The Fossil Record of Insectivores (Mammalia: Eulipotyphla) in Greece

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1 Introduction

Eulipotyphla is today the third largest mammalian order (after Rodentia and Chiroptera), comprising four extant (Talpidae, Erinaceidae, Soricidae, Solenodontidae) and several extinct families (e.g., Nesophontidae, Amphilemuridae, Dimylidae, Heterosoricidae, Plesiosoricidae). Until the end of the last century, all these families were included in the order Insectivora, which was, however, also included in the Tenrecomorpha (tenrecs and golden moles) now assigned to the order Afrotheria. They are all small (2–1 kg), mostly insectivorous animals, with a long, narrow and mobile snout, and most of them are nocturnal (Macdonald 2009). Today, the Solenodontidae inhabit only the Caribbean Islands of Hispaniola and Cuba, whereas the erinaceids (hedgehogs and moonrats), talpids (moles and desmans), and soricids (shrews) have an almost worldwide geographical distribution (except for Australia and Antarctica). They are often considered as the most primitive living placental mammals and are, thus, morphologically closer than all other living placentals to the common mammal ancestors (Macdonald 2009). In any case, the dentition is generally close to the ancestral tribosphenic condition.

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Insectivore fossils have always been a by-product of large fossil rodent assemblages, and they are collected using the same methodology (sediment collection, wet screen-washing, dry sieving, picking under a stereoscopic microscope). Even though the importance of fossil rodents for biostratigraphy and paleoenvironmental reconstructions has for long been established, the use of the less common insectivores, particularly for paleoecological inferences, was only acknowledged much later. In Greece, the fossil insectivore research has essentially started in the 1970s; since then, 47 late Oligocene–late Pleistocene localities have revealed mainly isolated dental (main diagnostic elements) and a few postcranial elements. Eight species have been described from Greek Neogene localities are still recognized: three Erinaceidae (*Galerix symeonidisi*, *Parasorex kostakii*, *Schizogalerix macedonica*), two Talpidae (*Myxomygale engesseri*, *Desmanella dubia*) and one Heterosoricidae species (*Heterosorex ruemkeae*), and two Soricidae (*Amblycoptus jessiae*, *Deinsdorfia kerkhoffi*). In addition, three more species have disappeared in the synonymy (*Desmanodon meuleni*, *Galerix atticus*, *Dibolia dekkersi*).

2 Historical Overview

The first mention to fossil Eulipotyphla in a Greek locality was given by Thenius (1952), who reported the presence of *Galerix exilis* (assigned to *Schizogalerix moedlingensis* by Doukas et al. 1995) in the classic Pikermi locality. In the 1970s, studies mainly by researchers of the Geological Institute and the University of Utrecht (The Netherlands) communicated the presence of important eulipotyphlan faunas in well-studied localities such as Arnissa, Maritsa 1 and Pikermi-Chomateri (Mayhew 1978; de Bruijn et al. 1970; Rümke 1976). During the next two decades, many new eulipotyphlan faunas became known, mainly through Ph.D. theses in Greek universities (e.g., Doukas 1983; Koliadimou 1996), in Dutch universities (e.g., Rümke 1985), and also in collaborations between Greek and Dutch institutes (e.g., Reumer and Doukas 1985; Doukas et al. 1995). During the past 20 years, postgraduate studies in Greek universities resulted in the revealing of some more faunas (e.g., Sylvestrou 2002, Vasileiadou et al. 2003; Chatzopoulou 2014), and so did the ongoing collaboration of Greek and Dutch institutes (e.g., Doukas and Van den Hoek Ostende 2006; De Bruijn et al. 2012; Van den Hoek Ostende et al. 2015). In 2005, in the frame of an effort to revise the fossil record of the Eurasian Neogene insectivores known until then, Doukas presented a review of the Greek fossil record (Doukas 2005). This review made apparent that important Greek insectivore faunas had been till then only partially studied, some of which are still, after almost 15 years, not visited (e.g., the faunas of the Ptolemais Basin).

3 Phylogenetic Relationships

For over a century, the order Insectivora has been used as a “waste-basket” for extant insectivorous eutherian mammals with unspecialized dentition (Douady et al. 2002:200–2001 for short review on taxonomic concept of “Insectivora”). The monophyly of the order collapsed in the 1980s, when molecular analyses excluded from the order Afrotheria (golden moles and tenrecs), that had been included in Insectivora since the nineteenth century (Nikaido et al. 2003). Since then, Insectivora has been divided into Afrosoricida and Eulipotyphla (erinaceids, talpids, soricids and solenodons). The monophyly of Eulipotyphla has been frequently challenged (see Nikaido et al. 2003 for examples). However, studies based on nuclear genes (Douady et al. 2002), and also based on mitochondrial DNA sequences (Nikaido et al. 2003), support the monophyly of Eulipotyphla. Yet, the phylogenetic relationships within the order are controversial. As Nikaido et al. (2003:277) reported: “McKenna and Bell’s (1997) morphological analysis suggested that moles and hedgehogs are more closely related to each other than either is to shrew, and Butler’s (1988) morphological analysis suggested closer relationship between shrews and moles than to hedgehogs, while Murphy et al.’s (2001a, b) molecular analyses based mainly on nuclear DNA suggested a hedgehog/shrew clade excluding mole as an outgroup.” Douady et al. (2002), using molecular data, indicated a sister–taxon relationship of soricids and erinaceids to the exclusion of talpids. Nikaido et al. (2003) investigated the interfamiliar relationships in eulipotyphlans using mitochondrial protein data; their results indicated that the relationships cannot be resolved. Even though this issue is still a matter of debate, most molecular studies seem to agree on a late Cretaceous origin for Eulipotyphla and that the Solenodontidae split from the other extant eulipotyphlan families soon afterwards, before the end of the period (Springer et al. 2018). For example, Bininda-Emonds et al. (2007) constructed a species-level phylogeny of extant mammals (4510 of the 4554 extant species) and estimated that Eulipotyphla originated 91.8 ± 2.6 Ma, whereas the time of their basal diversification (of Solenodontidae) was determined at 84.2 ± 2.1 Ma, whereas Springer et al. (2018) dated this basal diversification at 78.5–65.4 Ma.

4 Distribution

Fossils of Eulipotyphla have been recovered from 47 Greek localities, distributed in continental (35 localities) and insular Greece (12 localities in Lesbos, Evia, Chios, Crete, Samos, Rhodos, Kalymnos, Naxos); see Fig. 1 and Appendix for detailed information. The oldest one is correlated with the late Oligocene, six are correlated with the early Miocene, three with the middle Miocene, 11 with the late Miocene, three with the Turolian/Ruscinian boundary, eight with the Pliocene, seven with the early Pleistocene, two with the middle Pleistocene, and six with the late Pleistocene. Unfortunately, some of them have only yielded scanty and fragmentary materials,

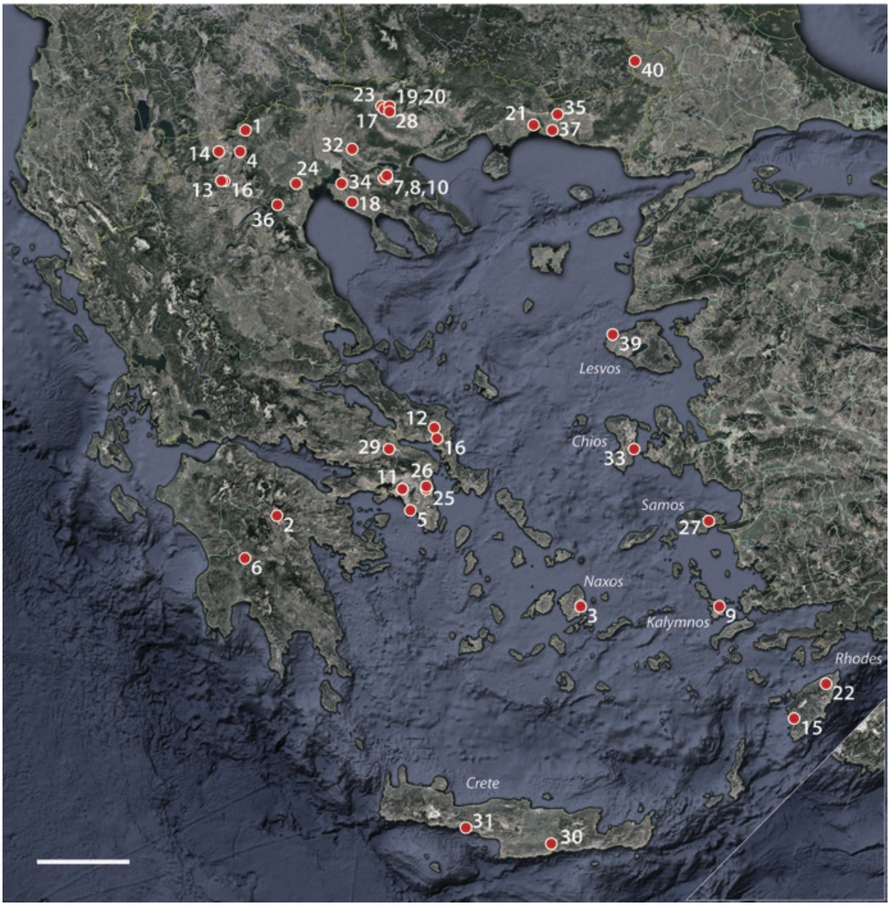

Fig. 1 Map of Greece showing the geographic distribution of the most important localities with insectivore fossils. **1**, Loutra Almopias Cave; **2**, Kitseli pothole; **3**, Naxos; **4**, Arnissa; **5**, Varkiza 2; **6**, Choremi localities; **7**, Apollonia; **8**, Ravin Voulgarakis; **9**, Kalymnos; **10**, Marathoussa; **11**, Tourkovounia localities; **12**, Limni 6; **13**, Ptolemais localities; **14**, Vevi; **15**, Apolakkia; **16**, Kardia; **17**, Spilia localities; **18**, Nea Silata; **19**, Maramena; **20**, Ano Metochi; **21**, Kessani; **22**, Maritsa 1; **23**, Monasteri; **24**, Paliambela-A; **25**, Pikermi; **26**, Chomateri; **27**, Samos-S3; **28**, Lefkon; **29**, Biodrak; **30**, Kastellios K1; **31**, Plakias; **32**, Chryssavgi 1; **33**, Thymiana localities; **34**, Antonios; **35**, Komotini; **36**, Moschopotamos; **37**, Karydia; **38**, Aliveri; **39**, Lapsarna; **40**, Kyprinos. See Appendix for more information. Image exported from Google Earth Pro © 2019, map data from US Dept. of State Geographer, SIO, NOAA, U.S. Navy, NGA, GEBCO, image from Landsat/ Copernicus. Scale bar equals 80 km, North faces upward

inadequate to allow identification even to generic level (e.g., Lapsarna, Thymiana, Monasteri, Choremi), whereas materials from other localities have not been studied adequately yet (e.g., localities in the Ptolemais Basin). Some other localities, however, have offered quite diverse eulipotyphlan faunal lists: the early Miocene localities Aliveri and Karydia have revealed six and eight species, respectively (Doukas

1986; Doukas and Van den Hoek Ostende 2006), the locality Maramena correlated with the Turolian/Ruscinian boundary has revealed eleven species (Doukas et al. 1995), the Pliocene locality Apolakkia and the early Pleistocene localities Marathoussa (North Greece) and Ravin Voulgarakis six species each (Doukas 2005; Koufos et al. 2001; Koliadimou 1996), and the late Pleistocene localities Loutra Almopias Cave LAC and LAC Ia eight and six species, respectively (Chatzopoulou 2014). Nevertheless, these findings are far from enough to present a complete picture of the Neogene and Quaternary eulipotyphlan faunas in Greece and their evolution.

5 Systematic Paleontology

Eulipotyphla Waddell, Okada, and Hasegawa, 1999

Erinaceidae Fischer, 1814

Type Genus *Erinaceus* Linnaeus, 1758.

Remarks Vasileiadou and Zouros (2012) reported the presence of Erinaceidae indet. at the early Miocene locality Lapsarna: they found the metacone area of a right M1, with a size similar to that of *Schizogalerix pasalarensis* and *Schizogalerix anatolica*.

Subfamily Galericinae Pomel, 1848

Type Genus *Galerix* Pomel, 1848.

Remarks The generic assignment of many galericine species in one of the genera *Galerix*, *Schizogalerix*, and *Parasorex*, and their evolutionary relationships are still a matter of debate (Ziegler 2005; Doukas and Van den Hoek Ostende 2006; Prieto et al. 2012). Since the present work does not aim to revise the subfamily, we follow Van den Hoek Ostende (2001), Doukas and Van den Hoek Ostende (2006), Prieto et al. (2010, 2011) and Zijlstra and Flynn (2015) in the galericine taxonomy.

Parasorex von Meyer, 1865

Type Species *Parasorex socialis* von Meyer, 1865.

Other Taxa Included *P. depereti* (Crochet, 1986); *P. ibericus* (Mein and Martín-Suarez, 1993); *P. pristinus* (Ziegler, 2003); *P. kostakii* (Doukas and Van den Hoek Ostende, 2006).

Distribution From the early–late Miocene of Austria, France, Germany, Greece, Hungary, Italy, Moldova, Romania, Spain, Switzerland to the Pliocene of France, Spain.

★*Parasorex kostakii* (Doukas and Van den Hoek Ostende, 2006)

Nomenclatural and Taxonomical History *Galerix* sp. in Doukas (2005) (initial identification); *Galerix kostakii* in Doukas and van den Hoek Ostende (2006) (new species); *Parasorex kostakii* in Prieto et al. (2012) (new combination).

Type Material Left M1, KRD 3/04, Department of Paleontology and Historical Geology, University of Athens (Doukas and van den Hoek Ostende 2006: Pl. 1.5).

Type Locality Karydia, Thrace, Greece, early Miocene (MN4).

Distribution The species has until now only been found in its type locality.

Remarks Doukas and Van den Hoek Ostende (2006) described the Karydia material (one d3, one d4, six p4, eight m1, five m2, one m3, one C, 10 P3, two P4, 10 M1, 17 M2, 10 M3, including the holotype; Fig. 2) as *Galerix kostakii* (in memory of our dear colleague Constantin "Kostaki" Theocharopoulos), even though they mentioned that some of its characters are typical for *Schizogalerix* and *Parasorex*, such as the presence of a hypocone on all P3 and the bi-partitioned posterior cingulum on all M1/2. They also mentioned the absence of the protocone–metaconule connection from around 80% of the M1/2. What led them to the grouping of this species within *Galerix* is mainly the p4 morphology, which lacks a continuous paralophid connecting the tip of the protoconid to the paraconid and bears a small or even no metaconid. However, the (rare) presence of a paralophid on the p4, as well as the absence of a protocone–metaconule connection from the M1, and its rare presence on the M2 (on 3 out of 13) of the species from its type locality led Prieto et al. (2012) to classify the species within the genus *Parasorex*. The above authors explained the occasional presence of a protocone–metaconule connection on the upper molars of the species from Karydia, as well as of their *Parasorex* sp. from Sámsonháza 3 (Hungary), as the result of the relatively narrow shape of the molars of these two primitive *Parasorex* species and preferred to evaluate this character as a less important one for the generic attribution.

Galerix Pomel, 1848

Type Species *Viverra exilis* de Blainville, 1839.

Other Taxa Included *G. stehlini* (Gaillard, 1929); *G. africanus* Butler, 1956; *G. rutlandae* Munthe and West, 1980; *G. symeonidisi* Doukas, 1986; *G. aurelianensis* Ziegler, 1990; *G. saratji* Van den Hoek Ostende, 1992; *G. uenayae* Van den Hoek Ostende, 1992; *G. iliensis* (Kordikova, 2000); *G. remmerti* Van den Hoek Ostende, 2003; *G. wesselsae* Zijlstra and Flynn, 2015.

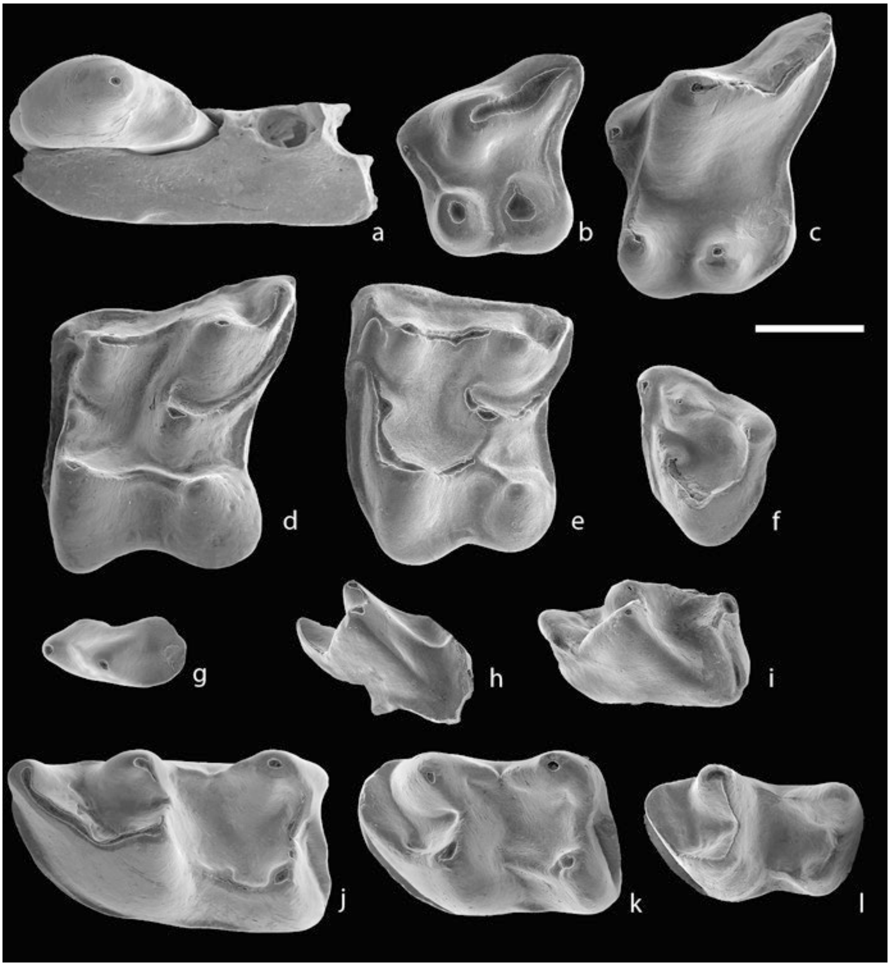

Fig. 2 *Parasorex kostakii* from Karydia (type locality). (**a**) Partial maxilla with C, (**b**) P3, (**c**) P4, (**d**) M1 holotype, (**e**) M2, (**f**) M3, (**g**) d3, (**h**) d4, (**i**) p4, (**j**) m1, (**k**) m2, (**l**) m3. Images CD, personal data. All specimens are figured as left; **f**, **h**, **i**, **k**, **l** are reversed. Scale bar equals 1 mm

Distribution Latest Oligocene of Turkey to the early–middle Miocene of Eurasia (Portugal, Spain, France, Switzerland, Austria, Germany, Czech Republic, Hungary, Moldova, Serbia, Greece, Turkey, Russia, Pakistan).

Remarks Apart from *Galerix symeonidisi* (see below), the only material from Greece attributed to this genus is a single M1 from Komotini, described as *Galerix* sp. by Doukas and van den Hoek Ostende (2006) (mentioned as *Schizogalerix* sp. in Doukas 2005), which is larger and more robust than the M1 of its contemporary galericine *Parasorex kostakii* from Karydia.

★*Galerix symeonidisi* Doukas, 1986

Nomenclatural and Taxonomical History *Galerix symeonidisi* in Doukas 1983 (nomen nudum); *Galerix symeonidisi* in Doukas 1986 (new species).

Type Material Left M2, AL 3036, Department of Paleontology and Historical Geology, University of Athens (Doukas 1986:Pl. 1.6).

Type Locality Aliveri, Evia Island, Greece, early Miocene (MN4).

Distribution Early Miocene (MN4) of Greece (Aliveri); early Miocene (MN4 to the lowermost part of MN5) of Serbia, Germany, Austria, and Spain.

Remarks The materials from Aliveri (Fig. 3) comprise 72 dental elements (including the holotype: one p2, three p3, 14 p4, two m1, nine m2, four m3, seven P3, three P4, four M1, 14 M2, 11 M3). The species was initially described in Doukas (1983; PhD thesis, in Greek). As this publication does not meet the criteria of the ICZN, it constituted nomen nudum and was later made available for the same concept by Doukas (1986). This new *Galerix* species was described on the basis of its small size, the longer p2 than p3, and the presence of two lingual cusps on the P3, of which the posterior side is noticeably emarginated.

Schizogalerix Engesser, 1980

Type Species *Schizogalerix anatolica* Engesser, 1980.

Other Taxa Included *S. zapfei* (Bachmayer and Wilson, 1970); *S. voesendorfensis* (Rabeder, 1973); *S. moedlingensis* (Rabeder, 1973); *S. pasalarensis* Engesser, 1980; *S. sarmaticum* (Lungu, 1981); *S. sinapensis* Sen, 1990; *S. macedonica* Doukas, 1995 in Doukas et al., 1995; *S. duolebulejinensis* Bi et al., 1999; *S. intermedia* Selänne, 2003; *S. evae* De Bruijn et al., 2006.

Distribution Miocene of Eurasia (France, Switzerland, Austria, Germany, Romania, Slovakia, Greece, Turkey, Moldova, Ukraine, Pakistan, Kazakhstan, China).

Remarks Dental elements attributed to *Schizogalerix* sp. have been found in several Miocene–Pliocene localities in Greece. In Antonios, *Schizogalerix* sp. is represented by one d3, three m1, one m2, one m3, two P4, two M1, six M1/2, and seven M3 and shows mixed morphology found in both *S. pasalarensis* and *S. anatolica* (Vasileiadou and Koufos 2005). De Bonis et al. (1997) reported the presence of *Schizogalerix* sp. in Thymiana A and C, but no information on the material has been published. One p2, one p4, and one M3 from Chryssavgi 1 were attributed to cf. *Schizogalerix* sp. by Koliadimou (1996). One M2 and one M3 from Kastellios K1 included in the collections of the Faculty of Geosciences, Utrecht University, the Netherlands, were attributed to *Schizogalerix* sp. by Doukas (2005), but Furió et al. (2014:166) commented that “*The material from this Greek locality fits better the*

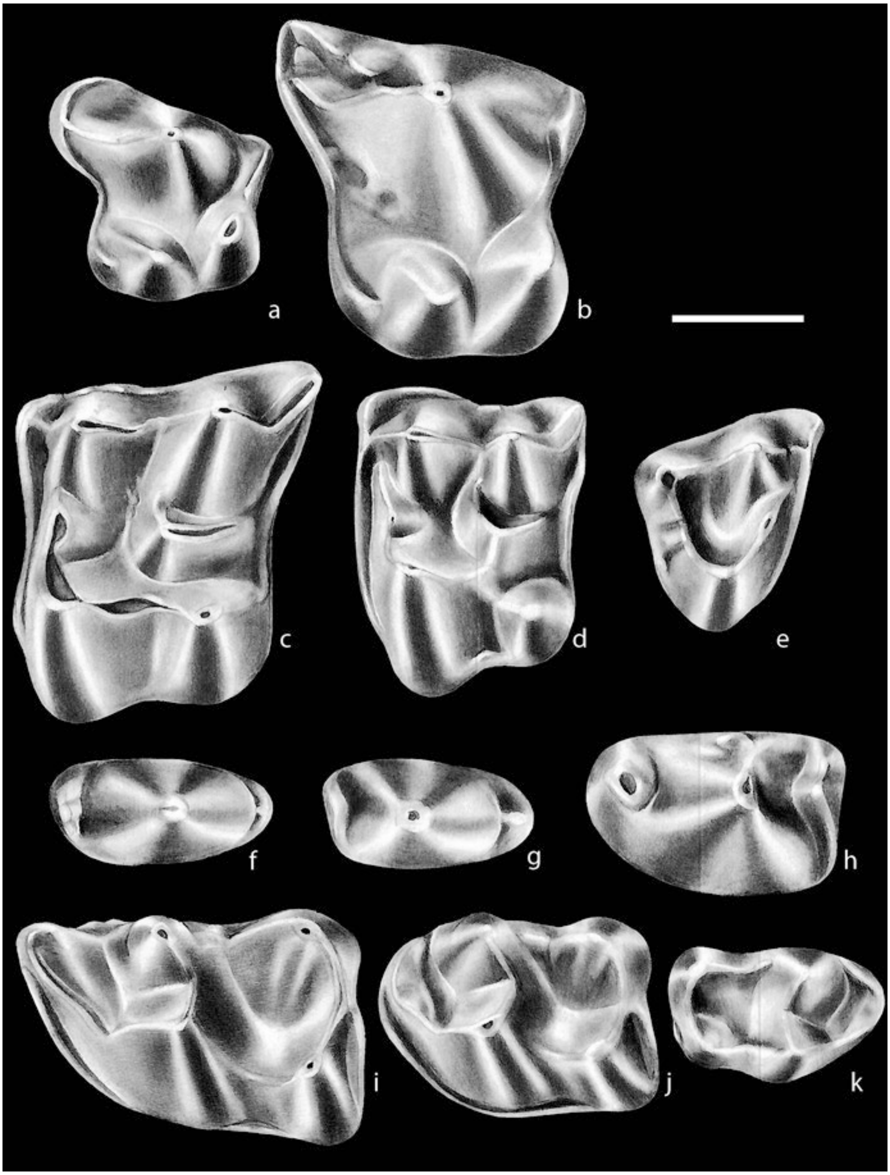

Fig. 3 *Galerix symeonidisi* from Aliveri (type locality). (**a**) P3, (**b**) P4, (**c**) M1, (**d**) M2 holotype, (**e**) M3, (**f**) p2, (**g**) p3, (**h**) p4, (**i**) m1, (**j**) m2, (**k**) m3. Images CD, personal data. All specimens are figured as left; a, b, f, g, k are reversed. Scale bar equals 1 mm

morphology of other Eastern Europe species like S. macedonica *or* S. zapfei/S. attica"). Two p4, one m1, one m2, three m3, one M1, and one M3 (most specimens fragmentary) from Biodrak were initially described as *Galerix* sp. by Rümke (1976), but transferred to *Schizogalerix* sp. by Doukas (2005). Finally, Doukas (1989) mentioned the presence of *Schizogalerix* sp. in Lefkon, but there is no additional information on this material.

★*Schizogalerix macedonica* Doukas, 1995 in Doukas et al. (1995)

Type Material Left M1, MA 3041, Department of Paleontology and Historical Geology, University of Athens (Doukas et al. 1995:Pl. 2.2).

Type Locality Maramena, Strimon basin, N Greece, Turolian/Ruscinian boundary.

Distribution The species has been reported only from Greece, from its type locality and the nearby locality Ano Metochi 2–3.

Remarks Doukas described this new species from Maramena (in Doukas et al. 1995) based on its large size, the clearly divided mesostyles, and the presence of an extra cuspule next to the hypocone on the M1–2, as well as the presence of an extra cuspid at the base of the entoconid on the ml–2 (better developed on the m2 than on the ml). This species is one of the largest and youngest *Schizogalerix* species. Maramena (Fig. 4) and Ano Metochi 2–3 have collectively yielded 40 isolated dental elements (one p3, three p4, three m1, six m2, six P3, two P4, nine M1, eight M2, two M3, including the holotype) (Doukas et al. 1995).

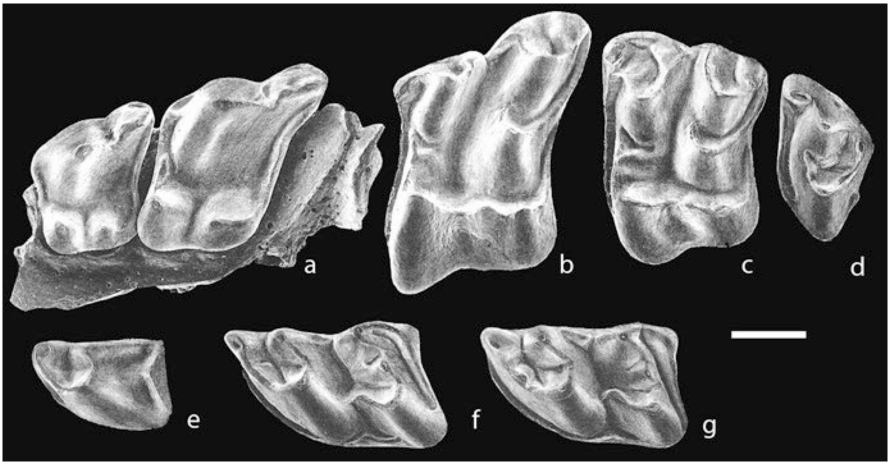

Fig. 4 *Schizogalerix macedonica* from Maramena (type locality). (**a**) Maxillary fragment with P3 and P4, (**b**) M1 holotype, (**c**) M2, (**d**) M3, (**e**) p4, (**f**) ml, (**g**) m2. Images CD, personal data. All specimens are figured as left. Scale bar equals 1 mm

Schizogalerix moedlingensis (Rabeder, 1973)

Nomenclatural and Taxonomical History *Galerix moedlingensis* in Rabeder (1973) (new species); *Schizogalerix moedlingensis* in Engesser (1980) (new combination).

Type Material Left M2, UWPI 1953/10/4, Institut für Paläontologie der Universität Wien (Rabeder 1973:Abb. 3.19).

Type Locality Eichkogel, Austria, late Miocene, early Turolian (MN11).

Distribution Late Miocene of Austria, Greece and possibly Ukraine (*S.* cf. *moedlingensis*).

Remarks The presence of a hypocone on the P3, of a posterior arm joining the metaconule with the posterior cingulum on the M1–2 and of a paralophid and a strong metaconid on the p4 led Engesser (1980) to transfer this species to *Schizogalerix*. The deeply divided mesostyle on the M1–2 is considered as an evolved character that differentiates this species from earlier *Schizogalerix*. It differs from *S. zapfei* on the presence of a hypoconid–entoconid ridge on the lower molars. Other diagnostic characteristics are the long talon on the P4 with median longitudinal ridge and the relatively large M3 with a distinct protoconule (Rabeder 1973). The species has been reported from two Greek localities: Pikermi–Chomateri and Pikermi. The Pikermi–Chomateri material consists of 59 isolated dental elements, some fragmentary (one p2, six p3, five p4, four m1, 14 m2, nine m3, two P3, one P4, seven M1, three M2, seven M3), which, according to Rümke (1976), differ slightly in morphology and size from the type material from Eichkogel. Thenius (1952) described one partial mandible with p2–m2 from the classic locality Pikermi (not to be confused with Pikermi–Chomateri) as *Galerix exilis*. The mandible, also mentioned by Rümke (1976) and Engesser (1980), was recovered from the collections of the Department of Paleontology and Historical Geology (University of Athens) and transferred to *S. moedlingensis* by Doukas et al. (1995:48) due to "*the pattern of the hypoconid–entoconid–posterior cingulum complex*."

Schizogalerix zapfei (Bachmayer and Wilson, 1970)

Nomenclatural and Taxonomical History *Galerix zapfei* in Bachmayer and Wilson (1970) (new species); *Schizogalerix zapfei* in Engesser (1980) (new combination). ★*Galerix atticus* Rümke, 1976, is considered a junior synonym of *S. zapfei*, according to Engesser (1980).

Type Material Right lower jaw with p3–m3, No 1970/1386, Naturhistorisches Museum Wien (Bachmayer and Wilson 1970:Pl. 5. 17–17a).

Type Locality Kohfidisch, S Burgenland, Austria, late Miocene, Turolian (MN11).

Distribution Besides its type locality, this species has also been found in the late Miocene of Greece (Pikermi–Chomateri and S3 in Samos Island) (described as the species *Galerix atticus* Rümke, 1976).

Remarks The mesostyles of *S. zapfei* are slightly more developed than in *Galerix exilis*; there is a single alveolus for the p2, and the posterior cingulum of the m1–2 is continuous to the tip of the entoconid (Bachmayer and Wilson 1970).

★*Galerix atticus* Rümke, 1976

[Junior subjective synonym of *Schizogalerix zapfei* (Bachmayer and Wilson, 1970) according to Engesser (1980)].

Type Material Left M2, PK 606, Department of Palaeontology and Historical Geology, University of Athens (Rümke 1976:PI. 1.9).

Type Locality Quarry of the Pikermi Brick and Tile Factory (Pikermi–Chomateri), lignitic clay with mollusk fragments (Turolian).

Remarks In 1976, Rümke named the new species *Galerix atticus*, based on an assemblage of one p2, one p3, one p4, five m1, four m2, three m3, seven P3, one P4, two M2, one M3 (including the holotype) from the Turolian locality Pikermi–Chomateri. She mentioned that *G. atticus* differs from previously described *Galerix* species (apart from *G. zapfei*) in the isolated position of the hypoconid of the m1–2. Rümke (1976) noticed that the morphology of the talonid of her species and *G. zapfei* is very close, based on the descriptions given by Bachmayer and Wilson (1970). She also noticed the overall similarities of *G. atticus* with *G. zapfei*, with the exception of the p2, which seems to be single-rooted in the Austrian but double-rooted in the Greek species. Later, Bachmayer and Wilson (1980:358–359) noted that the type locality of *G. atticus* had only revealed one p2 with the roots broken off, and the only proof of the presence of two roots was the "*constriction of the crown enamel*." The same authors stated the probable presence of both single-rooted and double-rooted p2 in the type locality of *G. zapfei*, and the possibility that "G. atticus *may eventually prove to be a synonym of* G. zapfei" (Bachmayer and Wilson 1980:360). Engesser (1980) synonymized the two species and transferred *zapfei* to the genus *Schizogalerix*. Black et al. (1980) assigned one m1, one P4, and one M2 from the locality S3 in Samos Island to Rümke's species; these specimens can be thus safely referred to *S. zapfei*.

Lantanotherium Filhol, 1888

Type Species *Erinaceus sansaniense* Lartet, 1851.

Other Taxa Included *L. robustum* Viret, 1940; *L. sanmigueli* de Villalta and Crusafont, 1944; *L. longirostre* Thenius, 1949; *L. piveteaui* Crusafont, de Villalta and Truyols, 1955; *L. sawini* James, 1963; *L. dehmi* James, 1963; *L. lactorensis* Baudelot and Crouzel, 1976; *L. sabinae* Mein and Ginsburg, 2002.

Distribution Miocene of Austria, China, Czech Republic, France, Germany, Greece, Hungary, Poland, Portugal, Serbia, Slovakia, Spain, Switzerland.

Remarks The genus name is often misspelled as *Lanthanotherium*, initially by its author Filhol in 1891 and by many authors since then (e.g., Rabeder 1973; see Furió and Alba 2011 for further examples). Furió and Alba (2011) presented a detailed discussion on the issue and concluded that the original spelling (*Lantanotherium*) is correct, and all other subsequent spellings (*Lanthanotherium*) are unjustified emendations.

Lantanotherium sanmigueli de Villalta and Crusafont, 1944

Nomenclatural and Taxonomical History *Lantanotherium sanmigueli* in de Villalta and Crusafont (1944) (new species); *Lanthanotherium sanmigueli* in Rabeder (1973) (unjustified emendation of the generic name).

Type Material Partial left mandible with m1–2, Institut de Paleontologia Miquel Crusafont de Sabadell, Barcelona (de Villalta and Crusafont 1944:Fig. 10; Pl. II.5).

Type Locality Can Purull, Vallès–Penedès Basin, Spain, late Miocene (MN10).

Distribution Late Miocene (lower Vallesian, MN9) of southern Greece (Plakias); late Miocene (Vallesian–Turolian, MN9–11) of Spain, France, Austria, Germany, Czech Republic, Hungary, China.

Remarks The species has been assigned to *Lantanotherium* based on the centrally placed and isolated metaconule on the M1–2, the presence of the "hypocone" on the M3, and the shape of the protocristid in the lower molars, characters unique, and easily recognizable for this genus. The material found in Plakias includes one p1 one p2, three p3, two p4, one m2, one P1, one P2, one M1, one M2, and one M3; De Bruijn et al. (2012) concluded that the Plakias species has a complete dental formula, unlike *L. sansaniense* and similar to *L. sanmigueli* from Austria; the small size of the dental elements also led to the allocation to the latter species.

Subfamily Erinaceinae Fischer, 1817

Type Genus *Erinaceus* Linnaeus, 1758.

Remarks The presence of the erinaceine *Palerinaceus* sp. in Ravin de la Pluie has been reported by de Bonis et al. (1986) without description of the material. During the past few years, some of the *Palerinaceus* species have been transferred to the genus *Amphechinus*, whereas the former *Palerinaceus* subgenus *Postpalerinaceus* was upgraded to generic level, leaving no species in the genus *Palerinaceus*. Since the Ravin de la Pluie material cannot be located, we cannot confirm the presence of any of the genera. As there is no information on the Ravin de la Pluie erinaceine, its presence is not mentioned in the Supplementary Information.

Erinaceus Linnaeus, 1758

Type Species *Erinaceus europaeus* Linnaeus, 1758 (extant).

Other Taxa Included Extant: *E. concolor* Martin, 1838, *E. amurensis* (Schrenk, 1858), *E. roumanicus* Barrett-Hamilton, 1900. extinct: *E. mongolicus* Schlosser, 1924, *E. praeglacialis* Brunner, 1933, *E. lechei* Kormos, 1934, *E. olgai* Young, 1934, *E. koloshanensis* Young and Liu, 1950, *E. samsonowiczi* Sulimski, 1959, *E. ostramosi* Jánossy, 1972, *E. davidi*, Jammot 1973.

Distribution From the late Miocene (MN10) to the present of Europe, Middle East, Russia, China.

Remarks *Erinaceus* sp. has been reported from the locality Nea Silata (one partial M1; Vasileiadou 2001) and from Tourkobounia 1 (one p3, two m2, and one I3; Reumer and Doukas 1985). Fossil remains of the extant *E. europaeus* have been described from the Biharian locality Apollonia (one partial mandible with i1, p4–m3; Koliadimou 1996) and of *E.* cf. *europaeus* from the late Pleistocene locality Loutra Almopias Cave LAC (one M1 and one M3; Chatzopoulou 2014).

Erinaceus praeglacialis Brunner, 1933

Type Material Brunner (1933) did not designate a holotype for his new species. The available material from Windloch based on which he described the species (thus syntypes) consists of one partial left mandible with p3–4 and m1, one partial left mandible with I1, I3 and C, one partial left mandible with m1, one partial right mandible with i1, and one isolated left m2 (Brunner 1933:Pl. 6.9–10).

Type Locality Windloch, Germany, early Pleistocene.

Distribution From the early Pleistocene of Greece to the early–middle Pleistocene of Europe (Spain, Austria, Germany, Czech Republic, Hungary, Italy).

Remarks This is a large *Erinaceus* species, with dental dimensions close to those of the extant European hedgehog *E. europaeus*. Brunner (1933) mentions that *E. praeglacialis* is characterized by a size slightly larger than that of the extant *E. europaeus*, by the elongated metastyle on the P4 and M2 and a special morphology and position of the upper P3. Rabeder (1972) noticed that the M3 of *E. praeglacialis* is larger than that of any other species. Rzebik-Kowalska (2000) considered that the longer metacrista on the M1, with a less labial and more posterior orientation, differentiates the species from *E. europaeus*. Reumer and Doukas (1985:114) differentiate their

E. praeglacialis from Tourkobounia 5 (one M1 and one M2) from *E. europaeus* based on the "considerably less trapezoidal M2" of the former species.

Erinaceus samsonowiczi Sulimski, 1959

Type Material Left lower jaw with p3–m3 and partial articular processes, No. 1051, Museum of the Earth, Polish Academy of Sciences, Warsaw (Sulimski 1959:Pl. II.2).

Type Locality Węże, Poland, Pliocene, Ruscinian (MN15).

Distribution Turolian/Ruscinian boundary (MN13/14) of Greece; late Miocene (MN10) of the Czech Republic; Pliocene of Poland.

Remarks Sulimski (1959) described the species based on its small size that differentiates it from other European species (apart from *E. lechei*). He based his species in the following: "*characteristic low position of mental foramen, smaller length of the tooth-row i1–m3, strong structure of the whole lower jaw, smaller dimensions of cardinal length, differences of length in tooth-rows p3–m3 and p4–m3, shape of p3 and p4 which, as a rule, are with a slightly posteriorly curved protoconid, finally frequent strong reduction of trigonid in m3*" (Sulimski 1959:32). An assemblage of four p4, two ml, four m2, one m3, four P3, three P4, three M1, and four M2 from Maramena, initially reported as *Erinaceus* sp. in Doukas (1989), was later described and attributed to *E. samsonowiczi* by Doukas et al. (1995). It shows minor metrical and morphological differences from the material from the type locality (i.e., absence of buccal cingulum on the p4, presence of buccal cingulum on the m2 and fairly better developed metaconule on the M2; Doukas et al. 1995).

Dimylidae Schlosser, 1887

Type Genus *Dimylus* von Meyer, 1846.

Plesiodimylus Gaillard, 1897

Type Species *Plesiodimylus chantrei* Gaillard, 1897.

Other Taxa Included *P. huerzeleri* Müller, 1967; *P. crassidens* Engesser, 1980; *P. bavaricus* Schötz, 1985; *P. helveticus* Bolliger, 1992; *P. johanni* Kälin and Engesser, 2001; *P. gaillardia* Mein and Ginsburg, 2002; *P. similis* Fejfar and Sabol, 2009; *P. ilercavonicus* Crespo et al., 2017.

Distribution Miocene (MN3–11) of Europe (Spain, France, Switzerland, Austria, Germany, Poland, Czech Republic, Greece) and middle Miocene (MN7/8) of Turkey.

Comments The taxonomy of *Plesiodimylus* is still mostly unresolved (see discussion in Klietmann et al. 2014:474–476), with many species considered to be invalid (e.g., *P. bavaricus* in Van den Hoek Ostende, 1995); since this work does not aim to revise the genus, we here list all the species that have been assigned to the genus, without discussing their validity.

Plesiodimylus crassidens Engesser, 1980

Type Material Left M1, Sar. 109, Naturhistorisches Museum, Basel (Engesser 1980:Abb. 27.a).

Type Locality Sari Çay, Turkey, middle Miocene (MN7/8).

Distribution From the middle Miocene of Turkey (MN7/8) and Czech Republic (MN10) to the early Miocene (MN4) of Greece.

Remarks The teeth of *P. crassidens* are large, with thick enamel, bulky cusps, and shallow valleys; the M1 bears a strong parastyle, no mesostyle and very weak or no cusp in the central valley; the m1 bears a low paraconid and a very reduced trigonid valley; the m2 has a wider trigonid valley, but the talonid is reduced (Engesser 1980). The species shows more exodaenodontous (overlapping dentary in occlusal view) and amblyodontous (inflated) teeth than all other *Plesiodimylus* species, characters that have been linked with a higher specialization in a malacophagous diet (Ziegler 1999). The few dental elements from the early Miocene locality Karydia (one p4, one m1 and two m2, two P4, two M2) have dimensions intermediate between *P. crassidens* from Sari Çay and *P. huerzeleri* from Aliveri. There are morphological similarities with the Turkish species (e.g., thick enamel, low paracristid not reaching the tip of the protoconid on the m1), but also important differences (e.g., the posterior width of the p4 and m2 is more reduced in the Turkish than in the Karydia species) (Doukas and van den Hoek Ostende 2006). As the morphology of the M1 plays a key role for the diagnosis of the *Plesiodimylus* species, the absence of this molar from the Karydia assemblage led the authors to the assignment of their material to *P.* aff. *crassidens*.

Plesiodimylus huerzeleri Müller, 1967

Nomenclatural and Taxonomical History *Plesiodimylus huerzeleri* in Müller (1967) (new species). The species has frequently been considered a junior synonym of *P. chantrei* (e.g., Engesser 1976, 1980; Doukas 1986), but other authors consider it as a valid species (e.g., Schötz 1985; Ziegler 1999; Kälin and Engesser 2001; Fejfar and Sabol 2009; Klietmann et al. 2014). We here follow the latter opinions and maintain both as valid species.

Type Material Partial left mandible with m1–2, Slg. M 1937 II 10460, Bayerische Staatssammlung für Paläontologie und Historische Geologie München (Müller 1967:Pl. 1.8a–b).

Type Locality Wintershof-West, Germany, early Miocene (MN3).

Distribution Early Miocene (MN3–4) of Central Europe (France, Germany, Czech Republic) and early Miocene (MN4) of Greece.

Remarks The diagnosis by Müller (1967) mentions that the m1–2 are equally large, the m1 is triangular, the hypoconid and entoconid are equally large, and the talonid valley is small and labially slightly open on the m1, the talonid valley opens lingually and slightly labially on the m2, the M1 is only slightly wider posteriorly than anteriorly, the parastyle is prominent, the mesostyle small and not split, and the protocone and hypocone are almost equally large. According to Klietmann et al. (2014:475), *P. huerzeleri* from its type locality includes M1 of their Morphotype I of *P.* aff. *chantrei* from Petersbuch 28: "*the mesostyle is small, the parastyle just a curved ridge; the anterior arm of the protocone ends at the parastyle or between parastyle and paracone; therefore, there are only two basins, formed by the paracone, parastyle, protocone and central cuspule or central cuspule, hypocone, metacone and posterior cingulum, respectively; the margins of all cusps are round*" (Klietmann et al. 2014:473). Doukas (1983), in his PhD thesis (in Greek) assigned two m2, one P4, and one M1 from Aliveri to *P. huerzeleri*, after comparisons with *P. chantrei* from La Grive. Later, the author agreed with Engesser (1976) in synonymizing the two species and described the Aliveri material as *P. chantrei* (Doukas 1986). Van den Hoek Ostende et al. (2015:276), in a revision of the Aliveri materials, listed the Aliveri dimylid as *P. huerzerleri*. Until the taxonomy of *Plesiodimylus* is better known, we prefer to retain both species as valid.

Heterosoricidae Viret and Zapfe, 1951

Type Genus *Heterosorex* Viret and Zapfe, 1951.

Dinosorex Engesser, 1972

Type Species *Dinosorex pachygnathus* Engesser, 1972.

Other Taxa Included *D. sansaniensis* (Lartet, 1851); *D. zapfei* Engesser, 1975; *D. anatolicus* Van den Hoek Ostende, 1995; *D. grycivensis* Rzebik-Kowalska and Topachevsky, 1997; *D. engesseri* Rabeder, 1998.

Distribution Late Oligocene–late Miocene of Europe (Spain, France, Switzerland, Austria, Germany, Poland, Slovakia, Czech Republic, Hungary, Moldova, Ukraine, Serbia, Greece) and Turkey.

Remarks Among the few representatives of Heterosoricidae in Greece, *Dinosorex* sp. is present with one lower antemolar, two m1, two m3, four A1, and three M1/2 in the late Oligocene locality Kyprinos (Doukas and Theocharopoulos 1999). In comparison with the late Oligocene *Quercysorex huerzeleri* (originally described as a

Dinosorex) and the early Miocene *D. anatolicus*—*Dinosorex* sp. from Kyprinos is larger than the former and smaller than the latter, whereas there are also some morphological differences of the Greek species with both species (Doukas and Theocharopoulos 1999). The absence of P4 from Kyprinos, an element essential for the *Dinosorex* taxonomy, hampered a specific identification. Moreover, in the absence of the diagnostic lower incisor, we even cannot exclude that the Kyprinos species represents a *Quercysorex*. Further, Van den Hoek Ostende (1995) mentioned the presence of *Dinosorex* sp. in the early Miocene locality Komotini. However, Doukas and Van den Hoek Ostende (2006), in their report on the insectivores from Karydia and Komotini, mentioned that the material seen by the latter author in 1995 could not be recovered. The occurrence of this genus in Komotini is, thus, uncertain.

Heterosorex Gaillard, 1915

Type Species *Heterosorex delphinensis* Gaillard, 1915.

Other Taxa Included *H. neumayrianus* (Schlosser, 1887); *H. neumayrianus subsequens* (Doben-Florin, 1964); *H. ruemkeae* Doukas, 1986; *H. wangi* Storch and Qiu, 1991.

Distribution From the early–middle Miocene of Europe (Spain, France, Switzerland, Austria, Germany, Poland, Slovakia, Czech Republic, Slovak Republic, Greece) to the late Miocene (MN11/12) of China; possible presence in the late Oligocene of Germany.

Remarks Apart from *H. ruemkeae* from Aliveri (see below), the only other Greek representative of the genus has been reported from Karydia, described as *Heterosorex* sp. (Doukas and Van den Hoek Ostende 2006; initially reported as *Dinosorex* sp. by Doukas, 2003). According to Doukas and Van den Hoek Ostende (2006), the Karydia species (two i1, one lower antemolar, one I1, three upper antemolars, two P4, four M1, and two M2) can be attributed to either *H. ruemkae* or *H. neumayrianus*, but due to the scarcity of the material and the absence of complete mandibles, identification at the species level is not possible.

★*Heterosorex ruemkeae* Doukas, 1986

Type Material Left M2, AL 3361, Department of Paleontology and Historical Geology, University of Athens (Doukas 1986:Pl. 4.4).

Type Locality Aliveri, Greece, early Miocene (MN4).

Distribution Early Miocene (MN4) of Greece (Aliveri) and Serbia (Snegotin; Marković 2003; Marković and Milivojević 2010).

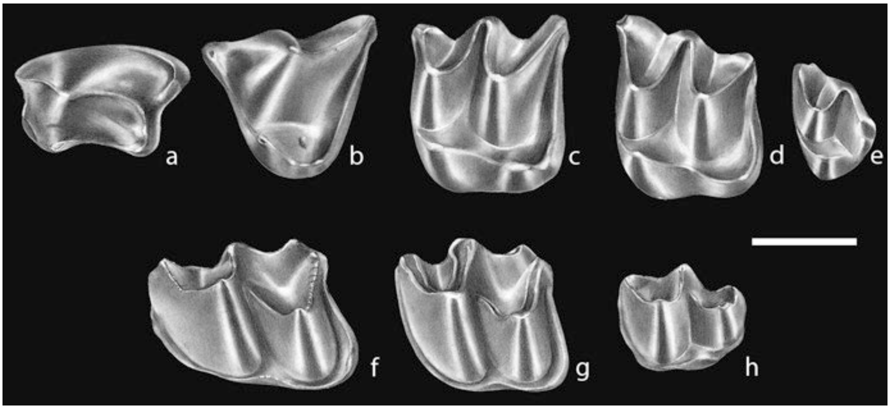

Fig. 5 *Heterosorex ruemkeae* from Aliveri (type locality). (**a**) Right A1, (**b**) right P4, (**c**) right M1, (**d**) left M2 (holotype), (**e**) left M3, (**f**) left ml, (**g**) left m2, (**h**) right m3. Images CD, personal data. All specimens are figured as left; **a**, **b**, **c**, **h** are reversed. Scale bar equals 1 mm

Remarks *Heterosorex ruemkeae* is considerably smaller than the other European *Heterosorex* species. Furthermore, its M1–2 bear an undivided mesostyle, its P4 has a strong and isolated parastyle, a narrow anterior cingulum and triangular to trapezoid outline, and its M3 bears a free-ending posterior arm on the protocone (Doukas 1986). The Aliveri material (five i1, six m1, nine m2, one m3, three I1, one A1, three P4, eight M1, four M2 and three M3; Fig. 5) was initially assigned to *Dinosorex huerzeleri* by Doukas (1983). Later, Doukas (1986) assigned the material to *Heterosorex*, based on the presence of a high entoconid crest on the m1–2 and the weak development of the lingual and posterior parts of the M1–2.

Plesiosoricidae Winge, 1917

Type Genus *Plesiosorex* Pomel, 1848.

Remarks The only plesiosoricid material found in Greece is one *Plesiosorex* sp. M2 from the early Miocene locality Karydia; although not possible to be identified to the species level, this material is important because it represents the southernmost occurrence of this family—Plesiosoricidae is present in Central Europe but absent from southern Europe (Doukas and Van den Hoek Ostende 2006).

Talpidae Fischer, 1814

Type Genus *Talpa* Linnaeus, 1758.

Remarks Talpid elements of unknown generic affinities have been reported from the late Oligocene locality Kyprinos (one m2; Doukas and Theocharopoulos 1999), the early Miocene locality Lapsarna (one m1 and one M3; Vasileiadou and Zouros 2012), and the Pliocene (MN15) locality Vevi (material under study; Doukas 2005).

Subfamily Talpinae Fischer, 1814

Type Genus *Talpa* Linnaeus, 1758.

Remarks In various cases, the finding of only a few dental elements with no mandibles and humeri hampers the precise identification of talpine assemblages, but nevertheless the attribution of these elements to the family-level is certain.

Myxomygale Filhol, 1890

Type Species *Myxomygale antiqua* Filhol, 1890.

Other Taxa Included *M. hutchisoni* (Ziegler, 1985); *M. engesseri* Doukas, 1986; *M. gracilis* Ziegler, 2003.

Distribution From the middle Oligocene to the middle Miocene of Europe (Spain, France, Austria, Germany, Czech Republic, Serbia, Greece).

★*Myxomygale engesseri* Doukas, 1986

Type Material Left M2, Al 3152, Department of Paleontology and Historical Geology, University of Athens (Doukas 1986:Pl. 2.2).

Type Locality Aliveri, Greece, early Miocene (MN4).

Distribution Early Miocene (MN4) of Greece (Aliveri) and Serbia (Snegotin; Marković and Milivojević 2010), possibly latest Oligocene of Germany (Eggingen-Mittelhart 2; Van den Hoek Ostende 1989).

Remarks The material from the type locality (Fig. 6) consists of one m2, one M1, two M2, and four M3 (including the holotype). Doukas (1986) described this species based on the small size of its dental elements, the presence of a prominent protoco-

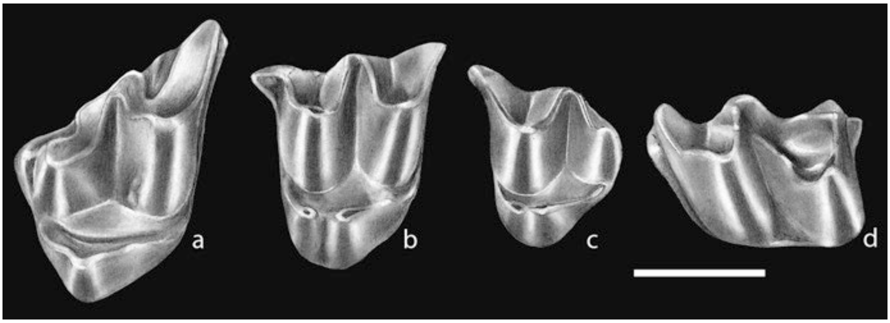

Fig. 6 *Myxomygale engesseri* from Aliveri (type locality). (**a**) M1, (**b**) M2 (holotype), (**c**) M3, (**d**) m2. Images CD, personal data. All specimens are left. Scale bar equals 1 mm

nule close to the protocone on the M2–3, the weak hypocone on all upper molars, and the absence of anterior cingulum on the Ml. Hugueney and Maridet (2017) described the new genus *Percymygale* to include species initially described as *Myxomygale* (i.e., *M. vauclusensis* Crochet, 1995 and *M. minor* Ziegler, 1990). They differentiated their genus from *Myxomygale* based on the presence of ten alveoli anterior to the p4 and the posterior mental foramen below the p4 on the mandible of the former genus versus the presence of seven alveoli anterior to the p4 and the posterior mental foramen below the m1 on the mandible of the latter genus. Since the mandible of *M. engesseri* is not known, Hugueney and Maridet (2017) mentioned that "M. engesseri *cannot be assigned to* Myxomygale *with certainty*"—however, they preferred to maintain its original combination of *M. engesseri* until more material is known.

Myxomygale hutchisoni **(Ziegler, 1985)**

Nomenclatural and Taxonomical History *Palurotrichus hutchisoni* in Ziegler (1985) (new species); *Myxomygale hutchisoni* in van den Hoek Ostende (1989) (new combination).

Type Material Partial left mandible with m2 and the alveoli of i1–m3, 1976 XXII 3176, Bayerische Staatssammlung für Paläontologie und Historische Geologie München (Ziegler 1985:Taf. 3.1).

Type Locality Petersbuch 2, Germany, early Miocene (MN4).

Distribution Early–middle Miocene of Europe.

Remarks Many of the diagnostic characters of the species are based on the morphology of the humerus (e.g., distinctive "Scalopine ridge," with straight, mediolateral course, moderately deep fossa brachialis; moderately deep in lateral half fossa olecrani; Ziegler 1985). The dental diagnostic characters of the species include (from Ziegler 1985): the dental formula of the mandible is 3–1–3–3; the lower incisors are slightly enlarged; the p1, p2, and p3 are approximately of the same size and single-rooted; the lower molars are brachyodont; the crista obliqua on the m1 runs to approximately the middle of the trigonid posterior wall, whereas on the m2–3 it ends more lingually; mental foramens are situated under the m1 and the p1; mesostyle on the upper molars is unsplit; the metaconule is just present on the M1 and pronounced on the M2. Doukas and Van den Hoek Ostende (2006) reported the presence of one M2 and two M3 of a talpid they assigned to *M.* cf. *hutchisoni* at the Greek early Miocene locality Karydia. The molars are larger than those of *M. engesseri* and *M. gracilis* and closer in size to those of *M. hutchisoni*, but the scarcity of the material did not allow the certain assignment to the latter species (Doukas and Van den Hoek Ostende 2006).

Urotrichus **Temminck, 1841**

Type Species *Urotrichus talpoides* Temminck, 1841 (only extant species).

Other Taxa Included Extinct: *U. dolichochir* Gaillard, 1889; *U. giganteus* Ziegler, 2006.

Distribution From the late Miocene of Europe (France, Austria, Germany, Poland, Slovakia, Ukraine, Greece) to the present of Japan.

Remarks A few teeth of *Urotrichus* sp. have been reported from Maramena (three M1, five M2, and one M3); they were attributed to the genus based on the morphology of the M1–2, but the absence of humeri and lower dental elements hampers identification at species level (Doukas et al. 1995).

Talpa Linnaeus, 1758

Type Species *Talpa europaea* Linnaeus, 1758 (extant).

Other Taxa Included Extant: *T. caeca* Savi, 1822; *T. altaica* Nikolsky, 1883; *T. davidiana* (Milne-Edwards, 1884); *T. romana* Thomas, 1902; *T. levantis* Thomas, 1906; *T. occidentalis* Cabrera, 1907; *T. caucasica* Satunin, 1908; *T. stankovici* Martino and Martino, 1931; *T. aquitania* Nicolas et al., 2016; extinct: *T. minuta* de Blainville, 1840; *T. fossilis* Petényi, 1864; *T. minor* Freudenberg, 1914; *T. gracilis* Kormos, 1930; *T. praeglacialis* Kormos, 1930; *T. vallesensis* de Villalta and Crusafont, 1944; *T. tyrrhenica* Bate, 1945; *T. csarnotana* Kretzoi, 1959; *T. gilothi* Storch, 1978; *T. neagui* Rădulescu and Samson, 1989; *T. tenuidentata* Ziegler, 1990. This genus, which includes a large number of extant and extinct species, is in need of a revision, which is out of the scope of the present chapter; thus, all species that have been described until now are listed above but several synonymies between them have been proposed and even more are possible.

Distribution From the early Miocene to the present of Europe and Asia.

Remarks Koliadimou (1996) described six *Talpa* sp. teeth (one I, one C, two P4, one M1 and one M2) from the Pleistocene (MNQ20) locality Ravin Voulgarakis; the identification to species level is hampered by the absence of lower molars and metacranial elements. Chatzopoulou (2014) described a nearly complete right humerus from the late Pleistocene locality Loutra Almopias Cave LAC as *Talpa* sp., mentioning that its size is similar to that of the humerus of *Talpa minor*. In the same cave, in both levels LAC and LAC Ia, the extant species *T. europaea* has also been reported, represented by two M1, one M3, and the proximal part of one ulna (Chatzopoulou 2014).

Talpa fossilis Petényi, 1864

Nomenclatural and Taxonomical History *Talpa vulgaris fossilis* in Petényi (1864) (new subspecies). *T. praeglacialis* Kormos, 1930, is considered a junior synonym of *T. fossilis*, according to Kretzoi (1938).

Type Locality Beremend, Hungary, Pliocene, early Villanyian (MN16).

Distribution The earliest record of the species is from the Greek Turolian/ Ruscinian locality Maramena and has a continuing presence in Europe from the Pliocene up to the middle Pleistocene (Doukas et al. 1995; Kurtén 1968).

Remarks Van Cleef-Roders and Van den Hoek Ostende (2001) provided an English translation of Petényi's (1864) original description of his subspecies, given in Old Hungarian. According to this description, the fossil bone material of this animal is similar to that of the recent common mole (*T. europaea*), in both morphology and size, the only difference being that in *T. europaea* the labial side of the mandible has only two mental foramina, one under the second premolar and one under the first molar, whereas in *T. fossilis* three foramina are present, one under the first premolar and two under the first molar. According to Kormos (1930), the presence of an anterior cingulum in m1 is an important diagnostic feature for *T. fossilis* (van den Meulen 1973). Since the size and morphology of the dental elements of *T. fossilis* are within the range for the extant *T. europaea* (a fact that has made some researchers tentatively consider the two species as synonymous, e.g., von Koenigswald 1970; Rabeder 1972; Van Cleef-Roders and Van den Hoek Ostende 2001), many of the identifications of Plio–Pleistocene assemblages might be incorrect. Van Cleef-Roders and Van den Hoek Ostende (2001:62–64) noticed that whereas the middle-sized *Talpa* is usually referred to *T. europaea* in late Pleistocene deposits, in older deposits it is often classified as *T. fossilis* in the German literature, but as *T.* cf. *europaea* in the French literature; the authors concluded that "*presumably this split in* T. fossilis *and* T. *cf.* europaea *presents a linguistic barrier only*". On the other hand, Sansalone et al. (2015) applied a geometric morphometrics analysis on a large sample of *T. fossilis* and *T. europaea* humeral remains from the Plio-Pleistocene of Hungary, and their results suggest that the two species are separate.

The material of a middle-sized *Talpa* from Maramena is quite rich, consisting of two p3, four p4, 12 m1, 24 m2, 23 m3, 17 M1, 39 M2, 24 M3, and eight humeri (some fragmented) (Doukas et al. 1995). These authors commented that the assignment of the Maramena material in *T. fossilis* should be considered as preliminary and that "*a revision of* Talpa *should particularly clarify the status of* Talpa fossilis*, and could therefore influence the identification of the Maramena species*" (Doukas et al. 1995:54). As Doukas et al. (1995:52) pointed out "*few insectivore genera are as badly in need of revision as the genus* Talpa." Here, we prefer to maintain the original identification, but with caution and in accordance with Van Cleef-Roders and Van den Hoek Ostende (2001:64), who consider *T. fossilis* a junior synonym of *T. europaea*, however, they pointed out that "*older assemblages previously assigned to* T. fossilis *(the name has been used for various Pliocene and even an Upper Miocene assemblage) could also belong to a fossil species, which is now extinct.*"

Subfamily Desmaninae Thomas, 1912

Type Genus *Desmana* Güldenstädt, 1777.

Remarks The genera included in this subfamily are mainly distinguished on the basis of incisor and premolar morphological features. Koufos et al. (2001) described a small collection of desmanine dental elements (two partial mandibles, one p2, three p3, one p4, one m1, one m2, four m3, one P4, three M1, three M2, and three M3) has been recovered from the early Pleistocene locality Marathoussa (Chalkidiki, N Greece), classifying the material as Desmaninae indet.

Archaeodesmana Topachevski and Pashkov, 1983

Type Species *Desmana pontica* Schreuder, 1940.

Other Taxa Included *A. verestchagini* (Topachevski, 1961), *A. vinea* (Storch, 1978), *A. bifida* (Engesser, 1980), *A. getica* (Terzea, 1980), *A. turolensis* (Rümke, 1985), *A. adroveri* (Rümke, 1985), *A. luteyni* (Rümke, 1985), *A. major* (Rümke, 1985), *A. brailloni* (Rümke, 1985), *A. acies* Dahlmann, 2001, *A. baetica* Martín-Suárez et al., 2001, *A. elvirae* Minwer-Barakat et al., 2008.

Distribution From the late Miocene to the Pliocene of Eurasia (Spain, France, Austria, Germany, Romania, Poland, Czech Republic, Moldova, Slovakia, Hungary, Bulgaria, Greece, Turkey, Ukraine).

Remarks *Archaeodesmana* was initially described by Topachevski and Pashkov (1983) as a subgenus of *Desmana* Güldenstädt, 1777, with *Desmana pontica* Schreuder, 1940 as the type species. Rümke (1985) created the genus *Dibolia* with *D. dekkersi* as a type species. This genus was found to be a junior homonym of *Dibolia* Latreille, 1829, a genus of Coleoptera, and the genus *Ruemkelia* Rzebik-Kowalska and Pawlowski, 1994, was created as a replacement name. Hutterer (1995) noticed that Rümke (1985) had included the species *Desmana pontica* in her genus *Dibolia* and thus suggested that the replacement name was not needed and included in *Archaeodesmana* all species which Rzebik-Kowalska and Pawlowski (1994) had included in *Ruemkelia* (= *Dibolia* Rümke, 1985), elevating *Archaeodesmana* to generic level. The synonymy of *Archaeodesmana* and *Ruemkelia* has also been followed by several other authors (e.g., Martín-Suárez et al. 2001, Minwer-Barakat et al. 2008). However, Rzebik-Kowalska (2005a, b) and Rzebik-Kowalska in Rzebik-Kowalska and Rekovets (2015) do not agree with the synonymy and prefer retaining the genus name *Ruemkelia* (for the species of *Dibolia* Rümke, 1985), as the two genera have different type species and there is currently no study that proves their congenerity. Despite her own opinion on the matter, Rzebik-Kowalska used the genus name *Archaeodesmana* instead of *Ruemkelia* in her reviews of the insectivores from Poland and Romania (2005a, b, respectively) "*to make uniform the generic name for this talpid in the whole volume*" (Rzebik-Kowalska 2005a:124). Since the present work cannot review the type material of *Archaeodesmana* and *Ruemkelia* species, we here tentatively follow Hutterer (1995). Dental elements of *Archaeodesmana* sp. have been reported from the Pliocene (MN15) Greek locality Vevi (Doukas 2005).

Archaeodesmana bifida (Engesser, 1980)

Nomenclatural and Taxonomical History *Desmana bifida* in Engesser (1980) (new species); *Dibolia bifida* in Rümke (1985) (new combination); *Archaeodesmana bifida* in Hutterer (1995) (new combination).

Type Material Left M1, Akc. 1, Naturhistorisches Museum Basel (Engesser 1980:Abb. 45a, 46).

Type Locality Afyon–Dinar–Akçaköy, Turkey, Pliocene, Ruscinian (MN15).

Distribution Pliocene of Turkey, Greece, Romania, and perhaps Slovakia.

Remarks According to the diagnosis by Engesser (1980), the species has a small size, similar to that of *Galemys pyrenaicus*. The I1 is straight and its scoop-shaped crown has two cusps. The P4 is significantly longer than wide, with relatively poorly developed protocone and a faint ridge anteriorly to the paracone. The P3 has three roots. The p4 lacks a lingual cuspid, but bears a clear paraconid. The canines and premolars are relatively delicate. The p2 is somewhat smaller than the p3. The roots of the p3 are straight. The p1 usually bears a non-transversally broadened root. The M1 is short lingually, as the metaconule protrudes slightly to the rear, and a relatively extended angle between the two metacone arms. The M2 is very short. The lower molars lack a lingual cingulid, and the enamel in the talonid is wrinkled. The crista obliqua of the m3 connects with the protoconid–metaconid ridge approximately in the middle of the tooth. The i2 is not much bigger than the i1 and bears a lingual cingulum. The mental foramina are very variable, but they are mostly four. Rümke (1985) gave an emended diagnosis for the species: the mean length of the p2 is about 1.32 mm, that of the p3 about 1.40 mm, and that of the p4 about 1.66 mm, the p2/p3 ratio is about 0.94, the p1 has one or two roots, the mean length of the C is about 1.40 mm, that of the P3 about 1.61 mm, and the P1 has two roots. Rümke (1985), apparently having noticed similarities of the only mandible from Ciuperceni 1 with the Turkish species, synonymized Terzea's (1980) *Desmana getica* with *D. bifida*. This opinion is not shared by most authors (e.g., Hutterer 1995, Martín-Suárez et al. 2001, Minwer-Barakat et al. 2008) who keep the two species separated, an opinion also tentatively followed here. The material from Limni 6 assigned to *A. bifida* by Rümke (1985) is rather poor, consisting of two partial mandibles and the following dental elements (including both in situ and loose teeth): one i1, one p1, four p2, one p3, one p4, two m1, two m2, two m3, one I1, three C, two P2, three P3, two P4, and two M3 (no mention on i2/3 and I2/3).

Archaeodesmana getica (Terzea, 1980)

Nomenclatural and Taxonomical History *Desmana getica* in Terzea (1980) (new species); *Ruemkelia getica* in Terzea (1997) (new combination); *Archaeodesmana getica* in Hutterer (1995) (new combination). ★*Dibolia dekkersi* Rümke, 1985, is considered a junior synonym of *A. getica*, according to Van den Hoek Ostende et al. (1989).

Type Material Lower jaw with p2–4 and m2–3, Institute of Speleology "Émile Racovitza", Bucharest (see Terzea 1980).

Type Locality Ciuperceni 1, Romania, Pliocene (MN14).

Distribution From the latest Miocene-Pliocene of Greece to the Pliocene of Europe (Spain, Romania).

Remarks The p2/p3 ratio has a middle value, the P2/P3 ratio a low value, and the C is short. The lower ml has an entostylid of medium height, whereas the lower m3 has a very small or absent entostylid. The upper P4 rarely shows a "bifid" protocone. The P1 has a single root. The lower molars have a broad posterior cingulum and lack a parastylid. The P4 lacks both a metacone and a widening of the posterocrista. The M1–2 show no metastyle. Terzea (1980) described the new species *Desmana getica* based on a mandible from the early Ruscinian Romanian locality Ciuperceni 1. Rümke (1985) included that specimen in the species *Dibolia bifida* (Engesser 1980) (see above). In the same work, she published the new species *Dibolia dekkersi*, based on material from the Greek early Ruscinian locality Kardia. Van den Hoek Ostende et al. (1989) included the Romanian mandible in the species *Dibolia dekkersi*, as its dental dimensions and the p2/p3 ratio are within the ranges of the latter species (van den Hoek Ostende pers. commun. Jan. 2019). However, as Rzebik-Kowalska (2005a) mentioned, "*the name* getica *has priority upon the name* dekkersi." Rzebik-Kowalska and Pawlowski (1994) transferred *Dibolia* species in their new genus *Ruemkelia* and Hutterer (1995) to *Archaeodesmana* (see discussion above).

Apart from Kardia (type locality of *Dibolia dekkersi*, see below), *A. getica* has also been found in Ptolemais 3 and Maramena. The material from Ptolemais 3 available to Rümke (1985) includes three i1, three c, one p1, eight p2, two p3, seven p4, 11 m1, 13 m2, 13 m3, seven I1, 10 C, four P1, 11 P2, 18 P3, 12 P4, six M1, three M2, and 14 M3 (no mention to the i2/3 and I2/3). The material from Maramena studied by Rümke (1985) included six partial mandibles and the following dental elements (including in situ and loose teeth, but with no mention to the i2/3 and I2/3): seven i1, three c, four p1, nine p2, seven p3, nine p4, 10 m1, six m2, eight m3, 10 I1, seven C, eight P1, seven P2, eight P3, six P4, seven M1, four M2, and seven M3. The material from Maramena collected after 1986 and studied by Doukas et al. (1995) is much richer, including one partial mandible with p3–4, one with p4–m2, two with p4–m1, one with m2–3, six p4, 12 m1, 13 m2, 12 m3, one partial maxilla with P1–3 and two with P4–M1, seven P2, five P3, 22 P4, 31 M1, 25 M2, 16 M3, one fragmented humerus, and one chevron bone.

★*Dibolia dekkersi* Rümke, 1985

[Junior synonym of *Archaeodesmana getica* (Terzea, 1980) according to Van den Hoek Ostende et al. (1989)].

Type Material Right p3, Ka-646, Faculty of Geosciences, Utrecht University, The Netherlands (Rümke 1985: Fig. 53.2).

Type Locality Kardia, Greece (early Ruscinian).

Remarks In the diagnosis and the differential diagnosis of her new species, Rümke (1985) mentioned that the mean length of the p2 is about 1.44 mm, of the p3 about 1.24 mm, of the p4 about 1.58 mm, the p2/p3 ratio is about 1.16 (thus average), the p1 is single-rooted, the mean length of the C is about 1.28 mm (thus short), of the P2 about 1.59 mm, of the P3 about 1.46 mm, the P2/P3 ratio is about 1.09 (thus low), and the P1 is double-rooted. The material from the type locality is rather rich, consisting of four partial mandibles and the following dental elements (including both in situ and loose ones, with no reference to the i2/3 and I2/3): 22 i1, eight c, 16 p1, 29 p2, 20 p3 (including the type specimen), 28 p4, 30 m1, 27 m2, 44 m3, 22 I1, 29 C, 18 P1, 29 P2, 31 P3, 35 P4, 34 M1, 44 M2 and 31 M3.

Archaeodesmana verestchagini **(Topachevski, 1961)**

Nomenclatural and Taxonomical History *Desmana verestchagini* in Topachevski (1961) (new species); *Archaeodesmana verestchagini* in Martín-Suárez et al. (2001) (new combination).

Type Material Partial right mandible with p2–m3, No. 26967 (Rümke 1985:Fig. 76).

Type Locality Kosyakin, Russia, early Pliocene (MN14).

Distribution Pliocene of Bulgaria, Russia, Greece, and possibly Ukraine.

Remarks According to Rümke's (1985) emended diagnosis for the species, the mean length of the p2 is about 1.80 mm, of the p3 about 1.55 mm, of the p4 about 2.10 mm, and the p2/p3 ratio is about 1.16. She also gave some additional diagnostic features, based on material from the Greek locality Spilia 1: the mean length of the C is about 1.32 mm, of the P2 about 2.00 mm, of the P3 about 1.71 mm, the P2/P3 ratio is about 1.17, and the p1 and P1 are single-rooted. She mentioned that the species is characterized by its small size (Rümke 1985:96) and that the small size mainly of the p3 and P3 distinguishes it from all other *Desmana* species (Rümke 1985:188). Martín-Suárez et al. (2001) included the species to *Archaeodesmana*, following the diagnoses of the genus, and Minwer-Barakat et al. (2008) followed the same nomenclature. The species has been reported from the Greek localities Spilia 0 and 1, Kardia, Ptolemais 1 by Rümke (1985). The material from Spilia 1 studied by Rümke (1985) was limited, consisting of eight partial mandibles and the following dental elements (including in situ and loose teeth, no mention to i2/3 and

I2/3): six i1, five c, seven p1, eight p2, nine p3, seven p4, eight m1, six m2, eight m3, four I1, five C, five P1, four P2, 10 P3, three P4, four M1, six M2, and three M3. The scarce material from Kardia Rümke (1985) studied consisted of two i1, one c, five p2, two p3, five p4, seven m1, eight m2, eight m3, two P2, one P3, one P4, four M1, three M2, and five M3 (no mention to i2/3 and I2/3; the presence of partial mandibles is mentioned, but their quantity is not given). The material available to Rümke (1985) from Ptolemais 1 included five i1, seven c, nine p1, 15 p2, 20 p3, 24 p4, 17 m1, 12 m2, five m3, 13 C, 12 P1, 10 P2, 17 P3, 14 P4, nine M1, four M2, and five M3 (no mention to i2/3 and I2/3; the presence of partial mandibles is mentioned but their number is not given). Doukas (2005), in his review on the Greek insectivores, listed the material as *Desmana* and not *Archaeodesmana*.

Subfamily Uropsilinae Dobson, 1883

Type Genus *Uropsilus* Milne-Edwards, 1871.

Desmanella Engesser, 1972

Type Species *Desmanella stehlini* Engesser, 1972.

Other Taxa Included *D. crusafonti* Rümke, 1974; *D. fejfari* Gibert, 1975; *D. dubia* Rümke, 1976; *D. sickenbergi* Engesser, 1980; *D. cingulata* Engesser, 1980; *D. amasyae* Engesser, 1980; *D. engesseri* Ziegler, 1985; *D. gardiolensis* Crochet, 1986; *D. storchi* Qiu, 1996; *D. rietscheli* Storch and Dahlmann, 2000; *D. woelfersheimensis* Dahlmann, 2001; *D. gudrunae* Van den Hoek Ostende and Fejfar, 2006.

Distribution From the late Oligocene to the late Pliocene of Eurasia (Spain, France, Switzerland, Austria, Germany, Poland, Romania, Greece, Turkey, China).

Remarks *Desmanella* sp. has been reported from the Greek localities Lefkon (no information on material; Doukas 1989) and Limni 6 (unpublished material; Doukas 2005).

★*Desmanella dubia* Rümke, 1976

Type Material Right M1, PK 565, Department of Paleontology and Historical Geology, University of Athens (Rümke 1976:Pl. 2.13).

Type Locality Pikermi (Chomateri), Greece, late Miocene, Turolian (MN12).

Distribution From the late Miocene to the Pliocene of Europe (Spain, France, Poland, Bulgaria) and late Miocene of Greece.

Remarks The diagnosis by Rümke (1976) mentions that this is a small *Desmanella* species (m1 length = 1.43 mm), with a relatively small m1, not much larger than the

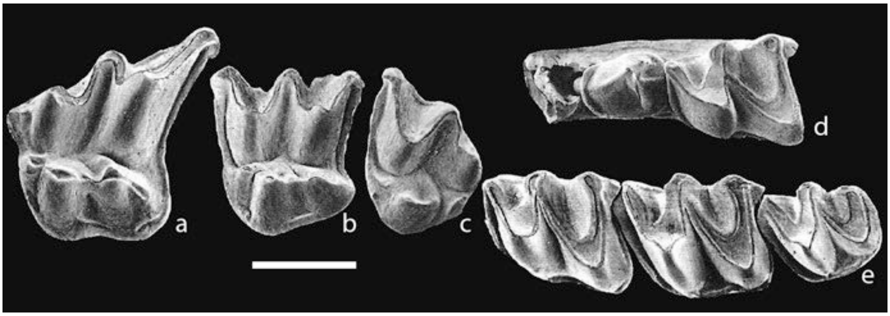

Fig. 7 *Desmanella dubia* from Maramena. (**a**) M1, (**b**) M2, (**c**) M3, (**d**) partial mandible with p4–m1, (**e**) partial mandible with m1–3. Images CD, personal data. All specimens are figured as left. Scale bar equals 1 mm

m3. The lower molars bear a continuous cingulum along their anterior, labial and posterior sides. The M1 shows a concave posterior outline, due to the strongly elongated hypocone. The lingual cusps of the M1 and M2 form slightly curved crests. The posterior cingulum of the M1 and M2 ends at the posterolabial corner of the teeth. Finally, the M3 is relatively large, with a wide valley separating the hypocone from the protocone. The material from the type locality is rather scanty, consisting of two m1 (one fragmented), two m2, two m3, one P4, one M1 (holotype), two M2 (one fragmented), and one M3 (Rümke 1976). The species name "*dubia*" reflected the author's doubt on the generic allocation, as both *dubia* and even the type species of *Desmanella* could also belong to *Asthenoscapter* Hutchison, 1974, based on the published collections back in 1976 (which did not include lower antemolars or mandibles that could reveal the number of roots, a main distinctive feature between the two genera; see Rümke (1976) for discussion). Materials published since then have confirmed the generic allocation of *dubia* to *Desmanella* (e.g., Crochet and Green 1982; Ziegler 2003; Rzebik-Kowalska 2005c). The material of *D. dubia* from Maramena (Fig. 7) is richer than that from the type locality: one partial mandible with m1–3, nine partial mandibles with p4–m1, three partial mandibles with p4–m2, 14 partial mandibles with m1–2, six partial mandibles with m2–3, 24 ml, 31 m2, 22 m3, three partial maxillae with M1–3, 23 P4, 45 M1, 51 M2, and 28 M3 (Doukas et al. 1995). The mandibles from Maramena show six alveoli for the antemolars in front of the double-rooted p4, confirming Rümke's (1976) allocation of the species to *Desmanella* instead of *Asthenoscapter* (that shows some double-rooted antemolars) (Doukas et al. 1995).

Talpidae incertae sedis

Desmanodon Engesser, 1980

Type Species *Desmanodon major* Engesser, 1980.

Other Taxa Included *D. minor* Engesser, 1980; *D. antiquus* Ziegler, 1985; *D. ziegleri* Van den Hoek Ostende, 1997; *D. burkarti* Van den Hoek Ostende, 1997; *D. daamsi* Van den Hoek Ostende, 1997; *D. crocheti* Prieto, 2009; *D. fluegeli* Prieto et al., 2010.

Distribution Early-middle Miocene of Europe (Portugal, Spain, France, Austria, Germany, Czech Republic, Slovakia, Greece) and Turkey.

Remarks Three upper molars from the early/middle Miocene Greek locality Antonios have been identified as *Paratalpa/Desmanodon* (Vasileiadou and Koufos 2005), based on the remark of Van den Hoek Ostende (2003) that the distinction between *Desmanodon* and *Paratalpa* requires information from the humeri. Since *Paratalpa* has been found only in latest Oligocene–early Miocene W and C European localities, it is probable from a paleobiogeographic and a biostratigraphic point of view that the Antonios talpid belongs to *Desmanodon*.

Desmanodon antiquus Ziegler, 1985

Taxonomical History ★*Desmanodon meuleni* Doukas, 1986, is considered a junior synonym of *D. antiquus*, according to Doukas and Van den Hoek Ostende (2006).

Type Material Right M1, 1959 XXVIII 589, Bayerische Staatssammlung für Paläontologie und Historische Geologie, München (Ziegler 1985:Taf. 6.6).

Type Locality Rembach bei Vilsbiburg, Germany, early Miocene (MN4).

Distribution Early Miocene of Europe (Austria, Germany, Czech Republic) and early Miocene of Greece.

Remarks Ziegler (1985), in his diagnosis, mentions that this is a small *Desmanodon* species. The P4 has three separate roots, and its protocone is faint. The upper molars bear a deeply split mesostyle, a clear metaconule, a short and not isolated parastyle, but lack a protoconule. The m2–3 bear a prominent precingulid, and the crista obliqua is sloping toward the middle of the trigonid wall. The p4 shows a subtle metaconid. The humerus is slender, with a long tuberculum teres, distally placed pectoral tubercle, a sharp-edged crista pectoralis and a laterally compressed caput parallel to the longitudinal axis of the humerus. The material from Aliveri, on which the species *D. meuleni* Doukas, 1986, was based, is rather scanty, consisting of three m1, six M1, ten M2, and nine M3 (Doukas 1983). It has been included in *D. antiquus* after the synonymy of the two species was established by Doukas and Van den Hoek Ostende (2006). The material from Karydia, initially mentioned as *Desmanodon* sp. in the locality faunal list given by Doukas (2005) but later described as *D. antiquus* by Doukas and Van den Hoek Ostende (2006), is even scantier: one mandibular fragment with the p4, one m2, and four M2 (Doukas and Van den Hoek Ostende 2006).

★*Desmanodon meuleni* Doukas, 1986

[Junior synonym of *Desmanodon antiquus* Ziegler, 1985, according to Doukas and van den Hoek Ostende (2006)].

Type Material Right M2, AL 3162, Faculty of Geosciences, Utrecht University, The Netherlands (Doukas 1986:Pl. 2.5).

Type Locality Aliveri, Greece, early Miocene (MN4).

Remarks Doukas first published the species *D. meuleni* in his PhD thesis in 1983, based on material from Aliveri. As his Greek thesis did not qualify as a publication, a few years later, the same name was used for the same concept, as *Desmanodon meuleni* Doukas, 1986. In the meantime, Ziegler (1985) had already published the species *D. antiquus* from Germany. As the two species seem to be conspecific, the German species predated the Greek one, and *D. meuleni* is considered as a junior synonym of *D. antiquus* (see discussion in Doukas and Van den Hoek Ostende 2006).

Desmanodon minor Engesser, 1980

Type Material Partial right mandible with p3–m3, Sar.2, Naturhistorischen Museum Basel (Engesser 1980:Abb.55b, 56b).

Type Locality Sarı Çay, Turkey, middle Miocene (MN7/8).

Distribution Besides its type locality, it is also found in the middle Miocene of Greece.

Remarks Engesser's (1980) diagnosis mentioned that the species has somewhat smaller size than the type species of *Desmanodon* and, mainly, more delicate molars. The protocone of the upper molars is less massive. The p3 has two roots. The m1 is much smaller than the m2. The M1 bears a very prominent parastyle. The lingual and posterior roots of the P4 are usually not fused. The p3–4 are relatively large. The mandible is relatively strong. The humerus is significantly smaller and less specialized than that of *D. major*, with comparatively shorter teres edges. Koliadimou (1996) reported the presence of one *D. minor* M2 from the middle Miocene locality Chryssavgi 1. Even though the material is scarce, it can be assigned to this species with certainty due to its dimensions, the absence of an anterior and lingual cingulum and the presence of a small posterior cingulum, a small cuspule on the labial area and a strong mesostyle (Koliadimou 1996), characteristics also present in the M2 from the type locality.

Soricidae Fischer, 1814

Type Genus *Sorex* Linnaeus, 1758.

Remarks Several Greek localities have yielded small collections of isolated dental elements that cannot be determined at genus level and are only reported as Soricidae indet. Vasileiadou and Zouros (2012) reported the presence of one upper incisor and one M2 of Soricidae indet. From Lapsarna De Bonis et al. (1997) listed Soricidae indet. in the faunal list from Thymiana A (unpublished material). One m2 and a partial mandible with the alveoli of the m2–3 of an unidentified soricid have been found at Paliambela-A (Sylvestrou 2002; Sylvestrou and Kostopoulos 2007). Doukas (1989, 2005) reported the presence of Soricidae indet. at Monasteri and Spilia 0,1, without giving further details on the material. Three partial upper incisors of an unidentified soricid were recovered from Kessani (Vasileiadou et al. 2012). Van de Weerd (1979) and Doukas (2005) mentioned the presence of Soricidae indet. in Ptolemais 1, with no further information. Soricidae indet. is also reported from the localities Limni 6 (Doukas 2005) and Elaiochoria (one specimen: cf. *Deinsdorfia*; Hulva et al. 2007), without further details. Undeterminable soricid dental elements were also found at Varkiza 2 (Van de Weerd 1973) and Choremi 1 and Choremi 4 (Van Vugt et al. 2000).

Subfamily Crocidosoricinae Reumer, 1987

Type Genus *Crocidosorex* Lavocat, 1951.

Remarks Two i1, one p4, 13 m1, 10 m2, two m3, three I1, one P4, four M1, and four M2 from Aliveri were initially assigned to Soricidae indet. by Doukas (1983) and later to Crocidurinae indet. by Doukas (1986), based on the crocidurine-type p4. A small number of molars (three m1, one m2, one m3, two M1, and one M2) from the early–middle Miocene locality Antonios have been assigned to Crocidosoricinae indet. (Vasileiadou and Koufos 2005), but the absence of the subfamily's diagnostic element (p4) makes this identification uncertain.

Lartetium Ziegler, 1989

Type Species *Sorex prevostianum* Lartet, 1851.

Other Taxa Included *L. dehmi* (Viret and Zapfe 1951); *L. africanum* (Lavocat 1961); *L. petersbuchense* Ziegler, 1989; *L. ziegleri* Mein and Ginsburg, 2002.

Distribution Early–middle Miocene of Europe (Spain, France, Austria, Germany, Czech Republic, Slovakia, Serbia, Greece), Turkey, and Morocco.

Lartetium dehmi (Viret and Zapfe, 1951)

Nomenclatural and Taxonomical History *Sorex dehmi* in Viret and Zapfe (1951) (new species); *Lartetium dehmi* in Ziegler (1989) (new combination).

Type Material Viret and Zapfe (1951) did not designate a holotype of their new species; lectotype, by subsequent designation by Hugueney et al. (2012): left mandible with a2–m2, MC 230, Museum of Lyon, France (Viret and Zapfe 1951:Fig. 6a–b).

Type Locality Vieux-Collonges, France, middle Miocene (MN5).

Distribution Early–middle Miocene of Europe (France, Germany, Slovakia, Serbia) and possible presence in the early Miocene of Greece.

Remarks The species is characterized by wide upper molars with a well-developed hypocone, weak entocristids and a labial termination of the oblique cristid on the lower molars, and a broad talonid and wide labial cingulum under the protoconid on the m1. Doukas and Van den Hoek Ostende (2006) assigned one m1, one m2, two P4, and four M1 from Karydia to *L.* cf. *dehmi*. The material shares metrical and morphological characteristics with the material from the type locality; however, its scantiness and the presence of only isolated dental elements instead of complete jaws did not allow the certain assignment to the species.

Subfamily Paenelimnoecinae Fejfar, Storch and Tobien, 2006

Type Genus *Paenelimnoecus* Baudelot, 1972.

Paenelimnoecus Baudelot, 1972

Type Species *Paenelimnoecus crouzeli* Baudelot, 1972.

Other Taxa Included *P. pannonicus* (Kormos, 1934); *P. micromorphus* (Doben-Florin, 1964); *P. repenningi* (Bachmayer and Wilson, 1970); *P. truyolsi* (Gibert, 1975); *P. obtusus* Storch, 1995; *P. chinensis* Jin and Kawamura, 1997.

Distribution From the early Miocene to the Pliocene of Europe (Spain, France, Austria, Germany, Poland, Moldova, Romania, Czech Republic, Slovakia, Hungary, Greece), Turkey, and China.

Remarks A single m2 from the early Miocene locality Karydia and a single m1 from the middle Miocene locality Plakias have been attributed to this genus (as *Paenelimnoecus* sp. and cf. *Paenelimnoecus* sp., respectively), based on their reduced entoconid (Doukas and Van den Hoek Ostende 2006 and De Bruijn et al. 2012, respectively). Since no additional material is available in both localities, a specific identification is impossible. However, Doukas and Van den Hoek Ostende (2006) mention that the Karydia specimen is remarkably larger than the m2 of *P. micromorphus* and *P. crouzeli*.

Subfamily Soricinae Fischer, 1814

Type Genus *Sorex* Linnaeus, 1758.

Crusafontina Gibert, 1975

Type Species *Crusafontina endemica* Gibert, 1975.

Other Taxa Included *C. kormosi* (Bachmayer and Wilson, 1970); *C. magna* (Hutchison and Bown, 1980 in Bown 1980), *C. minima* (Hutchison and Bown, 1980 in Bown 1980), *C. fastigata* Van Dam, 2004; *C. vandeweerdi* Van Dam, 2004.

Distribution From the middle Miocene to the Pliocene of Europe (Spain, France, Switzerland, Austria, Germany, Poland, Moldova, Ukraine, Czech Republic, Hungary, Greece) and Turkey.

Crusafontina endemica Gibert, 1975

Type Material Partial left mandible with p4–m2, Nr. 9002, Institut de Paleontologia Miquel Crusafont de Sabadell, Barcelona (Gibert 1975:Pl. 2.7a–b).

Type Locality Can Llobateres 1, Spain, late Miocene (MN9).

Distribution Late Miocene (MN9–MN10) of Europe (Spain, France, Austria, Moldova, Hungary) and possible presence in the late Miocene of Greece.

Remarks The species has a rather complete dental formula (1–4–3/1–2–3), as all *Crusafontina* species. The original diagnosis for the species by Gibert (1975) gives the following characteristics: two rooted P4, presence of a small postero-internal depression and presence of a labial crest but absence of a lingual one on the P4, a very wide trigonid basin and a long paralophid on the m1, presence of a hypoconid and an entoconid on the m3, a not bifid upper incisor, presence of a narrow interarticular area separating the articular facets of the mandible. Mészáros (1998:147) gave an emended diagnosis for the species: "*small* Crusafontina *species with hypoconid and entoconid on the third lower molar. The apex of the upper incisor is long, I1 L/H > 1.40. The P4 hypoconal flange is short. The second upper antemolar is relatively elongated, the A1/A2 length ratio is less than 1.62. The lower incisor may be monocuspulate or bicuspulate. The m1/m3 length ratio is less than 2.20. The mental foramen is below the m1 trigonid or the middle of the tooth.*" Van Dam (2004) discussed the differences between *C. endemica* and *C. kormosi* and proposed changes in Mészáros (1998) emended diagnosis (see van Dam 2004:746–749 for reasoning): *C. endemica* is a small *Crusafontina* species, its I1 has a long apex, and the L/H ratio is not smaller than about 1.40, the metastyle of the M1 extends more buccally than the parastyle does and the hypoconal flange does not protrude lingually, the I1 bears 2–3 cusps, the m3 shows a talonid with a small basin and the Lm3/Lm1 ratio is not smaller than about 0.40. Van Dam (2004) assigned one m1 from the locality Biodrak to *C.* cf. *endemica*, as it fits morphologically and metrically with *C. endemica*.

Crusafontina kormosi (Bachmayer and Wilson, 1970)

Nomenclatural and Taxonomical History *Anourosorex kormosi* in Bachmayer and Wilson 1970 (new species); "*Anourosorex*" *kormosi* in Storch (1978) (new combination); *Crusafontina kormosi* in Storch and Qiu (1991) (new combination). The species *Amblycoptus vicinus* Kretzoi, 1954—described based on fragmentary material from Csákvár (Hungary)—is regarded as a synonym of *C. kormosi*, even though the name *vicinus* has priority (see discussion in Mészáros 1998:149).

Type Material Right mandible with complete dentition, 1970/1389, Natural History Museum of Vienna (Bachmayer and Wilson 1970:Pl. 1.3).

Type Locality Kohfidisch, Austria, Late Vallesian (MN10).

Distribution From the late Miocene (MN10–MN13) of Europe (France, Austria, Germany, Hungary, Czech Republic, Moldova) and possible presence in the late Miocene (MN10) of Greece.

Remarks The original diagnosis by Bachmayer and Wilson (1970) mentions that this species' size is somewhat smaller than in the living *Anourosorex squamipes*, its teeth have a faint pigment, and its dental formula is 1–4–3/1–2–3. The posterior borders of the P4–M1 are emarginated, the P4 shows a somewhat pointed anterior margin, the M1 is transversally relatively wide, the m3 is reduced but shows a small basined talonid, the lower molars bear weak labial cingula and slightly crested entoconids. The upper articular condyle of the mandible has an oval rather than triangular shape, the lower articular condyle is only slightly visible in lingual view, and its anterior edge does not extend forward beyond the posterior border of the superior pterygoid fossa, and the pterygoid spicule is relatively obscure. Mészáros (1998) gave an emended diagnosis, according to which the species is relatively large among the *Crusafontina* species; the m3 bears neither a hypoconid nor an entoconid, and its trigonid is reduced to a single cusp or even without cusps or is totally missing; the I1 apex is shorter than in *C. endemica*; the P4 shows a long hypoconal flange; the second upper antemolar is long; there are always two cusps on the lower incisor; the Lm1/Lm3 ratio is higher than 2.20; the mental foramen is below the middle of the m1 or backward. As with *C. endemica*, Van Dam (2004:746–749 for reasoning) changed some points in Mészáros' (1998) emended diagnosis. According to Van Dam (2004), *C. kormosi* is a medium-sized *Crusafontina* species. The I1 shows a long apex and its L/H ration is smaller than about 1.40. On the M1, the metastyle and parastyle extend buccally about equally far, and the hypoconal flange does not protrude lingually. The i1 is bicuspulate. On the m3, the talonid might show a closed basin or a terminal heel or might be absent. The Lm3/Lm1 ratio is smaller than about 0.40. Van Dam (2004) argues that the morphology of the talonid of the m3 is not a good morphological feature to distinguish between *C. endemica* and *C. kormosi* (as Mészáros 1998 had proposed), and the Lm3/Lm1 ratio could be used instead. One m1 and one m2 from the locality Lefkon, previously mentioned as

Amblycoptus sp. by Doukas (1989), have been attributed to *C.* cf. *kormosi* by Van Dam (2004). The material is too limited to allow certain specific identification.

Amblycoptus **Kormos, 1926**

Type Species *Amblycoptus oligodon* Kormos, 1926.

Other Taxa Included *A. jessiae* Doukas, 1995 in Doukas et al. (1995).

Distribution From the late Miocene to the Pliocene (MN12–14) of Europe (Spain, Hungary, Russia, Greece) and Turkey.

★*Amblycoptus jessiae* Doukas, 1995 in Doukas et al. (1995)

Nomenclatural and Taxonomical History *Amblycoptus* n. sp. in Doukas (1989); *Amblycoptus jessiae* Doukas in Doukas et al. (1995) (new species).

Type Material Partial mandible with a1, p4, ml and m2, AMPG MA 3296 (Doukas et al. 1995:Pl. 6.10).

Type Locality Maramena, Greece, late Miocene, Turolian/Ruscinian boundary.

Distribution From the late Miocene to the early Pliocene (MN12–14) of Europe (Spain, Greece).

Remarks The diagnosis by Doukas et al. (1995:54) mentions that the species' size is intermediate between *A. oligodon* and *A. topali*, its A1 bears a parastyle, the P4 shows a well-developed protocone, and the ml shows "*neither well separated nor entirely merged*" entoconid and entostylid. The differential diagnosis mentions that this species "*differs from* A. oligodon *in the morphology of the talonid of ml, in having less separated entoconid and entostylid, and by having a relatively smaller m2. It also differs in the morphology (parastyle, hypoconal flange) and size of the A1. It differs from* A. topali *in the relative size and the L/W ratio of the ml and in the morphology of the A1. The entoconid/entostylid complex in* A. jessiae *is not fused as in* A. topali. *It finally differs from Amblycoptus sp. (Osztramos 7) in the less advanced morphology of the A1.*" Mészáros (1997) introduced the genus *Kordosia*, which differs from *Amblycoptus* in a number of features including the absence of an A3, and suggested that *A. jessiae* could be included in *Kordosia* with uncertainty until mandibles from the type locality Maramena are recovered. Later, Van Dam (2004:755) discussed the similarities and differences of *jessiae* with *A. oligodon* and *K. topali* and concluded that "*in short, whereas the P4 and M1 of* jessiae *are more* Amblycoptus-*like, the m1 and A1–2 are more* Kordosia-*like. Assignment to* Amblycoptus *is preferred, taking into account the probable presence of the A3.*" We here follow the opinions of Van Dam (2004) and Doukas (2005) in retaining the species in the genus *Amblycoptus*. The material from the type locality (Fig. 8) includes four lower incisors, five a1, 19 p4, 52 m1, 20 m2, a partial mandible with a1, p4–m2 (holotype), 14

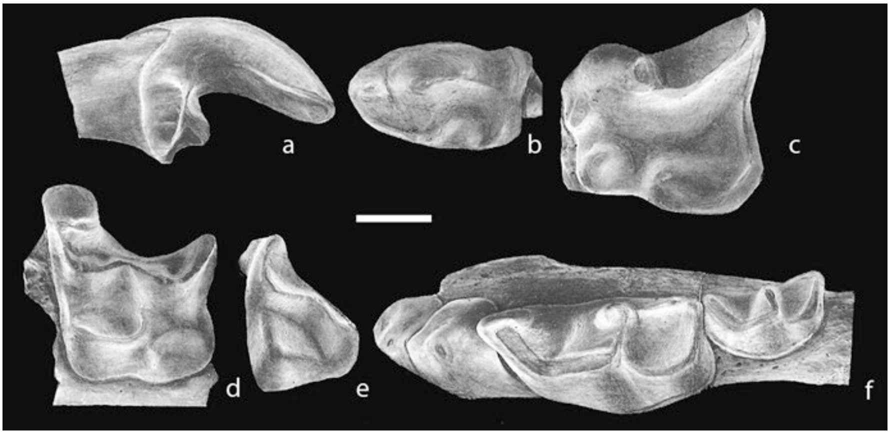

Fig. 8 *Amblycoptus jessiae* from Maramena (type locality). (**a**) I sup., (**b**) A1, (**c**) P4, (**d**) M1, (**e**) M2, (**f**) right mandibular fragment with a1, p4, ml and m2 (holotype). Images CD, personal data. All specimens are figured as left. Scale bar equals 1 mm

upper incisors, 53 A1, 12 A2, 62 P4, 59 M1, and 12 M2 (Doukas et al. 1995). Doukas (1989) mentioned the presence of *Amblycoptus* sp. in the locality Ano Metochi 3 (with no information on the material); Doukas (2005) included the insectivore material from Ano Metochi 2, 3 in that from Maramena, the type locality of the species *A. jessiae*. Apparently, the Ano Metochi 3 *Amblycoptus* also belongs to this species. Vasileiadou et al. (2003) reported the presence of one lower incisor, two m1, one m2, two upper incisors, and two M1 of *A.* cf. *jessiae* at the locality Nea Silata. The material is damaged, and no measurements are available, but the morphological features and the relative size fit well with those of the Maramena species.

Blarinella Thomas, 1911

Type Species *Sorex quadraticauda* Milne-Edwards, 1872 (extant).

Other Taxa Included Extant: *B. griselda* Thomas, 1912; *B. wardi* Thomas, 1915; Extinct: *B. dubia* (Bachmayer and Wilson, 1970); *B. europaea* Reumer, 1984.

Distribution From the late Miocene to the Pleistocene of Europe (Hungary, Greece) and Asia (China), and extant in Southeast Asia.

Remarks Storch (1995) created the genus *Alloblarinella* to separate extinct from extant species that had been included to *Blarinella* and made *B. europaea* the type species of his new genus (he included the species *dubia* in *Petenyia*, as originally allocated by Bachmayer and Wilson, 1970). Doukas (2005) mentioned the presence of cf. *Blarinella* sp. in the Pliocene locality Vevi, without additional information on the material.

Blarinella dubia (Bachmayer and Wilson, 1970)

Nomenclatural and Taxonomical History *Petenyia dubia* in Bachmayer and Wilson 1970 (new species); *Blarinella dubia* in Reumer (1984) (new combination).

Type Material Left lower jaw with m1–3, No. 1970/1387, Naturhistorisches Museum, Wien (Bachmayer and Wilson 1970:Pl. 2.6).

Type Locality Kohfidisch, Austria, late Miocene (MN11).

Distribution From the early Pliocene (Ruscinian) of Europe (Poland, Czech Republic, Hungary) and possible presence in Greece.

Remarks According to the diagnosis by Bachmayer and Wilson (1970:546), the species' size is similar to that of *Petenyia hungarica*, its lower incisor is relatively smooth in dorsal profile, with some pigment, "*but not as intense as now preserved*," and its coronoid spicule is not particularly prominent. Later, Reumer (1984) transferred the species to *Blarinella* and gave an emended diagnosis: the P4 shows a normally developed protocone, the M1–2 bear a protocone and a talon but lack an endoloph and a hypocone, the lower molars show a very strong cingulum on both lingual and labial sides, as well as high entoconid crests, and there is a horizontal bar in the internal temporal fossa. De Bruijn et al. (1970) reported the presence of one partial mandible with i, p4–m2 and one partial maxilla with P4–M2 of *Blarinella* sp. at the locality Maritsa 1 (Rhodos Island). Later, Reumer (1984) assigned these two specimens to *B. dubia* based on the absence of a continuous endoloph on the upper molars.

Blarinella europaea Reumer, 1984

Type Material Partial maxilla with M1–2, no. V.12705, Vt.99, Hungarian State Geological Survey, Budapest (Reumer 1984:Pl. 21.6).

Type Locality Csarnóta 2, Hungary, early Pliocene, Ruscinian (MN14–15).

Distribution Early Pliocene (Ruscinian) of Europe.

Remarks The diagnosis, as given by Reumer (1984), mentions that this is a large *Blarinella* species with heavily pigmented teeth, both upper and lower incisors bear a strongly spatulate apex, the P4 shows a faint protocone, the upper molars bear a well-developed paracone and metacone as well as a continuous endoloph, the lower molars are quadrate, with sharp buccal edges of the protoconids and the hypoconids due to sharp angles of the lophids and with extremely high entoconid crests. Two lower incisors from the late Ruscinian Greek locality Apolakkia were assigned to *Blarinella* sp. by Van de Weerd et al. (1982), based on their similarity with the lower incisor on the partial mandible from Maritsa 1. Reumer (1984) assigned the specimens to *B.* cf. *europaea*.

Petenyia Kormos, 1934

Type Species *Petenyia hungarica* Kormos, 1934.

Other Taxa Included *P. robusta* Rzebik-Kowalska, 1989; *P. katrinae* Qiu and Storch, 2000 (see Rzebik-Kowalska 1989 for synonymies among *Petenyia* species and transfer of former *Petenyia* species to other genera).

Distribution From the early Pliocene to the early Pleistocene of Europe (Spain, France, Switzerland, Germany, The Netherlands, Poland, Italy, Slovakia, Romania, Russia, Hungary, Bulgaria, Greece), and Asia (Turkey and China).

Petenyia hungarica Kormos, 1934

Type Material Skull with nearly complete dentition, no. Ob.3684, Hungarian State Geological Survey, Budapest (Reumer 1984:Pl. 15.1).

Type Locality Villány Kalkberg (= Villány 3), Hungary, early Pleistocene, late Villanyian (MNQ17).

Distribution From the early Pliocene to the early Pleistocene (early Ruscinian to early Biharian) of Europe (Spain, France, Switzerland, Germany, The Netherlands, Poland, Italy, Slovakia, Romania, Russia, Hungary, Bulgaria, Greece) and Turkey.

Remarks Kormos (1934) gave only a description for his species and not a formal diagnosis. His description includes the following morphological features: the rostral part of the skull above the antemolars is excavated; the upper incisor has a strong talon; there are four upper antemolars, which reduce in size backward; the P4 and M1–2 show nearly straight posterior margins; the mandible is short and robust; the mental foramen is situated between the paraconid and the protoconid of the m1; the coronoid process shows concave anterior edge and an undulate tip; the coronoid spicule is strongly pronounced; the lower incisor is bicuspulate and lacks a buccal cingulum; the m3 bears a single-cusped talonid (Reumer 1984). Reumer (1984) commented that Kormos' (1934) description of the position of the mental foramen is probably wrong, as all the specimens he studied bear the mental foramen between the protoconid and the hypoconid of the m1. Reumer (1984) also proposed some characters as diagnostic: the upper incisor is not fissident; the upper molars lack a hypocone, but show a small metaloph; the lower molars bear entoconids close to the metaconids and usually high entoconid crests; the lower incisor reaches buccally the end of the p4; the anterior edge of the coronoid process shows a small spicule that results in a slight "3″-shape in side view; the external temporal fossa is divided into two roughly equal parts by the coronoid spicule; the lower condylar facet is high; the interarticular area is broad and low; all teeth are pigmented dark red. This species has been found in Maramena, where it is represented by one p4, five m1, four m2, three m3, one upper incisor, four P4, nine M1, and four M2 (Doukas et al. 1995). The same material had been reported as *Petenyia* sp. by Doukas (1989).

Sulimskia Reumer, 1984

Type Species *Sorex kretzoii* Sulimski, 1962.

Other Taxa Included *S. ziegleri* Qiu and Storch, 2000.

Distribution Pliocene of Europe (Poland, Slovakia, Hungary, Greece) and Asia (China).

Sulimskia kretzoii (Sulimski, 1962)

Nomenclatural and Taxonomical History *Sorex kretzoii* in Sulimski (1962) (new species); *Sulimskia kretzoii* in Reumer (1984) (new combination).

Type Material Rostral fragment of a skull with the mandibles (left mandible nearly complete, only lacking the angular process; right mandible with a damaged coronoid process; both mandibles with complete dentition), No. M.Z. VIII/Vm–312/1, Museum of the Earth, Polish Academy of Sciences, Warsaw (Sulimski 1962:Text-Plate 2, Fig. 10).

Type Locality Weze 1, Poland, Pliocene, Ruscinian (MN15).

Distribution From the Pliocene to the early Pleistocene (Ruscinian to Villanyian) of Europe (Germany, Poland, Slovakia, Hungary, Greece).

Remarks The diagnostic features of *S. kretzoii* given by Sulimski (1962) are the following: the dental formula is 3–1–3–3/2–0–1–3; the i2 is small, compressed, with one cusp and a strong cingulum; the p4 is high, with a robust cingulum, strongly posteriorly directed; all cingulums of the lower molars are thick and uniform; the entoconid is separated on all molars; the m3 bears a small entoconid; the mental foramen is situated in a shallow depression between the proto- and hypoconid; the coronoid process is wide and spade-like; the masseteric crest bears a spine; the pterygoid fossa is triangular, wide and deep; the upper articular facet of the condyloid process is oblique, expanded lingually; the lower articular facet of the condyloid process is long and wide, not so oblique, bears a slight notch on its upper edge and its lingual end distinctly curves downward; the I1 shows a strong talon and a cingulum, but lacks a cusp; the arrangement ratio of the upper unicuspid antemolars and premolars is: 2:2:1:1:0.5; the P3 is small, pushed below the P4; the M3 is small and reduced; the rostrum of the skull is short. Two almost complete m1 and three partial lower molars (two trigonids and one talonid) found in Apolakkia (Rhodos Island) were attributed to Blarinini indet. by Van de Weerd et al. (1982), based on the absence of an entoconid crest. The authors mentioned that two partial lower incisors, one partial P4 and one partial M1 from the locality might also belong to the same species (Van de Weerd et al. 1982:93). Reumer (1984) attributed the fragmentary lower molars from Apolakkia to *S. kretzoii*, based on their size, the absence of an entoconid crest, the anterior position of the entoconid, the deep trigonid valley and the narrow and pointed metaconid; however, he did not mention the lower incisors and upper teeth from Apolakkia.

Asoriculus Kretzoi, 1959

Type Species *Crocidura gibberodon* Petényi, 1864.

Other Taxa Included *A. similis* (Hensel, 1855); *A. corsicanus* (Bate, 1945); *A. castellarini* (Pasa, 1947); *A. tornensis* (Jánossy, 1973); *A. borsodensis* (Jánossy, 1973); *A. adroveri* (Jammot, 1977); *A. thenii* (Malez and Rabeder, 1984); *A. maghrebiensis* Rzebik-Kowalska, 1988; *A. burgioi* Masini and Sarà, 1998. Some of the species (*similis*, *corsicanus*, *burgioi*) are Plio–Pleistocene endemic insular species from Mediterranean islands (Sardinia, Corsica, Sicily) and the generic name *Nesiotites* Bate, 1945, also used for the endemic shrew from the Balearic Islands, has been proposed for them (e.g., Reumer 1984:132), an opinion not widely accepted in the literature (e.g., Masini and Sarà 1998). Furthermore, some synonymies have been proposed among the above species [e.g., *A. tornensis* and *A. borsodensis* are thought to be synonyms of *A. gibberodon* by Reumer (1984:89)]. Since this work is not a review of the genus *Asoriculus* and original material has not been studied, we give here the complete list of species that have occasionally been thought to belong to the genus.

Distribution From the late Miocene to the Pleistocene of Europe (Portugal, Spain, France, Austria, Germany, Poland, Slovakia, Czech Republic, Romania, Italy, Croatia, Bulgaria, Hungary, Greece), Asia (Turkey),and North Africa (Morocco).

Remarks *Asoriculus* was initially described as a subgenus of *Soriculus* by Kretzoi (1959) and was later raised to generic rank by the same author (Kretzoi 1962). It is a widely distributed genus in the Plio–Pleistocene of Europe, where it is represented mainly by the species *A. gibberodon*, a species also present in many Greek localities. *Asoriculus* sp. is mentioned by Doukas (2005) in Vevi, with no additional information on the available material.

Asoriculus castellarini (Pasa, 1947)

Nomenclatural and Taxonomical History *Neomys castellarini* in Pasa (1947) (new species); *Asoriculus castellarini* in Hutterer (1994) (new combination).

Type Material See Pasa 1947.

Type Locality Cava Sud, North Italy, Pleistocene, Biharian.

Distribution Pleistocene of Europe (Italy, Slovakia, Greece).

Remarks The species has a large number of features in common with *A. gibberodon*, including the size of the dental elements. There seem to be some differences in the area of the mandibular articulation, but since *A. castellarini* is not known from many localities and *A. gibberodon* shows a large variation in the mandibular articulation morphology, the differences cannot be fully evaluated. Both Reumer (1984) and Rzebik-Kowalska (2013) mentioned that *A. castellarini* might be a junior synonym of *A. gibberodon*. We here prefer to include the species as valid without, however, implying that Reumer's and Rzebik-Kowalska's opinions are rejected; the material from the type locality of the species needs to be revised before definite conclusions are drawn. Koliadimou (1996) attributed two lower incisors, three m1, five m2, five m3, one partial mandible with m1–3, one partial mandible with m2–3, one partial mandible with m1–2, one upper incisor, two P4, and two M1 from the Biharian locality Ravin Voulgarakis to *A.* cf. *castellarini*. The author based the identification on the morphology of the vertical blade of the mandible, which is closer to that of *A. castellarini* than to that of *A. gibberodon*. However, the limited number of specimens that retain this part of the mandible attributed to *A. castellarini* does not allow a good assessment of its morphological variation. Finally, as stated above, detailed study of the *A. castellarini* type material might prove that the species is synonymous with *A. gibberodon*, and thus, the Ravin Voulgarakis material should be attributed to the latter species.

Asoriculus gibberodon (Petényi, 1864)

Nomenclatural and Taxonomical History *Crocidura gibberodon* in Petényi (1864) (new species); *Soriculus gibberodon* in Kretzoi (1956) (new combination); *Soriculus* (*Asoriculus*) *gibberodon* in Kretzoi (1959) (new subgenus); *Asoriculus gibberodon* in Kretzoi (1962) (new combination); *Episoriculus gibberodon* in Repenning (1967) (new combination). *Soriculus kubinyii* Kormos, 1934, is considered a junior synonym of *A. gibberodon*, according to Reumer (1984).

Type Material The type material of *Crocidura gibberodon* Petényi, 1864, from Beremend has been lost and the type material of *Soriculus kubinyii* Kormos, 1934, from Villány 3 (Hungary) has been proposed as a neotype (Reumer 1984): skull with nearly complete dentition, Ob.3685, Hungarian State Geological Survey, Budapest (Reumer 1984:Pl. 27.3).

Type Locality Villány Kalkberg (Villány 3), Hungary, Pliocene, Villanyian (late MN17) (original locality of the neotype, type locality of *Soriculus kubinyii* Kormos, 1934).

Distribution From the late Miocene (Turolian, MN13) to the Pleistocene of Europe (Spain, France, Austria, Germany, Poland, Romania, Slovakia, Hungary, Italy, Bulgaria, Greece) and Turkey.

Remarks Reumer (1984) mentioned that some parts of Kormos' (1934) original diagnosis for his species *S. kubinyii* can be used as diagnostic features for *A. gibberodon*. These include the following: the upper incisor is fissident, and the lower one bearing weak cuspules; pigmentation is only present at some tips. Furthermore, Reumer (1984) gave an emended diagnosis, according to which the species is rather small and bears weakly pigmented teeth; it bears four upper antemolars, of which the A4 is variable in its development; the upper molars show a variable morphology, with a moderate posterior emargination; the lower incisor is bicuspulate and bears a well-developed buccal cingulum; the a1 is elongate; the lower molars have high entoconid crests; the m3 shows a talonid basin; the mental foramen is situated below the posterior half of the m1. A large number of Greek localities have yielded dental elements of this species. De Bruijn et al. (1970) reported the presence of one complete mandible, three partial mandibles with m1–3, three partial maxillas and numerous isolated lower and upper teeth of *A. gibberodon* in Maritsa 1 (Rhodos Island). The locality Maramena has yielded five lower incisors, 17 m1, 20 m2, 10 m3, six upper incisors, five P4, nine M1, and 12 M2 of this species (Doukas et al., 1995; material previously mentioned as *Episoriculus* sp. by Doukas, 1989). One lower incisor, one m1, one m2, and one M2 from Kessani and one lower incisor, three m1, two upper incisors, nine P4, four M1, seven M2, and one M3 from Nea Silata have also been assigned to this species (Vasileiadou et al. 2012 and Vasileiadou 2001, respectively). Van de Weerd et al. (1982) have assigned one fragmentary lower incisor, one m1, and one m2 from Apolakkia (Rhodos Island), and Reumer and Doukas (1985) have assigned six lower incisors, one p4, 11 m1, six m2, one m3, 11 upper incisors, ten P4, 17 M1, 16 M2, two M3, and nine condyles from Tourkobounia 1 to *A. gibberodon*. Finally, one lower incisor, four m1, two m2, three upper incisors, eight M1, and three M2 from the Biharian locality Marathoussa (Chalkidiki, N Greece) also belong to this species (Koufos et al. 2001).

Deinsdorfia **Heller, 1963**

Type Species *Sorex hibbardi* Sulimski, 1962.

Other Taxa Included *D. fallax* (Heller, 1936); *D. kordosi* Reumer, 1984; *D. janossyi* Reumer, 1984; *D. insperata* Rzebik-Kowalska, 1990; *D. reumeri* Rzebik-Kowalska, 1990; *D. kerkhoffi* Reumer, 1995 in Doukas et al. (1995); *D. doukasi* Furió and Mein, 2008.

Distribution From the late Miocene to the early Pleistocene of Europe (Spain, France, Switzerland, Germany, Poland, Slovakia, Romania, Bulgaria, Hungary, Greece).

★*Deinsdorfia kerkhoffi* Reumer in Doukas et al. (1995)

Type Material Partial ramus with m1–3, MA 6092, Department of Paleontology and Historical Geology, University of Athens (Doukas et al. 1995:Pl. 8.6).

Type Locality Maramena, Strimon basin, Greece, Miocene/Pliocene boundary.

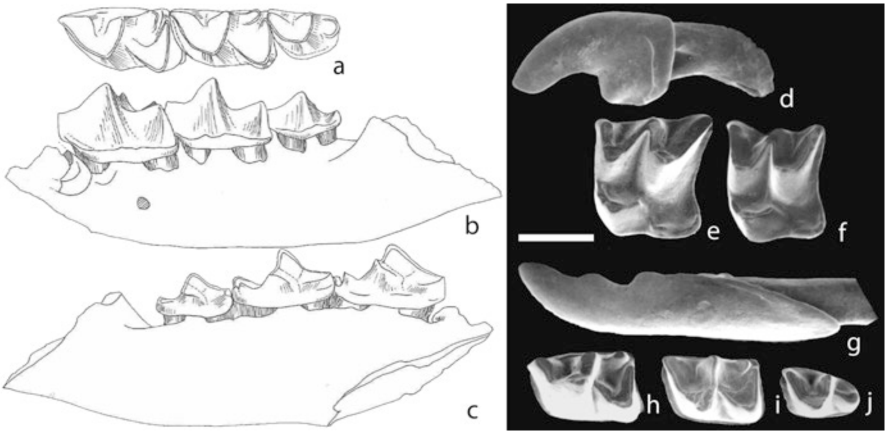

Fig. 9 *Deinsdorfia kerkhoffi* from Maramena (type locality; **a**–**c**; drawings CD, personal data.) and Silata (**d**–**j**; images KV, personal data). (**a**) Partial right mandible with m1–3 holotype—occlusal view, (**b**) same—buccal view, (**c**) same—lingual view, (**d**) I sup., (**e**) M1, (**f**) M2, (**g**) i inf., (**h**) m1, (**i**) m2, (**j**) m3. All specimens are figured as left; **a**–**c**, **f**, **h** are reversed. Scale bar equals 1 mm

Distribution From the late Miocene/early Pliocene (Turolian/Ruscinian boundary) of Greece and Bulgaria (*D.* cf. *kerkhoffi* in Dorkovo).

Remarks The diagnosis of the species in Doukas et al. (1995) includes the following features: *Deinsdorfia* species of a large size; the lower incisor bears three weak cuspules; the lower molars bear short talonid and moderately high entoconid crest; the m3 has a reduced, single-cusped talonid; the upper incisor is not fissident; the upper molars bear a metaloph and a low and small hypoconal flange, surrounded by a weak cingular ridge; the M3 is relatively long and has a small pointed parastyle; the coronoid process has a forward-pointing apex and its lower part leans backward; the condyle is large; the coronoid spicule is well-developed. Apart from the holotype, the type locality has also yielded (Fig. 9) three lower incisors, one p4, 10 m1, 14 m2, four m3, eight upper incisors, two upper antemolars, four P4, 17 M1, 11 M2, one M3, and three rami with condyles (Doukas et al. 1995). This species has also been reported from two localities in N Greece of similar age with Maramena (Turolian/Ruscinian boundary): 11 lower incisors, nine m1, 12 m2, eight m3, 12 upper incisors, two P4, seven M1, and 12 M2 have been found in Nea Silata (Vasileiadou 2001) and one m2, one m1, and one M1 in Kessani (Vasileiadou et al. 2012).

Beremendia Kormos, 1934

Type Species *Beremendia fissidens* (Petényi, 1864).

Other Taxa Included *B. pohaiensis* (Kowalski and Li, 1963); *B. minor* Rzebik-Kowalska, 1976.

Distribution From the early Pliocene to the middle Pleistocene of Europe (Spain, France, Switzerland, Austria, Germany, The Netherlands, United Kingdom, Poland, Italy, Czech Republic, Slovakia, Romania, Russia, Hungary, Bulgaria, Greece) and Asia (Siberia and China).

Beremendia fissidens (Petényi, 1864)

Nomenclatural and Taxonomical History *Crossopus fissidens* in Petényi (1864) (new species); *Neomys fissidens* in Kormos (1911) (new combination); *Beremendia fissidens* in Kormos (1930) (new combination). *Beremendia ucrainica* (Pidoplichko, 1956) is a junior synonym of *B. fissidens*, according to Rzebik-Kowalska (1976).

Type Material (syntypes) Six maxillary and 37 mandibular fragments, Hungarian Natural History Museum, Department of Paleontology and Geology (Petényi 1864:Pl. 1.5a–o).

Type Locality Beremend limestone quarry (locality 2), Hungary, Pliocene, early Villanyian (MN16).

Distribution Early Pliocene to middle Pleistocene of Europe.

Remarks According to the original diagnosis (in Old Hungarian) by Petényi (1864), this species has a bifid upper incisor and an acuspulate lower one (Botka and Mészáros 2014). Botka and Mészáros (2014) gave an emended diagnosis that includes the following: the teeth are intensively pigmented dark red; the upper incisor is strongly fissident and shows a bifid apex; there are four upper antemolars; the A1–2 have almost the same size, the A3 is smaller, and the A4 is even smaller, hidden and not visible in buccal view or might be completely absent; the P4 and M1–2 show a moderate posterior emargination; the M1 has a moderately developed parastyle; the M3 is relatively small; the lower incisor is grooved and acuspulate, with an upward curved apex; the a2 is bicuspid and has a posterolingual basin; the m3 is reduced; the ramus is strong and massive; the coronoid process is robust and anterolaterally curved with a variable angle; the angular process is short and flat; the external pterygoid fossa is more or less deeply pocketed, with a narrow upper facet of which the shape varies from elliptic to oval; the interarticular area is broad and shows a lingual margin; the lower facet leans strongly anteriorly and is invisible in buccal view; the internal temporal fossa is small, deep, and pocketed. One upper antemolar from Tourkobounia 1, one lower incisor, two lower a1, two m1, two m3, two partial mandibles with m1, two upper incisors, three M1, and one M2 from Ravin Voulgarakis and one m1, one partial mandible with m1, two P4, two M1, one M2, and one M3 from Marathoussa (N Greece) have been attributed to this species (Reumer and Doukas 1985; Koliadimou 1996; Koufos et al. 2001).

Sorex Linnaeus, 1758

Type Species *Sorex araneus* Linnaeus, 1758.

Other Taxa Included As reported by Reumer (1984:22): "*the genus* Sorex *has long been the waste-basket for soricid remains. Large numbers of* 'Sorex' *species have been described, many of which belong to other genera, tribes or even to other subfamilies*." Although many of these issues have been resolved at the end of the last century and at the beginning of the present, a revision of the fossil material attributed to this genus is certainly needed. For the list of extant *Sorex* species see Hutterer (2005). Many of the extant species can be found in fossil assemblages correlated back to the Pliocene (e.g., *S. minutus* MN15, today). According to Rzebik-Kowalska (2008), at least 16 extinct forms have been described from Asia, 34 from North America and 28 from Europe. One of the extinct subgenera of *Sorex* is *Drepanosorex* Kretzoi, 1941, originally described as a separate genus, but later included as a subgenus in *Sorex* by Reumer (1985), an opinion shared by many authors since then and also followed herein. The subgenus includes five species from the Pleistocene of Europe: *S.* (*D.*) *savini* Hinton, 1911, *S.* (*D.*) *margaritodon* Kormos, 1930, *S.* (*D.*) *praearaneus* Kormos, 1934, *S.* (*D.*) *austriacus* Kormos, 1937, *S.* (*D.*) *rupestris* Zaitsev and Baryshnikov, 2002.

Distribution From the early Pliocene (Ruscinian) to the present of Eurasia and North America.

Remarks The oldest occurrence of *Sorex* in Greece is *Sorex* sp. from the Turolian/Ruscinian boundary locality Maramena, where the genus is represented by one broken m1, one toothless ramus, two upper incisors, two P4, seven M1, and four M2 (Doukas et al. 1995; material previously mentioned as "*Sorex*" sp. in Doukas 1989). The authors discussed that this *Sorex* is of medium size, larger than both *S. minutus* and the early Ruscinian *S. bor*, but similar in size with the late Ruscinian *S. bor* from Osztramos 7, with which both morphological similarities and differences can be observed. *Sorex* is a common element of Greek Pleistocene localities, where it is present with the extant species *S. minutus* Linnaeus, 1766 (Eurasian pygmy shrew) and *S. araneus* Linnaeus, 1758 (common Eurasian shrew). The former species is represented by six lower incisors, four m1, nine m2, one m3, one partial mandible, ten upper incisors, two P4, six M1, and one M2 from Marathoussa (N Greece; Koufos et al. 2001), one lower incisor, two m1 and five partial mandibles from Arnissa (Mayhew 1978), two partial mandibles with m2, one upper incisor, and two P4 from Loutra Almopias Cave LAC and one partial mandible with i–m1, one partial mandible with m1–3, one upper incisor, one M2, and one partial maxilla with P4–M1 from Loutra Almopias Cave LAC Ia (Chatzopoulou 2014), whereas Koliadimou (1996) assigned one lower incisor, one m1, two partial mandibles with m1–2, one partial mandible with m1–3, one upper incisor, three M1, and one partial maxilla with P4–M1 from Ravin Voulgarakis to *S.* cf. *minutus*; the dental elements show similarities with *S. minutus*, but some metrical parameters are slightly higher than those of the corresponding elements from Plio–Pleistocene Hungarian and Dutch localities, hence the uncertain identification. *Sorex araneus* is represented in Arnissa by one lower incisor, one partial mandible, one P4, and one M2 (Mayhew 1978), in Loutra Almopias Cave LAC by one m1, one M1 and one M2 and in Loutra Almopias Cave LAC Ia by one p4, one partial mandible with i–p4, one partial mandible with m2, one upper incisor, one P4, one M1, one partial maxilla with A2–3, one partial maxilla with P4, and one partial maxilla with M1–2 (Chatzopoulou 2014).

Sorex (Drepanosorex) praearaneus Kormos, 1934

Nomenclatural and Taxonomical History *Sorex praearaneus* in Kormos (1934) (new species); *Drepanosorex* n. g. *praearaneus* in Kretzoi (1941) (new combination); *Sorex* (*Drepanosorex*) *praearaneus* in Reumer (1985). *Sorex pachyodon* Pasa, 1947, is a junior synonym of *S. praearaneus*, according to Reumer (1985).

Type Material Skull with partial dentition, no. Ob.3681, Hungarian State Geological Survey, Budapest (Kormos 1934:Fig. 32; Reumer 1984:Pl. 9.1).

Type Locality Villány Kalkberg (= Villány 3), Hungary, early Pleistocene, late Villanyian (MNQ17).

Distribution From the early to the middle Pleistocene of Europe (Spain, The Netherlands, Poland, Italy, Czech Republic, Slovakia, Romania, Hungary, Greece).

Remarks Reumer (1984) used the following characters given by Kormos (1934) as diagnostic features for the species: the A5 is smaller than the A4; the mental foramen is situated below the posterior edge of the p4; the external temporal fossa reaches the upper condylar facet; the internal temporal fossa reaches half-way up the coronoid process. Reumer (1984) gave an emended diagnosis for the species, according to which *praearaneus* is a small *Drepanosorex* species with fissident upper incisor, slightly exoedaenodont dentition, five upper antemolars of which the A1–2 are the largest, and the A4 is slightly smaller than the A3 and A5, poorly developed hypocones on the P4 and the upper molars, a tricuspulate lower incisor with bulbous cuspules and a well-developed talonid on the m3. Koufos et al. (2001) described six lower incisors, one a1, six p4, six m1, nine m2, six m3, ten partial mandibles, 12 upper incisors, 14 upper antemolars, six P4, three M1, eight M2, and four M3 of *S.* (*D.*) *praearaneus* from Marathoussa (N Greece); the small degree of exoedaenodonty in the antemolars and the small size of the dental elements assigned them to the most primitive *Drepanosorex* species known. Furthermore, Koliadimou (1996) described three lower incisors, two p2, one partial mandible with p4–m2, three upper incisors, and two P4 of *S.* (*D.*) cf. *praearaneus* from Ravin Voulgarakis; the reason for the uncertain determination is the slightly larger width of the lower premolar and molars from Ravin Voulgarakis in comparison with that of the corresponding teeth from the Hungarian and Dutch materials described by Reumer (1984).

Neomys Kaup, 1829

Type Species *Sorex fodiens* Pennant, 1771 (extant).

Other Included Taxa At present, there are three extant species of *Neomys* widespread in Eurasia: *N. fodiens* (Pennant, 1771) (Eurasian water shrew), *N. anomalus* Cabrera, 1907 (Mediterranean water shrew) and *N. teres* Miller, 1908 (Transcaucasian water shrew). Furthermore, four extinct species have been described up to now from

European fossil localities: *N. newtoni* Hinton, 1911, *N. browni* Hinton, 1911, *N. hintoni* Zaitsev and Baryshnikov, 2002, and *N. intermedius* Brunner, 1952.

Distribution From the early Pliocene (Ruscinian) to the present in Eurasia and North America.

Remarks The presence of *Neomys* sp. in the Biharian locality Tourkobounia 2 (one upper incisor) has been reported by Reumer and Doukas (1985), as well as in the late Pleistocene localities Loutra Almopias Cave LAC (one partial mandible with i–m1, one partial mandible with m1, two upper incisors, one P4) and Loutra Almopias Cave LAC Ia (three lower incisors, two m1, one m3, one partial mandible with p4–m3, one partial mandible with m1–2, one partial mandible with m2, three upper incisors, one partial maxilla with I–A2, one partial maxilla with I–A1, one partial maxilla with P4–M1, one partial maxilla with P4–M2, one partial maxilla with M1–2, one partial maxilla with M2) has been reported by Chatzopoulou (2014). The species from the Loutra Almopias Cave could belong to either *N. fodiens* or *N. anomalus*, as it shows metrical and morphological similarities with both; the difference between the two species is located mainly in the height of the coronoid process, an area which is not preserved in the Loutra Almopias Cave material (Chatzopoulou 2014).

Subfamily Crocidurinae Milne-Edwards, 1872

Type Genus *Crocidura* Wagler, 1832.

Crocidura Wagler, 1832

Type Species *Sorex leucodon* Hermann, 1780.

Other Included Taxa Today there are at least 183 valid *Crocidura* species living in South Eurasia and Africa (for the list of extant species see Hutterer 2005). Some of them are present in Greek Pleistocene fossil assemblages (see below).

Distribution From the Pliocene (Ruscinian) to the present of Eurasia and Africa.

Remarks The oldest occurrence of *Crocidura* in Europe seems to be the single m3 described as *Crocidura* sp. from the Pliocene locality Apolakkia, showing the characteristic reduction of the talonid to a single cuspid, i.e., the hypoconid (Van de Weerd et al. 1982; Reumer 1984). Furthermore, a number of fossil assemblages have been described as *Crocidura* sp. from Greek Pliocene–Pleistocene localities: one lower incisor, two m1, four m2, two m3, one upper incisor, one M1, and one fragmentary M2 from Tourkobounia 1 were described by Reumer and Doukas (1985) and are considered as the oldest *Crocidura* of the European mainland; Kotsakis et al. (1980) listed two species of *Crocidura* sp. for Kalymnos without giving details on the material; Van der Geer et al. (2014) figured a partial mandible with m1–3 and a partial maxilla with P4–M2 found in the Faculty of Geosciences, Utrecht University, The Netherlands, together with material from Naxos that had never been reported before; Tsoukala et al. (2006) assigned to *Crocidura* sp. a partial mandible with m2, one M1 and two M2 from Kitseli pothole. Additionally, three extant species have been found in late Pleistocene localities: the greater white-toothed shrew *C. russula* is represented by two partial mandibles at Arnissa (Mayhew 1978); the bicoloured shrew *C. leucodon* is known with two partial mandibles, two upper incisors, two P4, two M1, and two M2 from Arnissa (Mayhew 1978), four lower incisors, one a1, six m1, three m2, one m3, one partial mandible with i–a2, one partial mandible with m1–2, seven upper incisors, one A1, one M1, and one M2 from Loutra Almopias Cave LAC and one partial mandible with i–m2, one upper incisor, and one partial maxilla with A2–M2 from Loutra Almopias Cave LAC Ia (Chatzopoulou 2014); finally, the lesser white-toothed shrew *C. suaveolens* is known with two m2, one partial mandible with m1–2, one upper incisor, and two M1 from Loutra Almopias Cave LAC and one partial mandible with i–m1, three partial mandibles with m1–2 and one upper incisor from Loutra Almopias Cave LAC Ia (Chatzopoulou 2014). The endemic Cretan shrew *C. zimmermanni* has been reported in late Pleistocene localities in Crete (Lyras et al. this volume).

Crocidura kornfeldi Kormos, 1934

Type Material Skull with partial dentition (the left A4 got lost after 1934), no. Ob. 3686, Hungarian State Geological Survey, Budapest (Reumer 1984:Pl. 1.1).

Type Locality Villány Kalkberg (= Villány 3), Hungary, early Pleistocene, late Villanyian (MNQ17).

Distribution From the early to the middle Pleistocene of Europe (Spain, Austria, Czech Republic, Slovakia, Romania, Hungary, Greece).

Remarks Since Kormos (1934) did not give a formal diagnosis but only a description for his new species, Reumer (1984) separated some of the features given by Kormos as diagnostic: the P4, M1 and M2 are relatively short and broad and the molars show a short emargination; the lower incisor is acuspulate; the al–2 are broad; a thick bar is present between the anterior base of the coronoid process and the condyle, under the internal temporal fossa, below which there is a deep groove. Furthermore, Reumer (1984) gave an emended diagnosis, according to which *kornfeldi* is a fairly small *Crocidura* species with relatively short and broad P4 and molars. Furthermore, the A1 is much larger than the A2–3, while the A2 is slightly smaller than the A3, which is nearly as high as the parastyle of the P4 in buccal view. The P4 has a buccally situated protocone far from the antero-lingual corner of the premolar. The lower molars bear a narrow, undulating cingulum. The ascending ramus is robust, the internal temporal fossa is bordered ventrally by a thick bar, and the condyle is relatively large. There are several Greek localities that have revealed elements of this extinct *Crocidura*. Three lower incisors, two p4, 16 m1, 11 m2, two m3, two condyles, five upper incisors, one A1, one A2/3, two P4, five M1, and two M2 have been reported from Tourkobounia 2, one m1, four m2, one m3, and two condyles from Tourkobounia 3, and two m1, one m2, one m3, one condyle and one P4 from Tourkobounia 5 (Reumer and Doukas 1985). Koliadimou (1996) described one mandibular fragment with m1–m3, one with m1–m2, one upper incisor, and five M1 from the late Biharian locality Rema Voulgarakis. Finally, the richest *C. kornfeldi* material has been reported from Marathoussa (N Greece) by Koufos et al. (2001): five lower incisors, four a1, six p4, 12 m1, 10 m2, five m3, 13 upper incisors, six P4, eight A1, five A2/3, five M1, 11 M2, and one M3. The materials from Ravin Voulgarakis and Marathoussa are morphologically identical and metrically very close to *C. kornfeldi* from Osztramos 3/2 described by Reumer (1984) (Koufos et al. 2001).

6 Concluding Remarks

The Greek insectivore fossil record, even though represented by fragmentary or inadequately studied assemblages, can give some valuable information on the evolution of the faunas in the southern part of the Balkans. The highest peak in the Greek eulipotyphlan diversity occurred during the early Miocene, when all six families were present (with at least three erinaceid, two dimylid, one heterosoricid, one plesiosoricid, three talpid, and two soricid species), whereas by the late Miocene, only the three extant ones remained. As the extinct families disappeared, soricids started showing a larger diversity (with at least five species in the late Miocene of Greece and afterwards, versus two species in the early Miocene). Extant genera started emerging in the late Miocene in Greece (*Erinaceus*, *Talpa*, *Blarinella*, *Sorex*), and by the end of the early Pleistocene, all extinct genera had disappeared from the Greek faunas (last representatives being *Asoriculus* and *Beremendia*). All extant genera present in Greece since the early Pleistocene are also represented today in the area, albeit some of them by different species (e.g., *Erinaceus europaeus* in the Pleistocene but *Erinaceus roumanicus* today). The importance of the Greek insectivore fossil record is also reflected in the description of eight valid new species from Greek Neogene faunas (*Galerix symeonidisi*, *Parasorex kostakii*, *Schizogalerix macedonica*, *Myxomygale engesseri*, *Desmanella dubia*, *Heterosorex ruemkeae*, *Amblycoptus jessiae*, *Deinsdorfia kerkhoffi*).

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Editorial Note The works in this book (lagomorphs, rodents, insectivores) are the last of Katerina, who left us recently after a long battle with cancer. Katerina deeply believed in this collective project and worked with passion and dedication for its implementation, giving even her very last strength. Unfortunately, she could not deal with the constructive comments and suggestions of the reviewers, a task undertaken by the co-authors of the articles and her friends in the same scientific field.

Appendix

Occurrences of insectivores in Greece. Locality numbers refer to the collection numbers of the PaleoBiology Database (PBDB). Type localities are marked with boldface

Localities$^{\text{PBDB no.}}$	Age (MN, GPTS)	Taxon
Loutra Almopias Cave LAC Ia^{204954}	Younger Dryas (13,000–14,500 BP)	*Talpa europaea*[1] *Sorex araneus*[1] *Sorex minutus*[1] *Neomys* sp.[1] *Crocidura leucodon*[1] *Crocidura suaveolens*[1]
Kitseli pothole^{204955}	Late Pleistocene	*Crocidura* sp.[2]
Naxos^{203848}	Late Pleistocene	*Crocidura* sp.[3]
Arnissa^{204957}	Late Pleistocene [penultimate interglacial (Eemian) age]	*Sorex araneus*[4] *Sorex minutus*[4] *Crocidura russula*[4] *Crocidura leucodon*[4]
Loutra Almopias Cave LAC^{203847}	Middle Würm (42,500 BP)	*Erinaceus* cf. *europaeus*[1] *Talpa europaea*[1] *Talpa* sp.[1] *Sorex araneus*[1] *Sorex minutus*[1] *Neomys* sp.[1] *Crocidura leucodon*[1] *Crocidura suaveolens*[1]
Varkiza 2^{204167}	Middle or late Pleistocene	Soricidae indet.[5]
Choremi 4^{200082}	Middle Pleistocene (late Biharian, ~580–620 ky)	Soricidae indet.[6]
Choremi 1^{200079}	Middle Pleistocene, (late Biharian, ~840–880 ky)	Soricidae indet.[6]
Apollonia^{34784}	Pleistocene (MNQ20)	*Erinaceus europaeus*[7]
Ravin Voulgarakis^{34783}	Pleistocene (MNQ20)	*Talpa* sp.[7] *Asoriculus* cf. *castellarini*[7] *Beremendia fissidens*[7] *Sorex* cf. *minutus*[7] *Sorex* cf. *praearaneus*[7] *Crocidura kornfeldi*[7]
Kalymnos^{34770}	Early Pleistocene (Biharian, MNQ19)	*Crocidura* sp. (two species)[8]
Marathoussa^{34765}	Early Pleistocene (Biharian, MNQ19)	Desmaninae indet.[9] *Asoriculus gibberodon*[9] *Beremendia fissidens*[9] *Sorex minutus*[9] *Sorex praearaneus*[9] *Crocidura kornfeldi*[9]
Tourkovounia 5^{34592}	Early Pleistocene (Biharian)	*Erinaceus praeglacialis*[10] *Crocidura kornfeldi*[10]
Tourkovounia 3^{34592}	Early Pleistocene (Biharian)	*Crocidura kornfeldi*[10]

(continued)

Localities[PBDB no.]	Age (MN, GPTS)	Taxon
Tourkovounia 2[34767]	Early Pleistocene (Biharian, MNQ19)	*Crocidura kornfeldi*[10] *Neomys* sp.[10]
Limni 6[34590]	Pliocene (Villanyian, MN16)	*Archaeodesmana bifida*[11] *Desmanella* sp.[12] Soricidae indet.[12]
Tourkovounia 1[34589]	Pliocene (Villanyian, MN16)	*Erinaceus* sp.[10] *Asoriculus gibberodon*[10] *Beremendia fissidens*[10] *Crocidura* sp.[10]
Ptolemais 3[35088]	Pliocene (late Ruscinian, MN15, ~4.95–4.77 Ma)	*Archaeodesmana getica*[11–12]
Vevi[214354]	Pliocene (late Ruscinian, MN15)	*Archaeodesmana* sp.[12] Talpidae indet.[12] *Asoriculus* sp.[12] cf. *Blarinella* sp.[12]
Apolakkia[202499]	Pliocene (late Ruscinian, MN15)	Galericinae indet.[12] *Asoriculus gibberodon*[14] *Blarinella* cf. *europaea*[14, 15] *Sulimskia kretzoii*[14, 15] *Crocidura* sp.[14, 15] Echinosoricinae indet.[12]
Ptolemais 1[35086]	Pliocene (uppermost part of the early Ruscinian, MN14, ~5.04–4.95 Ma)	*Archaeodesmana verestchagini*[11] Soricidae indet.[12]
Kardia[35087]	Pliocene (early Ruscinian, MN14, ~5.23–5.22 Ma)	*Archaeodesmana verestchagini*[11] *Archaeodesmana getica*[11]
Spilia 0, 1[31931,31,299]	Pliocene (early Ruscinian, MN14, ~5.23–4.95 Ma)	*Archaeodesmana verestchagini*[11] Soricidae indet.[16]
Nea Silata[191612]	Miocene/Pliocene, (Turolian/Ruscinian, MN13/14, ~5.4–5.23 Ma)	*Erinaceus* sp.[18, 19] *Amblycoptus* cf. *jessiae*[18, 19] *Asoriculus gibberodon*[18, 19] *Deinsdorfia kerkhoffi*[18, 19]
Maramena[32189][a]	Miocene/Pliocene, (Turolian/Ruscinian, MN13/14, ~5.4–5.23 Ma)	*Erinaceus samsonowiczi*[16, 20] ***Schizogalerix macedonica***[20] *Archaeodesmana getica*[11, 20] *Desmanella dubia* [20] *Urotrichus* sp.[20] *Talpa fossilis*[20] ***Amblycoptus jessiae***[20] *Asoriculus gibberodon*[16, 20] *Sorex* sp.[16, 20] *Petenyia hungarica*[16, 20] ***Deinsdorfia kerkhoffi***[20]
Kessani[205296–7]	Miocene/Pliocene, (Turolian/Ruscinian, MN13/14, ~5.4–5.23 Ma)	*Asoriculus gibberodon*[21] *Deinsdorfia kerkhoffi*[21] Soricidae indet.[21]
Maritsa 1[68046]	Late Miocene (Turolian, MN13)	*Asoriculus gibberodon*[22] *Blarinella dubia*[22, 15]

(continued)

Localities^PBDB no.^	Age (MN, GPTS)	Taxon
Monasteri[31940]	Late Miocene (Turolian, uppermost MN13, ~5.96–5.33 Ma)	Soricidae indet.[16]
Paliambela-A[205335]	Late Miocene (Turolian, uppermost MN13, ~5.96–5.33 Ma)	Soricidae indet.[23, 24]
Pikermi[68214]	Late Miocene (end of middle Turolian, MN 12, ~7.1 Ma)	*Schizogalerix moedlingensis*[26, 20]
Chomateri[195562]	Late Miocene (Turolian, MN12)	*Schizogalerix moedlingensis*[27] *Schizogalerix zapfei* = ***Galerix atticus*[27]** ***Desmanella dubia*[27]**
Samos-S3[205351]	Late Miocene (middle Turolian, MN12, near the fossil level MYT, ~7.3 Ma, Chron C3Br.2r)	*Schizogalerix zapfei*[28]
Lefkon[31223]	Late Miocene (latest Vallesian, MN10)	*Schizogalerix* sp.[16] *Desmanella* sp.[16] *Crusafontina* cf. *kormosi*[30]
Biodrak[205342]	Late Miocene (latest Vallesian, MN10)	*Schizogalerix* sp.[27, 12] *Crusafontina* cf. *endemica*[30]
Kastellios K1[205360]	Late Miocene (late Vallesian, MN10, 9.3–9.1 Ma, C4Ar.1r)	*Schizogalerix* sp.[32]
Elaiochoria[219100]	Late Miocene (late Vallesian to early Turolian, MN10–11)	Soricidae indet.[33]
Plakias[183151]	Late Miocene (early Vallesian, lower part of MN9, ~9.9 Ma or 9.311–9.6 Ma)	*Lantanotherium sanmigueli*[34] Galericinae indet.[34] cf. *Paenelimnoecus* sp.[34]
Chryssavgi 1[205366]	Middle Miocene (late Astaracian, MN7 and 8)	cf. *Schizogalerix* sp.[7] *Desmanodon minor*[7]
Thymiana C[205390]	Middle Miocene (Orleanian, MN5, ~15.5 Ma, interval of Chrons C5Bn.1n—C5Cr)	*Schizogalerix* sp.[36]
Thymiana A[205389]	Middle Miocene (Orleanian, MN5, ~15.5 Ma, interval of Chrons C5Bn.1n, C5Cr)	*Schizogalerix* sp.[36] Soricidae indet.[36]
Antonios[73861]	Early Miocene (Orleanian, MN4/5)	*Schizogalerix* sp.[37] *Desmanodon* sp.[37] Crocidosoricinae indet.[37]
Komotini[68085]	Early Miocene (Orleanian? MN4)	*Galerix* sp.[38]
Moschopotamos[208601]	Early Miocene (Orleanian, MN4)	Eulipotyphla indet.[39]
Karydia[69435]	Early Miocene (Orleanian, MN4)	***Parasorex kostakii*[38]** *Plesiodimylus* aff. *crassidens*[38] *Heterosorex* sp.[38] *Plesiosorex* sp.[38] *Myxomygale* cf. *hutchisoni*[38] *Desmanodon antiquus*[38] *Lartetium* cf. *dehmi*[38] *Paenelimnoecus* sp.[38]

(continued)

Localities$^{\text{PBDB no.}}$	Age (MN, GPTS)	Taxon
Aliveri^{68032}	Early Miocene (Orleanian, MN4, 18–17.5 Ma)	***Galerix symeonidisi***[40] *Plesiodimylus huerzeleri*[40, 41] ***Heterosorex ruemkeae***[40] ***Myxomygale engesseri***[40] *Desmanodon antiquus*[40, 38] Soricidae indet.[40]
Lapsarna^{186558}	Early Miocene (Orleanian, MN4, older than 18.4 ± 0.5 Ma)	Erinaceidae indet.[42] Talpidae indet.[42] Soricidae indet.[42]
Kyprinos^{196839}	late Oligocene	*Dinosorex* sp.[43] Talpidae indet.[43]

MN Mammal Neogene Zone, *MNQ* Mammal Quaternary Zone

[1]Chatzopoulou (2014), [2]Tsoukala et al. (2006), [3]van der Geer et al. (2014), [4]Mayhew (1978), [5]van de Weerd (1973), [6]van Vugt et al. (2000), [7]Koliadimou (1996), [8]Kotsakis et al. (1980), [9]Koufos et al. (2001), [10]Reumer and Doukas (1985), [11]Rümke (1985), [12]Doukas (2005), [13]Hordijk and De Bruijn (2009), [14]van de Weerd et al. (1982), [15]Reumer (1984), [16]Doukas (1989), [17]Koufos and Vasileiadou (2015), [18]Vasileiadou (2001), [19]Vasileiadou et al. (2003), [20]Doukas et al. (1995), [21]Vasileiadou et al. (2012), [22]de Bruijn et al. (1970), [23]Sylvestrou (2002), [24]Sylvestrou and Kostopoulos (2007), [25]Koufos (2013), [26]Thenius (1952), [27]Rümke (1976), [28]Black et al. (1980), [29]Koufos et al. (2009), [30]van Dam (2004), [31]Zachariasse et al. (2011), [32]Furió et al. (2014), [33]Hulva et al. (2007), [34]de Bruijn et al. (2012), [35]Koufos (2006), [36]de Bonis et al. (1997), [37]Vasileiadou and Koufos (2005), [38]Doukas and van den Hoek Ostende (2006), [39]Benda and Steffens (1981), [40]Doukas (1986), [41]van den Hoek Ostende et al. (2015), [42]Vasileiadou and Zouros (2012), [43]Doukas and Theocharopoulos (1999)

[a]The insectivore fauna from the locality Maramena includes also the material from Ano Metochi 2–3, as the two localities are very close by and the faunas are thought to be identical (Doukas 2005)

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