerix intermedius* Selänne, 2003; *Schizogalerix pristinus* Ziegler, 2005; *Schizogalerix evae* de Brujin et al., 2006.

Revised diagnosis (modified from van den Hoek Ostende, 2001): Middle to large-sized Parasoricini. p2 smaller than p3. p4 with a well-developed metaconid and paralophid (continuous or not), with the metaconid located more mesially than protoconid. Enlarged m1 compared to p4 (more than 150% of p4) but not much larger than m2 (being approximately between the 105 and 120% of m2). Trigonid on m2 most often very compressed. P3 always with hypocone. M1-2 elongated distolabially-mesiolingually and wide, with winding centrocrista, often more or less divided and with or without divided mesostyle. Shortened premolar series compared to the molar row. Labial cingulum on M2 reduced, present only anteriorly to the metacone, vestigial or even absent. Protocone connected only with the hypocone on M1-2.

PALEOBIOGEOGRAPHICAL AND STRATIGRAPHIC IMPLICATIONS

The projection of the dendrogram on the geological time scale permits a tentative reconstruction of the evolutionary history of the major groups of Galericinae consistently with the fossil record currently available (Fig. 8). The early species closest to the Galericinae are known from the Middle-Late Eocene of Central Asia (Mongolia): *Eogalericius* and in particular *Microgalericulus* are probably the closest genera to the last common ancestor of all Galericinae.



← Figure 8 - Summary dendrogram indicating the divergence times of Galericinae genera, based on the systematics proposed in this paper. Dashed bars indicate uncertain phyletic lines. Geological time scale obtained using TimeScale Creator (https:// timescalecreator.org/index/index.php).

There are not equivalent species in Europe at that time, and we can assume a dispersion from Asia to Europe. The last common ancestor of all Galericinae likely dispersed at the time of the "Grande Coupure", which dates to around the Eocene/Oligocene transition, between 34.5 and 33.9 Ma, at the end of MP 19 (Costa et al., 2011). The first record of Galericinae are remains of *Tetracus nanus* from Coyrou 1-2 from Quercy (France), dated to MP 20-MP 21 (Legendre et al., 1995). Therefore, the ancestors of *Tetracus* and especially of *Eotetracus* most likely arrived during the great faunal change. The primitive *Eotetracus* survived in Majorca until MP 23, and may be the closest genus to the ancestor of all Galericinae. *Tetracus*, on the other hand, is a relatively more advanced genus; it was close to *Galerix* morphologically and probably diversified in Europe. In fact, at this time Galericinae of comparable age are still unknown in Asia, thereby suggesting an European origin for the subfamily.

Tetracus became extinct in the early Chattian (MP 26). Galericines are then unknown until the latest Oligocene (MP 30) of Anatolia, when *Galerix saratji* appeared (van den Hoek Ostende 1992; 2001c, d). There are two possible explanations for this gap: 1) *Tetracus*-like galericines were more widespread than the imperfectly known stratigraphical record is able to show. Van den Hoek Ostende (2018) reports *Tetracus* from Anatolia; if so, the genus possibly survived in East Europe or in the Near East (after *Tetracus* became extinct in West-Central Europe), and gave rise to the earliest *Galerix* at the end of the Oligocene; 2) *Galerix* may have arisen from a more basal, Asian species immigrated in Anatolia in the latest Oligocene. This option is not supported, because the absence of early, pre-MP 30 galericines in Asia.

The history of the genus *Galerix* may be more complex than previously thought: *Galerix uenayae* seems to be positioned at the base of an "European clade" of *Galerix*, which includes *G.*

aurelianensis and, probably, also *G. remmerti* and *G. exilis*. The genus would thus have soon dispersed in Europe shortly after its origin in Western Asia, possibly in MN 1-2, as suggested by the presence of *Galerix aurelianensis* and *Galerix remmerti* in MN 3 deposits respectively in Germany (Ziegler, 2006) and Spain (van den Hoek Ostende, 2003a). Furthermore, this early dispersal event possibly reached as far east as Central Asia too, giving rise to *Galerix wesselsae* in the early MN 3 of Pakistan around 19.0 Ma (Zijlstra and Flynn, 2015). The ancestor of *Galerix africanus* may also have originated in Central Asia approximately in the time period, as already suggested by Butler (1984).MN 2-3 seems to be the time when Galericinae most diversified: many phyletic lines of Parasoricini possibly appeared, except *Galerix*, in both Europe and Asia. In fact, the most primitive species of the group, *Schizogalerix evae*, is MN 3 in age. This suggests an earlier origin of *Schizogalerix* and *Epigalerix* (in particular the latter one) which might be parsimoniously dated to MN 2, perhaps at the end of the Mi-1 global cooling event, around 19.8 Ma (Liebrand et al., 2011; Zou et al., 2016). Possibly all the phyletic lineages of Parasoricini arose in MN 2; this fast radiation in such a short time span may blur the reconstruction somewhat of the phylogenetic relationships at the base of the tribe (see also Borrani et al., 2018).

Van den Hoek Ostende (2018) was skeptical about the use of cladism to investigate the phylogenetic affinities of *Deinogalerix*. The author noted that, due only to the anterior placement of the mental foramen, *Deinogalerix* groups up with the most primitive species of Parasoricini ("transitional forms" in Borrani et al., 2018) Moreover, van den Hoek Ostende (2018) underlined that the short distal branch of the metaconule in M1-2 of many M1-2s of *Deinogalerix* is possibly a result of parallelism (reversion) with earlier Galericinae. In fact, in *Deinogalerix masinii*, as well as in some specimens of *D. freudenthali* and *D. minor*, the distal arm of the metaconule still reaches the postero-labial corner of M1-2; therefore, the ridge, at least in the Gargano species, was originally long and robust and then shortened. Nonetheless, the position of the mental foramen and the development of the distal branch of the metaconule in the upper molars do not figure among the many synapomorphies (43 and 18 in the full-taxa and 37-taxa strict consensus trees, respectively) taken into account for the present analysis. The synapomorphies of *Deinogalerix* by far outnumber the autapomorphies found in the endemic genera *Eotetracus* (10 in both tree topologies), *Riddleria* (16) and *Apulogalerix* (17 and 13, respectively), thereby suggesting a much longer time (as is especially by the full-taxa tree) of divergence from their continental (non-endemic) ancestors than in the other endemic genera. Unfortunately, the most primitive species of *Deinogalerix* (*Deinogalerix masinii* and *D. samniticus*) already exhibit a large number of derived characters that shade their affinities with other galericines. A divergence of this group from other pre-MN 4 Parasocini (such as *Parasorex kostakii*) is plausible, and would also explain the considerable number of synapomorphies (in addition to the very large size, which is so a unique case among erinaceids) present in this genus.

Van den Hoek Ostende (2018) also remarked that an ancient origin (MN 2 or MN 3, depending on the tree topology or potential ancestors that are considered) of *Deinogalerix* from Eastern Europe would be not consistent with the paleontological record. Van der Sar et al. (2017) explained that the absence of *Galerix* from the Late Oligocene locality of Banovíci (Bosnia-Herzegovina) could simply depend on low sample size. Unfortunately, no Galericinae is known between MP 26 (last occurrence of *Tetracus nanus*) and MP 30 (first occurrence of *Galerix saratj*), and there are very few fossiliferous localities in Eastern Europe dated between MP 30 and MN 2. Similarly, there are virtually no localities nor species known so far outside Anatoli for a key moment of diversification of Galericinae, the Early Miocene (MN 1-2), which was probably a key moment for the diversification of Galericinae, are virtually unknown outside Anatolia. Hence, there is a substantial gap in the documentation of Galericinae in Europe and Asia between the Late Oligocene and Early Miocene, regardless of whether *Deinogalerix* may have had an Eastern origin or not. Paleobiogeographic arguments for ruling out an archaic or eastern origin of *Deinogalerix* are not sufficiently compelling. These issues can only be addressed once new, earlier (and, likely, less derived) species of the giant erinaceid from Gargano should be discovered and, most importantly, our knowledge of the Late Oligocene-Early Miocene evolutionary history of the subfamily should ever improve.

In sum, *Deinogalerix* might have stemmed from a primitive, *Epigalerix*-like ganeusin MN 2 (*Galerix-Parasorex* transitional species in Borrani et al., 2018). The 37- taxa analysis suggests closer affinities with *Parasorex*, as proposed by van den Hoek Ostende (2001d), maybe with basal *Parasorex*-like species like *P. kostakii*. The phyletic lineage of the *Deinogalerix* originated much earlier than the Middle-Late Miocene, around MN 2 or to MN, depending on the options set. The many diagnostic traits of *Deinogalerix* likely evolved in the insular realm during the long MN 2/3 and MN 10 time period. On the other hand, the ancestor of *Apulogalerix pusillus* possibly immigrated in Gargano during MN 9 (Masini and Fanfani, 2013; Savorelli et al., 2017; Borrani et al., 2018), thereby indicating not only a different origin of the two taxa (also made evident by the more derived, peculiar morphologies of *Deinogalerix* compared to *Apulogalerix*) but also the existence of at least two different phases of colonization of the Apulia Platform, the first during MN 2-3 and the second before MN 10 (Borrani et al., 2018), contrarily to what was suggested by van den Hoek Ostende (2001d). There are high chances that the ancestors of both *Deinogalerix* and *Apulogalerix* immigrated in the Apulia Platform from Balkans (Borrani et al., 2018).

As mentioned above, the earliest species of *Schizogalerix* is *Schizogalerix evae* from Anatolia, although the basal-most *Schizogalerix*, morphologically, is *S. pristinus* from the MN 5 of Gaindorf Formation (Austria). The earliest *Schizogalerix* species were therefore more widespread than previously thought, as already supposed by Ziegler (2003). The genus probably arose in East Europe or Near East at the end of MN 2 from an *Epigalerix*- or *Parasorex*-like ancestor, then dispersed both towards East (giving rise to the ancestor of *S. evae* and other more-derived species of

Schizogalerix) and towards EuropeThe genus may have become extinct in its western range after MN 5, because it is unknown in Middle Miocene of central Europe. The genus *Schizogalerix* dispersed again in Central-Eastern Europe in MN 9 with the species *S. voesendorfensis* (Prieto et al., 2014; van den Hoek Ostende, 2001d; Ziegler, 2006). On the other hand, the genus diversified and evolved in Anatolia, possibly dispersing in Asia before MN 6, giving rise to *Schizogalerix duolebulejinensis* in China (Bi et al., 1999), and in Africa in MN 8, with *Schizogalerix* cf. *anatolicus* (Engesser, 1980). In Africa the genus became extinct with the very derived *Schizogalerix* nov. sp. from Amama II (MN 12; Engesser, 1980). Very derived species of *Schizogalerix* dispersed one last time in East Europe from Anatolia in MN 9, with *S. sarmaticum* in Moldavia (Rzebik-Kowalska and Lungu, 2013). The genus became extinct in the Late Miocene with *Schizogalerix macedonicus*, in MN 13 of Greece (Doukas et al., 1995), which is very similar to *Schizogalerix* nov. sp. from Amasya (MN 13 of Turkey; Engesser, 1980: p. 80, fig. 19c).

6 – Conclusion

The Galericinae (=Galericini sensu van den Hoek Ostende, 2001d) are a group of erinaceids (Eulipotyphla: Erinaceomorpha) known from the Early Oligocene to the Early Pliocene, with at least six genera: *Apulogalerix* Masini and Fanfani (2013), *Deinogalerix* Freudenthal (1972), *Galerix* Pomel (1848), *Parasorex* von Meyer (1865), *Riddleria* van den Hoek Ostende (2003b), *Schizogalerix* Engesser (1980), and *Tetracus* Aymard (1850). Their phylogenetic relationships, particularly those of the endemic *Apulogalerix* and *Deinogalerix* from the "Terre Rosse" fauna (Apulia, Italy), have never been investigated in detail except by van den Hoek Ostende (2001d), Borrani et al. (2018) and Masini and Fanfani, (2013, concerning *Apulogalerix*). Moreover, affinities have been proposed between the living Galericinae (= Hylomyinae *sensu* Frost et al., 1991) and the extinct Galericini (see van den Hoek Ostende, 2001d). To date, the whole of the extinct and extant members of the family Erinaceidae have never been subjected to detailed research, except by Gould (1995); fossil members have especially been neglected by cladistic analysis. The present study aims at investigating past representatives of Galericinae, as well as comparing them with other extinct (e.g., "Tupaiodontinae") and living (e.g., gymnures such as *Echinosorex*) insectivores, in order to improve our understanding of the phylogenetic relationships of the various genera, with special focus on the relationships between the various species of the Apulia Platform. A cladistic approach, under the optimality criteria of maximum parsimony and maximum likelihood (which is perhaps more accurate than Bayesian inference approaches for morphological datasets; see Schrago et al., 2018), appeared being particularly suitable to the task.

The phylogenetic relationships of Galericinae are largely unclear or controversial. Elucidating them was desirable, but certainly challenging. Most of the difficulties arise from the fact that the fossil records of this subfamily are very incomplete. Generic characters and boundaries between the various taxa are often blurred, whereby interrelations are difficult to establish.

This study is based both on observational evidence and on literature data. Screening the taxonomic literature in order to select the characters that could be used would have been time-consuming, but above all, would have involved considerable subjectivity. To reduce the impact of subjective character selection, the phylogeny of Galericinae has been investigated using the free and widely accepted software TNT v. 1.5 (Goloboff and Catalano, 2016).

Cladistics has the ability to discover informative features and taxonomic groups within a natural system. It has the advantages that it can deal with qualitative descriptive characteristics and that it reduces subjective decisions on the taxonomic importance of characters, but at the same time it can expose to the creation of fluctuating and transient phylogenies, especially when the analysis involves fossil records, which are notoriously only an extremely small sampling of the totality of morphological traits and of species that have existed (see Appendix V). In fact, one inherent logical and structural weakness of cladistics is that its explanatory power weakens as it is extrapolated farther and farther into the past, because of the fewer and fewer species and fewer and fewer morphological traits one finds as he travels back in time. This is an inevitable bias in cladistic analysis.

To reduce the impact of this bias, the present study is based both on a large amount of direct observational data and on an even larger volume of literature information. The most important diagnostic characters of genera have been examined and for each of them the apomorphic and the plesiomorphic state have been inferred. This decision-making process was a very important segment of the research and was largely based on the results from successive runs of the cladistic analysis. Unfortunately, the analysis is not exempt from the limits listed above: some species are only known from very fragmentary remains, and the sizes of the samples the various species, as well as the number and quality of their discriminating characters, are not comparable. This imposed careful screening, revision and evaluation to minimize the impact of these impediments, not to mention that recent analyses (e.g., He et al., 2012) include or are even largely based on molecular sequence analysis, which is virtually impossible to perform for most fossils. A further difficulty arises from the fact that several species of Galericinae are known only from dental characters: Gould (2001) cautioned that teeth may be exposed to ontogenic, sexual or even pathological variations, and may display non-independent characters. All this considered, at the end the analysis was performed on a matrix of 38 ingroup taxa, 3 outgroup species, i.e., *Eogalericius butleri*, *Microgalericulus esuriens,* and *Zaraalestes minutus,* and 128 characters.

The analysis reached a number of important results. A first, major one is that, against common belief that Oligo-Miocene Galericini form a tribe of present-day Galericinae, cranial characters separate Hylomyinae (modern gymnure) from Galericinae at the subfamily rank within Erinaceidae. Only 3 skeletal characters (i.e., the absence of the anterior process of the alisphenoid, possibly the small paroccipital process and the fusiform and elongated metacromion process of the scapula) against the 27 listed by Frost et al. (1991) link the present-day gymnure to Galericini. The large majority of characters are probably primitive features, inherited from earlier Erinaceidae. Hylomyinae and Galericinae are also distinct dentally: the upper molars are differently shaped (squarish in Hylomyinae, usually sub-rectangular in Galericinae); the P3 lingual lobe is well-developed and may have two cusps in Galericinae, and is very reduced or even absent in Hylomynae; M3 has a neo-metastylar-cusp in Hylomyinae, unknown in Galericinae.

A second significant result from this study is that Tupaiodontinae is probably a paraphyletic group of Eocene-early Miocene insectivores, which possibly includes species (as *Zaraalestes minutus*) closely related to derived clades, among which Galericinae. Members of Tupaiodontinae share several plesiomorphic features (e.g., transverse paralophid on m1, presence of hypoconulid on m3), and their dental proportions are overall similar to those of other Paleogene erinaceids, which suggests the existence of a heterogeneous group of relatively advanced early erinaceids rather than a true clade.

All the results of this analysis on the ancestral stocks of these insectivores converge to a consistent picture where Galericinae emerge as a group of erinaceids that appeared in the earliest Oligocene (MP 20/21 boundary) and that thrived up to the early Pliocene (MN 15). The principle of maximum parsimony used to test the phylogenetic relationships permitted to score the phylogenetic networks on the basis of the minimum number of state changes for each character. This provided considerable solidity and reliability to the results.

Galericinae ancestors, probably reminiscent of *Microgalericulus* or *Zaraalestes,* immigrated in Europe from Asia during the so-called “Grande Coupure” event, in the latest MP 19 (ca. 34.5-33.9 Ma). Six genera of Galericinae are generally recognized: *Tetracus, Galerix, Parasorex, Deinogalerix, Apulogalerix* and *Schizogalerix.* A remarkable result of the present analysis is that it revealed the existence of two more genera, *Eotetracus* gen. nov. and *Epigalerix* gen. nov.

Eotetracus includes the most primitive Galericinae, *Tetracus daamsi* Hugueney and Adrover, 2003. On the other hand, the advanced species *Galerix symeonidisi* Doukas, 1986, which is transitional between *Galerix* and *Parasorex*, typifies *Epigalerix*.

Another important result was discovering a clade of *Parasorex*-like species of *Epigalerix, Deinogalerix, Parasorex, Apulogalerix* and *Schizogalerix*. The members of this new tribe, indicated as Parasoricini, share several synapomorphies, among which p4s with relatively high paracone and usually with evident paralophid, m3s with entoconid often placed distally to the hypocone, P3s with hypocone, which, however, might sometimes grow small or be secondarily lost; M3s with usually well-developed parastyle. Derived dental features indicate that *Galerix iliensis* can confidently be assigned to *Parasorex*, in spite of its having M1-2s without metaconule distal arm extended to the disto-labial corner of the tooth, which is a typical trait of other species of the genus.

Two of the most solidly-based clades detected by this study are *Deinogalerix* and *Schizogalerix*. The two genera display a large number of synapomorphies, and their nodes are well-supported by high retention indexes and high bootstrap values. Despite its chronological distance (MN 5) from the earliest member of the genus (*Schizogalerix evae*, MN 3), *Parasorex pristinus* is here assigned to *Schizogalerix* on the basis of dental proportions and on a series of synapomorphies (e.g., metaconid placed more mesially compared to protoconid on p4, M1-2 elongated mesiolingually-distolabially, reduced labial cingulum on M2), as originally proposed by Ziegler (2003). The presence of this species in the European middle Miocene, which is less derived than its Anatolian congeners, may imply that primitive representatives of the genus were more widespread in Europe than the fossil record seems to suggest (as already proposed by Ziegler, 2003). *Schizogalerix* presumably diversified between MN 3 and 5 in Anatolia; it then became extinct in Europe by the end of MN 5 and dispersed towards East in MN 5, towards North Africa before MN 8, and back to central Europe with *Schizogalerix voesendorfensis* and to Eastern Europe with *S. sarmaticum* in MN 9.

Incidentally, in regard to *Parasorex*, another striking finding in this study is that *Galerix* and *Parasorex* may be paraphyletic. The unclear relationships between these genera, which at least in some cases may be of evolutionary significance, possibly arise from rapid early Miocene speciation events in connection with the end of the Mi-1 global cooling episode (MN 2; Liebrand et al., 2011; Zou et al., 2016).

Some scholars (e.g., Freudenthal and Martín-Suárez, 2010; van den Hoek Ostende, 2001d) relate *Deinogalerix* to *Apulogalerix*. This hypothesis is not supported by the results of the present study: *Apulogalerix* appears to be closely related to *Parasorex,* in particular to the Spanish species *Parasorex ibericus*, and *Deinogalerix* to earlier *Epigalerix* or *Parasorex*-like species. *Apulogalerix* may have stemmed from *Parasorex* in late Miocene (MN 9; Masini and Fanfani, 2013; Borrani et al., 2018). The genus is identified by a very high number of autapomorphies (e.g., peculiar dental proportion, progressive reduction to possible total absence of P3 hypocone in most recent populations), which are likely endemic features acquired during insular isolation. In consideration of this, *Apulogalerix* is here considered a valid genus. *Deinogalerix* diverged from other Galericinae much earlier than *Apulogalerix*, presumably during MN 2, or MN 3 at most; this may explain its many distinctive, endemic features (e.g., giant size, bulbous shape of P4/p4, enlarged P4 compared to M1, elongated snout with large diastemas in the largest species). Indeed, many of these morphologic traits may have freely developed in the absence of natural enemies in the Gargano "Terre Rosse" context: it cannot be excluded that galericines achieved great stature with dietary shifts that led them to become kind of ecological equivalents to the modern giant tenrec (*Tenrec ecaudatus*), and thus to occupy, *de facto*, the niche of small, primarily insectivorous continental carnivores, such as coati and jackals.

The various lines of evidence collected for this study support the model of at least two distinct dispersal events during the Miocene, through which the Messinian “Terre Rosse” fauna would have been formed, as suggested *inter alios* by Borrani et al. (2018).

Several problematic aspects of the the phylogeny of Galericinae and, more generally, of fossil erinaceids, still deserved to be cleared. Some of the more notable issues are *Galerix* and *Parasorex* are monophyletic or not, what are the real affinities of *Riddleria atecensis* and the early evolutionary history of Parasoricini. Unfortunately, these questions will only be addressed properly by the discovery of new fossils that can hopefully complete the picture of poorly known early species (e.g., *Parasorex iliensis*, *P. kostakii*, and *Schizogalerix evae*) and, most importantly, shed light on the status of the subfamily between the Late Oligocene and Early Miocene (MP 27-MN 2) outside of Anatolia. Similar phylogenetic analyses should be extended to other groups of extinct erinaceids in the future, with the aim of reconstructing as precisely as possible the origin,

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Appendix I - Erinaceidae of the Neogene of Italy

In Italy, Neogene insectivores range from moles, shrews, and giant insular *Deinogalerix* hedgehogs to the *Parasorex depereti* from a number of localities dating all the way back to the early-middle Burdigalian (MN3). Nonetheless, the systematics of these animals have rarely been analyzed in-depth in previous studies, with the exception of Fanfani (1999). Moreover, new localities have been discovered in the meantime and many taxa have been given new genus or species names. Taking the cue from Doukas (2005) and Ziegler et al. (2005), who listed the insectivores from Aliveri and Karydia (Greece) and from Germany, respectively, the present section focuses on the Italian Neogene fossil record of insectivores, and in particular on that of Erinaceidae. The complete list of Italian Neogene insectivores, with updated nomenclature and divided for localities, is reported in Table 3.

LIST OF LOCALITIES WITH ERINACEIDS

Tortonian (Late Miocene)

Scontrone (prov. L'Aquila, Abruzzo).

Stratigraphy and sedimentology: The vertebrate-bearing deposits from Scontrone are biostratigraphically correlated with the *Lithothamnion* Limestone of Roccamorice (northern Majella; Patacca et al. 2013) and are therefore assigned an estimated age of 9 Ma (Tortonian, MN 10). The "Scontrone calcarenites" crop out on the east side of Monte Civita; they are fine-grained marginal-marine calcarenites of the so-called Sasso-Gananza Unit (Mazza and Rustioni, 2008;

Epoch/Age	Stage	Mammal age	Neogene Mammal Zone (MN)	Region	Locality	Family	Subfamily	Species
Pliocene	Piacenzian	Early Villanyian	MN 16a	Sardinia	Nuraghe Su Casteddu	Soricidae	Soricinae	*Asoriculus* aff. *gibberodon* (Petényi, 1864)
						Talpidae	Talpinae	*Talpa* sp.
				Piedmont	Arondelli quarry	Soricidae	Soricinae	cf. *Asoriculus gibberodon* (Petényi, 1864)
								Beremendia fissidens (Petényi, 1864)
								Blarinoides mariae Sulimski, 1959
								Deinsdorfia hibbardi (Sulimski, 1962)
								Petenyia hungarica Kormos, 1934
								Sorex sp.
						Talpidae	Talpinae	*Talpa* cf. *minor* Freudenberg, 1914 vel *Talpa fossilis* Petényi, 1864
				Tuscany	Arcille	Soricidae	Soricinae	*Blarinoides* sp.
	Zanclean	Ruscinian	MN 14 or 15	Sardinia	Capo Mannu	Erinaceidae	Galericinae	*Parasorex depereti* (Crochet, 1986)
						Soricidae	Soricinae	*Asoriculus gibberodon* (Petényi, 1864)
								cf. Soricini indet.
						Talpidae	Talpinae	*Talpa* cf. *minor* Freudenberg, 1914
Miocene	Messinian/ ?earliest Zanclean	Late Turolian/ ?earliest Ruscinian	MN 13/ ?earliest MN 14	Apulia	"Terre Rosse" faunas	Erinaceidae	Galericinae	*Apulogalerix pusillus* Masini and Fanfani, 2013
								Deinogalerix brevirostris Butler, 1980
								Deinogalerix freudenthali Butler, 1980
								Deinogalerix intermedius Butler, 1980
								Deinogalerix koenigswaldi Freudenthal, 1972
								Deinogalerix masinii Villier et al., 2013
								Deinogalerix minor Butler, 1980
								Deinogalerix sp. 1
								Deinogalerix sp. 2
						Soricidae	Crocidosoricinae	*?Lartetium* cf. *dehmi* (Viret and Zapfe, 1952)
	Messinian	Late Turolian	MN 13	Emilia-Romagna	Monticino quarry	Erinaceidae	Erinaceinae	*"Mioechinus"* sp.
							Galericinae	*Parasorex depereti* (Crochet, 1986)
						Soricidae	Crocidosoricinae	cf. *Miosorex desnoyersianus* (Lartet, 1851)
							Soricinae	*Neomiosorex sp.*
				Piedmont	Moncucco Torinese	Erinaceidae	Galericinae	*Parasorex* aff. *ibericus* (Mein and Martín-Suárez, 1993)
						Soricidae	Soricinae	*Petenyia* cf. *hungarica* Kormos, 1934
								Neomyini indet.
						Talpidae	Talpinae	*Talpa* sp.
					Ciabòt Cagna	Erinaceidae	Galericinae	*Parasorex depereti* (Crochet, 1986)
				Tuscany	Borro Strolla	Erinaceidae	Galericinae	*Parasorex* cf. *depereti* (Crochet, 1986)
				Piedmont	Verduno	Erinaceidae	Galericinae	*Parasorex* sp.
						Soricidae	Soricinae	cf. *Asoriculus gibberodon* (Petényi, 1864)
				Tuscany	Velona basin	Erinaceidae	Galericinae	*Parasorex* vel *Schizogalerix* sp.
					Baccinello V3	Erinaceidae	Indet.	Erinaceidae indet.
		Middle Turolian	MN 12	Tuscany	Baccinello V2	Soricidae	Crocidosoricinae?	cf. Crocidosoricinae indet.
	Tortonian	Early Turolian	MN 11	Tuscany	Baccinello V1	Soricidae	Crocidosoricinae	cf. *Lartetium* sp.
								?*Crocidosorex* sp.
					Baccinello V0	Soricidae	Indet.	Soricidae indet.
		Late Vallesian	MN 10	Abruzzo	Scontrone	Erinaceidae	Galericinae	*Deinogalerix samniticus* Savorelli et al., 2017
								Deinogalerix sp.
	Burdigalian	Ramblian	MN 3	Sardinia	Oschiri	Soricidae	Crocidosoricinae	*Oligosorex antiquus* (Pomel, 1853)
						Talpidae	Talpinae	*"Geotrypus" oschiriensis* De Brujin and Rümke, 1976
							Indet.	*Nuragha schreuderae* De Brujin and Rümke, 1976

Table 3 - List of Italian taxa with revised systematic.

Patacca et al., 2008, 2013). The vertebrates are fragmental, disarticulated and markedly weathered (Mazza and Rustioni, 2008; Patacca et al., 2013).

Species: Rustioni et al. (1992) attributed a fragmental maxillary with P3-P4 from the "Scontrone calcarenites" to an extinct otter. It was then assigned to the morphologically primitive *Deinogalerix freudenthali* (Mazza and Rustioni, 2008), known from "Terre Rosse" faunas of Gargano (Apulia). Later studies assigned the remain, alongside others found successively, to two distinct species of *Deinogalerix* (*D. samniticus* and an unnamed, smaller form; Savorelli et al., 2017, 2019).

Remarks: Scontrone yielded the remains of no other small mammals than *Deinogalerix*, which can hardly be called a micromammal due to the giant size it achieved living in isolation. The presence at

Scontrone of this highly derived, endemic gymnure (subfamily Galericinae; Freudenthal, 1972; Butler, 1980; van den Hoek Ostende, 2001d; Masini et al., 2010; Villier, 2010, 2012; Villier et al., 2013; Savorelli et al., 2017, 2018, 2019; Borrani et al., 2018) along with those of other endemic taxa, such as the artiodactyl *Hoplitomeryx* and the anseriform *Garganornis* (Mazza and Rustioni, 2008; Pavia et al. 2017), indicate the existence of a so-called Abruzzo-Apulian Platform (Patacca et al., 2008, 2013). These morphologically primitive species of the genus provides an important chronological constraint for the younger “Terre Rosse” fauna (see below) (Savorelli et al., 2017, 2019).

Messinian (Late Miocene)

Baccinello V3 (prov. Grosseto, Tuscany).

Stratigraphy and sedimentology: The V3 fauna was found in “mudstones with lenticular pebbly sandstones and conglomerates” of the CB1e sub-synthem deposits, associated to a “alluvial plain with channel and floodplains” environment (Benvenuti et al., 2015: 240, tab. 1). The remains are dated to the pre-evaporitic Messinian, between 6.7 and 6.4 Ma (MN 13) (Rook et al., 2011).

Species: The scanty insectivore remains from Baccinello V3 are assigned to Erinaceidae indet. (Hürzeler and Engesser, 1976).

Remarks: In contrast to the V1 and V2 assemblages, Baccinello V3 fauna is not endemic and has affinities with coeval early MN 13 European faunas (Engesser, 1989; Rook et al., 1996; Bernor et al., 2011). The scanty erinaceid remains are usually reported as “Erinaceidae gen. et sp. nov.” in faunal lists (e.g., Rook et al., 1996). They are not properly figured nor discussed; for this reason, they possibly should be addressed to as “Erinaceidae indet.”.

Borro Strolla (prov. Siena, Tuscany).

Stratigraphy and sedimentology: The remains of Galericinae come from the so-called BS1 sub-synthem locality Piaggiole B quarry, as does the majority of the mammals. The sub-synthem, which consists of "[…] an alternation of greyish-purple coarse-grained sands, silty sands, and subordinate gravels" (Abbazzi et al., 2008b: 620), belongs to the Borro Strollo (BS) Synthem. This synthem ends, in the upper portion of the BS3 sub-synthem, with a lithofacies of marine origin belonging to the earliest Pliocene Argille Azzurre Formation (Bossio et al., 1993, 2001; Abbazzi et al., 2008b). The assemblage is dated to the uppermost Messinian (Abbazzi et al., 2008b).

Species: There is only one insectivore reported from Borro Strolla, *Parasorex* cf. *depereti* (*Galerix* cf. *depereti* in the original publication by Abbazzi et al., 2008b).

Remarks: The mammalian remains from the BS1 sub-synthem did not undergo transport after death and some are articulated, thereby indicating that they were preserved a low-energy environment, with slow-running waters. The depositional environment is transitional from high to low energy channels. The presence of terrestrial and freshwater mollusks suggests a relatively warm and semi-arid environment, susceptible to flooding (Abbazzi et al., 2008b).

Ciabòt Cagna (prov. Cuneo, Piedmont).

Stratigraphy and sedimentology: The micromammal remains come from one of two thin carbonaceous horizons at the top of the so-called lithozone B, which are associated with a deltaic environment (Cavallo et al., 1993). The fossiliferous horizon is associated to the "facies a *Congeria"*, that is correlated with the Conglomerati of the Cassano-Spinola Formation, and it is dated to the post-evaporitic ("Lago-Mare", MSC stage 3.2) late Messinian, close to the Miocene-Pliocene boundary (Cavallo et al., 1993; Angelone and Cavallo, 2010).

Species: The only species of insectivores known from Ciabòt Cagna, *Parasorex depereti* (see discussion below), was originally described as *P.* cf. *socialis* by Cavallo et al. (1993).

Remarks: Parasorex cf. *socialis* from Ciabòt Cagna is represented by a single, badly preserved gymnure tooth (considered as a labial portion of M1) and was assigned to this species by Cavallo et al. (1993) mainly on the basis of its size, the presence of labial cingulum and the straight centrocrista. However, the specimen figured by Cavallo et al. (1993: 13, fig. 6A) is actually a M2 fragment, because of some morphological details (i.e., less prominent disto-labial corner of the tooth, shorter metastylar crest and less developed paraconule, with the labial arm extending towards the mesio-labial corner of the crown). The labial margin of the tooth is more concave than in *Parasorex socialis*, as in *P. depereti* and *P. ibericus*. The fragment differs from many other known specimens of *Parasorex socialis* for its straight centrocrista, which is more suggestive of *P. depereti*. The sample from Brisighella, which is larger than that used by Crochet (1986) for its original description, shows that also in *P. depereti* M2 may have a continuous but narrow labial cingulum (Masini et al. 2019). The paraconule is smaller than in *P. socialis*; it is also simpler than in the latter species, in which a distal arm is usually present. The lingual portion of the tooth is almost absent; however, the protocone-metaconule connection is very strong, as in the specimens of *P. depereti* in which there is a protocone-hypocone-metaconule connection ("triple connection" in Borrani et al. 2018). In *Parasorex socialis*, only in 1 aberrant M2 out of 72 from Petersbuch the protocone is also connected with the metaconule (Ziegler 2005). On the other hand, a protocone-hypocone-metaconule connection is reported in 26% of the sample of M2s of *Parasorex depereti* from BRS25. The size of the labial portion of the Ciabòt Cagna specimen (2.40 mm in length; Cavallo et al., 1993) falls in the dimensional variability of *P. depereti* from BRS25, in which the labial length of the tooth is comprised between 2.31 and 2.73 mm (Masini et al., 2019), and France, in which it is between 2.34 and 2.75 mm (Crochet, 1986). For this reason, the *Parasorex* from Ciabòt Cagna is assigned to *Parasorex depereti*; this is in line with the late Messinian age of the Piedmont assemblage and the faunal similarities with Monticino quarry (see below).

The few fragmentary micromammal remains were probably transported by flooding water from an open woodland upstream of the deltaic environment where the specimen was found (Cavallo and Repetto, 1988; Cavallo et al., 1993). The presence of remains of amphisbenians and sand boas (Erycidae) in the same level bearing those of the micromammals suggests temperate-warm climate (Cavallo et al. 1993). In particular, sand boas prefer clayey soils in relatively warm and arid environments such as steppe, savannah or, less frequently, beach-like environments (Rook et al., 2015; Speybroeck et al., 2016). The depositional environment was characterized by rich aquatic vegetation, including the riparine plant *Toddalia* (diffused today in Africa and South-East Asia) and reeds of the genus *Cyperus* and *Phragmites* (Cavallo and Repetto, 1988). The assemblage shows affinities with other West Europe and African faunas of similar ages; it is particularly interesting for the presence of a gerbillid rodent (Cavallo et al., 1993; Abbazzi et al., 2008b; Angelone and Cavallo, 2010).

Moncucco Torinese (prov. Asti, Piedmont).

Stratigraphy and sedimentology: The rich vertebrate fossil fauna comes from the assemblages MCC3, MCC3/4, MCC4, MCC/4, MCC5 and MCC7 of the clayey “facies a *Congeria*” deposits in the Moncucco quarry, that are considered as the lateral equivalent of the Conglomerati di Cassano-Spinola Formation (Clari et al., 2008; Angelone et al., 2011). All the fossil assemblages from Moncucco are bracketed within a time span ranging from 5.41 to 5.33 Ma (stage 3.2 of the Messinian Salinity Crisis; Angelone et al., 2011; Colombero et al., 2017), but were likely deposited in a shorter span of time (Colombero et al., 2017).

Species: There are four different species of insectivores: a gymnure (*Parasorex* aff. *ibericus*), a mole (*Talpa* sp.) and two shrews, *Petenyia* cf. *hungarica* (present only in MCC3/4, MCC4 e MCC7) and Neomyini indet. (Colombero et al., 2017).

Remarks: The remains of the most common species of shrews were assigned to *Asoriculus gibberodon* by Angelone et al. (2011); however, Colombero et al. (2017) considered them as belonging to Neomyini indet.

A paralic, coastal environment existed in the late Messinian at Moncucco Torinese, with oligo-mesohaline waters and temporary or permanent freshwater bodies, dominated by an open woodland landscape under mesic and warm conditions. The small mammal assemblage is dominated by murids (more than 75%); Soricidae represents between 1.6 to 3%, whereas *Parasorex* is around 2% and *Talpa* is poorly represented (less than 1%) (Colombero et al., 2017). *Parasorex ibericus* is considered an opportunistic species (García-Alix et al., 2008), and so probably was also *Petenyia*, which preferred relatively warm and dry environments with open forests (García-Alix et al., 2008; Popov, 2003; Reumer, 1984). On the other hand, present-day Neomyini (water-shrews) have semi-aquatic habits in a variety of freshwater environments (inter alios Scott et al., 2012). Interestingly, according to the scheme proposed by Colombero et al. (2017: 35, fig. 18) for the relative variation in the importance of the different habitats (i.e., forest, woodland/bushland, grasslands, rocky outcrops and water edges), *Petenyia* is only present in assemblages with relatively limited forested habitats and widespread grasslands and bushlands, under presumably relatively dry conditions.

Monticino quarry (prov. Ravenna, Emilia-Romagna)

Stratigraphy and sedimentology: The remains from Monticino quarry come from a network of cavities (numbered from 1 to 28), mainly of karstic origin, which are sealed by the brackish sediments of the Colombacci Formation and are possibly slightly older or contemporaneous with the latter. The fissure fillings are dated to the post-evaporitic Messinian, being deposited after the tectonic processes that tilted the earlier Gessoso Solfifera unit but before the earliest Pliocene Argille Azzurre Formation (Marabini and Vai, 1989; Rook et al., 2015).

Species: Four different species are known from the cavities: *Parasorex depereti* (from fissures 2, 3, 5, 6, 12, 14, 24, 25, 26, 27 and 29), *Neomyosorex* sp. (from fissures 2, 3, 4, 5, 6, 8, 9, 11, 12, 25, 27 and 29) and scanty remains of "*Mioechinus"* sp. (from fissures 5 and 9) and cf. *Miosorex desnoyersianus* (just from fissure 20) (De Giuli et al., 1988; De Giuli, 1989; Masini, 1989; Masini and Thomas, 1989; Fanfani, 1999; Rook et al., 2015).

Remarks: The presence of Galericinae in the Brisighella deposits has been reported by many authors since the discovery of the assemblages (Costa et al., 1986; De Giuli et al., 1988; De Giuli, 1989; Masini, 1989; Masini and Thomas, 1989; Torre, 1989; Masini and Rook, 1993). It was assigned to various different species over time, but consensus was finally reached on *Parasorex depereti* (Fanfani, 1999; Masini and Fanfani, 2013; Rook et al., 2015; Masini et al., 2019).

De Giuli (1989), Masini (1989), Masini and Thomas (1989) and Torre (1989) assigned the most abundant remains of the shrews from Brisighella to *Asoriculus* (=*Episoriculus*) aff. *gibberodon*; this interpretation was questioned by Fanfani (1999), who preferred attributing it to *Neomyosrex* sp.; he also attributed the scanty remains of a small-sized Crocidosoricinae to cf. *Miosorex pusilliformis*, which is a junior synonym of *Miosorex desnoyersianus* according to Klietmann et al. (2013).

Some authors (De Giuli et al., 1988; De Giuli, 1989; Masini, 1989; Masini and Thomas, 1989; Torre, 1989; Fanfani, 1999; Rook et al., 2015) reported *Mioechinus* or *Postpalerinaceus* sp. from the Monticino quarry fissure infillings. The taxonomic status of *Mioechinus*, coined by Butler (1948) to accomodate *Erinaceus oeningensis* (from the Middle Miocene of Deutschland; Ziegler 1999), is currently disputed: McKenna and Bell (1997) considered it as a synonym of *Hemiechinus*, and Mein and Ginsburg (2002) attributed it to the genus *Atelerix* (Prieto et al., 2015). On the other hand, Ziegler (2005) considered *Mioechinus* as a valid genus but limitedly to the type species; he also stated that the Miocene hedgehogs cannot be distinguished from each other if not based on cranial features. According to this criterion, the scanty remains of "*Mioechinus*" from Brisighella cannot be discriminated from *Postpalerinaceus* or *Atelerix*. Given the disputed validity of

Mioechinus and the fragmentary state of its cranial remains, the Brisighella hedgehog is tentatively assigned to "*Mioechinus*" sp.

Monticino quarry has been associated to "a flat, brackish, shallow environment not far from a distributary channel system and from an alluvial flash plain" (Marabini and Vai, 1989: p. 372).

Terre Rosse faunas (prov. Foggia and Barletta-Andria-Trani; Apulia)

Stratigraphy and sedimentology: The Terre Rosse insular faunas are recorded from several karstic fissure infillings, typically reddish in color (from which the name of these fossiliferous deposits), mainly exposed by quarry activities, between the cities of Foggia and Poggio Imperiale (Foggia) and in an unknown locality between Barletta and Andria (Freudenthal, 1971; Masini et al., 2010). The fissures are attributed to five different phases, from 0 to 4 (further subdivided into sub-units 1a, 1b, 2a, 2b, 3a, 3b and 3c; see Masini et al., 2013 and Savorelli et al., 2019) on the basis of the evolutionary degree of the faunal content, in particular of the abundant small mammal record (Freudenthal, 1976; De Giuli et al., 1987; Masini et al., 2008, 2010, 2013; Rinaldi and Masini, 2009; Maul et al., 2014). The Gargano fissure infillings are not vertically staked stratigraphically and can thereby only be dated biochronologically. The method proposed by Freudenthal (1976) was based mainly on the increase in size and in the number of molar crests of the endemic murid *Mikrotia*, using the evolutionary degree of the endemic cricetid *Hattomys* to cross-check the resulting succession of fissures. De Giuli et al. (1987) refined the criteria, focusing mainly on the morphological evolution of *Mikrotia* and *Prolagus* through time assuming the minimum number of bioevents (extinction, speciation/migration) and evolutionary changes (Savorelli et al., 2019). The fauna is dated to the late Messinian (MN 13) (De Giuli et al., 1987; Freudenthal, 1985) or, at most, to the earliest Pliocene (MN 14) (De Giuli et al., 1987).

Species: The insectivores are all endemic genera, maybe except ?*Lartetium* cf. *dehmi* from phase 0-1 fissures (M013, Rinascita 1, Biancone 1, F15 and F21 a-b) (Fanfani, 1999; Masini et al., 2013).

There are two endemic Galericinae genera: *Apulogalerix* and *Deinogalerix*. The former includes only one species, *Apulogalerix pusillus*, which ranges from phase 0 (*Apulogalerix* cf. *pusillus*) to 4 (Masini and Fanfani, 2013; Masini et al., 2013). The giant gymnure *Deinogalerix* includes a number of species, belonging to different evolutionary lineages, which are often present in the same fissure (Savorelli et al., 2019: 246, Tab. 5). *Deinogalerix masinii* is the smallest and earliest one, for being present only in phase 0 (fissure M013) (Villier et al., 2013). *Deinogalerix freudenthali* is present in fissures of phases 1a (Rinascita 1) and 1b (Biancone 1 and F15); however, scanty remains may suggest its presence already in phase 0 (M013) (Butler, 1980; Savorelli et al., 2019). A jawbone fragment, from the younger fissure P81D (phase 2), which is tentatively attributed to *Deinogalerix* sp. 2, may belong to the same lineage or be a *D. freudenthali*-like ancestor of *D. minor* (Savorelli et al., 2019). *Deinogalerix minor*, a relatively larger and more derived species, belongs to a lineage that includes the latest species *D. brevirostris* (from the latest phase 3 deposit San Giovannino) and maybe another earlier unidentified species (i.e., *Deinogalerix* sp. 1 from the fissure fillings F15 and F21C of phase 1b). It is reported from deposits of phases 2 and 3 (Fina D, Chirò 7A, Chirò 14A, Fina H, F9, Gervasio and possibly F1, Chirò 20C and M010, the latter originally described as *D. brevirostris* by Villier 2010) (Butler, 1980; Savorelli et al., 2019). *Deinogalerix intermedius*, a large-sized species, has also been found in the phase 2 and 3 fissures (Fina D, NBS, Nazario 4, P81D, Pizzicoli 4, F1, Chirò 5A, Posticchia 1B, Fina H, F8, F9, Gervasio and Chirò 20C) and maybe in latest phase 1b deposit F21C (Butler, 1980; Savorelli et al., 2019). Finally, aside with *D. brevirostris*, another large-sized species of *Deinogalerix* is known from San Giovannino (latest phase 3), i.e., *D. koenigswaldi*, that is probably related to *D. intermedius* (Freudenthal, 1972; Butler, 1980; Savorelli et al., 2019). No remains of *Deinogalerix* are known from fissure infilling F32 (phase 4) (Savorelli et al., 2019).

Remarks: Villier (2012) and Villier and Carnevale (2013) supposed that all the species of *Deinogalerix* from phases 1-3 could actually represent distinct ontogenetic stages and individuals of the two sexes of the largest sized representative *Deinogalerix koenigswaldi*. Savorelli et al. (2019) excluded this hypothesis due the evident dentary differences shown by these representatives as well as by the absence of marked sexual dimorphism in present-day Eulipotyphla (see Lindenfors et al., 2007). *Deinogalerix* and *Apulogalerix* have been considered related to each other based on their sharing common traits, such as, for instance, the absence of i3 and the bulbous shape of the teeth (van den Hoek Ostende, 2001d). This hypothesis, however, has been dismissed not only based on the possibility that the overall aspect of the teeth may likely result from parallelism by living in similar environments, but also after the discovery of *Deinogalerix masinii*, which still retains a reduced i3. In alternative to supposing it somehow linked to *Parasorex* and *Apulogalerix*, *Deinogalerix* has been supposed to be related to more basal, *Galerix*-*Parasorex* transitional species (Borrani et al., 2018).

A small Crocidosorinae was originally assigned to "*Sorex" dehmi* or to "*Myosorex*" (De Giuli et al., 1987, 1990), and to *Lartetium* cf. *dehmi* by Fanfani (1999). However, the absence of the third antemolar excludes this species from Gargano from *Lartetium*; for this, it has been named ?*Lartetium* cf. *dehmi* by Masini et al. (2013).

The "Terre Rosse" faunas, together with those from the older localities of Scontrone and Palena (Abruzzo), belong to the Abruzzo-Apulian Palaeobioprovince (Mazza and Rustioni, 2008), better known as Abruzzo-Apulian Platform (Patacca et al., 2013). The faunas from Scontrone show lower degree of endemism and are dated stratigraphically to the Tortonian (ca. 9 Ma; Patacca et al. 2008, 2013). Savorelli et al. (2016) dated the dispersal of the ancestors of the endemic murid *Apatodemus* in the insular domain to the Messinian (MN 13). However, the ancestors of the endemic *Deinogalerix* and of the artiodactyl *Hoplitomerix* are posited to have arrived much earlier, in the Late Oligocene-Early Miocene (Mazza and Rustioni, 2008; Borrani et al., 2018). *Apulogalerix pusillus* has been considered related to the Iberian species *Parasorex ibericus*, based on some common traits (e.g., absence of i3); if this interpretation is correct, its ancestor dispersed in Gargano at the beginning of the Tortonian (MN 9) (Masini and Fanfani 2013; Borrani et al., 2018).

Velona basin (prov. Siena, Tuscany)

Stratigraphy and sedimentology: All the vertebrate remains come from the lacustrine deposits of Fosso Casotto and Gretoni, which are indicated as subunit B localities of the Lower Synthem of the Velona basin (Ghetti et al., 2002). These deposits are included in the so-called lithofacies $VB1b_m$ (Benvenuti et al., 2015) and are dated to the pre-evaporitic Messinian (early MN 13); they are considered to have accumulated in a low-energy environment, i.e., a marsh with oligo-mesohaline waters (Ghetti et al., 2002; Benvenuti et al., 2015).

Species: There is only one species of insectivores reported from the Velona basin, *Parasorex* cf. *depereti* (*Galerix* sp. in Ghetti et al., 2002).

Remarks: The mammal remains are considered similar with those of the V3 faunas of the Baccinello-Cinigiano basin (Benvenuti et al., 2015). Ghetti et al. (2002) identified the remains of erinaceids from Velona as *Galerix* sp., but failed to figure or describe them. However, the genus is not known after the Middle/Late Miocene transition (MN 7/8-9; van den Hoek Ostende, 2001d; Prieto et al., 2011).

The only remain of Galericinae is a lingual fragment of a right M2, about 1.73 mm long (Fig. 9). The fragment preserves the lingual portion of the mesial cingulum and, most importantly, a large protocone, connected to the hypocone by a continuous ridge and apparently also to the metaconule. This last character is present only in two species between *Parasorex*, *Parasorex depereti* and *P. kostakii*, of which only the former is present in Italy at the end of the Miocene; however, the rather small size and the scanty remains prevent a confidant classification in the latter species. Therefore, it is herein provided the attribution to *Parasorex* cf. *depereti*.

Figure 9 - Lingual fragment of *Parasorex* cf. *depereti* from the Velona Basin, in (a) mesial and (b) occlusal view. Scale bar=1 mm.

Verduno (Cuneo, Piedmont)

Stratigraphy and sedimentology: The rich vertebrate-bearing levels of the site of Verduno are correlated with stage 3.1 of the Messinian Salinity Crisis (5.55-5.41 Ma) (Colombero et al., 2014). The clayey lithofacies 1, 2 and 5 that yielded the small mammal remains belong to the Cassano Spinola Conglomerates Formation (Colombero et al., 2013, 2014).

Species: The assemblage includes only two species of insectivores: cf. *Asoriculus gibberodon* (Soricidae), from lithofacies 1 and 2, and *Parasorex* sp. (Erinaceidae), from lithofacies 5 (Colombero et al., 2014).

Remarks: The fossiliferous lithofacies that provided the remains of the two species formed in different depositional environments: lithofacies 1 and 2 deposited in an oligo-mesohaline costal setting, probably a lake several meters deep with oligotrophic water (Colombero et al., 2014). Lithofacies 5 is associated with a fluvio-deltaic environment, with brackish water (Dela Pierre et al., 2011). The probable presence of *Asoriculus gibberodon* could be related to a relatively wet and warm habitat (Reumer, 1984; Popov, 2003; García-Alix et al., 2008).

Zanclean (Early Pliocene)

Capo Mannu (Oristano, Sardinia).

Stratigraphy and sedimentology: The assemblage has been biostratigraphically dated to a time period between MN 13/14 and MN 16 (Furió and Angelone, 2010). The remains come from lens of quartzite sandstone enclosed within the lower part of the Calcari di Mandriola Formation, which has been interpreted "as a damp or pond accumulation at the base of the first dune unit" (Furió and Angelone, 2010: p. 219 and references therein).

Species: The fauna from Capo Mannu D (Dune) 1 unit was described by Pecorini et al. (1974), who reported the presence of Erinaceidae gen. indet. and of a non-Desmaninae mole. Later on, the two species have been ascribed to *Parasorex depereti* and *Talpa* cf. *minor*, respectively, by Furió and Angelone (2010), which also reported the presence of two Soricidae, *Asoriculus gibberodon* and cf. Soricini indet.

Remarks: Asoriculus gibberodon and *Talpa* cf. *minor* may indicate the presence of a relatively warm and wet habitat, maybe a forest edge (Reumer, 1984; Popov, 2003; García-Alix et al., 2008).

DISCUSSION

Despite Italian Neogene insectivores are known from relatively few localities, the Late Miocene (MN 10-13) provided a rich record, wherein two of the three main families of Eulipotyphla (Erinaceidae and Soricidae) are well represented.

The only spiny hedgehog (subfamily Erinaceinae) known is "*Mioechinus*" sp. from Brisighella. Rare remains of *Orycteropus* cf. *gaudryi* (Afrotheria: Tubulidentata) are reported from the same deposits (Rook and Masini 1994). Present-day aardvarks primarily live in habitats with soft soils and high availability of ants and termites, but can also be found in arid (not desertic) environments, as well as from rainforests to grasslands (Taylor 2011). Modern hedgehogs of the genus *Atelerix* can also be found in a variety of environments, except for rainforests and deserts, and arid grasslands to steppe are home to *Hemiechinus* (Corbet 1988; see He et al. 2012 for an updated classification of present-day Erinaceinae). If at least some Miocene species of hedgehogs are placed in the synonymy of *Hemiechinus* or (more probably) of *Atelerix*, the presence of these animals in the Monticino quarry deposits alongside the aardwaark may indicate relatively xeric environmental conditions. This is also supported by the presence in the same deposits of Erycidae (sand boas) remains (Kotsakis 1989; Rook et al. 2015): these snakes prefer relatively arid environments with soft soils, such as steppe or savannahs (Rook et al. 2015; Speybroeck et al. 2016). Interestingly, an Erycidae indet. is also reported from Ciabòt Cagna (Piedmont; Cavallo et al. 1993), alongside with *Parasorex depereti*, that is also present at Monticino quarry.

The very poor record of the Erinaceinae is compensated by the richness of the Late Miocene Italian Galericinae one. The oldest are the *Deinogalerix* species from the late Vallesian of Scontrone (*D. samniticus* and *D.* sp.; Savorelli et al. 2017, 2019), albeit these highly derived and specialized insular species from both Scontrone and Gargano are not directly linked with younger mainland species. The oldest continental Italian Galericinae is *Parasorex* vel *Schizogalerix* sp. from the Velona basin (early MN 13). *Parasorex depereti* (which is known from four assemblages from MN 13 to MN 14 or 15; Abbazzi et al. 2008b; Fanfani 1999; Furió and Angelone 2010; Masini and Fanfani 2013; Masini et al. 2019) and related species occurs in some Messinian and one Pliocene assemblages.

Appendix II – List of taxa used for comparisons

Taxon	**Stratigraphic range**	**Site**	**References**
Anatolechinos	Middle (*Anatolechinos huadianensis*) -Late Eocene (*Anatolechinos neimongolensis*)	Member (=Sequence) III of the Huadian Formation (China; *Anatolechinos huadianensis*); Houldjin Formation, Ulan Gochu Formation and Qagan Bulag (=Chaganbulage) Formation (China; *Anatolechinos neimongolensis*)	Wang (2008), Wang and Li (1990)
Brachyerix macrotis	Late Oligocene (late Arikaarean, Ar3-early Barstovian)	Deep River Beds (upper zone), Montana; Split Rock (upper porous sandstone sequence), Wyoming; Sheep Creek Formation (base), Nebraska; Harrison o Marsland Formation, Nebraska; Troublesome Formation (lower part), Colorado	Matthew and Mook, 1933; Rich and Rich (1971)
Changlelestes dissetiformis	Early Eocene	Wutu Formation (China)	Lopatin (2006); Storch and Dashzveg (1997); Tong and Wang (1993)
Echinosorex gymnurus	Extant	Brunei Darussalam, Indonesia, Malaysia, Myanmar and Thailand	Butler (1948); Corbet (1988); Frost et al. (1991); Gureev (1979); Ziegler (1983)

Entomolestes	Late Early (*Entomolestes grangeri*: Barstovian, Br2)-early Middle Eocene (*Eontomolestes westgatei*: Uintanian, Ui1)	Grizzly Buttes West, Bridger B, Bridger Formation, Wyoming (*Entomolestes grangeri*); UCM 92189, 2 m above the base of the Turtle Bluff Member, Bridger Formation, Wyoming (*Entomolestes westgatei*)	Krishtalka (1976); Kirshtalka and Munthe (1976); Matthew (1909); Novacek et al. (1985); Murphey e Kelly (2017)
Eochenus sinensis	Middle Eocene	Members (=Sequences) III and IV of the Huadian Formation (China)	Wang and Li (1990)
Exallerix gaolanshanensis	Early Miocene (Xiejian)	Lanzhou Basin, Gansu (China)	Qiu and Gu (1988)
Gymnurechinus	Early Miocene	Hiwegi and Rusinga Formation, Rusinga Island, Kenya (*Gymnurechinus camptolophus* and *G. leakeyi*); Kamathangere and Kathwanga, Kenya (*Gymnurechinus camptolohpus*); Songhor, Ghana (*G. songhorensis*)	Butler (1956b; 1969)
Hemiechinus	Extant	Central-West Asia (South Russia, China, Mongolia, Turkestan, Afghanistan, west Pakistan, Iran) to Lybia (*Hemiechinus auritus*); central and east Pakistan and north-west India) (*Hemiechinus collaris*)	Butler (1948); Corbet (1988); Frost et al. (1991)
Hylomys	Early Middle Miocene (MN 4, *Hylomys engesseri*) - extant	Li Mae Long (Thailand; *Hylomys engesseri*); Brunei Darussalam, Cambodia, China, Indonesia, Lao People's Democratic Republic, Malaysia, Myanmar, Thailand, Vietnam (*Hylomys suillus*); Sumatra (Indonesia) (*Hylomys parvus*)	Butler (1948); Corbet (1988); Engesser and Jiang (2011); Frost et al. (1991); Mein and Ginsburg (1997); Ziegler (1983)

Lantanotherium	Early (MN 3; *Lantanotherium lactorense*) - late Miocene (*Lantanotherium dehmi*)	Beaulieu (France; *Lantanotherium lactorense*); Cuyama Valley badlands (California; *L. dehmi* and *L. sawini*); Dorn-Diirldaeim (Germany; *L. sanmigueli*); Götzendorf, Richardhof-Golfplatz, Richardhof-Wald, Schernham (Austria; *L. sanmigueli*); La Grive-Saint-Alban (France; *L. robustum*and *L. sabinae*); Leoben, Steiermark (Austria; *L. longirostre*); Lufeng (China; *L.sanmigueli*); Mae Moh (Thailand; *Lantanotherium anthrace*); Observation Quarry (Nebraska; *L. observatum*); San Llobateres (Spain; *L. sanmigueli*); Viein Basin (Austria; *Lantanotherium* cf. *sansaniense*); Sansan (France; *L. sansaniense*)	Cailleux et al. (2020); Engesser (1979, 2009); Korth and Evander (2016); Jones (1963); Mein and Ginsburg (2002); Rabeder (1973); Storch and Qiu (1991); de Villalta Comella and Crusafont Pairó (1944); Ziegler (2006)
Leptictis dakotensis	Early Oligocene (Orellan)	Corral Draw (South Dakota); White River Formation (Wyoming and South Dakota)	Butler (1956a, as *Ictops dakotensis*); Novacek (1986); Rose (2006, 2012)
Litocherus lacunatus	Middle-Late Paleocene (Ti4-5)	Various localities (*Titanoides* locality, Rock Springs Uplift, Battle Mountain and Type Chappo) of Wyoming; Roche Perceé (Saskatchewan, Canada)	Gazin (1956); Gingerich (1983); Rankin (2018)

Litolestes ignotus	Late Paleocene (Ti5)	Princeton Quarry (Park County, Wyoming); Silver Coulee Quarries, Polecat Bench Formation, (Wyoming)	Butler (1988); Jepsen (1930); Krishtalka (1976); Novacek et al. (1985); Scott (2006, as *L.* cf. *ignotus*); Schwartz and Krishtalka (1976); Secord (2008)
Macrocranion	Early (MP7, *Macrocranion vandebroeki*; Wa0, *M. junnei*)- Middle Eocene (*M. tenerum* and *M. tupaiodon*)	Dormaal (Belgium; *M. vandebroeki*); Grube Messel (Germany; *Macrocranion tenerum* and *M. tupaiodon*) Willwood Formation, Bighorn basin (Wyoming; *M. nitens* and *M. junnei*); Quarry 88, San Jose Formation (New Mexico; *M. nitens*); Lost Cabin and Lysite Members, Wind River Formation (Wyoming; *M. nitens*)	Bown and Schankler (1982); Maier (1977, 1979); Matthew and Granger (1918); Krishtalka (1976); Novacek et al. (1985); Quinet (1964); Smith and Smith (1995, as *Dormaalius vandebroeki*); Smith et al. (2002); Tobien (1962)
Megaleptictis altidens	Latest Eocene (Chadronian) or earliest Oligocene (Orellan)	Lower or middle White River Group (South Dakota)	Meehan and Martin (2012)
Mesechinus dauuricus	Extant	China, Mongolia and Russia	Corbet (1988, as *Hemiechinus daauricus*); Frost et al. (1991)
Neohylomys hainanensis	Extant	Island of Hainan (China)	Corbet (1988), Engesser and Jiang (2011); Frost et al. (1991; as *Hylomys hainanesis*)
Neotetracus sinensis	Extant	China, northern Myanmar and northern Vietnam	Butler (1948); Engesser and Jiang (2011); Frost et al. (1991)

Ocajila makpiyahe	Late Oligocene-early Miocene? (Arikaarean)	S.D.S.M. V5360, Sharps Formation (South Dakota); Blue Ash Local Fauna (South Dakota)	Engesser (1979); Korth (2009, as cf. *O. makpiyahe*); Macdonald (1963)
Paraechinus	Extant	*Paraechinus aethiopicus*: Algeria; Bahrain; Chad; Djibouti; Egypt; Eritrea; Ethiopia; Iran, Islamic Republic of; Iraq; Israel; Jordan; Kuwait; Libya; Mali; Mauritania; Morocco; Niger; Oman; Qatar; Saudi Arabia; Somalia; Sudan; Syrian Arab Republic; Tunisia; United Arab Emirates; Western Sahara; Yemen. *P. hypomelas:*Afghanistan; Iran, Islamic Republic of Oman; Saudi Arabia; Tajikistan; Turkmenistan; Uzbekistan; Yemen. *P. hypomelas* and *P. micropus*: Pakistan. *P. nudiventris* and *P. micropus*: India	Butler (1948); Corbet (1988); Frost et al. (1991)
Podogymnura truei	Extant	Island of Mindanao (Philippines)	Corbet (1988); Frost et al. (1991); Ziegler (1983)
Protogalericius averianovi	Uppermost early Eocene	Andarak 2, lower part of the Alai Beds (Kyrgyzstan)	Lopatin (2006)
Tupaiodon morrisi	Latest Eocene/earliest Oligocene (Chadronian-Orellan transition)	Hsanda Gol formation, Red beds, Loh (Mongolia)	Butler (1980), Matthew and Granger (1924)
Scenopagus	Early- early Middle Eocene (*Scenopagus curtidens*: Wasatchian-early Uintanian)	Andarak 2, lower part of the Alai Beds (Kyrgyzstan)	Murphey and Kelly (2017); Novacek et al. (1985); Krishtalka (1976)

Scymnerix tartareus	Early Oligocene	Ulan-Khureh, Shand-Gol Formation (Mongolia)	Lopatin (2003b)
Silvacola acares	Early Eocene (Bridgesian)	Driftwood Creek, Driftwood Canyon Provincial Park, (British Columbia)	Eberle et al. (2014)
Zaraalestes russelli	Middle Eocene	Quarry Tsagan Tsav II, Tsagan Tsav Section (Mongolia)	Storch and Dashzveg (1997)

Table 4 - List of taxa used for comparative purposes, with time span, geographical distribution and main references.

Appendix III – Data matrix

Eogalericius_butleri

??00????????????0?00?[012]00?000001?0??0??001100010001002[01]0[01]1000[02]00001000000000000[12]??????????000?00000000000000000020000000200?????????

Micrograleriuculus_esuriens

?????????0???0000?00?400?0200??????0??0??11000021010200100021001010010100 10???

Zaraalestes_minutus

??00???????????????0?400?0200020000[03]??2111[01][01]0002[01][01]2020010000000[01]010010000000000?200000000020?0001[01]00000[01]0001[01]0[02]?5200[01]001101100000?

Apulogalerix_pusillus

??01??000000100000000[26]1300003021100[023]10?0[01]140112111[01]00100110[12]1000014110[02]10[01]2011300110130[01][123]0200021?001000010[134][01]2[23]10[35]0042[23]1[02]110[01]00411?

Deinogalerix_brevirostris

1?1211??????????1??0?41211022222111???0??2401101310041002 0?3????????1???2??????10113120110222020301200?210????0?5004250?120010?21?

Deinogalerix_freudenthali

?????00100120001000?412?10021?????2??01124011012110410020 0[34]1022203110[02][12]2010013?????1????02010203012001[02]100[01]25005[01]042[56]01100[01]10121?

Deinogalerix_intermedius

?????112111221111121412?2002?22112200011240110131004100200???222??????????0013?01131201102[02]2020301200111 0?0[12]?005[02]03250112?????21?

Deinogalerix_koenigswaldi

2112[12][12]112121221211112241212022322112200011240110131004100200[34]0022233210202

01001310113120110222020301200111020250052042501120110121?

Deinogalerix_masinii

0?11??00100020000000?41210002122011200011240110121104100200[12]102220311001001001

3101131201[01]02[01]112030120010100125[01]0500125[01]1100110121?

Deinogalerix_minor

1112111010012[01]001000141211022222111200011240110131004100200[34][01]0222332100[0

1]2010013?01131201102[12]10203012001[02]10[23]1[12]500500[14]2501120110121?

Deinogalerix_samniticus

?????????????????????412???11????????????24011012110410020001?22203?100?2??00?????31

2011?2001?????200??1?????????0?2?2?10?110??1?

Galerix_africanus

??11????????????0?00??10?011402?0?10??00110000111100010011000010115210000030013??0

1001000020?010?0010003100[13]102[01][35]300102[13]10?10?401?

Galerix_aurelianensis

???0??????????0?0?00?60???1100???0?0100001[04]000[13][01]11100100[01]100[013]00[01]111

2100[01]01[13]00[12]3?010000002020?00121010001100[13][0123]0[12]03[23]00[0123]01[13]10

0[12]00001?

Galerix_exilis

0000000000000000000[345]0[01]?011502?0[01]0[012]10000[012][045][01]001111[12][01]110

0[01]10[12][01]0[01]011[25][12]10[02][01][01][01][13]0[01][12]3?010[01][01][01]00[012]02010[

12][012]3[01]010001100[13][123]0[02]0[34]20[02][123]01[13]100[012]00[04][01][01]?

Galerix_iliensis

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011020?1212001001[12]1000221?5[02]002[23]1[01]110200101?

Galerix_remmerti

????????????????????????????40?????00???????0011?12[01]01000101[01]0001111102[01]00100

13????00[01]002010?0112[01]0100011001[13]0[12]?1200[013]121100[12]00001?

Galerix_rutlandae

???????????????????0??????0240?????101001100001[01]112[01]0100[01]10[02]00001111101[01

]0120013?01[01]00000[01]020?01??001000[123]100[13][234]0205[123]00[123]02[13]100[012]00

401?

Galerix_saratji

?????????????????????[45]0??01000?1?0?[12][01]001110000[01]111200100[01]10[01][01]00[01]

11[01][12]10[02]100[01][01][01]13?0??00[01]00[02]0[12]0?01[01]2201000[012]100[01][13]0[12]

0[235][02]00[13]0[12]1100[02]0[012][04][01]1?

Galerix_stehlini

??????0010000[01]0000000[2345]1[12]?01130210110??00111000[13]1112101001000[03]000112

110011020013?01100000[01]020?0[12]1300100011001102?520[02][12]02[13]100000401?

Galerix_symeonidisi

?????????????????????[45]????1000????????0001101[01][013]11120210[01][01]0000000111[12]

100[01]10101[12]3????0?20[01][03]020?0[12]1200100011001[12]0[02]?[35][02]00[012]0[01][01]

110[01]0[01]001?

Galerix_uenayae

??????????????0????0?[45]0??01100?????[012]1001[01]10000[13]1112001000100100011121001

1010013?0??00[01]00[02]020?0012001000[01]1[01]0[01][234]0[12]0[235][02]02[012]01[01]100[

01]00401?

Galerix_wesselsae

??????????????????????????1140?????101011100001[01]?1200100[01]00[02]0000112110?[01]01

10?13?011012003020?0?[12]?00100?11001[34]020?[02]00[01]021110[02]0[02]401?

Parasorex_depereti

???????00000100000000604?00?0021000[02]10[012]001[34]0110111[12]12101110210001 1[02]110[02]110201130110[0124]12[01][01][23]020[01][01]21[23]00100001001[12]110[13]00[01][12][12]1111[01][01]00[04]01?

Parasorex_ibericus

???1??0000?0??000?00?[456]12?0005021100?10[012]0014011011110210[01]100[012]10[01]0112110[02]110201[15]31?1?0120120[12]0?0212001000010[01][01]2[234][01]030002[23]11110100401?

Parasorex_kostakii

???????????????????????????050??????????????11[013]1?1?121011101100 01[01][12][12]102100[12]0153????0120[01][12]020?00030010000100 12[02]2?500[01][123][02]1111[01][01]00001?

Parasorex_pristinus

???????????????????????????160???????????140110211??2100110?1000112121011010??3????0120?2??0????????1[01]00100022??100222?1110[01]00301?

Parasorex_socialis

??00??000000100000000[3456]02?000502?00??100001[03]0110111[12]121011000100011[12]110[01]11[01][12]01[15]301110120[01][023]020?0[12]12001000010012210[35]0002[023]1[01]110[12]00[04]01?

Riddleria_atecensis

?????????????????????????????0???????????????????????1???102001?3201111?10?0043????000?0202???11????00012001122?12044021110100001?

Schizogalerix_anatolicus

???????????0??000?01?50??000602?0000100001601102112[02]31011111[04]000111121[02][03]1010113????00201[12]020?021[23]003110010312[34]00300[34]2[34]02210[02]00201?

Schizogalerix_duolebulejinensis

????????????????????????????60??????????????110211223111?10?0000121?2120101?????????????????0?0?0233003110010312400????????????????1?

Schizogalerix_evae

????????????????????????????60??????????????1102112021011000?00011?121011010153??????????020?023?20311101011230?????????????????1?

Schizogalerix_intermedius

????????????????0?01?61??02060210000100001601102112?31011112400012?121[12][03]10101[16]3??110120120?0??213003110010412900500?2A02210100301?

Schizogalerix_macedonicus

???????????????????????????060??????????????1102112231011110510012112104101????????012013120?0214003110011[34][12]280050142A02210100301?

Schizogalerix_moedlingensis

??????0000?01000000?0502??0250?????0?????170110211213101111?[01]000111221011010113????012012020?023400311001011290030042A0221001030[01]?

Schizogalerix_pasalarensis

???????????????????????????050??????????????01102112221011101100011121211010113????012012020?021200311001011220030022300210100201?

Schizogalerix_sarmaticum

???????????????????????????06??????2?????170110211223101111151001211211410101[16]3????0120?3120?011400311001011290050032A02310000201?

Schizogalerix_sinapensis

????????????????0?01?61??000602100?01000016011021120310111114[01]001[12]1121141010163??11012013120?021300311001041290050 0[34]2A02210000[34]01?

Schizogalerix_voesendorfensis

??????0000?01[01]0000010[45]12?000602?0??0??0??17011021122310111110000111221001010113?1??01201202010234003110010112700300032[38]20210000[24]01?

Schizogalerix_zapfei

?????????0??????0?01?50??020602?0??0??20027011021122311111040001212210410101163????
?????????????????11001032290???????????????????

Tetracus_daamsi

??????????????????????????1130???00201010120001111110101100000100111000001?013?0??
000000010?0001[12]0100011000102?130010201??210?01?

Tetracus_nanus

????????00?000000?00?[45]00?011000?000[02]0[01]0[01][01]10000[13]1111011[01]0110000001
1[01]010011000[01]13?0[01][01]000000020?000220100011001102 0[35]200[01]020100[012]0000

Appendix IV – List of characters

Cranial characters

0) Nasals, posterior end (from He et al., 2012, modified): (0) anterior to antorbital rim; (1) approximately in line with antorbital rim; (2) posterior to orbital rim. Ordered. This character can be observed only in *Galerix exilis*, *Deinogalerix brevirostris*, *D. koenigswaldi*, *D. masinii* (Villier et al., 2013) and *D. minor*. In *G. exilis* and *D. masinii* the posterior rim of the nasals does not reach the antorbital rim. In *D. minor* and *D. brevirostris* the posterior end of the nasals is approximately in line with, or slightly posterior to, the antorbital rim; in *D. koenigswaldi* it is posterior to the antorbital rim.

1) *Foramen palatinum magnum*, extension of distal margin (modified from Gould, 1995; He et al., 2012): (0) posterior to maxillo/palatina suture; (1) in line with maxillo/palatina suture. Unordered. The position of the distal margin of the *foramen palatinum magnum* can be only observed in three species: *Deinogalerix koenigswaldi*, *D. minor* and *Galerix exilis.* He et al.'s (2012) original character was changed here to better fit the configurations present in Galericinae: in *G. exilis* the distal margin of the *foramen palantinum magnum* is located behind the maxillo/palatina suture; in *D. koenigswaldi*, *D. brevirostris* and *D. minor* it is in line with the suture.

2) Position of anterior opening of infraorbital canal (from Frost et al., 1991; Gould, 1995; He et al., 2012, modified): (0) dorsal to P3; (1) dorsal to P4. Ordered. The polarity of this character was changed with respect to He et al., 2012: in early species of Erinaceomorpha and Erinaceidae, e.g., *Macrocranion nitens* and *Silvacola acares*, the anterior opening of the infraorbital foramen can be aligned between P2 and P3. However, in

early Galericinae-like species, e.g., *Eogalericius butleri* and *Zaraalestes minutus*, as well as in *Macrocranion tupaiodon* (specimen F.2 in Maier, 1979: p. 47, fig. 6A), is in line with P3. A comparable position can also be observed in *Apulogalerix pusillus*, *Galerix exilis* and *Parasorex socialis*. In *G. africanus* it is positioned "above the anterior end of P4" (Butler, 1984: p. 143), as it is also in *Deinogalerix brevirostris*, *D. koenigswaldi*, *D. masinii* and *D. minor*.

3) Base of zygomatic arch: (0) from metastyle of M1 to metastyle of M2; (1) from metastyle of M1 to whole M2; (2) from M1 to between M2-M3. Unordered. In *Eogalericius butleri* and *Zaraalestes minutus,* the base of the zygomatic arch extends from the metastyle of M1 to the metastyle of M2. Maier (1979, p. 43) reports that even in *Macrocranion tupaiodon* "the zygomatic roots above M2; it is a rather slender structure […]". In *Apulogalerix pusillus*, *Parasorex ibericus*, *Deinogalerix masinii* and *Galerix africanus,* the zygomatic arch is stronger and extends from the metastyle of M1 to the whole M2. *G. aurelianensis*, *G. exilis* and *Parasorex socialis* have a plesiomorphic, short-based zygomatic arch. In contrast, *D. koenigswaldi*, *D. brevirostris* and *D. minor* have a long-based zygomatic arch, extended from above M1 to between M2-M3.

4) Development of sagittal crest (from Gould, 1995; He et al., 2012, modified): (0) weak; (1) well-developed; (2) hypertrophic. Unordered. The early species *G. exilis*, alongside other erinaceids, e.g., members of extant *Echinosorex*, *Hylomys*, *Neohylomys* and *Neotetracus* - some of which totally lacking this structure-, has a poorly-developed sagittal crest (Ziegler, 1983: p. 170, fig. 156; Butler, 1948: p. 449, fig. 3; Ziegler, 1983: p. 166 – 168, fig. 150-154; Frost et al., 1991: p. 51- 56, pl. 1-6). In Erinaceinae, only members of the genera *Hemiechinus*, *Mesechinus* and *Paraechinus* (Butler, 1948: p. 450, fig. 4; Frost et al., 1991: p. 64-68, pl. 13-17) have no sagittal crest. A relatively well-developed sagittal crest can be found only in the enigmatic North American Eocene species *Proterix bicuspis*

(Gawne, 1968; Bjork, 1975), but whether this character was widespread or not among the basal-most Erinaceidae is not clear. Only *Macrocranion tupaiodon* from Grube Messel, among basal Erinaceomorpha, preserves complete skulls: Sespedectidae show a weak sagittal crest and strong nuchal crests. Among Galericinae, this character can only be checked in three species other than *G. exilis*: *D. koenigswaldi*, *D. minor* and *D. brevirostris*. *D. minor* (Villier and Carnevale, 2013: p. 907, fig. 4, as *D. koenigswaldi*), *D. brevirostris* (Butler, 1980: p. 11, fig. 4) and the holotype RGM 177 777 of *D. koenigswaldi* show a well-developed sagittal crest (although different in shape from the more elongated, less curved crest in *Proterix*). However, the putative male *D. koenigswaldi* specimen RGM 179 194 has much higher and strong sagittal (and nuchal) crest, which distinguishes it from the holotype . All the described skulls of “Galericini” possess a variously developed sagittal crest; for this reason, the state of character “absent or poorly developed” was changed into “poorly developed”, a new one, “hypertrophic”, was added, and the polarity reversed compared to that proposed by Gould (1995) and He et al. (2012).

5) Exoccipital: (0) almost straight, external occipital protuberance overhanging occipital condyles; (1) weakly convex, external occipital protuberance approximately dorso-distal to occipital condyles; (2) very convex, external occipital protuberance dorso-distal to occipital condyles. Unordered. This character can only be observed in *Deinogalerix brevirostris*, *D. koenigswaldi* and Galerix *exilis* among the species considered for this study. In other taxa, e.g., *Hylomys suillus* (Ziegler, 1983: p. 166, fig. 150c) the external occipital protuberance is concave, and displaced anteriorly to the occipital condyles. This state of character could be primitive for Erinaceidae, because Erinaceinae (e.g., *Hemiechinus auritus* in Butler, 1948: p. 485, fig. 4) and Brachyericinae (e.g., *Brachyerix macrotis* in Rich and Rich, 1971: p. 9, fig.1) show this configuration of the interparietal bone, or one where the interparietal bone is approximately overhanging the occipital condyles (e.g., *Atelerix*

albiventris, line *A. kilimanus* in Butler, 1948: p. 451, fig. 5). Nevertheless, in the morphologically primitive, extant Hylomyinae species *Echinosorex gymnurus* (Butler, 1948: p. 449, fig. 5) the development of the interparietal stretches the external occipital protuberance more caudally, so that it is located only slightly anterior to the occipital condyle. In *Macrocranion tupaiodon* (Maier, 1979: p. 44, fig. 4) and *G. exilis*, (Ziegler, 1983: p. 159, fig. 141c) the external occipital protuberance lies approximately over the occipital condyle and the exoccipital is almost straight. In the genus *Deinogalerix* the nuchal crest is more developed: in *D. brevirostris* (Butler, 1980: p. 9, fig. 4) and *D. minor* (Villier and Carnevale, 2013: p. 907, fig. A and B1) the exocipital is convex, and the external occipital protuberance is placed slightly dorso-distally. In the holotype of *D. koenigwaldi*, RGM 177 777, the external occipital protuberance and the exocipital are approximately developed like in the other *Deinogalerix* species, whereas in another specimen, RGM 179 194, the exocipital is somewhat more convex and the external occipital protuberance is stretched distally with respect to the occipital condyles.

Mandibular characters

6) Antero-medial fossettes of condyles: (0) well developed; (1) poorly developed. Ordered. In *Apulogalerix pusillus*, *Deinogalerix freudenthali* (Savorelli et al., 2019), *D. masinii* (Savorelli et al., 2019), *Galerix exilis* (Ziegler, 1983: p. 161, fig. 143; *ibid*. p. 162, fig. 136-147), *G. stehlini* (Ziegler, 1983: p. 164, fig. 149), *Parasorex ibericus* (Mein and Martín Suárez, 1993, p. 725, fig. 3), *P. socialis* (Savorelli et al., 2019), *Schizogalerix moedlingensis* (Bachmayer and Wilson, 1970: tab. 1) and *S. voesendorfensis* (Prieto et al., 2014: p. 137, fig. 1, a1-2) the antero-medial fossettes of the condyles are well-individuated and clearly visible. In contrast, in more derived species of *Deinogalerix*, such as *D.*

intermedius, D. minor and *D. koenigswaldi*, the articular surfaces of the condyles are weaker and the antero-medial fossettes are barely visible (Savorelli et al., 2019).

7) Articular surface of condyle: (0) not extended; (1) flat and extended rostrally. Ordered. This character can be checked in the same taxa as character 6 as well as in *Parasorex depereti*; with the exception of *D. intermedius* and *D. koenigswaldi*, in which the condyles are typically flat and extended anteriorly, in all the other species the condyles are roughly globular and non-extended rostrally.

8) Condyle height above toothrow (from Borrani et al., 2018, modified): (0) high; (1) low; (2) very low. Ordered. The condyles are high in all the species of *Apulogalerix*, *Galerix*, *Parasorex*, *Schizogalerix* and *Tetracus* (Butler, 1980; Ziegler, 1983). In contrast, *G. stehlini* has low condyles, somewhat like those of *Deinogalerix masinii*, *D. freudenthali* and *D. minor* (Savorelli et al., 2019). In *D. intermedius* and *D. koenigswaldi*, the condyles are very low, approximately at level of the cheek teeth or even lower. In Galericinae the height of the condyles depends on the height of the ascending rami relative to the cheek toothrows: species with high ascending rami have high condyles, and vice versa.

9) Orientation of angular process: (0) aligned with ascending ramus; (1) displaced labially. Ordered. All mainland species, including the primitive Galericinae*sensu lato Microgalericulus esuriens*, and *Apulogalerix* have the angular processes aligned with the ascending rami; only in *Deinogalerix intermedius* and *D. koenigswaldi*, the angular processes are bent labially (Butler, 1980; Savorelli et al., 2019).

10) Dorso-medial groove of angular process: (0) delimited by sharp crests; (1) delimited by crests but labial ones blunt; (2) shallow, delimited by blunt crests. Ordered. In mainland taxa, *Apulogalerix, Deinogalerix freudenthali*, *D. masinii* and *D. minor,* the dorso-medial grooves of the angular processes are fairly deep and encased between two sharp crests (Savorelli et al., 2019). In *D. intermedius* there is a reduction of the labial crests, which

appear blunt; in *D. koenigswaldi* the dorsal grooves are shallow and both lingual and labial crests are blunt (Savorelli et al., 2019).

11) Dorso-ventral thickness of angular process: (0) relatively strong; (1) relatively weak. Ordered. In *Deinogalerix*, the angular processes are rod-shaped; they are relatively weaker than the hook-shaped angular processes of mainland species and *Apulogalerix*.

12) Ventral profile of angular processes, in labial view: (0) poorly-arched dorsally; (1) very arched dorsally; (2) almost straight and more or less oriented disto-ventrally. Unordered. In the early Galericinae *Tetracus nanus*, the angular processes are weakly hook-shaped, with ventral margin poorly-arched dorsally. The angular processes are shaped similarly in some *Galerix* species, i.e., *G. exilis* and *G. stehlini*. In *Parasorex depereti* and *P. socialis* the angular processes are more hook-shaped, with more concave ventral margin; the same occurs also in *Apulogalerix*, *Schizogalerix moedlingensis* and *S. voesendorfensis*. Members of the genus *Deinogalerix* have straight angular processes, directed more or less disto-ventrally.

13) Shape of ventral margin of *musculus temporalis* fossae: (0) straight and located high compared to *foramina mandibularis*; (1) slightly arched ventrally; (2) arched ventrally and low compared to *foramina mandibularis*. Ordered. The Galericinae *sensu lato* species *Microgalericulus esuriens* has the ventral margins of these fossae delimited by straight and high ridges; this character is shared by all the other mainland species of Galericinae, by *Apulogalerix pusillus*, as well as by the earlier species of *Deinogalerix D. freudenthali, D. masinii* and *D. minor*. However, in *G. stehlini, Schizogalerix voesendorfensis* and also in one mandible of *D. minor* (Savorelli et al., 2019), the ventral margin is lower and more arched ventrally, and in *D. intermedius* (Savorelli et al., 2019) and *D. koenigswaldi*, the crest is even more arched ventrally and low compared to the insertion of the *musculus temporalis*.

14) Ascending rami (0) not or (1) protruding distally. Ordered. *Deinogalerix intermedius* and *D. koenigswaldi* are characterized by possessing ascending rami that extend distally (Savorelli et al., 2019).

15) Curvature of posterior margin of mandibles, between angular processes and condyles: (0) open; (1) narrow; (1) very narrow. Unordered. Based on pictures in Lopatin (2006: p. 284, fig. 9b-c) and Crochet (1995: p. 48, fig. 11a), the mandibles of *Microgalericulus esuriens* and *Tetracus nanus* have rear margins in the form of open arches, similar to those of the mandibles of other mainland species and *Apulogalerix*, *Deinogalerix freudenthali*, *D. masinii* and *D. minor*. In specimens of *Galerix exilis*, *G. stehlini* and *D. intermedius*, the rear outlines form arches that are closer, narrower than equivalent margins in other specimens (e.g., specimen Goldberg 1966 XXXIV 1006 in Ziegler, 1983, p. 162, fig. 145). In the mandibles of *D. koenigswaldi* the curves of the posterior margins are even narrower.

16) Position of ascending rami: (0) uplifted; (1) low. Ordered. Savorelli et al. (2017) pointed out that *Deinogalerix masinii* has mandibles with uplifted ascending rami (i.e., “base sensibly higher than the ventral profile of the horizontal ramus”: Savorelli et al., 2017), as have the mandibles of mainland Galericinae*sensu lato* and *sensu stricto*. In mandibles of more advanced *Deinogalerix* species, the ventral outlines under the ascending rami are levelled off with those of the horizontal rami.

17) Posterior margins of masseter fossae: (0) delimited by prominent border; (1) flat, opened posteriorly. Ordered. In mainland species where this character can be observed (i.e., *Apulogalerix*, *Galerix exilis*, *G. stehlini*, *Parasorex depereti*, *P. socialis*, *Schizogalerix moedlingensis* and *S. moedlingensis*) and in the morphologically primitive species of *Deinogalerix*, i.e., *D. freudenthali*, *D. masinii* and *D. minor*, the rear margins of the masseter

fossae are bounded by a crest; in the mandibles of *D. intermedius* and *D. koenigswaldi* the masseter fossae are flat and not closed posteriorly.

18) Masseter fossae: (0) deep; (1) shallow. Ordered. In general, the masseter fossae in Erinaceidae and Erinaceomorpha are very deep (e.g., *Hemiechinus auratus*, *Erinaceus europaeus* and *Macrocranion tupaiodon*); the same occurs in Galericinae, except in *Deinogalerix intermedius* and *D. koenigswaldi*, which have shallow masseter fossae (Savorelli et al., 2019).

19) Inclination of ascending rami respect to horizontal rami: (0) weakly inclined backward; (1) almost vertical (ca. 90°); (2) very inclined backwards. Unordered. With the exception of the members of the genus *Schizogalerix*, in which the ascending rami are almost vertical, in mainland Galericinae *sensu lato* and *sensu stricto* species and in *Apulogalerix*, *Deinogalerix brevirostris*, *D. freudenthali*, *D. masinii* and *D. minor* ascending rami are slightly inclined backwards; in *D. intermedius* and *D. koenigswaldi* they are much more inclined.

20) Height of coronoid processes (from Borrani et al., 2018, modified): (0) high; (1) low; (2) very low. Ordered. Coronoid processes are high in mainland Galericinae species as well as in the Terre Rosse species *Apulogalerix pusillus*, the are lower in *D. intermedius* and *D. minor* and very low in *D. koenigswaldi*.

21) Mental foramen (modified from Borrani et al., 2018): (0) two mental foramen, one under p2 and one under p3; (1) two mental foramina, fused in a single large foramen placed between p2 and the anterior root of p3; (2) three mental foramina, two under p2 and one under p3; (3) two foramina, one under p3 and one under p4; (4) one foramen under p2; (5) one foramen under p3; (6) one foramen between p3 and p4; (7) one mental foramen under p4. Unordered. The position of the mental foramen is usually very variable in the Eulipotyphla; however, in some genera (such as the Crocidosoricinae *Myosorex* and the

Galericinae *Deinogalerix*; Furió et al., 2007; Savorelli et al. 2017, 2019) this character is diagnostic. As a general rule, in the earlier erinaceids a displacement distally and a reduction of the number of mental foramina through time may be observed: in the Paleocene-Middle Eocene genera there are usually two mental foramina placed under p2 and p3 (*Litolestes ignotus*, *Oncocherus* and one specimen of *Eochenus*). In *Eogalericius*, the position and number of the metal foramina is very variable: there are usually two mental foramina under p2 and p3 (as in the other Early-Middle Eocene erinaceids), but there should be present even three foramina (two under p2 and one under p3) or a very large one, placed between p2 and the anterior root of p3 (Lopatin, 2004, 2006). The latter seems to anticipate the usual position of the mental foramen in the early Galericinae *sensu lato*, i.e., *Zaraalestes* and *Microgalericulus*, in which it is under p3, as well as in many Galericinae *sensu stricto* such as *Deinogalerix*, *Galerix africanus*, *G. rutlandae* and *G. saratji*. In general, the position of the mental foramen is very variable in other Galericinae, with the exception of *Schizogalerix*, in which it lies under p4 or between p3 and p4 (with the exception of *S. voesendorfensis*, where it is under p3 or between p3/p4). In *Apulogalerix*, the mental foramen is usually under p4, however in some specimens there is an additional mental foramen under p2, which mimic the plesiomorphic state of character of Erinaceomorpha (e.g., *Macrocranion* and *Scenopagus*).

22) Height of horizontal rami under the molars, compared to p2-m3 toothrow length: (0) low; (1) high. Unordered. In general, the horizontal rami are rather slender in Galericinae (in contrast to other erinaceid subfamilies, such as Erinaceinae and Brachyericinae), in particular in earlier Galericinae. In contrast, *Apulogalerix*, *Deinogalerix*, *Galerix africanus*, *G. stehlini*, *Parasorex ibericus*, as well as some species of *Schizogalerix* have robust mandibles, with heights of the horizontal rami that are about 30-40% the length of the p2-m3 toothrows.

23) Aboral extension of mandibular symphysis: (0) under p2; (1) between p2 and p3; (2) under p3; (3) under p4; (4) under c. Unordered. The presence of a not extended mandibular symphysis behind p2 is characteristic of the primitive Galericinae *sensu lato* and also of *Tetracus nanus*, *Galerix africanus* and some specimens of *Galerix exilis.*

Diastema and ratios

24) Diastema between I3 and C (from He et al., 2012, modified): (0) absent or minimum; (1) present. Ordered. The premaxilla is poorly known in almost all Galericinae taxa (as well as in many early Erinaceomorpha, with a few, notable exceptions, such as *Macrocranion nitens, M. tupaiodon* and *Eochenus sinensis*). In general, there are no true diastemas; only *M. tupaiodon* has I3 and C fairly spaced from one another (Maier, 1979: p. 47, fig. 6A). In *Macrocranion nitens*, *Eochenus* and *Apulogalerix* upper third incisor and canine are next to one anotherIn contrast, there is a marked I3 - canine diastema in *Deinogalerix*, which is diagnostic for this genus.

25) C - P2 and c - p4 diastemas (from He et al., 2012, modified): (0) absent or minimum; (1) present, reduced; (2) present, long. Ordered. The diastemas between these upper and lower teeth are considered together, because these teeth are reciprocally engaged in occlusion. In general, these teeth are placed against each other or just slightly spaced in Galericinae; this dental pattern is common to almost all early Erinaceomorpha (including *Macrocranion*, *Changlelestes* and *Eochenus*), to all Galericinae *s.l* and to *Deinogalerix masinii* (Villier et al., 2013). Ziegler et al. (2007) reports the presence of a diastema between the upper canine and P2 in *Zaraalestes minutus*; the same occurs in *Apulogalerix pusillus*, but in this species the diastema is generated by the absence of p1 and cannot be considered homologue of the true diastemas shown by *Deinogalerix*. True diastemas are only present in advanced representatives of *Deinogalerix*: the longest diastemas are shown by *D.*

intermedius and *D. koenigswaldi*, whereas more primitive species, such as *D. brevirostris*, *D. freudenthali* and *D. minor*, have shorter diastemas.

26) p2/p3 (Fig. 9; Tab. 5 and 6) (van den Hoek Ostende, 2001d; Borrani et al., 2018): (0): p2<p3; (1): p2≥p3; (2) p2 very reduced compared to p3. Unordered. As a general rule, the p2 is considered as large as or larger than p3 when the ratio is 90% or more. This character is considered diagnostic for *Galerix* (van den Hoek Ostende, 2001d), but it is also for *Tetracus* (Hugueney and Adrover, 2003); therefore, this character state is probably plesiomorphic for Galericinae *sensu stricto.* In the Asian species *G. rutlandae* the p2 is smaller than p3 (Zijlstra and Flynn, 2015). In *Microgalericulus* and in *Zaraalestes* (although no measurements of p2 of the latter species are reported from Ziegler et al., 2007), as well as in *Schizogalerix intermedius* and *S. zapfei*, the p2 is very reduced (less than 65% of p3).

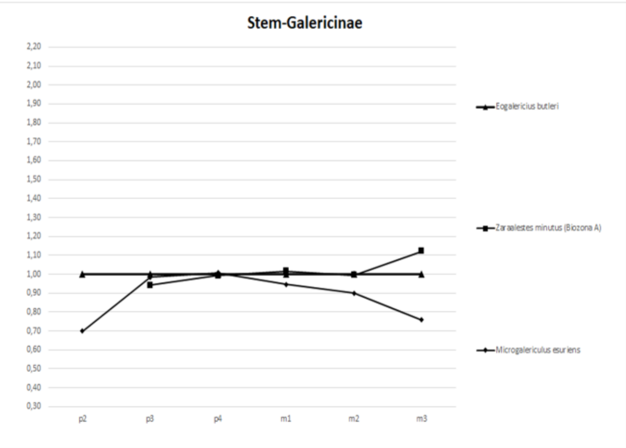
Tooth	N°	Measure	Mean	Min.	Max .	St. dev.
p2	23	Lp2	1.41	1.27	1.51	0.064
		Wp2	0.72	0.62	0.87	0.003

Table 5 – Measurements of p2 of *Apulogalerix pusillus* taken by the author, with basic statistics. N°: number of specimens. L: length of the lingual border of the crown. W: width taken orthogonal to the length (see Prieto et al., 2010 and Masini and Fanfani, 2013 for the used method). Min.: minimum value. Max.: maximum value. St. dev.: standard deviations. Measurements were taken from pictures taken with a digital microscope Dino-Lite AM4115ZTW and measured with the software DinoCapture 2.0.

27) p3/p4 (Fig. 10, Tab. 6): (0) p3 smaller than p4 (ca. between the 75 and 90 % of p4); (1) p3 much smaller than p4 (less than 75% of p4); (2) p3 about the same size as p4 (between the 90 and the 100% of p3). Unordered. Usually, in the Galericinae *sensu stricto* and *sensu lato,* the p3 is smaller than p4; however, in some of the more derived species of *Deinogalerix* (*D. brevirostris, D. koenigswaldi* and *D. minor*), *Galerix rutlandae* and *Schizogalerix moedlingensis* the two teeth are about of the same size, with the p3 only slightly smaller than p4. On the other hand, in *Deinogalerix samniticus*, many *Galerix* (*G.*

africanus, G. aurelianensis, G. exilis, G. iliensis, G. stehlini, G. uenayae and *G. wesselsae*), *Parasorex pristinus* and *Tetracus* the p3 is much smaller, being around the 75% or less of p4.

Ratio between m1 and adjacent teeth (from Gould, 2001, modified) (Fig. 10; Tab. 6): (0) m1 between 120 and 135% the size of p4, and 110 and 125% of m2; (1) m1 approximately as large as p4 but more than 170% of m2; (2) m1 approximately between the 115% and the 125% of p4 but more than the 140% of m2; (3) m1 approximately between the 120 and 135% of p4, and the 125 and 135% of m2; (4) m1 approximately between the 145 and 150% of p4 and the 110 and 115% of m2; (5) m1 approximately between the 145 and 150% of p4 but more than the 115% of m2; (6) m1 larger than the 150% of p4 but between the 105 and 120% of m2. Unordered. The development of m1 compared to the adjacent teeth varies greatly between the Galericinae as a whole: Galericinae *sensu lato*, *Tetracus nanus* and some early species of *Galerix* (*G. aurelianensis, G. saratjy, G. symeonidisi* and *G. uenayae*), together with *Parasorex depereti* show m1s relatively small compared to p4 and m2, *Deinogalerix samniticus* is a *unicum* between Galericinae, having a very large p4 (about as large as m1) and both much larger (more than the 170%) of m2. The other species of the genus *Deinogalerix*, even if they does not have a so extremized pattern, have m1 compared to m2 too (more than 140%, peaking around the 190% in *Deinogalerix intermedius*), but the m1 is always sensibly larger than p4 (being between 115 and 125% of it). Also *Galerix africanus, G. remmerti* and *G. wesselsae* have a distinctive dentary pattern, with a m1 much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p2
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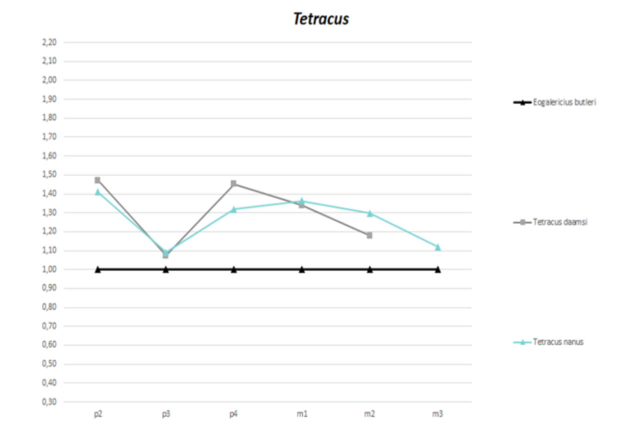
m3
Eogalericius butleri
Zaraalestes minutus (Biozona A)
Microgalericulus esuriens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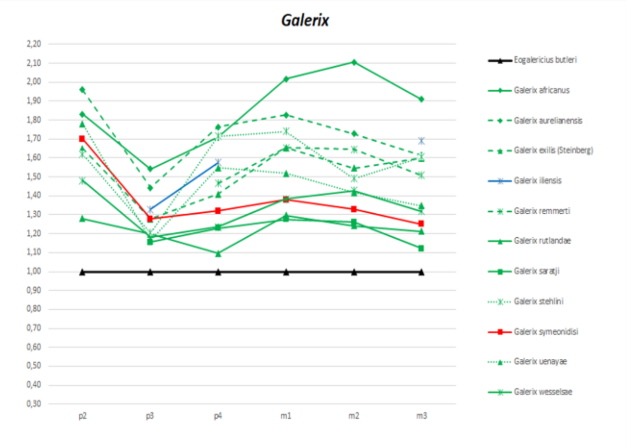
Eogalericius butleri
Tetracus daamsi
Tetracus nanus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p2
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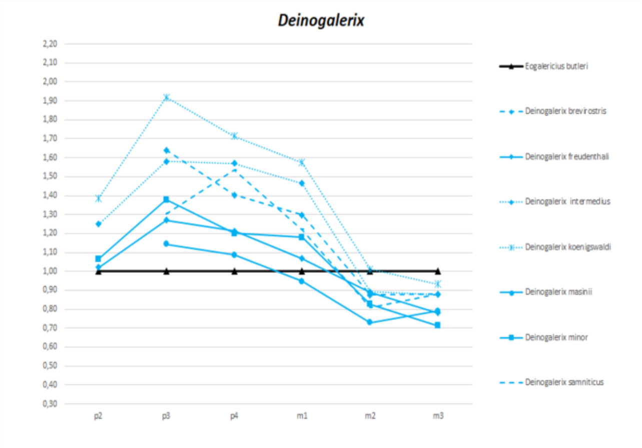
Eogalericius butleri
Galerix africanus
Galerix aurelianensis
Galerix exilis (Steinberg)
Galerix iliensis
Galerix remmerti
Galerix rutlandae
Galerix saratji
Galerix stehlini
Galerix symeonidisi
Galerix uenayae
Galerix wesselsae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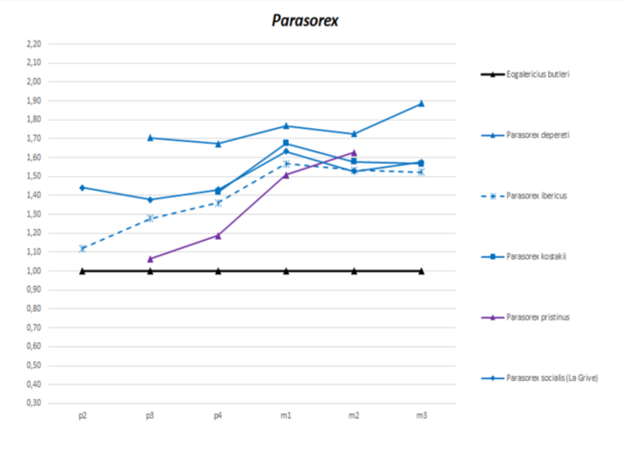
Eogalericius butleri
Deinogalerix brevirostris
Deinogalerix freudenthali
Deinogalerix intermedius
Deinogalerix koenigswaldi
Deinogalerix masinii
Deinogalerix minor
Deinogalerix samniticus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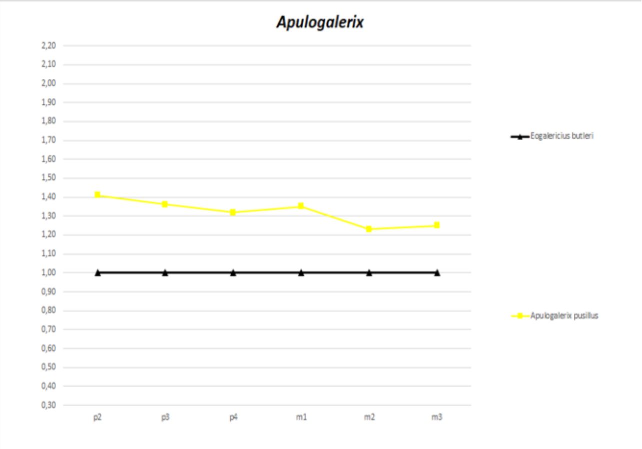
Eogalericius butleri
Parasorex depereti
Parasorex ibericus
Parasorex kostakii
Parasorex pristinus
Parasorex socialis (La Grive)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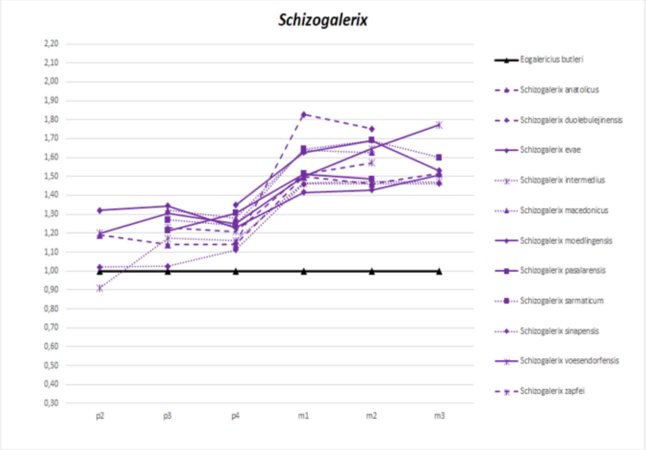
Eogalericius butleri
Apulogalerix pusillus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Eogalericius butleri
Schizogalerix anatolicus
Schizogalerix duolebulejinensis
Schizogalerix evae
Schizogalerix intermedius
Schizogalerix macedonicus
Schizogalerix moedlingensis
Schizogalerix pasalarensis
Schizogalerix sarmaticum
Schizogalerix sinapensis
Schizogalerix voesendorfensis
Schizogalerix zapfei

←Figure 10: Ratio diagrams comparing the labial length of lower teeth (see Prieto et al., 2010) in different genera of Galericinae and stem-Galericinae. Colours reflects the proposed revised systematics of this work (see "Systematic implications" and "Revised systematic"). For simpler comparisons with other Galericinae, dental lengths of *Deinogalerix* have been divided for 5. The considered standard is Eogalericius butleri; dental measurements are reported in Tables 1 and 2.

Species	p2	p3	p4	m1	m2	m3	References
Eogalericius butleri	1,00	1,22	1,44	1,85	1,61	1,32	Lopatin (2006)
Zaraalestes minutus [1]		1,15	1,43	1,88	1,60	1,48	Ziegler et al. (2007)
Microgalericulus esuriens	0,70	1,20	1,45	1,75	1,45	1,00	Lopatin (2006)
Apulogalerix pusillus	1,41	1,66	1,90	2,50	1,98	1,65	Masini and Fanfani (2013); this work[2]
Deinogalerix brevirostris		10,00	10,10	12,00	7,05	5,80	Savorelli et al. (2019)
Deinogalerix freudenthali	5,10	7,30	8,68	10,03	7,10	5,77	Savorelli et al. (2019); Butler (1980)
Deinogalerix intermedius	6,25	9,64	11,30	13,55	7,18	5,79	Savorelli et al. (2019)
Deinogalerix koenigswaldi	6,93	11,70	12,34	14,57	8,14	6,16	Villier (2012); Villier and Carnevale, 2013 (in Savorelli et al., 2019)
Deinogalerix masinii		6,97	7,82	8,77	5,88	5,22	Villier et al. (2013) (in Savorelli et al., 2019)
Deinogalerix minor	5,33	8,40	8,65	10,90	6,65	4,70	Butler (1980), Villier and Carnevale (2013) (in Savorelli et al., 2019)
Deinogalerix samniticus		7,95	11,05	11,28	6,50	5,80	Savorelli et al. (2016)
Galerix africanus	1,83	1,88	2,46	3,73	3,39	2,52	Butler (1956, 1969, 1984)
Galerix aurelianensis	1,96	1,76	2,54	3,38	2,78	2,13	Ziegler (1994, 1998); weigthed average from Klietmann (2013), Ziegler (1990) and van den Hoek Ostende and Fejfar (2006)
Galerix exilis (Steinberg)	1,65	1,56	2,03	3,06	2,49	2,11	Ziegler (1983)
Galerix iliensis		1,62	2,27			2,23	Kordikova (2000)
Galerix remmerti			2,11	3,06	2,65	1,99	Van den Hoek Ostende (2003a)
Galerix rutlandae	1,28	1,46	1,58	2,40	2,00	1,60	Zijlstra and Flynn (2015)
Galerix saratji		1,41	1,77	2,36	2,03	1,48	Medie ponderate da Van den Hoek Ostende (1992)
Galerix stehlini	1,62	1,47	2,47	3,22	2,4	2,12	Ziegler (1983)
Galerix symeonidisi	1,70	1,56	1,90	2,55	2,14	1,65	Doukas (1986)
Galerix uenayae	1,78	1,42	2,23	2,81	2,28	1,78	Van den Hoek Ostende (1992)
Galerix wesselsae	1,48	1,44	1,78	2,56	2,30	1,74	Zijlstra and Flynn (2015)
Parasorex depereti		2,08	2,41	3,27	2,78	2,49	Masini et al. (2019)
Parasorex ibericus	1,12	1,56	1,96	2,9	2,47	2,01	Mein and Martín-Suárez (1993) in Masini and Fanfani (2013)
Parasorex kostakii			2,04	3,10	2,54	2,07	Doukas and van den Hoek Ostende (2006)
Parasorex pristinus		1,3	1,71	2,79	2,62		Ziegler (2003)
Parasorex socialis (La Grive)	1,44	1,68	2,06	3,02	2,46	2,08	Masini and Fanfani (2013); Ziegler (2005)[3]
Riddleria atecensis						1,96	Van den Hoek Ostende (2003b)
Schizogalerix anatolicus	1,19	1,39	1,64	2,77	2,35	2,00	Weighted mean from Selänne (2003)
Schizogalerix duolebulejinensis			1,65	3,38	2,82		Bi et al. (1999)[4]
Schizogalerix evae			1,94	3,01	2,72	2,02	De Brujin et al. (2006)
Schizogalerix intermedius	0,91	1,43	1,67	2,71	2,37	1,94	Weighted mean from Selänne (2003)
Schizogalerix macedonicus		1,61	1,84	3,03	2,62		Doukas (1995)
Schizogalerix moedlingensis	1,32	1,64	1,77	2,62	2,30	1,99	Ziegler (2006) and weighted mean from Rabeder (1973)
Schizogalerix pasalarensis		1,48	1,88	2,80	2,39		Engesser (1980) in Masini and Fanfani (2013)
Schizogalerix sarmaticum		1,55	1,79	3,04	2,72	2,11	Rzebik-Kowalska and Lungu (2009)[5]
Schizogalerix sinapensis	1,02	1,25	1,60	2,70	2,35	1,93	Weighted mean from Selanne (2003)
Schizogalerix voesendorfensis	1,20	1,59	1,80	2,77	2,65	2,34	Prieto et al. (2010)
Schizogalerix zapfei		1,5	1,74	2,80	2,53		Engesser (1980) in Masini and Fanfani (2013)
Tetracus daamsi	1,47	1,31	2,09	2,48	1,9		Hugueney and Adrover (2003)
Tetracus nanus	1,41	1,33	1,90	2,52	2,09	1,48	Hugueney and Adrover (2003)

28)

← Table 6 – Mean length of lower teeth used for the ratio diagrams in Figure 10, with references. [1]The measurements of Zaraalestes minutus are those of the earlier population of biozone A (see Ziegler et al., 2007). [2]See Table XXX. [3]Only for p2s length from the population of Petersbuch 6, chosen because it is dimensionally similar to that of La Grive. [4]One measurement of m1 has been excluded, because it is here considered unreliable. [5]Mean between dimensional extremes (n=3).

Species	P4	M1	P4/M1 ratio	References
Eogalericius butleri	1,70	1,70	1,00	Lopatin (2006)
Zaraalestes minutus[1]	1,54	1,61	0,96	Ziegler et al. (2007)
Apulogalerix pusillus	2,42	2,19	1,11	Masini and Fanfani (2013)
Deinogalerix brevirostris	12,50	8,50	1,47	Butler (1980); Savorelli et al. (2019)
Deinogalerix freudenthali	10,30	7,65	1,35	Butler (1980); Savorelli et al. (2019)
Deinogalerix intermedius	14,85	8,70	1,71	Butler (1980); Savorelli et al. (2019)
Deinogalerix koenigswaldi	16,35	9,40	1,74	Butler (1980); Savorelli et al. (2019)
Deinogalerix masinii	9,25	6,80	1,36	Villier et al., 2013; Savorelli et al., 2019
Deinogalerix minor	11,9	7,95	1,50	Butler (1980); Savorelli et al. (2019)
Galerix africanus	3,21	3,42	0,94	Butler (1984)
Galerix aurelianensis	2,86	2,90	0,99	Ziegler (1994, 1998); weighted mean from Klietmann (2013), Ziegler (1990) and van den Hoek Ostende and Fejfar (2006)
Galerix exilis[2]	2,41	2,61	0,92	Ziegler (1983)
Galerix iliensis	2,45	2,85	0,86	Kordikova (2000)
Galerix remmerti	2,65	2,49	1,06	Weighted mean from van den Hoek Ostende (2003a)
Galerix rutlandae	2,00	2,09	0,96	Zijlstra and Flynn (2015)
Galerix saratji	2,03	2,17	0,94	Weighted mean from van den Hoek Ostende (1992)
Galerix stehlini	2,71	2,93	0,92	Ziegler (1983)
Galerix symeonidisi	2,20	2,30	0,96	Doukas (1986)
Galerix uenayae	2,61	2,33	1,12	Van den Hoek Ostende (1992)
Galerix wesselsae	2,27	2,51	0,90	Zijlstra and Flynn (2015)
Parasorex depereti	2,86	2,93	0,98	Masini et al. (2019)
Parasorex ibericus	2,22	2,45	0,91	Mein and Martín-Suárez (1993)
Parasorex kostakii	2,21	2,46	0,90	Doukas and van den Hoek Ostende (2006)
Parasorex socialis[3]	2,46	2,53	0,97	Ziegler (2005)
Schizogalerix anatolicus	2,20	2,55	0,86	Weighted mean from Selänne (2003)
Schizogalerix duolebulejinensis	2,31	2,95	0,78	Bi et al. (1999)
Schizogalerix evae	2,16	2,69	0,80	De Brujin et al. (2006)
Schizogalerix intermedius	2,40	2,55	0,94	Weighted mean from Selänne (2003)
Schizogalerix macedonicus	2,41	2,72	0,89	Doukas et al. (1995)
Schizogalerix moedlingensis	2,25	2,58	0,87	Ziegler (2005) and weighted mean from Rabeder (1973)
Schizogalerix sinapensis	2,26	2,38	0,95	Weighted mean from Selänne (2003)
Schizogalerix voesendorfensis	2,41	2,54	0,95	Prieto et al. (2010)
Tetracus daamsi	2,16	2,14	1,01	Hugueney and Adrover (2003)
Tetracus nanus	2,03	2,29	0,89	Hugueney e Adrover (2003)

← Table 7 – Mean of the labial length of P4 and M1, with references. [11]The measurements of Zaraalestes minutus are those of the earlier population of biozone A (see Ziegler et al., 2007). [2]Steinberg population. [3]Petersbuch 10 population.

larger than p4 (approximately between the 145 and 150% of it) but not much larger than m2 (around 110 and 115% ot the latter one). *G. stehlini* also have a similar pattern, but the m1 is sensibly larger compared to m2, being approximately between the 125 and the 135% of m2; this feature is shared also with *Apulogalerix pusillus* and *Tetracus daamsi*. On the other hand, *Galerix exilis*, *Parasorex* and *Schizogalerix* have very large m1s compared to p4; however, *Parasorex pristinus*, as the majority of *Schizogalerix* species (*S. anatolicus, S. duolebulejinensis, S. evae, S. intermedius, S. macedonicus, S. sarmaticum, S. sinapensis, S. voesendorfensis* and *S. zapfei*) have a larger m1 compared to p4 (more than 150% of p4) but relatively smaller compared to m2 (being approximately between the 105 and 120% of m2).

29) Ratio between P4 and M1 (from Borrani et al., 2018, modified) (Tab. 7): (0) P4 smaller than 115% the size of M1; (1) large P4, between 130 and 139% the size of M1; (2) large P4, between 140 and 145% the size of M1; (3) P4 larger than 165% the size of M1. Ordered. In continental Galericinae, as well as in *Apulogalerix*, the P4 is smaller or slightly larger than M1. In *Deinogalerix*, however, the P4 is sensibly larger: in the early species *D. freudenthali* and *D. masinii* the P4 is from 130% to 136% the size of M1, in *D. brevirostris* and *D. minor* from 140% and 145% and in *D. koenigswaldi* the ratio reaches 169%. This means that in *Deinogalerix* P4 (as well as the other upper premolars) grows larger through the evolution of the genus.

Dental characters

30) Lower incisors (from Gould, 2001; Frost et al., 1991; He et al., 2012, modified): (0) subequal; (1) i1 subequal to i2, i3 smaller than i2; (2) decreasing distally. Unordered.

Lopatin (2006) reported that *Eogalericius* had subequal i1s and i2s, and smaller i3; this derived condition is not shared by early Erinaceomorpha, where lower incisors are all subequal (e.g., *Changlelestes*) or have i2 that exceeds the size of i1 and i3, which are similar to one another in size (*Macrocranion vandebroeki*). Early erinaceids (e.g., *Litolestes*) possess incisors that decrease in size distally; this is also shared by Galericinae and *Zaraalestes*, with the only exception of *Tetracus nanus*, whose lower incisor alveoli are all of similar size (Crochet, 1995).

31) i1-2 crown (Gould, 2001; Borrani et al., 2018, modified): (0) not bilobed, with accessory distal denticle; 1) not bilobed, without distal denticle; (1) bilobed. Ordered. The first two incisors of Erinaceomorpha are rarely preserved in the fossil record and are usually difficult to distinguish from each other when found isolated. They are possessed by all the genera of Galericinae, where they are usually procumbent and spatulate-shaped. Lopatin (2006) reports that the incisors of early Erinaceidae genera (e.g., *Changlelestes, Eochenus* and *Litolestes*), bear a distinct distal cuspulid. Similar denticles are also present in *Zaraalestes minutus* (Lopatin, 2003a in Lopatin, 2006), which indicates that it belongs to an early group of erinaceids, relative to Galericinae. The lower incisors of Sespedictidae are only known through *Macrocranion tupaiodon*, which is generically reported to have spatulated teeth (Tobien, 1962: p. 12). *Deinogalerix*, possessed distinctive bilobed first two lower incisors, unlike any other Galericinae (and Erinaceomorpha): it is therefore an apomorphy of the genus.

32) i3 (Gould, 2001; Borrani et al., 2018): (0) present; (1) absent. Ordered. The presence of the i3 is a plesiomorphic trait in Erinaceidae, due to their non-reduced dental formula: it is present in all early Erinaceomorpha in which this trait can be observed (e.g., *Changlelestes*, *Macrocranion*, *Litolestes*, *Litocherus*). A loss of the i3 is a synapomorphy of Brachyericinae (if the first two teeth are not homologous to the first two incisors in

Erinaceinae; see Lopatin, 2006 for a discussion about this character) among Erinaceidae Also three Galericinae taxa (*Apulogalerix*, *Deinogalerix* and *Parasorex ibericus*) lost i3, but this may be interpreted as an instance of homoplasy: the earliest, reasonably complete *Deinogalerix* known to date, *D. masinii*, has very reduced i3. In *Apulogalerix* and *P. ibericus* the tooth already disappeared; therefore, these three genera have lost their third lower incisor at least along two distinct evolutionary pathways.

33) Shape of c (from Gould, 2001, modified): (0) rounded and with distal cuspulid (incisiviform/premolariform canine); (1) pointed and single-cusped. Ordered. Usually, Erinaceomorpha have a low, blunt lower canine with distal cuspule; the tooth is very procumbent in Brachyericinae. The lower canine is pointed and single-cusped in at least two erinaceid genera, i.e., the basal Erinaceidae *Eochenus*, *Galerix africanus*, *G. stehlini* and *Deinogalerix*. Although not closely related, the two genera also shared other common traits (e.g., relatively low ascending ramus and high and piercing lower canine), thereby suggesting possible ecological convergence (see "Discussion").

34) Height of lower canine compared to p3 (from Corbet, 1988; Frost et al., 1991; Gould, 1995, 2001; He et al., 2012, modified. These authors compare the height of the canine to that of p1 and not of p3): (0) canine approximately as high as p3; (1) canine higher than p3; (2) canine much higher than p3. Ordered. The canine is usually poorly-developed in Erinaceidae and usually as high as the p3 whenever the latter is present. Erinaceinae are a remarkable exception, because their lower canine, albeit small and premolariform, is higher than p3. The same occurs in some species of Hylomyinae (*Echinosorex* and *Podogymnura* and, to a lesser extent, *Hylomys* and *Neohylomys*), as well as in the basal erinaceid *Eochenus*. Galericinae generally have a small canine, as high as the p3 or barely higher. *Galerix africanus* and *G. stehlini* , alongside some species of *Deinogalerix* (*D. brevirostris*,

D. masinii and *D. minor*), have a higher, pointed canine. In *D. intermedius* and *D. koenigswaldii*, this tooth is even more developed and higher.

35) Presence and number of roots in p1 (from Corbet, 1988; Frost et al., 1991; Gould, 1995, 2001; He et al., 2012, modified): (0) present, one-rooted; (1) present, two-rooted; (2) present, two fused roots; (3) p1 absent. Unordered. The plesiomorphic condition in Erinaceomorpha is the presence of simple, one-rooted p1, as shown by many Paleocene-Eocene species (*Changlelestes*, *Macrocranion*, *Litolestes*, *Oncocherus* and *Scenopagus*). This morphology is shared by a large number of Galericinae *sensu stricto* as well as by the Galericinae *sensu lato Eogalericius*, *Microgalericulus* and *Zaraalestes* (which may lack the p1). However, this character shows great intraspecific variability: in *Parasorex depereti* and *P. socialis*, as well as in *T. daamsi* and *Deinogalerix*, the p1 may have fused roots. The species assigned to the genus *Galerix* may have p1 with one, two well-separated, or two fused roots. Finally, in *Apulogalerix*, whenever present, the p1 may be single-rooted or with two fused roots. In those cases where it is lacking, its place is taken by a short diastema.

36) Disto-lingual cuspulid on p1 (from Gould, 2001, modified): (0) absent; (1) present. Unordered. In the early Galericinae species *Tetracus daamsi* and *T. nanus*, in *Galerix remmerti*, *G. rutlandae*, *G. wesselsae*, in some specimens of *G. saratji*, and in *Deinogalerix*, the p1 shows no disto-lingual cuspulid; this variously developed cusplet is present in other *Galerix* species (e.g., *Galerix exilis*), *Apulogalerix*, *Parasorex* and *Schizogalerix*.

37) Distal cingulid on p1: (0) absent; (1) present. Unordered. Crochet (1995) reports that the only known, single p1 of *Tetracus nanus*, which is figured by Hugueney and Adrover (2003: p. 315, fig. 1b), shows a weak distal cingulid. The same can be observed on the p1 of *T. daamsi*, as well as on the p1s of two species of *Galerix*, *G. rutlandae* and *G. wesselsae.*

38) Number of roots in p2 (Borrani et al., 2018; from Corbet, 1988; Gould, 1995, 2001; He et al., 2012, modified): (0) two roots, divided; (1) two roots, fused; (2) one root.

Unordered. In general, Galericinae show two-rooted p2s; however, *Zaraalestes* and *Schizogalerix zapfei* have single-rooted p2 and *Parasorex depereti* and *P. ibericus* p2s have either one, two fused, or two divided roots.

39) Paraconid (=anterior cuspulid) on p2 (from Gould, 2001, modified): (0) present; (1) absent. Unordered. *Eogalericius*, *Apulogalerix*, *Schizogalerix*, *Parasorex*, many species of *Galerix* and some specimens of *Tetracus nanus* display an anterior cuspulid on p2; it may be homologue of the paraconid on the other premolars. This cuspulid is absent in *Zaraalestes*, *T. daamsi*, in some specimens of *T. nanus*, in *Deinogalerix* as well as in the early *Galerix* species *G. saratji*, *G. uenayae* and *G. wesselsae*.

40) Distal cuspid on p2 (from Gould, 2001, modified): (0) present; (1) absent. Unordered. *Eogalericius*, *Zaraalestes*, *Deinogalerix*, some specimens of *Tetracus nanus* and many species of *Galerix* show no distal cuspid on p2.

41) Presence and shape of paraconid on p3: (0) present, crest-like; (1) present, tubercle-like; (2) absent. Unordered. In the early Erinaceidae *Changlelestes* and in some specimens of *Oncocherus* the paraconid is a low, crest-like structure; therefore, this is probably the plesiomorphic state of the paraconid for the family. In Galericinae *sensu lato*, the paraconid is already a tubercle-like cuspule. The paraconid is absent on the swollen p3s of *Deinogalerix* as it is on the p3s of *Schizogalerix zapfei*. *Galerix exilis* shows the whole variety of character states.

42) Shape of p3 talonid (from Gould, 2001; He et al., 2012, modified): (0) talonid with distal cingulid, without *crista mediana* or cuspulids; (1) talonid with distal cingulid and central cuspulid, without *crista mediana*; (2) talonid with medial cuspulid and narrow *crista mediana* on the distal cingulid; (3) talonid with distal cingulid and weak *crista mediana*, but without cuspulids; (4) talonid with distal cingulid and with disto-lingual cuspulid; (5) talonid with disto-lingual cuspulid, without distal cingulid; (6) talonid with strong and

triangular distal cingulid, without cuspulids or *crista mediana*; (7) talonid with strong and triangular distal cingulid, without cuspulids but with *crista mediana*; (8) very reduced talonid, without cuspulids and *crista mediana*, but with well-developed distal cingulid. Unordered. The talonid of p3 shows a full range of differences in the Galericinae: in *Eogalericius*, *Tetracus nanus*, in some specimens of *Zaraalestes* as well as in some species of *Galerix*, it is a simple structure, reduced to a distal cingulid without *crista mediana*, nor any cuspulid. This structure is slightly more complex in *Microgalericulus* and in some specimens of *Zaraalestes mintuus*, wherein it includes a medial cuspulid on the postcingulid, as it is in *G. symeonidisi* and *G. wesselsae.* In *T. daamsi*, a weak *crista mediana* is added to the talonid of p3. In the other more derived *Apulogalerix*, *Deinogalerix* and *Parasorex* the talonid of p3 has a disto-lingual cuspulid, maybe homologue of the entoconid; the only exception are *P. depereti* and *P. socialis*, in which the distal cuspulid may be absent. *P. socialis* may also possess a more primitive, simple talonid. A simple talonid can also be found in some specimens of *G. aurelianensis* and *G. exilis*. Finally, in *Schizogalerix* the talonid of p3 has a well-developed, triangular-shaped distal cingulid, either with or without (in the species from Anatolia) cuspulid and with (in the European species) or without *crista mediana.*

43) p3 metaconid (from Corbet, 1988; Gould, 2001; He et al., 2012, modified): (0) absent; (1) present. Ordered. Usually, the metaconid is absent on the p3 of erinaceids; it may sometimes be observed *Zaraalestes minutus* and *Galerix exilis*.

44) Height of paraconid, relative to protoconid on p4: (0) paraconid low or (1) relatively higher. Ordered. The paraconid, anyhow lower than the protoconid, is relatively higher in *Apulogalerix*, *Deinogalerix*, *Parasorex*, *Schizogalerix*, *Galerix iliensis* and *G. symeonidisi.*

45) Height of metaconid relative to protoconid on p4: (0) low; (1) relatively high, not much lower than protoconid. Ordered. The metaconid is relatively higher on the p4s of

Eogalericius; however, this probably is not a plesiomorphic trait in Galericinae, because in *Microgalericulus*, *Zaraalestes*, *Tetracus*, as well as in many *Galerix* (except *G. iliensis* and some specimens of *G. symeonidisi*, e.g., specimen BSP 1979 XV 426 in Ziegler and Falbusch, 1986: tab. 1, fig. 17) the metaconid is rather low on p4. In some primitive Erinaceidae (e.g., *Changlelestes*), the metaconid is as high as the protoconid, whereas it is markedly lower in other ones (e.g., *Eochenus*). Therefore, the plesiomorphic state of this character is difficult to establish in erinaceids. In *Apulogalerix, Deinogalerix*, *Parasorex* and *Schizogalerix* the metaconid is lower than the protoconid, but anyhow relatively higher than on the p4s of *Tetracus* and of many representatives of *Galerix*.

46) Metaconid on p4 (from Gould, 2001; van den Hoek Ostende, 2001d; Borrani et al., 2018, modified): (0) present, distinct from protoconid (linked, or not, to it by centrocrista); (1) present, reduced to cuspulid on lingual side of protoconid; (2) present, inflated and fused with protoconid in a metaconid-protoconid complex; (3) absent. Unordered. A well-developed and recognizable metaconid on p4 is the plesiomorphic state of this character in Erinaceomorpha: in Sespedictidae (e.g., *Macrocranion*), and early Erinaceidae (e.g., *Changlelestes*), the metaconid is very high, almost as the protoconid and is separate, or not, from it. In Galericinae, the metaconid is still usually well-distinct; however, there are exceptions, as, for instance, in the genera *Apulogalerix, Tetracus*, in many *Galerix* and one *Parasorex.* In *T. daamsi*, the metaconid is a small cuspulid placed on the lingual side of the protoconid; the same occurs in *T. nanus*, but in this species it may even be absent. Also on p4s of *G. africanus, G. exilis, G. remmerti, G. rutlandae* and *G. wesselsae* the metaconid is reduced to a cuspulid and in *G. aurelianensis, G. stehlini* and *G. uenayae* it may even be absent. Unlike other *Galerix*, in *G. iliensis*, in at least some specimens of *G. saratji* (e.g., Ha 3, 3136 in van den Hoek Ostende, 1992: p. 463, pl. 2, fig. 9) as well as in *G. symeonidisi*, the metaconid on p4 is still well developed. In *Parasorex* usually the cuspid is usually well-

developed; in contrast, in *P. kostakii* it may be reduced, or absent. Finally, in *Apulogalerix* the metaconid is inflated and fused with the protoconid, which gives the tooth a bulging shape. When the metaconid is well-developed the centrocrista, if present, is variously notched; when it is reduced, the trigonid basin is very reduced, or absent.

47) Location of metaconid with respect to protoconid on p4: (0) metaconid displaced distally; (1) protoconid and metaconid approximately aligned; (2) metaconid located more mesially. Unordered. In early erinaceomorph, such as *Macrocranion*, the metaconid is located distally to the protoconid, as it is in some *Galerix*, such as G. *aurelianensis* (specimen Me, FE-Li7408-00034 in van den Hoek Ostende and Fejfar, 2006: p. 193, fig. 1), *G. rutlandae* and *G. wesselsae*. Whether this is the plesiomorphic state of character for Galericinae it is difficult to tell, because in early Galericinae it is aligned with the protoconid (*Eogalericius, Tetracus*) or is placed slightly more anteriorly (*Microgalericulus, Zaraalestes*). The distally placed metacone of some *Galerix* specimens is probably a parallelism with Paleogene species. The metaconid is positioned mesially with respect to the protoconid in *Parasorex pristinus* and *Schizogalerix*; in other *Parasorex* species the metaconid is located only slightly mesially to the protoconid.

48) Mesial wall of paraconid on p4: (0) procumbent; (1) fairly straight; (2) inclined distally; (3) secondarily verticalized. Ordered. In *Eogalericius* as well as in some specimens of *Zaraalestes* (e.g., specimen Z. Pal. No. MgM-III/7 in Sulimski, 1970: pag. 59, fig. D), the paraconid is slightly inclined anteriorly; this character state can be observed in other early Erinaceomoprha, such as *Entomolestes grangeri* and *Macrocranion nitens*. In Galericinae the mesial wall of the paraconid is usually almost vertical, but with a few exceptions: the early *Deinogalerix* species *D. freudenthali, D. masinii* and *D. samniticus* have a distally inclined paraconid on p4. More derived species of *Deinogalerix* (*D. brevirostris, D. intermedius, D. koenigswaldi* and *D. minor*) show a verticalized paraconid, but this pattern

is caused by the swelling of the cuspid and is not a retained plesiomorphic state of the character.

49) Extension of p4 talonid (Gould, 1995, 2001; from He et al., 2012, modified): (0) elongated; (1) reduced. Ordered. An elongated talonid is typical of early Erinaceomorpha and erinaceids, such as *Changlelestes* and *Macrocranion*; this kind of pattern can still be observed in *Microgalericulus* as well as in some specimens of *Zaraalestes*, and is therefore the possible plesiomorphic state of the character also in Galericinae *sensu lato*. However, in *Eogalericius*, as well as in the Galericinae *sensu stricto*, the talonid is relatively shorter compared to the trigonid.

50) Presence and location of distal cuspulid on p4 (from Gould, 2001; He et al., 2012, modified): (0) present, median or lingual; (1) present, displaced disto-lingually; (2) absent. Unordered. The presence of a distal cuspulid on p4 is rather variable in Galericinae. When present, it is placed in median or lingual position, or disto-lingually, thereby forming a sort of “entoconid”. In *Galerix* (except *G. africanus*, *G. aurelianensis* and some specimens of *G. exilis*), in *Schizogalerix* (except *S. evae*) and in some specimens of *Parasorex depereti, P. socialis* and *Zaraalestes minutus*, it is usually absent.

51) Shape of distal cingulid on p4: (0) simple, without *crista mediana*; (1) with weak *crista mediana*; (2) with well-developed *crista mediana*. Unordered. Usually, the distal cingulid on p4 is a simple, crest-like structure, not interrupted by a *crista mediana* (the crest which divides the talonid in two, approximately equal halves; Lopatin and Zazhigin, 2003; Lopatin, 2006). The nomenclature “*crista mediana”* is here preferred to to the so-called “transverse ridge” (e.g., in Selänne, 2003) referred to some species of *Schizogalerix*, because similar terms are used for other talonid’s structure (e.g., the “crête transversale” in Crochet, 1975). To avoid any possible confusion with the cristid obliqua (=prehypocristid, see Lopatin, 2006), or with the postcristid, this cristid is called here *crista mediana*. A

variously developed, but generally weak, *crista mediana* is present in *Tetracus daamsi*, in some species of *Galerix* (*G. exilis, G. remmerti, G. rutlandae* and *G. stehlini*), *Parasorex* (*P. depereti*, *P. ibericus* and *P. socialis*) and in at least one species of *Schizogalerix* (*S. moedlingensis*). A well-developed *crista mediana* is typical of advanced members of *Schizogalerix* (*S. duolebulejinensis*, *S. macedonicus, S. sarmaticum, S. zapfei* and some specimens of *S. anatolicus*), as well as of earlier species (*S. pasalarensis* and *S. voesendorfensis*).

52) Connection between paraconid and protoconid on p4 (Gould, 2001; van den Hoek Ostende, 2001d; Borrani et al., 2018, modified): (0) absent; (1) paraconid connected to the protoconid by a low and fairly straight crest; (2) paralophid present and discontinuous, with carnassial notch; (3) paralophid present and continuous; (4) blunt paralophid. Unordered. The paralophid on p4 is absent in *Galerix* (except *G. iliensis* and some specimens of *G. symeonidisi*); however, a discontinuous paralophid is already present in *Eogalericiu*s, *Microgalericulus* and apparently in *Zaraalestes*. In *Tetracus* (e.g., specimen PgT5 in Hugueney and Adrover, 2003: p. 315 pl. 1, fig. 2b) and some specimens of *Galerix exilis* (e.g., specimen Ss 11005 in Ziegler, 1983: p. 100, fig. 88a) the paraconid is connected to the protoconid by a fairly low and straight cristid, which however doesn’t seem a “true” paralophid. In *Deinogalerix, Parasorex* and *Schizogalerix* the paralophid is invariably present (except in *P. kostakii*, wherein it is rarely present; see Doukas and van den Hoek Ostende, 2006: p. 112); however, in all these groups it has different shape. In *Parasorex* the paralophid has a distinct carnassial notch (even in some unworn teeth of *Parasorex socialis*; see Ziegler, 2006: p. 133); this trait is shared by early species of *Schizogalerix*, i.e., *S. evae* and *S. pasalarensis*. In more derived *Schizogalerix*, however, the paralophid of p4 is a more continuous crest, poorly or not notched. In *Deinogalerix*, the paralophid is markedly blunt and swollen and shows no carnassial notch. Finally, in *Apulogalerix* the paralophid is absent

on p4: Masini and Fanfani (2013: p. 12) remark that the lack may be a secondary loss that can be accounted for by the general bulbous shape acquired by the tooth, as well as by the contemporary loss of the hypocone on P3; alternatively, it may be a plesiomorphic character state; for this reason, the character is herein considered unordered.

53) Precingulid on p4 (Borrani et al., 2018): (0) present; (1) absent. Ordered. The presence of a precingulid on p4 is common in early Erinaceomorpha and erinaceids: the cingulid occurs in at least some specimens of *Anatolechinos*, *Eochenus, Macrocranion*, *Oncocherus*, *Litolestes* and *Litocherus*. It is still present in *Zaraalestes minutus*, *Microgalericulus esuriens*, *Tetracus daamsi* as well as in some specimens of *Eogalericius butleri*; in contrast, it is constantly absent in all other -Galericinae *sensu stricto* (including *T. nanus*).

54) Labial cingulid on p4 (from Gould, 2001, modified): (0) absent; (1) present. Unordered. A labial cingulid, divided from the precingulid when the latter is present, is usually absent on the p4s of Galericinae. In contrast, it is shown by those of *Galerix africanus, Schizogalerix duolebulejinensis, S. zapfei* (in the p4s of the latter, the labial cingulid resembles a “precingulid”; see Engesser, 1980: p. 68, fig. 5a), *Tetracus daamsi* and some specimens of *T. nanus*.

55) Shape of the p4 paraconid: (0) tubercle-like; (1) crest-like. Unordered. In the early Galericinae *sensu lato Eogalericius*, the paraconid may be tubercle- or crest-like. In *Zaraalestes* and *Microgalericulus* it is more or less crest-like, whilst in *Tetracus* the paraconid is similar to a cuspid; therefore, it is difficult to state *a priori* what is the plesiomorphic state of character for the early Galericinae. Usually, with some exceptions (i.e., *Galerix iliensis*, *P. depereti*, *P. kostakii*, *P. socialis*, *Schizogalerix* as a whole and some specimens of *G. symeonidisi* and *P. ibericus*), the paraconid is tubercle-like in the Galericinae *sensu stricto*.

56) Lingual closure of the talonid on p4: (0) talonid opened lingually; (1) talonid closed lingually by a sharp cristid; (2) talonid closed lingually by a blunt cristid. Unordered. Lopatin (2006) reports the presence in *Eogalericius* of a “metastylid” which closes lingually the talonid of p4; however, in *Zaraalestes* and *Microgalericulus* such cristid is absent and the talonid basin is open lingually. Since in earlier erinaceomorphs the talonid basin seems to be close (*Macrocranion, Litolestes, Scenopagus*) or open (*Oncocherus*), it is difficult to state what state of character is plesiomorphic for the Galericinae. A metacristid is present in *T. daamsi* but not in *T. nanus*, which usually doesn't have a metaconid; however, there is a cristid that slopes linguo-distally from the protoconid in *T. nanus,* still reminding the shape of the metacristid in *T. daamsi*; for this reason, it is simpler and probably more accurate to talk about the “closed” or “opened” appearance of the talonid instead of what crests close the distal basin. In *Galerix,* the talonid basin shows a high variability, being opened lingually (*G. iliensis*, *G. remmerti*, *G. uenayae*), closed (*G. africanus*, *G. stehlini*) or shows both the states of character (*G. aurelianensis, G. exilis, G. rutlandae, G. saratji, G. wesselsae*). In *Apulogalerix, Parasorex* and *Schizogalerix* the talonid basin is closed lingually; the same occurs in *Deinogalerix,* in which the lingual crest has a distinctive blunt appearance.

57) Shape of the paraconid on m1: (0) crest-like; (1) tubercle-like. Unordered. As a general rule, the paraconid is poorly distinct on m1, being usually a flattened cuspid joined to the paralophid; therefore, it is considered herein tubercle-like when a cuspulid can be observed more or less readily, otherwise crest-like. This character is difficult to state, because in worn out tooth the paraconid, if tubercle-like, can be easily abraded in a more crest-like shaped, leading to misinterpretation. The paraconid in *Eogalericius, Zaraalestes* (as reported in Ziegler et al., 2007: p. 67; although a cuspulid may be distinguished; see specimen of *Zaraalestes minutus* NHMW 2006z0174/0001 in Ziegler et al., 2007: p. 69, fig.

9A, and of *Z. russelli*, specimen PSS 40-61 in Storch and Dashzveg, 1997: p. 441, fig. 5) and *Microgalericulus* is a crest-like cuspid, virtually indistinguishable from the paralophid; it is possible that this is the plesiomorphic condition of the Galericinae). In the Galericinae *sensu stricto* the paraconid is usually tubercle-like, excepted for *Deinogalerix*, some *Galerix* (*G. stehlini, G. symeonidisi and G. wesselsae*), *Schizogalerix evae, Parasorex ibericus* and *P. socialis*. In *Schizogalerix* seems that in unworned specimens there is a small cuspulid at the end of the paralophid, that is worn through onthogenesis.

58) Placement of the hypoconid compared to the entoconid on m1: (0) more or less aligned and opposite to each other; (1) hypoconid placed distally to the entoconid. Ordered. In contrast with the other Galericinae, in which the two cusps are more or less aligned to each other, in the more derived *Schizogalerix*, the hypoconid is typically displaced distally to the entoconid.

59) Presence and development of the labial cingulid (=ectocingulid in Lopatin, 2006) on m1 (modified from Gould, 2001): (0) present, well developed and continuous with the precingulid; (1) present, poorly developed and not continuous with the precingulid when this is present; (2) labial cingulid absent, there is only the precingulid; (3) precingulid absent, there is only a hint of labial cingulid between the protoconid and hypoconid; (3) anterolabial cingulid absent. Unordered. As a general rule, it is herein considered the labial cingulid as continuous with the precingulid when the cingulid extends distally to the apex of the protocone. In many early Erinaceomorpha, e.g., *Enotomolestes, Macrocranion* and *Litolestes*, there is no clear labial cingulid; however, in *Litocherus* and *Oncocherus* a short labial cingulid, continuous with the precingulid, is present. In early Galericinae *sensu lato* such *Eogalericius* and *Zaraalestes*, as well as in *Tetracus*, the labial cingulid is present and continuous, therefore this is probably the plesiomorphic state of character for the Galericinae (although in *Microgalericulus* it is absent). Usually, this character is variable in

the various genera, although a general reduction or absence of the labial cingulid can be observed in the more derived species of *Deinogalerix*, *Galerix*, *Parasorex* and *Schizogalerix*. In *Apulogalerix* the labial cingulidp is reduced and might be even absent.

60) Shape of the distal margin of the m1 talonid (modified from Gould, 2001, van den Hoek Ostende, 2001d): (0) continuous postcristid, postcingulid present and connected with the postcristid; (1) continuous postcristid, postcingulid not connected with the postcristid; (2) postentocristid absent, postcingulid connected only with the posthypocristid; (3) postcristid partially divided, with the postcingulid mainly connected to the with the postentocristid; (4) posthypocristid more or less turned mesially, with the postentocristid turned distally and fused with the postcingulid; (5) posthypocristid more or less turned mesially, with the postentocristid strongly curved, turned distally and fused with the postcingulid, the latter with an accessory cuspulid (=entostylid in Rzebik-Kowalska aand Lungu, 2009). Unordered. In unworn specimens of *Deinogalerix masinii,* the postcingulid is not connected with the postcristid. In *Galerix aurelianensis*, the postcristid may be partially divided, with the postcingulid mainly connected to the posthtypocristid; such shape may be found in some specimens of *G. stehlini*. The relationship between postcristid and postcingulid cannot be readily observed in the specimen of *Riddleria* figured by van den Hoek Ostende (2003b, specimen 51.1051: p. 7, pl. 1, fig. 8), however it seems that the character 0 is the most likely to occur.

61) Accessory cuspulid of the hypoconid on m1: (0) absent; (1) present. Ordered. Although it has been named “hypoconulid” by several authors (e.g., Doukas et al., 1995; Rzebik-Kowalska and Lungu, 2009; Selänne, 2003), this cuspulid in Galericinae is clearly non-homologous with the “true” hypoconulid of the earlier erinaceids (see character 79). In the early Paleogene Erinaceomorpha, for example *Changlelestes, Entomolestes*, *Macrocranion*, *Litocherus*, *Litolestes, Oncocherus* and *Scenopagus,* an hypoconulid actually

occur on the first and second lower molar; however, in all the following erinaceids (except for the enigmatic Whitneyan-Arikareeian limit/Ar1 *Ocajila makpiyahe* from South Dakota, which probably still has a small hypoconulid on m2) a “true” hypoconulid on m1-2 cannot be observed. A cuspulid may origin from a bulge on the posthypocristid in some of the more derived *Schizogalerix* species (*S. macedonicus*, *S. sarmaticum* and at least some specimens of *S. sinapensis*).

62) Presence and development of the postparacristid on m1: (0) absent; (1) present, not connected with the metaconid; (2) present, inflated and steep. Unordered. The postparacristid is usually absent; however, a faint cristid may be present in *Galerix exilis* and *Parasorex ibericus,* while it is always present in *G. africanus* and *Riddleria atecensis.* In *Deinogalerix,* the postparacristid is invariably present, with a distinctive inflated and steep shape.

63) Relative width of the m1 talonid compared to the trigonid: (0) talonid larger than the trigonid; (1) talonid as large as the tringonid; (2) talonid narrower than the trigonid. Unordered. In the Paleogene erinaceomorphs the talonid is usually larger than the trigonid (e.g., *Entomolestes, Macrocranion, Onconcherus* and some specimens of *Sespedectes* and *Changlelestes*). Such development of the trigonid can be observed in the majority of the Galericinae; however, the trigonid may be as large as the talonid in *Microgalericulus, Zaraalestes, Galerix aurelianensis, G. rutlandae* and *G. stehlini.* Only in *Deinogalerix* the talonid is narrower than the trigonid even in m1.

64) Development and shape of the paralophid on m1 (modified from Gould, 2001): (0) paralophid quite short, relatively little oblique; (1) oblique paralophid, developed more anteriorly; (2) paralophid very elongated anteriorly; (3) paralophid very elongated anteriorly, almost diagonal. Unordered. In early erinaceomorphs and erinaceids (e.g., *Changlelestes, Litolestes, Litocherus, Macrocranion, Oncocherus, Scenopagus*), the m1

paralophid is clearly short and transversally placed. In later Erinaceidae (e.g., *Anatolechinos* and *Eochenus*), however, the paralophid is usually still quite short but more oblique: such state of character can be observed in the Galericinae *sensu lato* and in *Tetracus daamsi,* which have a comparably short paralophid. Also, *Apulogalerix pusillus* shows a similar paralophid (see Masini and Fanfani, 2013, p. 10); however, it seems unlikely that this depends on a primitiveness of the tooth, which is very derived for many other features. It is possible that the paralophid in *Apulogalerix* is relatively shorter and more oblique due to the closer and bulging cusps compared to the other Galericinae. Usually, in other Galericinae the paralophid is rather oblique and more elongated mesially. Aside from *Apulogalerix* and *T. daamsi,* there are two exception to the development of this crest: in *Deinogalerix,* the paralophid is very elongated anteriorly, as well as in *Riddleria.* However, in the first genus the paralophid is almost parallel for a trait to the lingual margin of the tooth, while in the latter it is more diagonal.

65) Position of the metaconid on m1 (modified from Gould, 2001): (0) metaconid sub-aligned with the protoconid; (1) metaconid slightly more mesial than the protoconid; (2) metaconid very mesial to the protoconid; (3) metaconid slightly distal to the protoconid. Unordered. In the erinaceids, the metaconid is usually slightly displaced mesially to the protoconid; this can be found even in some Sespedectidae, as *Scenopagus*. In *Macrocranion* and some Galericinae species (*Tetracus daamsi*, *Deinogalerix freudenthali, D. samniticus* and *D. masinii*), however, the metaconid is almost opposite to the paraconid; it is highly possible that the state of character in *Deinogalerix* is a parallelism with those of the earlier Erinaceomorpha. A metaconid displaced markedly mesially to the protoconid is typical of the later *Schizogalerix* (*S. duolebulejinensis, S. intermedius, S. macedonicus, S. sarmaticum* and some specimens of *S. sinapensis*) and also of *Riddleria*; however, because the earlier *Schizogalerix* don’t shows this trait, it is highly probable that the state of character shared by

these two genera is a convergence. In *D. minor* and *D. koenigswaldi* the metaconid is displaced slightly distally to the apex of the protoconid instead.

66) Presence and morphology of the metacristid on m1: (0) absent; (1) present, sharp, divided from the entocristid by a notch; (2) present, sharp, united to the entocristid; (3) present, blunt, divided from the entocristid by a notch; (4) present, blunt, united to the entocristid; (5) present, developed in a small cuspulid. Unordered. In the early Galericinae *sensu lato*, *Riddleria* and in some specimens of *T. nanus* the metacristid is absent on m1; however, this crest is usually present and divided from the entocristid in the Galericinae *sensu stricto*. A sharp metacristid continuous with the entocristid can be observed in many *Parasorex* and some *Galerix* (*G. exilis, G. stehlini, G. wesselsae*). In *G. africanus* and some specimens of *G. exilis* the metacristid may develop in a small accessory cuspulid, as in the Hylomyinae genus *Lantanotherium* (Butler, 1984). In both genera of the “Terre Rosse” fauna, *Apulogalerix* and *Deinogalerix,* the metacristid becomes a blunt, inflated crest; however, in *Apulogalerix* it makes a continuous crest with the entocristid, whilst in *Deinogalerix* it is divided from the mesial arm of the entoconid by a notch. This may reflect a distinct origin for the two structures: in *Apulogalerix* it may derive from a more derived, *Parasorex*-like crest, while in *Deinogalerix* from a more plesiomorphic, notched metacristid.

67) Presence and development of the postparacristid on m2: (0) absent; (1) present, does not reach the metaconid; (2) present, connected to the metaconid. Unordered. The postparacristid on m2 usually shows a higher variability than that on m1 (character 63): it is absent in the -Galericinae *sensu lato* and in *T. nanus*. In *T. daamsi,* it is present but doesn’t reach the metaconid, as in *Riddleria* and usually in *Schizogalerix* (except *S. moedlingensis, S. voesendorfensis* and *S. zapfei,* in which close the basin of the trigonid lingually), and it is invariably present in the other Galericinae genera, but it is usually variable between the

various species. In some *Galerix* (*G. exilis, G. saratji* and *G. symeonidisi*) and in *Parasorex kostakii* it may reach or not the metaconid.

68) m2 trigonid (modified from Borrani et al., 2018; Gould, 2001): (0) mesio-distally compressed, with oblique paralophid; (1) relatively less compressed, with more diagonal paralophid; (2) very compressed. Unordered. In the early Erinaceomorpha and Erinaceidae (e.g., *Changlelestes, Macrocranion, Litocherus, Litolestes, Oncocherus, Scenopagusi),* the paralophid on m2 is distinctively oblique, giving the trigonid a mesio-distally compressed shape. Such development of the trigonid is still present in *Eogalericius,* but not in the other Galericinae; in *Schizogalerix,* except for the early species *S. evae*, the trigonid is very compressed instead.

69) Metaconid on m2: (0) metaconid located mesially to the protoconid; (1) metaconid very mesial compared to the protoconid. Ordered. In erinaceids, the metaconid on m2 is usually located slightly mesially to the protoconid; however, in *Parasorex pristinus, Riddleria* and *Schizogalerix* the metaconid is remarkably located mesially to the protoconid.

70) Anterolabial cingulid on m2 (from Gould, 2001, modified): (0) present and continuous, extended distally to protoconid; (1) present, not extended distally to protoconid (=precingulid); (2) divided in precingulid and in labial cingulid. Unordered. In early Galericinae (*Eogalericius, Zaraalestes, Tetracus* and many species of *Deinogalerix, Galerix,* some *Parasorex* and *Schizogalerix*) the labial cingulid is usually a continuous structure, which extends from under the paralophid to distally to the protoconid. In *Microgalericulus esuriens* and *Riddleria,* however, as well as in *G. rutlandae, S. sarmaticum, S. sinapensins* and some specimens of *G. exilis,* and *P. socialis. S-intermedius*, it is nothing more than a precingulid, whereas in some Galericinae *sensu stricto* it may be divided into a precingulid and labial cingulid. Therefore, the polarity of this

character is difficult to establish, especially if character state 2 is considered intermediate between 0 and 1.

71) Distal margin of talonid on m2: (from Gould, 2001; van den Hoek Ostende, 2001d; He et al., 2012, modified): (0) continuous postcristid, postcingulid present and connected with postcristid; (1) continuous postcristid, postcingulid not connected with postcristid; (2) postrcistid imperfectly divided, with postcingulid connected mainly with postentocristid; (3) lingual arm of hypoconid (=posthypocristid) variously bent mesially, with labial arm of entoconid (=postentocristid) directed distally and fused with postcingulid; (4) posthypocristid variously bent mesially, with postentocristid strongly curved, bent distally and fused with postcingulid, the latter with accessory cuspulid (=entostylid in Rzebik-Kowalska and Lungu, 2009). Unordered. See character 61 for a discussion of this character on m1; the distal margin of the talonid seems to be less variable on m2 than on m1. Usually, Galericinae have m2s with continuous postcristid and with postcingulid either connected or not with it. Many species of *Schizogalerix*, especially most derived ones, have m2s with postcristid ranging from continuous to divided into a postentocristid and a posthypocristid, with the distal cingulid fused mainly or completely with the former. A divided postcristid can also be observed in some specimens of *Deinogalerix freudenthali* (see Savorelli et al., 2019).

72) Relative width of m2 talonid relative to trigonid: (0) talonid larger than trigonid; (1) talonid as large as tringonid; (2) talonid narrower than trigonid. Unordered. See character 64 for a general discussion on a similar character. On m2 the talonid tends to be relatively narrower than the trigonid in many species.

73) Position of hypoconid with respect to protoconid on m2: (0) hypoconid labial to protoconid; (1) hypoconid approximately aligned to protoconid. Unordered. With a few exceptions, in Galericinae the hypoconid is usually placed labially with respect to the

protoconid. In *Microgalericulus esuriens, Galerix aurelianensis, G. rutlandae, G. wesselsae* and some specimens of *Apulogalerix pusillus, G. exilis* and *Parasorex socialis* it may be aligned with the protoconid.

74) Metacristid on m2: (0) absent; (1) present, divided from entocristid by notch; (2) present, united to entocristid; (3) present, shaped as small cuspulid. Unordered. For a discussion on a similar cristid see character 67. A small cuspulid is also present on the m2 of *G. aurelianensis*, whereas such cusplet is absent on m1 (Klietmann, 2013).

75) Paraconid on m3: (0) crest-like; (1) crest-like, with tubercle. Unordered. Usually, the paraconid on m3 is reduced to a continuous, crest-like structure; however, in some specimes of *Galerix G. saratji* (e.g., Ha 1, 3201 in van den Hoek Ostende, 1992: p. 463, pl. 2, fig. 12) it may appear as a mesial bulge, which is the likely remnant of a small, tubercle-like cuspid.

76) Location of entoconid respect to hypoconid on m3: (0) approximately next to each other; (1) entoconid placed distally to hypoconid. Unordered. Usually, in Erinaceomorpha the entoconid is approximately placed next to the hypoconid; however, in some Galericinae taxa (e.g., *Apulogalerix*, *Parasorex* and *Schizogalerix*) the entoconid is placed somewhat more distally.

77) Shape of distal margin of m3 talonid: (0) postcristid absent, distal cingulid present; (1) postcristid present and continuous, distal cingulid absent; (2) postcristid present and continuous, distal cingulid present but not connected with postcristid; (3) postcristid present and continuous, with distal cingulid connected with postcristid; (4) postcristid and distal cingulid absent; (5) postcristid partially divided, distal cingulid absent; (6) hypoconulid absent, posthypocristid divided from postentocristid, which is directed distally forming a distal cingulid. Unordered. In early Erinaceomorpha, e.g., *Changlelestes*, *Litocherus*, *Litolestes,* the hypoconulid usually prevents the formation of a continuous postcristid,

because the cuspulid is connected only with the hypoconid, nor is it connected with the entoconid or the hypoconid. The m2s of *Macrocranion vandelbroeki* (e.g., specimen IRScNB M180 in Smith and Smith, 1995: p. 17, pl. 2, fig. 1) show a continuous postcristid. Therefore, the presence of a hypoconulid (character 78) should be regarded as an independent character from the postcristid and its relation with the postcingulid. In the early Galericinae *sensu lato Eogalericius*, *Microgalericulus* and *Zaraalestes* the postcristid is absent, whereas Galericinae *sensu stricto* usually have a continuous postcristid and no distal cingulid on m3. A distal cingulid not connected with the postcristid may be present in *G. aurelianensis*, *G. exilis* and *G. symeonidisi*. In *G. iliensis* the distal cingulid extends to the postcristid and in *Parasorex* has no distal cingulid and a continuous or imperfectly divided postcristid. In some species of *Schizogalerix*, i.e., *S. intermedius, S. sarmaticum, S. sinapensis* and *S. zapfei*, the postentocristid is not connected with the posthypocristid whereas it is with a “distal cingulid”. However, in some specimens of *S. intermedius* and *S. sarmaticum*, the postcristid is rather continuous and there is no trace of any distal cingulid. This character state is present in almost all the other *Schizogalerix*, with the exception of *S. evae*, in which the postcristid is already partially divided, although still without any distal cingulid. It is therefore highly probable that the “distal cingulid” on the m3s of some derived *Schizogalerix* is not homologous of that of earlier Galericinae, but rather is an evolutionary novelty due to the splitting of the postcristid (like in *S. evae*), with the postentocristid bent distally to form a sort of “pseudo-distal cingulid”.

78) Hypoconulid on m3 (from Borrani et al., 2018, modified): (0) present, well-developed, placed mesio-lingually, protruding posteriorly and not fused with entoconid; (1) present, poorly-developed, positioned mesio-lingually, protruding posteriorly and not fused with entoconid; (2) present, poorly-developed, positioned mesio-lingually and fused with entoconid; (3) absent. Ordered. A robust hypoconulid is present on the m3s of almost all

early Erinaceomorpha and erinaceids, including *Zaraalestes*; this is therefore the plesiomorphic state of the character in erinaceids. A more reduced cuspulid, placed more mesio-lingually, at times fused with the entoconid, can be found in *Eogalericius*: this is probably an intermediate condition between the more developed and distinguishable cuspulid of earlier Erinaceidae and that of Galericinae, in which the hypoconulid is completely absent.

79) Length of I2, compared with that of I3 (Gould, 1995; from Gould, 2001, modified; He et al., 2012): (0) I2 larger than I3; (1) I2 as large as or smaller than I3. Unordered. In *Deinogalerix* and *Parasorex ibericus* the I2 is smaller than I3. In *P. depereti*, the smaller tooth is tentatively assigned to the I3 and the larger one to I2; for a complete discussion of these incisors, see Masini et al. (2019), p. 441.

80) P1 (from Corbet, 1988; Frost et al., 1991; Gould, 1995, 2001; He et al., 2012, modified): (0) present, with two roots; (1) present, with one root; (2) absent. Unordered. In *Zaraalestes minutus*, the first premolar is absent; this is an advanced state, because P1 is present and single-rooted in earlier Erinaceomorpha (e.g., *Macrocranion*), as well as in the later *P. depereti*, where P1 often shows a deep furrowed single-root. In *Tetracus, Deinogalerix, Galerix, Parasorex socialis, Schizogalerix voesendorfensis* this tooth is two-rooted.

81) P2 mesial cuspule: (0) present; (1) absent. Unordered. An anterior cuspule is present in early Erinaceidae, such as *Silvacola acares*, in *Zaraalestes, Galerix africanus* and in some specimens of *Tetracus nanus*. In contrast, other Galericinae *sensu stricto* have no mesial cuspule on P2.

82) P2 distal cuspule: (0) present; (1) absent. Unordered. This cuspule is more often present than the mesial one in Galericinae *sensu stricto*. It is always present on the P2s of *Galerix exilis, G. aurelianensis* and *Parasorex depereti*; it may also be present in some

specimens of *G. rutlandae* and *Tetracus nanus*. Because a distal cuspule is present in the Galericinae *sensu lato Zaraalestes minutus* as well as in other early Erinaceidae (e.g., *Silvacola acares*), it is probably plesiomorphic for this group of animals.

83) P3 protocone: (0) present, tubercle-like, divided from hypocone whenever it occurs; (1) present, crest-like, divided from hypocone whenever it occurs; (2) present, crest-like, fused to hypocone; (3) present, bulging, joined with hypocone; (4) absent. Unordered. Usually, this cuspule is tubercle-like and divided from the hypocone; however, in some specimens of *Galerix exilis* the protocone is crest-like, and in *Parasorex depereti* it can show exceptional variability, ranging from tubercle-like to crest-like, to being fused to the hypocone; sometimes it may even be absent. A bulging protocone, variously fused with the hypocone, is peculiar to *Deinogalerix*.

84) Connection between protocone and distal cingulum on P3: (0) present; (1) absent. Unordered. The protocone probably formed on the labial cingulum during the transition from the peramurid to the tribosphenic molar (Butler, 1990). The third premolar may have experienced the same evolution: in many early Galericinae (i.e., *Tetracus, Riddleria* and many species of *Galerix*) alongside *Zaraalestes* the protocone is connected with the distal cingulum, but without the development of any disto-lingual cusp (hypocone). Noteworthy is the pattern shown by *G. uenayae*: in the specimens Ke, 6259 and Ke, 6260, figured by van den Hoek Ostende (1992: p. 465, pl. IV, fig. 3-4), the distal cuspule is separated from the continuous disto-labial cingulum. This cuspule might be supposed to have originated independently from a "true" hypocone, with which it would therefore be convergent, or that it emerged from an isolated, more lingual "patch" of the disto-labial cingulum; this would have left the latter uninterrupted. In the second alternative, the disto-lingual cusp in *G. uenayae* (and in other species of *Galerix*) would be homologue of the hypocone of other, more derived species of Galericinae; thereby a protocone would still be connected with the

distal cingulum even in presence of a hypocone. This would imply that characters 85 and 86 (= “presence and development of hypocone”) are independent from one another, at least to a certain extent. The protocone is usually connected with the distal cingulum in *Galerix*, with the exception of *G. iliensis*, *G. symeonidisi*, *G. wesselsae* and some specimens of *G. exilis* (in which the distal cingulum may be totally absent). In *Parasorex depereti*, the distal cingulum is connected with the hypocone, which may be connected with a crest-like protocone, whenever the latter occurs. In all the other species of *Parasorex*, and also in *Apulogalerix*, *Deinogalerix* and *Schizogalerix*, the distal cingulum ends always without getting in touch with the protocone.

85) Hypocone on P3 (from Frost, 1991; Gould, 1995, 2001; van den Hoek Ostende, 2001d; He et al., 2012; Borrani et al., 2018, modified): (0) absent; (1) present, weak; (2) present, strong; (3) secondarily reduced or even absent. Ordered. In many Erinaceidae and early Erinaceomorpha (e.g., Brachyericinae, Hylomyinae, Erinaceinae, *Macrocranion*, *Tupaiodon*, *Zaraalestes*, *Litocherus*, *Oncocherus*), the hypocone is always absent on the P3 and sometimes even the lingual lobe is reduced or totally absent. The same also occurs in other early Galericinae, such as *Tetracus*, *Riddleria* and some species of *Galerix* (*G. aurelianensis*, *G. rutlandae* and *G. stehlini*). In other species of *Galerix*, however, this lobe is variable: in fact, in *G., africanus*, G. *exilis*, *G. remmerti*, *G. saratji* and *G. uenayae* there may be a small hypocone. In *G. iliensis*, *G. symeonidisi* and *G. wesselsae*, as well as in *Parasorex*, *Deinogalerix* and *Schizogalerix*, the hypocone is distinct and well-developed. In *Apulogalerix*, the hypocone tends to be secondarily reduced, or totally absent (see Masini and Fanfani, 2013 for complete discussion), which gives the tooth a primitive aspect.

86) Distal accessory cups on P3 hypocone: (0) absent; (1) present. Ordered. In some specimens of *Parasorex depereti*, an accessory cusp may be present distal to the hypocone of P3.

87) Carnassial notch on P3: (0) absent; (1) present. Unordered. The metastylar crest is usually fairly straight and with no carnassial notch in *Zaraalestes*, *Galerix*, *Riddleria* and *Tetracus*. In contrast, a carnassial notch is present on the P3s of *G. iliensis* and some specimens of *G. symeonidisi* (e.g., specimen BSP 1959 XXVIII 539 in Ziegler and Fahlbusch, 1986: tab. 1, fig. 29). A carnassial notch is more common on the P3s of the genera *Apulogalerix*, *Deinogalerix*, *Parasorex* and *Schizogalerix.*

88) P3 parastyle: (0) present, tubercle-like; (1) present, shoulder-shaped; (2) present, crest-like; (3) absent. Unordered. A tubercle-like parastyle is present in *Zaraalestes*, *Tetracus* and *Galerix africanus.* In other species of the genus *Galerix*, however, this character is variable: in the type species *G. exilis*, for example, it may be tubercle-like, shoulder-like (without a clear shaped cuspule or crest) or even crest-like, whereas in *G. wesselsae* it may be absent. A similar variability can be observed in *Parasorex*. The parastyle of P3 is shoulder-like in all the species of *Deinogalerix* but *D. masinii*, in which it can be conule-like (Villier, 2010), and is either a small crest-like structure or totally absent in *Schizogalerix*.

89) Disto-labial cuspule on P4: (0) absent; (1) present. Ordered. In general, there is no true metacone on the P4s of Erinaceomorpha (Novacek et al., 1985; Smith et al., 2002); this cusp is replaced by a shearing metastylar crest. However, in some advanced species of *Schizogalerix* (*S. macedonicus*, *S. sinapensis* and probably *S. sarmaticum*) a disto-labial cuspule may be present on the metastylar crest. This cuspule is most likely not homologous of the metacones of upper molars. For this reason, identifying it as a “metacone” seems inappropriate.

90) Labial cingulum (=ectocingulum in Lopatin, 2006) on P4: (0) present, extended; (1) present, limited to distal portion of crown; (2) absent. Unordered. The state of this character varies considerably in early Galericinae *sensu lato*: in *Eogalericius butleri* the labial

cingulum is extended labially almost along the entire length of the crown, whereas in *Zaraalestes minutus*, *Z. russelli* and in most Galericinae it is absent. Klietmann (2013) reports that the P4 of *Galerix aurelianensis* has only the distal cingulum. However, in the specimen NMA 2012-23/2058 (p.337, pl. 2, fig. 5) a weak labial cingulum occurs on P4, distal to the paracone. A similar structure can be observed in *Tetracus daamsi*, *G. remmerti* as well as in some specimens of *G. saratji* (e.g., Ha 3,621 in van den Hoek Ostende, 1992: p. 463, pl. 2, fig. 5).

91) P4 hypocone: (0) undivided; (1) imperfectly divided; (2) well divided. Unordered. As Savorelli et al. (2019) pointed out, in *Deinogalerix* there are different degrees of division of the hypocone: in the early species *D. freudenthali* and *D. samniticus* the hypocone is undivided, as in mainland Galericinae species, whereas in *D. masinii* it may either be imperfectly divided, or not. In *D. minor* the cusp can either be superficially or more deeply divided. In *D. koenigswaldi* and *D. brevirostris* the hypocone of P4 is split into two portions; Villier and Carnevale (2013) called the well-separated anterior portion "hypoconule". Finally, in *D. intermedius* the hypocone can either be well divided or undivided: we cannot exclude that an imperfect division of P4 hypocones may be abraded with increasing wear.

92) Collar margin outline of P4 in mesial view: (0) straight; (1) sloping dorso-ventrally; (2) step-shaped. Unordered. This character is unfortunately only rarely examined in the literature: however, as Savorelli et al. (2019) pointed out, it is important to distinguish the various species of *Deinogalerix*. In the early species *D. samnitus* the collar margin in mesial view is straight, in *D. freudenthali*, *D. masinii* and *D. minor* it slopes dorso-ventrally and in the more advanced *D. brevirostris*, *D. intermedius* and *D. koenigswaldi* it shows a step-shaped pattern. In *Apulogalerix*, the collar of the P4 in mesial view is straight as in *D. samniticus*; the same also occurs in *Parasorex depereti*, alongside morphotypes with sloping

pattern. A sloping collar outline can also be observed on the P4s of *Galerix exilis*, and, possibly, of *Schizogalerix voesendorfensis* (see Rabeder, 1973: p. 434, fig. 2b).

93) Height of hypocone relative to protocone on P4 (from Gould, 2001; He et al., 2012, modified): (0) protocone higher than hypocone; (1) protocone approximately as high as hypocone. Unordered. Usually, the protocone is higher than the hypocone; however, in *D. masinii*, as well as in the holotype of *D. samniticus*, the protocone is as high as the hypocone or slightly higher. *G. iliensis* also shows a higher hypocone, as well as some specimens of *P. depereti*.

94) Mesial development of P4 parastyle: (0) very protruding; (1) moderately protruding; (2) poorly protruding. Unordered. In the early *Eogalericius, Zaraalestes* and *Tetracus* the P4 has a well-developed, mesially elongated parastyle. The same can be observed in *Galerix aurelianensis*, *G. uenayae* and *Parasorex kostakii*. In other species of the genus *Galerix* (*G. africanus*, *G. remmerti*, *G. rutlandae* and *G. saratji*), but also in *Riddleria*, the P4 parastyle is more reduced, unlike some other species of Galericinae (i.e., *Galerix exilis*, *G. stehlini*, *G. symeonidisi* and *P. socialis*) where it may either be well-developed, or relatively less protruding. Usually, in the derived species of the genera *Apulogalerix*, *Deinogalerix*, *Parasorex* and *Schizogalerix* the P4 parastyle is poorly developed, with the exception of *S. sarmaticum*, in which it seems relatively large.

95) Shape of P4 parastyle: (0) tubercle-like, undivided; (1) crest-like; (2) shoulder-shaped; (3) tubercle-like with crest. Unordered. In general, this character shows a certain degree of intraspecific variability, but in few species it has a specific state. Cuspule-like P4 parastyle can be found in the early genera *Eogalericius*, *Zaraalestes* (in which it is very developed) and *Tetracus*, and also in younger and more derived genera *Apulogalerix*, *Deinogalerix*, *Galerix* and *Parasorex*. However, among the latter genera a few species (i.e., *D. brevirostris*, D. *koenigswaldi*, *D. minor*, *G. africanus* and *P. kostakii*) exhibit only

tubercle-like parastyle, unlike all the other species that show one or two alternatives. For example, both *Apulogalerix* and *G. exilis* possess P4s with tubercle-, crest- or shoulder-like (i.e., without discernible cuspules or crests) parastyle. Conversely, in most *Galerix* species, in all the other species of *Parasorex* as well as in some *Schizogalerix* species (e.g., the early species *S. pasalarensis*), in which this character is recognizable, the parastyle is crest-like. This character is also present in different states in *Deinogalerix*: in *D. intermedius*, *D. masinii* and *D. freudenthali* it comes as a tubercle-like cuspule which sometimes is even split. Finally, in some species of the genus *Schizogalerix* (for instance, in the earliest known *Schizogalerix evae*) the parastyle appears as a tubercle-like cuspule associated with a crest: this cuspule probably derives from an originally crest-like parastyle, then enlarged into a tubercle.

96) P4 parastyle connections: (0) connected by crests with labial cingulum and paracrista; (1) connected by crests with mesial arm of protocone and with paracrista; (2) connected with mesial arm of protocone; (3) not connected with protocone nor with paracone; (4) connected with paracone by short crest but not with protocone. Unordered. Usually, early Erinaceomorpha or Erinaceidae display two different kinds of parastyles: shoulder-like, where the labial cingulum is connected with the mesial arm of the protocone (e.g., *Changlelestes, Macrocranion tupaiodon*), or tubercle-like, either connected only with the mesio-labial cingulum (*Macrocranion junnei*) or, more frequently, with the paraconid by a paracrista (*Macrocranion vandelbroeki, Litocherus, Litolestes, Tupaiodon*). The latter pattern can still be found in *Eogalericius*, whereas *Zaraalestes* and *T. daamsi* already have the simpler condition where the parastyle is connected only with the mesial arm of the protocone and with the paracone but not with the labial cingulum. In the other Galericinae *sensu stricto*, the parastyle may be connected only with the mesial arm of the protocone, or,

as occurs in some derived species of *Schizogalerix* (*S. macedonicus, S. moedlingensis, S. sarmaticum* and *S. voesendorfensis*), only with the paracone by a short paracrista.

97) Protocone-hypocone connection on P4: (0) protocone and hypocone not connected; (1) hypocone connected with protocone by low mesial arm of hypocone (=prehypocrista); (2) hypocone connected with protocone both by prehypocrista and distal arm of protocone (=postprotocrista). Unordered. Like the protocone, during the transition from a peramurid tooth to a tribosphenic one, the P4 hypocone probably developed from a distal cingulum (see Butler, 1990 and character 85). P4s of all earliest Erinaceomorpha (e.g., *Changlelestes, Litocherus, Litolestes, Macrocranion, Oncocherus, Silvacola, Scenopagus*), have no hypocone, but have a well-developed distal cingulum. A hypocone is present on the P4s of *Protogalericius averianovi*, *Eogalericius butleri* and *Zaraalestes minutus*, as well as on those of Brachyericinae, Erinaceinae and Hylomyinae (including early species, e.g., *Hylomys engesseri* and *Scymnerix tartareus*). Therefore, the presence of two lingual cusps is a derived character shared by many erinaceids. On the P4s of *Protogalericius*, *Eogalericius* and *Zaraalestes*, the protocone is not connected with the hypocone; in some specimens of *Zaraalestes*, however, there may be a low prehypocrista connecting the two labial cusps. Which is the plesiomorphic state of this character is difficult to say in Galericinae: on the P4s of *Hylomys engesseri* a lower prehypocrista may reach the protocone. In *Scymnerix tartareus*, a small accessory cuspid is present between protocone and hypocone, and is connected with the hypocone by a low crest. In the Brachyericinae *Brachyerix macrotis*, “no crest links these cusps either to one another or to the buccal structures of the tooth” (Rich and Rich, 1971: p. 27); the same seems to occur in *Exallerix gaolanshanensis*. To further complicate the picture, in the early Galericinae *Tetracus daamsi*, the hypocone is connected with the protocone either by a prehypocrista or by both a prehypocrista and postprotocrista, unlike *T. nanus* where two strong crests connect the lingual cusps with one another. There is

no connection between hypocone and protocone in *Apulogalerix*, *Deinogalerix*, *Parasorex* and *Schizogalerix*, perhaps as a primitive state of the character, or as a secondary loss. Usually, in *Galerix* there seems to be no connections (*G. africanus*, *G. iliensis*, *G. rutlandae*, *G. stehlini*, *G. wesselsae*, some specimens of *G. remmerti* and *G. symeonidisi* and, according to van den Hoek Ostende, 1992, *G. uenayae*).

98) Paraconule on P4: (0) absent; (1) present. Ordered. Usually, there is no such cuspule in Galericinae; however, a mesial cuspule or bulge is present in *Deinogalerix*, lingually to the paracone.

99) Occlusal outline of P4 (from Frost et al., 1991; Gould, 1995; He et al., 2012, modified): (0) poorly elongated and lingually expanded lingual lobe (short and wide P4); (1) lingual lobe more developed, tooth widened lingually (relatively long and wide P4); (2) well-developed and elongated lingual lobe, narrow and squat tooth with relatively rounded lingual lobe; (3) tooth elongated mesiolabially-distolingually. Unordered. A short and wide P4 is plesiomorphic and is possessed by early erinaceids, i.e., *Changlelestes*, *Tupaiodon* and *Silvacola*. This generalized shape is still present in *Eogalericius butleri* and, to some extent, in *Zaraalestes*; however, in Galericinae P4 usually appears relatively wider. An even more squarish and inflated P4 is present in *Deinogalerix*, unlike *Schizogalerix* in which the tooth is typically stretched mesiolabially-distolingually.

100) Mesiolingual-distolabial elongation of M1-2 (Borrani et al., 2018): (0) not elongated; (1) elongated. Ordered. In *Schizogalerix*, the mesiolingual-distolabial elongation is mostly given by the oblique development of the metaconule-metacone complex. A similar development of the M1-2s can also be observed in *Parasorex pristinus*.

101) Metacone on M1-2: (0) wide; (1) relatively narrow (compressed). Ordered. In *Schizogalerix* and at least in some specimens of *Parasorex pristinus* the metacone on M1-2 is relatively narrow compared to that of the other Galericinae *sensu stricto*.

102) M1-2 preprotocrista: (0) more or less joined with paraconule, when present; (1) well separated from paraconule by a groove. Unordered. In almost all Galericinae with paraconule on M1-2s, the conule is joined to (or issues from) the continuous preprotocrista. In contrast, in *Deinogalerix*, *Galerix iliensis* and *Schizogalerix evae* a deep notch separates the paraconule from the crest.

103) Distal arm of metaconule on M1 (from van den Hoek Ostende, 2001d; Borrani et al., 2018, modified): (0) present and extended to disto-labial corner of tooth; (1) present and not connected with distal cingulum; (2) present and connected with distal cingulum; (3) absent. Unordered. The presence of a posterior arm of the metaconule extended to the postero-labial corner of the tooth and interrupting the distal cingulum, is a plesiomorphic trait for Erinaceomorpha: this state of character can be observed in *Changlelestes*, *Litocherus*, *Litolestes*, *Macrocranion*, *Oncocherus*, *Scenopagus*, *Silvacola*, *Tupaiodon*, with the only exception of *Anatolechinos neimongolensis*, in which the distal arm of the metaconule is not extended enough to reach the distal cingulum. A similar development of the posterior arm of the metaconule can still be observed in *Eogalericius* and *Zaraalestes minutus*; however, in some specimens of the latter the crest is already too short to reach the distal cingulum. This is the plesiomorphic state of Galericinae, and can be observed in *Tetracus*, *Riddleria* and in many species of *Galerix*. In some specimens of *G. rutlandae*, as well as in *G. africanus*, the metaconule has no distal arm, unlike some specimens of *G. saratji* and *G. uenayae*, but also *Parasorex*, *Schizogalerix* and some early species of *Deinogalerix* (*D. masinii* and some specimens of *D. freudenthali* and *D. minor*), where the crest is well-developed, so much to reach the disto-labial corner of M1. Due to their primitiveness, *G. saratji* and *G. uenayae* supposedly retained the posterior arm of metaconule as it was in their last common ancestor; more advanced *Parasorex*-like species evolved this feature from an ancestral metaconule with short posterior arm by convergence. Alternatively, *G. saratji*, *G. uenayae* and the

Parasorex-like species are perhaps more strictly related to one another than to the other Galericinae. However, the transitional species (*sensu* Borrani et al., 2018) *G. iliensis* and *G. symeonidisi* have metaconule with short distal arm on their M1s, in most cases not long enough to reach the distal cingulum. The fossil record indicates that the first option is the most parsimonious.

104) Shape of M1 (from Gould, 2001, modified): (0) relatively short and wide molars, with more developed labial region than lingual one, approximately rectangular; (1) proportionally more elongated and narrower molars, sub-rectangular in shape; (2) elongated and relatively narrow molars, approximately sub-squarish but with all sides concave. Ordered. The shape of the upper molars, especially of the M1, is quite distinctive in Erinaceomorpha, and can easily be used to distinguish the various macro-groups of Erinaceidae. In earlier taxa (e.g., *Anatolechinos*, *Changleletes*, *Eogalericius*, *Tupaiodon* and *Zaraalestes*), the molars are well-developed lingually, with the labial margin more elongated than the lingual one: this gives the teeth a roughly rectangular shape, with a more antero-posteriorly extended labial portion and a somewhat narrower lingual one. In other groups of Erinaceidae, M1 achieves different proportions: in Hylomyinae, Erinaceinae and Brachyericinae, for example, the tooth has a squarish outline. In Galericinae *sensu stricto* the tooth is sub-rectangular, being proportionately more elongated antero-posteriorly and narrower labio-lingually. Finally, in *Riddleria* the tooth is squarish and with concave sides. This seems to be similar to the extreme shape achieved by M1 in some *Galerix*, e.g., *G. saratji*, in which the tooth is relatively squarish.

105) Accessory cuspule posterior to hypocone on M1: (0) absent; (1) present. Ordered. The presence of an additional cuspule is a typical character of *Schizogalerix macedonicus* and might be present in *G. uenayae*.

106) Labial cingulum (=ectocingulum in Lopatin, 2006; Villier et al., 2013) on M1: (0) present, continuous; (1) present, discontinuous; (2) present, discontinuous due to labial displacement of mesostyle; (3) present, vestigial; (4) absent. Unordered. Usually, in Galericinae *sensu lato*, the labial cingulum is a continuous, variously extended crest. However, in most advanced species of *Deinogalerix* (*D. brevirostris*, *D. koenigswaldi* and *D. minor*) the labial cingulum is discontinuous, due to the labial displacement of the mesostyle; sometimes, there is no trace of it on the M1s of *D. minor*. A discontinuous labial cingulum may also be observed on M1s of *Apulogalerix*, where the labial cingulum is always reduced and may even totally lack. On those of *Parasorex ibericus* the labial cingulum may either be continuous or not. In *Schizogalerix* the labial cingulum of M1 is usually discontinuous, but in some derived species it may be either very reduced or lacking.

107) Paraconule on M1: (0) present, with short distal arm direct towards paracone; (1) present, without distal arm; (2) present, crescent-shaped around paracone, with well-developed distal arm; (3) paraconule absent. Unordered. In early Palaeocene Erinaceomorpha and erinaceids, e.g., *Changlelestes*, *Macrocranion*, *Litolestes* and *Oncocherus*, the paraconule is a well-developed cuspule with short, strong distal arm, usually directed towards the paracone. This state of character can still be observed in *Eogalericius*, therefore it is probably primitive for the subfamily; yet, in *Zaraalestes*, as well as in other “Tupaiodontinae”, such as *Tupaiodon* and *Anatolechinos*, the paraconule is already reduced to a bulge with no distal arm. The reduction of the paraconule is common in Galericinae *sensu stricto*; the paraconules on the M1s often have no distal arm. Only the M1s of some specimens of *Schizogalerix macedonicus* and of *S. zapfei* have the paraconule with crescent-shaped distal arm around the base of the paracone and more developed than those of other Galericinae.

108) Protocone-hypocone-metaconule connections on M1 (from Gould, 2001; van den Hoek Ostende, 2001d; Borrani et al., 2018, modified): (0) protocone connected only with metaconule; (1) triple connection, higher crest between protocone and metaconule; (2) protocone connected only with hypocone; (3) triple connection, crests of approximately same height; (4) triple connection, higher crest between protocone and hypocone. Unordered. In earlier Erinaceomorpha and erinaceids, such as *Changlelestes*, *Litocherus, Litolestes, Macrocranion*, *Oncocherus* and *Scenopagus* (except *Silvacola acares,* which developed an anterior arm of the hypocone connected with the postprotocrista; Eberle et al., 2014) the postprotocrista is not connected with the hypocone, which is separated from the trigon and often crest-like. We find the postprotocrista connected with the hypocone on the M1s of *Eogalericius* as well as on those of some specimens of *Zaraalestes* and *G. aurelianensis* (Ziegler, 1990). The development of a low prehypocrista, connecting the hypocone with the postprotocrista, can be observed in *Tetracus,* in some specimens of *Zaraalestes* and in many species of *Galerix* and *Riddleria.* Doukas (1986) states that on M1s of *G. symeonidisi* the protocone is connected only with the hypocone. In contrast, Ziegler and Fahlbush (1986) report the presence of a triple connection; based on specimen BSP 1959 XXVII 40 (Ziegler and Fahlbush, 1986: tab.1, fig. 34), this connection seems higher than the one between protocone and hypocone. The protocone is connected only with the hypocone in *Apulogalerix*, *Galerix iliensis*, *Parasorex* (except *P. depereti*, which at times shows state 1; Masini et al., 2019), *Schizogalerix* and some species of *Deinogalerix* (*D. freudenthali*, *D. koenigswaldi* and *D. masinii*).

109) Centrocrista on M1 (from van den Hoek Ostende, 2001d; Borrani et al., 2018, modified): (0) centrocrista present, continuous and roughly parallel to labial margin, no mesostyle; (1) centrocrista present, divided and roughly parallel to labial margin of tooth; (2) centrocrista present, continuous and winding, without distinct mesostyle; (3) centrocrista

present, sinuous and partially divided, without mesostyle; (4) centrocrista present and divided, without mesostyle; (5) centrocrista absent, with single mesostyle; (6) centrocrista present, sinuous and divided, with mesostyle on posterior arm of paracone; (7) centrocrista present, sinuous and divided, with mesostyle on anterior arm of metacone; (8) centrocrista present only distally, with mesostyle on posterior arm of paracone; (9) centrocrista absent, with double mesostyle. Unordered. A simple centrocrista, with non-split mesostyle, is characteristic of the M1s of earlier erinaceids, such as *Changlelestes, Litocherus, Litolestes* and *Oncocherus,* as well of those of *Eogalericius, Zaraalestes, Tetracus* and many species of *Galerix* (with the exception of *G. iliensis,* see below). This pattern, therefore, is the plesiomorphic state of this character for earlier erinaceids as well as for Galericinae. In *G. iliensis*, as well as in *Riddleria*, *Parasorex pristinus*, *P. socialis* and some specimens of *P. ibericus* (which shows high variability in this character, due the presence of partially divided or completely divided centrocristae), the centrocrista is not parallel to the labial margin of the tooth but rather is somewhat S-shaped and sinuous, on account of the fact that the premetacrista is located more lingually than the postparacrista. In *P. depereti,* however, the centrocrista still has a primitive shape, roughly parallel to the labial margin of the tooth but also divided and with no mesostyle. A poorly divided, S-shaped centrocrista (“morphotype 1” in Selänne, 2003), without mesostyle, can also be observed in relatively early species of *Schizogalerix*, such as *S. evae* as well as in some specimens of *S. anatolicus*. In *S. pasalarensis* there is still a continuous, but sinuous crest, which is therefore the primitive state of character for *Schizogalerix.* In fact, the development of a central cuspule (mesostyle) and the progressive splitting of the centrocrista is typical of more derived species of *Schizogalerix*; in some species (*S. intermedius*, *S. moedlingensis*, *S. sarmaticum, S. sinapensis* and *S. zapfei*) the mesostyle itself appears split. In *Deinogalerix,* the general blunt shape of the cusps on M1 causes the loss of the centrocrista; nonetheless, a mesostyle is present also in this genus.

110) Distal arm of hypocone on M1 (from Gould, 2001; Borrani et al., 2018, modified): (0) present, connected with distal cingulum; (1) present, not connected with distal cingulum; (2) absent. Unordered. In the early erinaceomorphs, e.g., *Changlelestes*, *Eochenus*, *Macrocranion*, *Scenopagus* and *Oncocherus*, the distal cingulum progressively raises connecting directly with the hypocone. This pattern, however, cannot be observed in *Eogalericius*, where the hypocone is isolated from the distal cingulum and there is no distal arm; this is probably a derived condition compared to earlier erinaceids and is shared with some more derived Galericinae *sensu stricto*. In *Zaraalestes* there is still a connection with the distal cingulum. In *Tetracus* the hypocone is usually isolated, unlike *Galerix*, where this character is much more variable: in some species the hypocone is isolated (*G. africanus*, *G. rutlandae, G. stehlini* and *G. wesselsae*), in others it may not be connected, or the distal arm is absent (*G. aurelianensis, G. remmerti, G. saratji* and *G. uenayae*); eventually, in others the hypocone may either be connected with the distal cingulum or without distal arm (*G. symeonidisi* and *G. exilis*). The hypocone has no distal arm on M1s of *Parasorex kostakii*, whereas the distal arm is usually present, connected or not with the distal cingulum, in all the other species of *Parasorex*, in *Apulogalerix* and in *Deinogalerix*. Because in *Eogalericius, P. kostakii* and *Tetracus* and at least in some specimens of *Galerix* and *Zaraalestes* there is no arm connecting the disto-lingual cusp with the distal cingulum, this is probably the plesiomorphic state of the character for Galericinae. In *Schizogalerix*, the hypocone is constantly connected with the distal cingulum.

111) M1 lingual roots (from Butler, 1948; Frost et al., 1991; Gould, 1995; He et al., 2012, modified): (0) one root; (1) two roots. Ordered. Unfortunately, the lingual roots on M1 are largely undescribed nor figured, especially those of many Paleogene erinaceomorphs,

therefore the polarity and evolutionary significance of this character are not easily defined. In *Oncocherus* M1s have just a single, ungrooved lingual root (see specimen UALVP 43138 in Scott, 2006, p. 1698, fig 2J). A vertical furrow is present on the root of all the M1s of the many species of Galericinae considered for this study; therefore, it is probably not the result of the fusion of two separate roots, rather a sign of incipient division. The same was observed on the M1s of many different erinaceids, such as the early Hylomyinae *Lantanotherium sansaniense*, *Thaiagymnura* and *Hylomys engesseri*. According to Butler (1948) also members of the Erinaceinae subfamily have a single, vertically-furrowed lingual root; it is already shown both by early members of the subfamily, such as *Scymnerix*, and by Brachyericinae (e.g., *Brachyerix macrotis*, specimen AMNH 21335 in Rich and Rich, 1971: p. 13, fig. 4). In *Echinosorex gymnurus* and in the other present-day Hylomyinae (see Butler, 1948: p. 459, fig. 12a'), as well as in some M1s of *Galerix africanus* the lingual root is divided. Because three-rooted M1s are so diffused among the various subfamilies, M1s with one lingual root are very likely plesiomorphic at least for Galericinae. In fact, in almost all of them (including the early species *Tetracus nanus*) M1s only have a single lingual root, and M1s with double lingual roots evolved independently in present-day Hylomyinae as well as in *G. africanus*.

112) Outline of M2 labial margin: (0) concave, maximum concavity at the height of metacone; (1) concave, maximum concavity between metacone and paracone; (2) weakly concave, maximum concavity at the height of metacone; (3) weakly concave, maximum concavity between metacone and paracone; (4) weakly concave, maximum concavity at the height of paracone; (5) straight. Unordered. The labial margin of the M2 in early Galericinae *sensu lato* species *Eogalericius* is distinctively concave, with maximum concavity at the height of the metacone. Such state of character is not found in other more derived species of Galericinae, but it can also be observed in other early Erinaceomorpha, such as *Eochenus*

sinensis, *Changlelestes dissetiformis*, *Litolestes ignotus*, *Macrocranion vandebroeki* and *Oncocherus krishtalkai*. In all these species, with the exception of *Eochenus sinensis*, but also in the other members of the genus *Macrocranion* and *Silvacola*, the labial margin of M2 can be even more concave. In the early Oligocene species *T. daamsi* the labial margin is very concave, but with a concavity displaced mesially between the paracone and the metacone; on the contrary, in the Late Oligocene Galericinae *sensu lato Zaraalestes*, as well as in some specimens of *Tetracus nanus*, the labial margin of M2 is almost straight. In general, the M2s of more derived species of Galericinae show a weakly concave or straight labial margin, with a few exceptions (e.g., *Parasorex pristinus* and *Riddleria atecensis*) wherein the maximum concavity is usually placed between the paracone and the metacone or, as in some specimens of *Galerix exilis*, at the height of the paracone.

113) Distal arm of metaconule on M2 (from van den Hoek Ostende, 2001d; Borrani et al., 2018, modified): (0) present, extended to postero-labial corner; (1) present and connected with distal cingulum; (2) present and not connected with distal cingulum; (3) absent. Unordered. In M2, the distal arm of the metaconule (when present) is usually shorter than in M1; see character 104 for the discussion of a similar character.

114) Accessory cuspid of M2 hypocone: (0) absent; (1) present. Ordered. An additional cuspid is present behind the hypocone on the M2s of *Schizogalerix macedonicus*.

115) Labial cingulum on M2: (0) present and continuous; (1) present and divided; (2) present only mesially to metacone; (3) vestigial; (4) absent. Unordered. The labial cingulum is well-developed in all early Erinaceomorpha as well as in early Galericinae (*Eogalericius*, *Zaraalestes* and *Tetracus*). In *Galerix* the shape of this structure is still plesiomorphic but in some specimens of *G. exilis* (e.g., specimen MNHN Sa. 13726 in Engesser, 2009: p. 60, fig. 42c), *G. stehlini* (e.g., specimen NMB GA. 5925 in Engesser, 2009: p. 60, fig. 42b) and in *G. uenayae* the labial cingulum is still developed but present only mesially to the metacone;

this also the state of character of *Schizogalerix pasalarensis* and *Parasorex pristinus*. In the other species of *Parasorex* the labial cingulum on M2 may be either continuous or divided; it is also divided in the early *Deinogalerix masinii*, whereas in younger species of the genus it is usually absent. The progressive reduction and disappearance of the labial cingulum can also be observed in *Schizogalerix*. It is absent on the M2s of *Apulogalerix*.

116) Connection between protocone-hypocone-metaconule on M2 (from Gould, 2001; van den Hoek Ostende, 2001d; He et al., 2012; Borrani et al., 2018, modified): (0) protocone only connected with metaconule; (1) triple connection between protocone-hypocone-metaconule, higher crest between protocone and metaconule; (2) protocone only connected with hypocone; (3) triple connection between protocone-hypocone-metaconule, crests of approximately same height; (4) triple connection between protocone-hypocone-metaconule, higher crest between protocone and hypocone. Unordered. See character 109 for a general discussion of the connections between paracone, hypocone and metaconule on upper molars; usually this character is more variable on M2 than M1. Because protocone and metaconule are very rarely connected on the M2s of *Apulogalerix* (Masini and Fanfani, 2013) and of *Parasorex socialis* (one specimens out of 72 from Petersbuch 48; Ziegler, 2006), both species are coded as 2.

117) Centrocrista on M2 (from van den Hoek Ostende, 2001; Borrani et al., 2018, modified): (0) centrocrista present, continuous and approximately parallel to labial margin, without mesostyle; (1) centrocrista present, divided and approximately parallel to labial margin of tooth; (2) centrocrista present, continuous and sinuous, without distinct mesostyle; (3) centrocrista present, sinuous and partially divided, without mesostyle; (4) centrocrista present, sinuous and divided, without mesostyle; (5) centrocrista absent, with single mesostyle; (6) centrocrista absent, with mesostyle partially divided; (7) centrocrista present, sinuous and divided, with mesostyle on posterior arm of paracone; (8) centrocrista present,

sinuous and divided, with mesostyle on anterior arm of metacone; (9) centrocrista only present distally, with mesostyle on posterior arm of paracone; (10) centrocrista absent, with double mesostyle. Unordered. See character 110 for a general discussion; state 7 was added to better accommodate specimens of undescribed species of *Schizogalerix*, i.e., *Schizogalerix* aff. *anatolica* from Sofça (Engesser, 1980).

118) Distal arm of hypocone on M2 (from Gould, 2001; Borrani et al., 2018, modified): (0) present, connected with distal cingulum; (1) present, not connected with distal cingulum; (2) absent. Unordered. See character 111 for a general discussion on a similar character. Differences exist in the distribution of the state of characters (for example, on the M2s of *Zaraalestes* there is always a connection between hypocone and distal cingulum, in contrast to M1).

119) Paraconule on M2 and extension of its distal arm: (0) present, with distal arm direct labially toward base of paracone (Masini and Fanfani, 2013); (1) present, without distal arm; (2) present, with crescent-shaped distal arm bent around base of paracone; (3) paraconule absent. Unordered. Usually, the paraconule is present on the M2s of all Galericinae except some *Galerix* specimens belonging to *G. africanus, G. aurelianensis, G. exilis, G. rutlandae and G. stehlini*. Usually, this cuspule grows smaller through evolution of Galericinae. In the early Galericinae *sensu lato Eogalericius*, as well as in the early Galericinae of the genus *Tetracus*, the paraconule is well-developed and its distal arm is very short and directed against the base of the paracone. In *Zaraalestes minutus* the paraconule is small and has no distal arm. Several early Erinaceomorpha genera, such as *Changlelestes*, *Eocheus*, *Litocherus*, *Litolestes*, *Macrocranion*, *Oncocherus* and *Scenopagus*, have a well-developed paraconule and an elongated distal arm of the paraconule (except *Silvacola*, which shows a conical paraconule without distal crest) either directed labially toward the base of the paracone or bent around the paracone, like in *M. junnei*. The plesiomorphic state of this

character is possibly that of *Eogalericius* (and *Tetracus*) and not that shown by *Zaraalestes*. Although the distal arm of the paraconule is commonly lost in Galericinae, perhaps because of a general reduction or simplification of the paraconule, in more advanced members of the genus *Schizogalerix* the paraconule is well-developed and distinctly crescent-shaped.

120) M3 (from Borrani et al., 2018, modified): (0) very extended lingually; (1) relatively narrower lingually, not mesio-distally compressed; (2) relatively narrower lingually, not too mesio-distally compressed; (3) relatively narrower lingually, very mesio-distally compressed. Ordered. Judging from the alveoli, in *Eogalericius* this tooth has a triangular outline with well-developed lingual lobe, reminiscent of that of more ancient Erinaceomorpha (e.g., *Macrocranion*, *Changlelestes*). In contrast, Galericinae generally have a third upper molar with small lingual lobe. In *Schizogalerix*, this tooth is compressed mesio-distally, and it is particularly so in *S. sarmaticum.*

121) M3 parastyle: (0) poorly-developed; (1) well-developed; (2) poorly-developed, relatively shorter, determining a squarish outline of the mesio-labial corner of the crown. Unordered. In general, the parastyle on M3 is poorly-developed; however, in *Parasorex* and *Schizogalerix* it is prominent antero-labially, and in some species of *Deinogalerix* (i.e., *Deinogalerix brevirostris, D. intermedius, D. koenigswaldi* and *D. minor*) it is very short, giving a distinctive squarish shape to the mesio-labial corner of the crowns.

122) Connection between M3 parastyle and paracone: (0) parastyle connected with paracone; (1) parastyle not connected with paracone. Unordered. The parastyle is usually connected with the paracone by a crest; however, in *Zaraalestes,* as well as in some specimens of *Parasorex depereti (*e.g, specimen MSF 3020 in Masini et al., 2019: p. 452, pl. pl. 2, fig. 26a) and *P. kostakii* (e.g., specimen KRD 3/12 in Doukas and van den Hoek Ostende, 2006: p. 125, pl. 1, fig. 9) the parastyle is not connected.

123) M3 distal cingulum: (0) absent; (1) present, short; (2) present, elongated. Unordered. A weak distal cingulum, limited to the basis of the protocone (Ziegler et al., 2007), is present in *Zaraalestes*. In *Apulogalerix*, the posterior cingulum is very short or even absent. In the genus *Deinogalerix*, the distal cingulum is usually short or very short; however, in F15-037 specimen of *D. freudenthali*, as well as in *D. brevirostris*, it is absent. *Galerix africanus* seems to have a very short distal cingulum (Butler, 1984: p. 141, fig. 9A); in *G. aurelianensis* and *G. remmerti* this crest is sometimes better developed. In *G. exilis* the distal cingulum is very variable: it may be absent (e.g., Steinberg 1970 XVIII 769 in Ziegler, 1983: p. 31, fig. 18a), poorly-developed (e.g., Goldberg 1966 XXXIV 2048 in Ziegler, 1983: p. 31, fig. 20a) or even elongated along most of the disto-lingual margin of the tooth (e.g., Goldberg 1966 XXXIV 2046 in Ziegler, 1983: p. 31, fig. 19a). A similar variability can also be observed in *G. rutlandae*. In *G. iliensis* the distal cingulum of M3 is well-developed whilst in other species of *Galerix* it is usually porly developed when present(*G. wesselsae G. saratji G. symeonidisi* and *G., uenayae*) or absent at all (*G. stehlini*). In *Riddleria atecensis*, the distal cingulum is short and poorly-developed. In the genus *Parasorex* it is usually absent or poorly-developed, with the exception of *P. socialis*, in which it may be elongated (e.g., MNA 2007-204/2017 in Prieto and Rummel, 2009: p. 107, fig. 4H). *Schizogalerix* have a short distal cingulum on M3, with the exception of *S. anatolicus*, in which it may be elongated. In *Tetracus daamsi* the distal cingulum is strong and well-developed, whilst in *T. nanus* it is variable.

124) Distal arm of M3 protocone: (0) present, connected with metaconule or metacone; (1) present, unconnected. Unordered. The distal arm of the protocone is usually connected with a cusp, which may either be the metaconule or the metacone. In *Deinogalerix* it is separated from the metacone by a notch and in *Schizogalerix moedlingensis* it is not extended enough to reach the metacone.

125) Mesial arm of M3 protocone: (0) present, connected with paraconule or paracone; (1) present, connected with parastyle; (2) present, unconnected. Unordered. Usually, the mesial arm of the protocone ends against or is connected with the paracone or with the paraconule, as occurs in many Galericinae, i.e., *Apulogalerix, Deinogalerix, Riddleria, Parasorex, Tetracus, Zaraalestes* and many *Galerix*. This is probably the plesiomorphic state of the character in erinaceids, because it is present not only in the early Erinaceidae *Litocherus, Litolestes, Oncocherus* and *Tupaiodon*, but also in Sespedectidae (e.g., *Macrocranion*). However, in *G. saratji* the mesial arm of the protocone may be connected with the paracone, with the parastyle or may end unconnected (van den Hoek Ostende, 1992: p. 447). In *G. wesselsae* it may either be connected or not with the paracone, and in *G. symeonidisi* it may either be connected with the paracone or with the parastyle.

126) M3 paraconule: (0) present, without mesial or distal arm; (1) present, distal arm absent, mesial arm present and connected with anterior cingulum; (2) present, distal arm absent, mesial arm present and not connected with anterior cingulum; (3) present, crescent-shaped; (4) absent. Unordered. In *Zaraalestes*, the paraconule is just a bulge on the mesial arm of the protocone. In *Deinogalerix*, the paraconule is strong and has an anterior arm connected with the anterior cingulum or with the parastyle (barely visible in the holotype of *D. koenigswaldi*). The presence and shape of this cuspule is variable in *Galerix*: in *G. africanus* and *G. uenayae* it is absent, in *G. aurelianensis*, *G. remmerti* and *G. symeonidisi* the paraconule is reduced to a small bulge on the mesial cingulum whilst in *G. iliensis* this cuspule presents an anterior arm connected with the mesial cingulum. In *G. exilis* and *G. saratji* the paraconule may either be reduced or totally absent. In *Apulogalerix* the paraconule is absent, in *Riddleria* it is small, similar to that of *G. remmerti*. *Parasorex depereti* and *P. socialis* may either have or not a reduced paraconule; in *P. ibericus* the paraconule is absent, in *P. kostakii* it is present and reduced, without anterior or posterior

arm. *P. pristinus* is the only species of *Parasorex* with an anterior and posterior arm of the paraconule on M3. The same can be found only in some representatives of the genus *Schizogalerix*, such as *S. intermedius*, *S. macedonicus* and *S. moedlingensis*. In *S. anatolicus*, *S. pasalerensis* and *S. sarmaticum* the paraconule of M3 has only the anterior arm. *S. sinapensis* may show a forked paraconule, or have none (Selänne, 2003, p. 77, fig. 3.12.D). Finally, in *Tetracus nanus* the paraconule may be small and without arms, or absent.

127) M3 metacone (from Gould, 1995 [as the metastylar spur]; He et al., 2012, modified): (0) present, tubercle-like; (1) present, crest-like; (2) present, crest-like and extended as metastylar crest. Unordered. Hylomyinae, including *Lantanotherium*, have a metastylar crest on M3, sometimes developed into a hypocone-like cusp (e.g., *Lantanotherium sansaniense*; Engesser, 1979, 2009); a similar crest is a diagnostic character of *Deinogalerix* (see "Discussion"). In *Zaraalestes minutus*, *Galerix* (except some specimens of *G. exilis*, e.g., Sa 11067 in Ziegler, 1983, p. 31, fig. 21, and *G. saratji*, e.g., Ha 1,3414 in van den Hoek Ostende, 1992, p. 463, pl. II, fig. 4), *Riddleria, Schizogalerix* (in unworn teeth) and *Tetracus* the metacone is clearly a tubercle. In *Apulogalerix pusillus* the metacone is crest-like.

128) M3 metaconule (Gould et al., 2001): (0) present; (1) absent. Ordered. The presence of the metaconule on M3 is a primitive character in Erinaceomorpha: in fact, it is present in *Changlelestes*, *Litocherus*, *Litolestes* and *Macrocranion*. This cuspule is also present in *Zaraalestes*, whereas in Galericinae *sensu stricto* it is usually absent, with except in a few specimens of *Galerix exilis* and *Schizogalerix moedlingensis*. In the early species *Tetracus nanus* it is usually present, however Hugueney and Adrover (2003) report the presence of two teeth from Montalban without this feature.

Appendix V – Cladism and fossil record

BASIC PRINCIPLES OF CLADISM

The basic principles of phylogenetic systematics are 1) evolution occurs; 2) there is a single phylogeny of life and it is the result of genealogical descent; 3) characters are inherited, modified or not, in the course of genealogical descent (Wiley, 1975 in Brooks et al., 1984: p.2).

A **character** is a feature that can be observed in both an extant or fossil specimen. The phylogenetic system explicitly refuses the simple concepts of “similarity” or “archetype”. The concept of similarity may be subdivided into various categories (Hennig, 1965; Pratt, 1972), the most important of which is **homoplasy**. “Homoplasy is similarity that is the result not of simple ancestry, but of either reversal to an ancestral trait in a lineage or of independent evolution” (Wake et al., 2011: p. 1032); it is the opposite of **homology** (Wake et al., 2011). There are essentially three different kinds of homoplasy: **parallelism** (in which two similar characters are developed from the same ancestral, or plesiomorphic, trait), **convergence** (in which two similar characters are developed from two different ancestral features) or **reversal** (in which a derived, or apomorphic, trait reverses to a more plesiomorphic, ancestral trait). Homoplasy may emerge from adaptative evolution, when similar characters serve similar functions; homoplasic characters may also evolve for the lack of both adaptative and structural options (Wake, 1991) or may emerge, at least in some cases, from **reticulate speciation** (i.e., origin of a new species by hybridization of two ancestral ones; Mishler and Theriot, 2000). A **homologous** character is a trait shared by an ancestor and all its descendants. “Two structures are called homologous if they represent corresponding parts of organisms which are built according to the same body plan. The existence of corresponding structures in different species is explained by derivation from a common ancestor that had the same structure as the two species compared" (Wagner, 1989). Therefore, two characters are homologous if 1) they are the same or 2) they are two different traits in an ancestor/descendant genealogical relationship (Wiley et al., 1991). Condition 2 may generate three or more homologous characters (Wiley et al., 1991).

Other two important categories of similarity include apomorphy and plesiomorphy. An **apomorphy** is a derived feature, while a **plesiomorphy** is an ancestral one (inter alios Brooks et al., 1984; Crowson, 1970; Hennig, 1965, 1966; Schoch, 1986; Wiley et al., 1991). Because an apomorphy is an evolutionary novelty, it derives from an ancestral character with which it is homologous. By being inherited from a common ancestor, **synapomorphies** (i.e., homologous derived characters shared by two or more species) are key similarities for phylogenetic systematics, and are basic to cladistic classification (Rosen 1978, 1979). On the other hand, **symplesiomorphies** are shared primitive characters; in the phylogenetic systems, symplesiomorphy- or homoplasy-based similarity does not permit to identify groups of organisms with a common ancestor (*inter alios* Hennig, 1965). Synapomorphies and symplesiomorphies are not synonyms, but rather subsets of homology: they "represent different perspectives on the same phenomenon, i.e. correspondence by common origin rooted trees" (Richter, 2017: p. 540). Homology indicates common ancestry, symplesiomorphies and synapomorphies primitive and derived state of homologous characters, respectively (Richter, 2017). The **polarity of character states** (i.e., the process whereby establishing the plesiomorphic or apomorphic state of a character) is assessed by comparison with the relevant **outgroup** (i.e., one or more species that are related to the **ingroup** = group of species that are analyzed, but are not part of it) (Schoch, 1986; Wiley et al., 1991).

The fundamental unit in phylogenetic systematics is the **clade**, i.e., a monophyletic group of organisms. Clades are of two kinds, species and taxa. A clade is a group that shares its last common ancestor and all its descendants (**monophyly**). Monophyletic groups are clusters of species more closely related to each other than to other species and with common ancestry (Wiley et al., 1991).

Other groups, such as the **paraphyletic** (i.e., group of organisms that share the ancestor but that do not include all the descendants) and **polyphyletic** ones (i.e., group of organisms including descendants but that do not share a common ancestor; inter alios Schoch, 1986, Wiley et al., 1991) are explicitly rejected by those who use phylogenetic systematics (Hennig, 1965).

Although non-monophyletic, these groups are nonetheless meant to express specific **evolutionary grades** (i.e., "successive levels of organization defined as stages in the improvement of an organic design for some specified function"; Gould, 1976: p. 117)and are more intuitive than many genuine monophyletic ones; in fact, they are commonly entered in classical systematics. For example, traditional "Reptilia" group should be regarded as an evolutionary grade of early amniotes but non as a clade, because it includes the ancestors (i.e., parareptiles, non-mammalian synapsids and non-avian diapsids) but not all the descendants, excluding mammals and birds; therefore, it is a paraphyletic group. Another notorious paraphyletic group, for example, is "Insectivora" (=Lipotyphla in Butler, 1988) (including Chrisoclorydea, Lipotyphla and Tenrecoidea), which is based on a suite of symplesiomorphic features (e.g., the mobile snout or proboscis; Butler, 1988) shared by all the species of this group (Gunnell et al., 2007). There is no doubt whatsoever that the sheer concept of "insectivore" cannot refer to a true monophyletic group (=clade) of mammals; nonetheless, it is still of common use today, because the term is related to a number of clear and unequivocal, albeit plesiomorphic, characters. For these reasons, although they cannot enter in any formal phylogenetic classification (because they do not express true ancestor-descendant relationships), evolutionary grades can sometimes still be useful for practical purposes (Willner et al., 2014). Only paraphyletic and monophyletic groups should be considered as grades, because they are identified by evolutionary key innovations; for polyphyletic groups, "structural type" seems a more appropriate definition (Willner et al., 2014).

Crown-groups are defined on the basis of present-day living species: by definition, a crown-group includes all the living species of a monophyletic group (clade), their last common ancestor and all the extinct descendants from that ancestor. A **stem-group** only includes species that are more closely related to the crown-group than to other clades (Budd and Jensen, 2000; Budd and Mann, 2020). For example, all modern placentate mammals form the Eutheria crown-group alongside their last common ancestor; hence, *Juramaia*, from the Late Jurassic of China (Luo et al., 2011), cannot be included in it, because the retention of plesiomorphic traits, not shared by any living placental (i.e., unreduced dental formula I 5/4 C 1/1 P 5/5 M 3/3, with the retention of dP3/3 in adult individuals; Averianov and Archibald, 2015). Some authors (e.g., Aubert, 2015) claimed that, by involving extant taxa, the terms crown- and stem-group have purely practical purport. However, the concepts of crown- and stem-group improve our knowledge of morphological evolution through time (Donoughe, 2005). Crown- and stem-groups together made the **total group** (Budd and Mann, 2020). Interestingly, when the crown-group of a clade evolves, the stem-group tends to collapse and went extinct, except in case the total group is hit by a mass extinction event (Budd and Mann, 2020). Because the crown-group is a relative concept, the crown-group as it would be appeared in the past is termed as the **provisional crown group** (Budd and Mann, 2020). Even if as I am aware there is no definition of **sensu stricto** and **sensu lato** formal definitions, they should be considered as equivalents of "**provisional crown group**" and "**provisional stem group**" repectively; in my opinion, they should include only extinct species, for each crown- and stem-group concepts are more difficult to apply.

PROBLEMS OF CLADISM APPLIED TO FOSSIL RECORD

The fossil record should be particularly useful for cladism, essentially because it permits: 1) to recognize the apomorphic and plesiomorphic states of characters; 2) to estimate the age of a clade; 3) to falsify phylogenetic hypotheses. Although defective (see below), the fossil record may help to determine the degree of similarity of character states (Hennig, 1965). Ages may only be determined for monophyletic clades; this is particularly important because the association of fossil species with a specific clade provides not only a minimum age to the group, but also to all the other groups related to it (Hennig, 1965; Schoch, 1986). Finally, the fossil record is the best, and sometimes the only, option to falsify a phylogenetic hypothesis of polarity of characters (Nelson and Platnick, 1981It should anyhow be noted that the use of the fossil record in cladistic analysis is fraught with difficulties, in relation to the size of the samples that are studied, the number and quality of the characters, the amount of genetic and morphologic characters that are involved and whether, or not, dental characters are considered.

a) **Sample size of specimens**. The problem of the amount of specimens is often underestimated or totally overlooked, and yet it is often crucial and difficult to solve. Many extinct species are only known from a single or just a few often-incomplete specimens; micromammals are largely known only from isolated teeth. The variability of many characters of very underrepresented species can be very much underestimated. For example, Ziegler (1983) reports that 17 out of 100 M2s of *Galerix exilis* from Steinberg have the protocone only connected with the hypocone and not also with the metaconule to form the usual "triple connection" reported by Borrani et al. (2018). In particularly small samples, the variability could be lost to record: for example, in a sample (n) of 10 M2s this rare morphotype could be absent in about 14.05% of cases (i.e., P(E)= ((83/100) x (82/99) x … x (74/91)); if n=5, the character state would be lost in 38.56% of cases. Ziegler (1983) also reports that in only 27 out of 100 M2s of *G. exilis* from Goldberg the protocone is more strongly connected with metaconule than it is with the hypocone. This uncommon feature, which is however typical in earlier species of *Galerix*, has 3.59% probability to be missed in a sample of n=10; the probability rises to the 19.95% with n=5. It is not so improbable that the characters of species very imperfectly represented may be pathological or abnormal, as are, for examples, small conules or cingulids usually not observed in other species. Ziegler

(2005), for example, reports the presence of a single, abnormal M2 out of 72 other ones of *Parasorex socialis* from Petersbuch 10 in which the protocone is connected with both hypocone and metaconule. Assuming that this character state occurs in 1 specimen out of 72 M2s of *P. socialis* and is not rarer, in 10 M2s the probability that at least one shows this character is 13.89% and in 5 it is 6.94%. Very rare, trivial features may sometimes be considered meaningful character states and conversely, rare, uncommon morphotypes may be misleadingly thought not to have phylogenetic significance. There is also the possibility that a widely represented character may not be phylogenetically significant, but aimply an ontogenetic, sexual or pathological feature. Dental characters are especially susceptible to wear, and can be change or even be totally obliterated (see Gould, 2001 and below). This shows the relevance of sample size in assessing the phylogenetic significance of morphological characters, especially dealing with fossil remains.

b) **Number and quality of characters**. Simões et al. (2016) noticed that characters progressively outnumber taxa over time, thereby leading to huge morphological datasets. This parallels the increasing computational power of computers as well as the growing knowledge of clades and the improvements in cladistic methodology. In general, there may not be equivalent attention to the coding of characters, nor to the logical structure of character state; in some cases, the same state of character can be repeated between different characters (Wilkinson, 1995; Hawkins, 2000; Brazeu, 2011; Simões et al. 2016). This causes the introduction of erroneous or repetitive data in the matrix, possibly increasing the risk of biased results. The misleading concept of “cladistic objectivity” can also lead to discard characters and state of characters, confiding that the software algorithms are able to solve this kind of problems: if every statement of homoplasy is a hypothesis that has to be tested (Wiley et al., 1991), also potential homology, or homoplasy, should ideally be recognized and justified while building a matrix. It is worth noting, however, that characters and character states are selected *a priori*, which introduces variable degrees of subjectivity in the cladistic approach. Needless to say that characters and character states should not be subjected to subjective selection by analysts, which may bias the analysis possibly leading to unreliable results. The study, careful description and logical statement for each character, as well as the discrimination between simple similarities and phylogenetic relevant states of character, are equally important factors.

c) **Genetic vs morphological evidence.** Over the last few decades, DNA sequencing and genomic studies grew both in number and in technical sophistication. Many unexplored critical aspects still exist, though, using this source of information alone. They are essentially four: 1) DNA reversals and convergences; 2) role of transposable elements (TE) and horizontal transfer of DNA between species; 3) little or no morphological or molecular support to a node; 4) poor applicability to the fossil record.

    1. DNA reversals and homoplasies. DNA includes only four nucleobases: adenine, cytosine, guanine and thymine. During molecular evolution, a base could possibly revert to a plesiomorphic character state (adenine, for example, replaced by cytosine). As already noticed by Mishler (1994), this implies few “states of characters” for each nucleotide and homoplasies between different genomic sequences that difficult to detect. These kinds of events are much more difficult to detect respect to probably less frequent morphological reversals and they can remain concealed within long genomic sequences. Unrelated species may possibly share similar traits of DNA: this can occur for horizontal transfer of DNA (see below), but similar physiological adaptations can also affect the genotype epigenetically. For example, similar expression patterns in Pitx1 gene can affect the development of pelvic structures both in relatively distant-related fishes (*Gasterosteus aculeatus* and *Pungitius pungitius*) and manatees, the MC1r gene influence the pigmentation by parallel expressions manners in mices, several felids and

lizards, black bears (*Ursus americanus*) and mammoths (*Mammuthus primigenius*), and the lysozymes in langurs (*Presbytis entellus*), cows (*Bos taurus*) and in hoatzin birds (*Opistochomus hoazin*) are similar due to the same dietary needs between this species, despite at least 300 Ma of divergent evolution (Arendt and Reznik, 2008). At the same time, different genes may influence the same trait: in Atlantic Coast populations of *Peromyscus poliotiotus* (the beach mouse) the MC1r determinates the lighter colour of the coat; however, the same character is developed under different genes in the Gulf Coast population (Arendt and Reznik, 2008). In the light of all this, cladistic analysis of genetic characters alone is quite problematic: homoplasies between different DNA sequences are difficult to detect and even harder to justify. In place of considering long genomic sequences, focus should be directed on small, highly-coding portions of nucleic acid, e.g., the subunit S18 of the ribosomal RNA (see for example Redmond et al., 2013 for an experimental application to sponges and von der Heyden et al., 2004 for one on Euglenozoa at species level). These regions tend to evolve less than non-coding portions of the genome, because they are basic to fundamental cellular processes (e.g., protein synthesis), and are therefore rather stable among organisms with variable relationships. Although these genomic regions are less susceptible to reversals and convergencies, as well as to extensive modifications, they are nonetheless exposed to homoplasies; substitution models may also deeply influence the results (Letsch and Kjer, 2011). More classical genetic studies, e.g., karyotype or genome mapping, should be more effective in revealing phylogenetic relationships between organisms, because they are less likely to be involved in homoplasies and reversals, and whenever this occurs, they are more easily detected. Adopting a full-evidence approach, these aspects need to be considered and not excluded *a priori*.

2. Role of transposable elements (TE) and horizontal transfer of DNA between species. The TE are mobile genetic units; *Maverick* transposons are related to DNA viruses (inter alios Feschotte and Pritham, 2007), while others (as the Ty in yeast; Curcio et al., 2007) show similarities with retroviruses. These transposons are shared among all eukaryotic organisms, and are variously amplified between the species, probably under the influence of both extrinsic and intrinsic factors. Transposons have significant bearing on eukaryotic DNA, and are a recurring reservoir of genetic material for the generation of new genes (Feschotte and Pritham, 2007). Therefore, horizontal genetic transfer within a specific macrogroup of organisms is not a remote probability, but may possibly constitute one of the fundamental mechanisms of molecular evolution in eukaryotes (Feschotte and Pritham, 2007). All this may put more than a burden on phylogenies based on molecular evidence, because unrecognized TE in shared portions of their genome may cause distantly related organisms to look more alike and, vice versa, closely related ones to differ to some extent. One of the most notable examples is given by the BovB LINE (Long Intersped Nuclear Element), an about 3.2 Kb long retrotransposon widespread between mammals (especially Ruminantia and Afrotheria, but also in horses, marsupials and monotremes) and squamates (Serpentes, Gekkota and Scincomorpha) but not in Arcosauromorpha (Aves, Crocodylia and Testudines), some lizards (including some Lacertidae, the infraorder Diploglossa and Rhyncocephalia) and other mammals, pointing out to horizontal transfer of DNA between distantly related groups of vertebrates through retroviruses (Kordiš and Gubenšek, 1999; Walsh et al., 2013).
3. Little or no morphological support to a node. This conflicts directly with one of the fundamental principles of cladism, and is also a major problem when the fossil record is involved (see below). Discriminating derived characters (apomorphies), ancestral

characters (plesiomorphies) and non-homologous characters (homoplasies) is crucial to phylogenetic systematics; the distinction helps storing and retrieving a large amount of information for classification purposes (Nelson and Platnick, 1981). However, usually in molecular studies node identifications and synapomorphies on nodes are not clearly specified; what makes things worse, often the morphological information stored at each node is not provided. These kinds of matrices have very little, or no information at all, coming from the fossil record. For example, in the phylogenetic reconstruction of modern mammals proposed by Benton (2015) and based on Asher et al. (2009), Horovitz and Sánchez-Villagra (2003), Novacek et al. (1988) and O'Leary (2013), 5 clades on 24 (including Pegasoferae, i.e., the clade comprising Chiroptera, Perissodactyla, Carnivora and Pholidota) do not have underlying synapomorphies. It should also be noted that in this example the morphological synapomorphies are added *a posteriori*, and they are not recognized by the analysis itself. Morphological (fossil) and genetical data should only be compared using matrices with both genetical and morphological inputs, using an *a priori* approach. Leaving the nature of the synapomorphies unclear is in stark contrast with the basics of cladism, whose primary goal is providing the most complete possible picture of the derived traits inherited from the last common ancestor. Matrices built on molecular data alone have no concern for the fossil record and inevitably rule out clades for which a molecular dataset is still not available. Matrices of this kind often fail to provide suites of well-evident morphological character states.

4. Poor applicability to the fossil records. The fossil record is often incompatible with exclusively genetic matrices. The oldest known DNA belongs to diatoms dated to 1.4 Ma (Kirkpatrck and Walsh, 2014), and the oldest mammalian DNA is that of a mammoth dated to 1.2-1.1 Ma (van der Valk et al., 2021). Therefore, genetic data are

available in the best case for only 4x10^{-4}% of the whole number of organisms that lived on Earth (or to 7x10^{-4}% of eukaryotes). Most species, even those that went extinct in Quaternary, will likely never provide suitable amounts of genetic material. Therefore, it is much difficult to obtain a sufficient sample of genomic data for extinct species (Mishler, 1994). Hence, most fossil species will constantly be excluded from molecular studies, except those capable to yield more complex and durable molecules (e.g., the enamel proteome of at least Early Pleistocene specimens; Wadsworth and Buckley, 2014; Capellini et al., 2019; Welker et al., 2019, 2020).

d) **Dental characters**. Gould (2001) claimed that dental characters can be biased by ontogenetical, sexual, pathological or even ontogenetic or concerted evolution (i.e., “the non[-]independent evolution of repetitive DNA sequences resulting in a sequence similarity of repeating units that is greater within than among species”; Elder and Turner, 1995). Because many species of small mammals (including many insectivores) are only known from scanty dental remains, there is a high probability that their phylogeny is biased. This serious problem is difficult to solve without large amounts of remains (see point “a” above). Gould (2001) however acknowledged that there are no alternatives but to use the available material - “a poor estimate of phylogenetic relationships may be preferable to no estimate of relationships at all” (Gould, 2001: p. 21).

Appendix IV – Character distribution between Tupaiodontinae and other Paleogene Erinaceomorpha

	Tupaidontinae						Sespedectidae	
Character	*Anatolechinos huadianensis*	*Anatolechinos neimongolensis*	*Ictopidium lechei*	*Tupaiodon morrisi*	*Zaraalestes minutus*	*Zaraalestes russelli*	*Macrocranion*	*Scenopagus*
Mental foramen	Under the anterior root of p3, with a groove directed antero-dorsally	Under the anterior root of p3, not located in a depressed area or with an antero-dorsal groove	Under the posterior root of p3; located in a depressed area or with an antero-	NA	Under the p3 roots or the posterior root of p3; not located in a depressed area or with an antero-dorsal	Under p3-4, in a depression on the lateral side of the mandible	Three mental foramina, one under p1, one between p2 and p3 and the last one under p4 or between p4/m1; or	Two mental foramina, one under p2 and one under p3 or the anterior root of
Shape of the upper molars	NA	M1 short and wide, approximately rectangular	NA	Short and wide molars, approximately rectangular	Short and wide molars, approximately rectangular	Short and wide molars, approximately rectangular	Short and wide molars, approximately rectangular	Short and wide molars, approximately rectangular
Hypocones on M1-2	NA	Low, connected to the distal cingulum, connected to the postprotocrista by a low crest	NA	Low, connected to the distal cingulum, not connected to the postprotocrista	Low, connected or not to the distal cingulum, connected or not to the postprotocrista	Low, connected to the distal cingulum, connected to the postprotocrista on M1 by a low crest but not on	Low, connected to the distal cingulum, connected or not to the postprotocrista by a low crest	Low, connected to the distal cingulum, not connected to the postprotocrista
c size	Small	Small	Small	NA	Small	Small	Small	NA
Relative size of p1-2 series compared to p3-4	Reduced	NA	Reduced	NA	Very reduced, due the absent or very reduced p1	Very reduced, due to the absent or very reduced p1	Not reduced, large	NA
p1	p1 present, one-rooted, similar in size to p2, smaller than c (=small p1)	NA	p1 present, one-rooted	NA	p1 present or absent, one-rooted	Absent	p1 present, one-rooted, larger than p2, larger than c	p1 present, one-rooted
p2	One-rooted, smaller than p3	One-rooted, smaller than p3	One-rooted, smaller than p3	NA	One-rooted, smaller than p3	One-rooted, smaller than p3	One-rooted, larger than p3	One-rooted
p3	Double-rooted	Double-rooted; without metaconid but with paraconid; short talonid, with one cuspulid	Double-rooted; without metaconid but with paraconid; short talonid	NA	Double-rooted,; without metaconid but with paraconid; short talonid, sometimes with one	Double-rooted	Single-rooted; without paracondi or metaconid; very short talonid without cuspulid	Double-rooted; without metaconid but with paracondi; very short talonid
Shape and height of the main cusps on p3-4	Relatively sharp and high	Relatively blunt and low	Relatively sharp and high	NA	Relatively sharp and high	Relatively sharp and high	Relatively low and blunt cusps on p3, higher and sharper ones on p4	Relatively sharp and high
m1-3 cristid obliqua	Ends under the protoconid	Ends under the protoconid	Ends under the protoconid	NA	Ends under the protoconid	Ends under the protoconid	Ends between the metaconid and the protoconid	Ends between the metaconid and the protoconid
Presence of m1-2 hypoconulid	Absent	Absent	Absent	Absent	Absent	Absent	Present	Present
Development of the m1-2 distal cingulid	Wide, not connected to the postcristid, descends to the base of the hypoconid	Wide, not connected to the postcristid, descends to the base of the hypoconid	Wide, not connected to the postcristid, descends to the base of the	NA	Wide, connected to the postcristid on m1 but not on m2, descends to the base of the hypoconid	Wide, connected to the postcristid on m1 but not on m2, descends to the base of the hypoconid	Absent	Absent
m1 paralophid (=development of m1 trigonid)	Short paralophid, slightly oblique	Short paralophid, slightly oblique	Short paralophid, placed trasversally	NA	Short paralophid, slightly oblique	Short paralophidt, slightly oblique	Short paralophid, placed trasversally	Short paralophid, placed trasversally
Height of the m1 paraconid	Low	High	High	NA	High	High	Low	Low
m3 hypoconulid	NA	Poorly developed, located near the entoconid	?	Present, poorly developed (?)	Well-developed, placed mesio-lingually	Well-developed, placed mesio-lingually	Well-developed, placed mesially or mesio-lingually	Well-developed, placed mesially

	Other Paleocene-Eocene basal Erinaceidae*											
Character	*Cedrocherus*	*Changlelestes dissetiformis*	*Eochenus sinensis*	*Eogalericius butleri*	*Entomolestes*	*Litocherus*	*Litolestes*	*Microgalericulus esuriens*	*Oncocherus krishtalkai*	*Oligochenus grandis*	*Protogalericius averianovi*	*Silvacola acares*
Mental foramen	One mental foramen under p3, not located in a depressed area or with an antero-dorsal groove	NA	One mental foramen, under p2 or p3, not located in a depressed area or with an antero-dorsal groove	Two mental foramen, under p2 and p3; rarely, three mental foramina (one under p3 and two under p2) or two small foramina forming a larger one under p2/p3	One mental foramen, under p3, the anterior root of p3 or p2, located in a depressed area	Two mental foramina, one under the anterior root of p2 and one under the posterior root of p3	NA	Under the anterior root of p3; not located in a depressed area or with an antero-dorsal groove	Two mental foramina, one under the anterior root of p2 and one under the posterior root of p3; rarely with the latter divided in two smaller foramina.	One mental foramen under p4; with an antero-dorsal groove	NA	NA
Shape of the upper molars	NA	Short and wide molars, approximately rectangular	Short and wide molars, approximately rectangular	Short and wide molars, approximately rectangular	NA	Short and wide molars, approximately rectangular	Short and wide molars, approximately rectangular	NA	Short and wide molars, approximately rectangular	NA	NA	Short and wide molars, approximately rectangular
Hypocones on M1-2	NA	Low, incipient, connected to the distal cingulum, not connected to the postprotocrista	Low, connected to the distal cingulum and to the postprotocrista	Low, not connected to the distal cingulum or to the postprotocrista	NA	Low, sometimes very reduced, connected to the distal cingulum, not connected to the postprotocrista	Low, connected to the distal cingulum, not connected to the postprotocrista	NA	Low, sometimes very reduced, connected to the distal cingulum, not connected to the postprotocrista	NA	NA	Low, connected to the distal cingulum and to the postprotocrista by a low crest
c size	NA	Small	Large	Small	Small	NA	Small	NA	Small	Small	NA	NA
Relative size of p1-2 series compared to p3-4	NA	Not reduced	Not reduced	Not reduced	Not reduced, large	Not reduced, large	Not reduced	Not reduced	Not reduced	Extremely reduced, due the very small p2 and absent p1	NA	NA
p1	p1 present, one rooted, similar in size to p2 (?)	p1 present, one-rooted, similar in size to p2, smaller than c (=small p1)	p1 present, one-rooted, smaller than p2, much smaller than c (=small p1)*	p1 present, one-rooted, smaller than p1, smaller than p2 (=small p1)	p1 present, one-rooted, larger than p2, smaller than c	p1 present, one-rooted, smaller than c, smaller than p1 (= small p1)	p1 present, one-rooted, smaller than c, smaller than p2 (=small p1)	p1 present, one-rooted, smaller than p2	p1 present, one-rooted, smaller than p2	Absent	NA	NA
p2	One-rooted, smaller than p3 (?)	One-rooted, smaller than p3	Two-rooted, smaller than p3	Two-rooted, smaller than p3	One-rooted, possibly larger than p3	Two-rooted, smaller than p3	Two-rooted, smaller than p3	Two-rooted, smaller than p3	Two-rooted, smalelr than p3	One-rooted, much smaller than p3	NA	NA
p3	Double-rooted; without metaconid or paraconid, with short talonid without cuspulid	Double-rooted<, without metaconid but with paraconid; short talonid without cuspulid	Double-rooted; without metaconid but with paraconid; short talonid without cuspulid	Double-rooted; without metaconid but with paraconid; short talonid without cuspulid	Double-rooted; without metaconid but with paraconid; short talonid without cuspulid	Double-rooted; without metaconid but with paraconid; short talonid with a cuspulid	Double-rooted; without metaconid but with paraconid; short talonid without distal cuspulid	Double-rooted; without metaconid but with paraconid; short talonid with a distal cuspulid	Double-rooted; without metaconid but with paraconid; short talonid with one or two cuspulid	Two-rooted	NA	NA
Shape and height of the main cusps on p3-4	Relatively blunt and low	Relatively sharp and high	Relatively sharp and high	Relatively sharp and high	Relatively sharp and high	Relatively sharp and high	Relatively sharp and high	Relatively sharp and high	Relatively blunt but high	Relatively blunt and high	Relatively sharp and high	NA
m1-3 cristid obliqua	Ends under the protoconid	Ends under the metaconid	Ends under the protoconid	Ends under the protoconid	Ends between the metaconid and the protoconid	Ends between the metaconid and the protoconid	Ends between the metaconid and the protoconid	Ends under the protoconid	Ends between the metaconid and the protoconid	Ends under the protoconid	NA	NA
Presence of m1-2 hypoconulid	Present	Present	Hypoconulid absent on m1, can be present on m2	Absent	Present	Present	Present	Absent	Present	Absent on m1	NA	NA
Development of the m1-2 distal cingulid	Absent	Absent (?)	Connected to the postcristid; descends under the hypoconid on m2	Wide, connected to the postcristid; descends under the hypoconid on m1	Absent on m1, narrow on m2 (*E. grangeri*); narrow on m1, absent on m2 (*E. westgatei*); not connected to the postcristid. Descend under the hypocone	Absent	Absent	Moderately developed on m1 but weak on m2, connected to the postcristid on m2 but not on m1, descends under the hypoconid.	Absent	Moderatly developed on m1, connected to the postcristid, descends under the hypoconid	NA	NA
m1 paralophid (=development of m1 trigonid)	Short paralophid, placed trasversally	Short paralophid, placed trasversally	Short paralophid, slightly oblique	Short paralophid, slightly oblique	Short paralophid, placed trasversally to slightly oblique	Short paralophid, placed trasversally	Short paralophid, placed trasversally	Short paralophid, slightly oblique	Short paralophid, placed trasversally	Short paralophid, placed trasversally	Short paralophid, placed trasversally	NA
Height of the m1 paraconid	High	High	Low	High	Low	Low	Low	High	Low	High	Very high	NA
m3 hypoconulid	Well-developed, placed mesio-lingually	Well-developed, placed mesially	Well-developed, placed near the entoconid or mesially	Poorly developed, protuding posteriorly or mesio-lingually and fused or not with the entoconid	Poorly developed, located near the entoconid	Well-developed, located near the entoconid	Well-developed, located mesio-lingually	NA	Poorly-developed, near the entoconid	NA	NA	NA

← Table 9 – Character distribution between Tupaidoontinae, Sespedectidae and other Paleogene erinaceids. *Basal Erinaceids are defined as all those Palaeogenic Erinaceids that do not belong to the subfamilies Erinaceinae, Brachyericinae, Galericinae and Hylomynae, including the Middle Eocene "Galericini" from Mongolia (see Lopatin, 2006).

Appendix VII – List of Paleogene Erinaceomorpha dental measurements

Species	**c**	**p1**	**p2**	**p3**	**p4**	**m1**	**m2**	**m3**	**References**
Anatolechinos huadianensis					1,64	1,84			Wang and Li (1990)
Anatalochinos neimongolensis	0,95		1,00	1,18	1,53	1,75	1,51	1,30	Wang (2008)[1]
Ictopidium lechei[2]				1,40	1,70	2,20	1,60	1,50	Zdansky (1930) (revised by Sulimski, 1970)
Zaraalestes minutus (Biozone A)				1,15	1,43	1,88	1,60	1,48	Ziegler et al. (2007)
Zaraalestes russelli[3]					1,49	2,16	1,88	1,60	Storch and Dashzeveg (1997)
Macrocranion tupaiodon[4]	1,20	1,87	2,00	1,63	3,00	3,07	3,06	3,08	Tobien (1962)
Macrocranion nitens					1,77	1,94	1,96	2,06	Krishtalka (1976)
Scenopagus edensis					2,06	2,23	2,25	2,38	Krishtalka (1976)
Cedrocherus aceratus				1,00	1,40		1,20	1,00	Gunnell (1994)
Cedrocherus ryani						2,00	1,50	1,30	Gingerich (1983)
Changlelestes dissetiformis	0,95	0,80	0,80	0,90	1,39	1,54	1,33	1,16	Tong and Wang (1993)
Eochenus sinensis	1,76	0,80	1,07	1,25	2,17	2,36	2,01	1,89	Wang and Li (1991)
Eogalericius butleri	0,74	0,61	1,00	1,22	1,44	1,85	1,61	1,32	Lopatin (2006)
Entomolestes westgatei					0,92	1,58	1,39	1,08	Murphey and Kelly (2017)
Litocherus notissimus					2,10	2,00	1,60	1,60	Simpson (1936)
Litolestes ignotus					1,67	1,72	1,48	1,37	Krishtalka (1976)
Microgalericulus esuriens		0,40	0,70	1,20	1,45	1,75	1,45	1,00	Lopatin (2006)
Oncocherus krishtalkai			0,94	1,08	1,48	1,41	1,16	1,04	Scott (2006)
Oligochenus grandis[3]	1,40		0,50	2,40	2,90	3,50	2,50	1,70	Lopatin (2005)

← Table 4 - Means of selected Paleogene Erinaceomorpha measurements on lower teeth length. [1]: Means of teeth between p2 and m2 based on dimensional extremes only. [2]: Sulimski (1970) and Storch and Dashzveg (1997) assert that *Ictopidium lechei* does not have p1; however, from Zdansky (1930: tab. 1, fig. 2) it appears to have this tooth. [3] p1 is always absent. [4] Used as standard in ratio diagrams.

Appendix VIII – States of root

The rooted tree has the following state of characters: (0) nasals anterior to the antorbital rim; (1) uncertain extension of the *foramen palatinum magnum*; (2) anterior opening of infraorbital canal dorsal to P3; (3) base of the zygomatic arch from metastyle of M1 to metastyle of M2; (4) weak or well-developed sagittal crest; (5) almost straight or weakly convex exoccipital, external occipital protuberance overhanging or disto-distal to the occipital condyles; (6) well developed antero-medial fossettes of confyles; (7) not extended articular surface of the condyle; (8) high condyle; (9) angular process aligned with the ascending ramus; (10) dorso-medial groove of angular process delimited by sharp crests; (11) relatively strong angular process, (12) poorly arched dorsally; (13) straight ventral margin of *musculus temporalis fossae*, located high compared to *foramina mandibularis*; (14) ascending rami not extending distally; (15) open posterior margin of the mandibles, between angular processes and condyles; (16) uplifted ascending rami; (18) masseter fossae (17) delimited by prominent border; (19) weakly inclined backward ascednding rami; (20) high coronoid process; (21) two mental foramen, one under p2 or p3 and one under p3 or p4 or even fused in a single large foramen under p2-3, or one foramen under p2; (22) low horizontal rami under the molars; (23) aboral extension of the mandibular symphysis under p2; (24) uncertain presence of diastema between I3 and C; (25) C – P2 and c- p4 diastemas absent; (26) uncertain size of p2 compared to p3; (27) p3 approximately between the 75 and 90% of p4; (28) m1 between 120 and 135% the size of p4, and 110 and 125% of m2; (29) P4 smaller than 115% the size of M1; (30) i1 subequal to i2, i3 smaller than i2, or lower incisors decreasing distally; (31) i1-2 not bilobed, with or without distal denticle; (32) i3 present; (33) lower canine rounded and with distal cuspulid; (34) canine approximately as high as p3; (35) one-rooted p1, (36) with distal cuspulid; (37) distal cingulid on p1 absent; (38) p2 with two roots divided, (39) uncertain presence of paraconid and (40) without distal cuspulid; p3 (41) with tubercle-like paraconid, (42) talonid with distal cingulid but without *crista mediana* or cuspulids and (43) without metaconid; (44) paraconid low, relative to protoconid, on p4; metaconid on p4 (46) present and distinct from protoconid but (45) with uncertain height and (47) uncertain location compared to the latter cusp; (48) mesial wall of paraconid on p4 procumbent or fairly straight; (49) reduced p4 talonid; (50) posterior cuspulid on p4 present, but uncertainty located; (51) distal cingulid on p4 simple, without *crista mediana*; (52) paralophid present and continuous on p4; (53) precingulid on p4 present; (54) labial cingulid on p4 absent; (55) uncertain shape of p4 paraconid; (56) talonid on p4 closed lingually by a sharp cristid; (57) crest-like paraconid on m1; (58) hypoconid more or less aligned and opposite to entoconid on m1; (59) labial cingulid on m1 present and continuous with the precingulid; (60) talonid on m1 with postcristid continuous, postcingulid present and continuous with the postcristid; (61) no accessory cuspulid of the hypoconid on m1; (62) postparactistid on m1 absent; (63) talonid larger or as large as the trigonid on m1; (64) paralophid quite short, relatively little oblique on m1; (65) metaconid slightly more emsial than the protoconid on m1; (66) metacristid and (67) postparacristid on m1 absent; (68) m2 trigonid mesio-distally compressed or relatively less compressed, with oblique or more diagonal paralophid; (69) metaconid on m2 located mesially to the protoconid; (70) anterolabial cingulid on m2 present and continuous, extended distally to protoconid; (71) distal margin of talonid on m2 with continuous postcristid, with postcingulid connected to the postcristid; (72) m2 talonid larger than trigonid; (73) hypoconid labial to protoconid on m2; (74) metacristid on m2 absent; (75) crest-like paraconid on m3; (76) entoconid approximately next to hypoconid on m3; (77) distal margin of m3 talonid without postcristid but with distal cingulid; (78) hypoconulid present, poorly-developed, positioned mesio-lingually, protruding posteriorly and fused or not with entoconid present; (79) I2 larger than I3; (80) P1 present, with two roots or absent; uncertain presence of (81) mesial and (82) distal cuspule on P2; (83) P3 protocone tubercle-like and divided from hypocone; (84) protocone connected to the distal cingulum on P3; (85) hypocone on P3 absent, (87) without distal cuspule;

(88) tubercle-like P3 parastyle; (89) no disto-labial cuspule on P4; (90) labial cingulum on P4 present and extended or absent; (91) undivided P4 hypocone; (92) sloping dorso-ventrally collar margin on P4, in mesial view; (93) protocone higher than the hypocone on P4; (94) very protruding P4 parastyle mesially, (95) tubercle-like and undivided; (96) P4 parastyle connected by crests with labial cingulum or mesial arm of protocone and with paracrista; (97) protocone and hypocone not connected on P4; (98) paraconule on P4 absent; (99) poorly elongated P4, with lingually expanded lingual lobe; (100) M1-2 not elongated mesiolabially-distolingually, (101) with wide metacone and with (102) preprotocrista more or less joined to the paraconule, when present; (103) distal arm of the metaconule on M1 present and extended to the disto-labial corner to the tooth or not connected to the distal cingulum; (104) relatively short and wide molars, with more developed labial region than lingual one, approximately rectangular; (105) accessory cuspule distal to hypocone on M1 absent; (106) labial cingulum on M1 present and continuous; (107) paraconule on M1 present, with or without distal arm direct towards the paracone; (108) protocone connected only to the metaconule on M1, or triple connection between protocone, hypocone and metaconule, with higher crest between protocone and metaconule; (109) centrocrista on M1 present, continuous and roughly parallel to labial margin, no mesostyle; (110) distal arm of hypocone on M1 absent; (111) M1 with one lingual root; (112) M2 labial margin straight or concave, with maximum concavity at the height of metacone; (113) distal arm of the metaconule on M1 present and extended to the disto-labial corner to the tooth or not connected to the distal cingulum; (114) accessory cuspid of M2 hypocone absent; (115) labial cingulum on M2 present and continuous; (116) protocone connected only to the metaconule on M1, or triple connection between protocone, hypocone and metaconule, with higher crest between protocone and metaconule; (117) centrocrista on M2 present, continuous and approximately parallel to labial margin, without mesostyle; (118) distal arm of hypocone on M2 absent; (119) paraconule on M2 present, with distal arm direct labially toward base of paracone; (120) M3 very extended or relatively narrower lingually, not mesio-distally compressed; (121)

poorly-developed M3 parastyle; (122) uncertain presence of connection between paracone and parastyle on M3; (123) M3 distal cingulum present, short or elongated; M3 protocone with (124) distal arm, connected with metaconule or metacone and (125) with mesial arm, connected with paraconule or paracone; (126) M3 paraconule present, without mesial or distal arm; (127) M3 metacone present, tubercle-like; (128) uncertain presence of metaconule on M3.