



THE FOSSIL RECORD OF FAT DORMICE: A REVIEW OF THE PAST DIVERSITY AND DISTRIBUTION OF THE GENUS *GLIS*

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Abstract: The familiar fat dormice, *Glis*, are among the most characteristic European rodents. With only two living species, their modern diversity represents but relics of an impressive past radiation, dating back to the Oligocene epoch, some 30 Ma. Throughout most of their evolutionary history, members of the genus have evolved little from what is considered the primitive glirid morphotype. In this sense, fat dormice might be called living fossils. This paper discusses the past diversity of the genus *Glis*, reviewing our knowledge of all eleven currently recognized species and some problematic taxa. The Early Miocene *G. complicatus* is identified as a full species, distinct from morphologically more derived and geologically younger *G. minor*. The Middle Pleistocene *G. percoi* is synonymised with *G. mihevci*. Morphological trends within the genus include an increase in size, a tendency towards more heavily built, isolated, straightened and transversal lophs on more flattened occlusal surfaces, rudimentary accessory ridges, weaker anterotropes, and more parallel protoloph and metaloph of M1–2.

Key words: *Glis*, fat dormice, biogeography, ecology, taxonomy, Cenozoic

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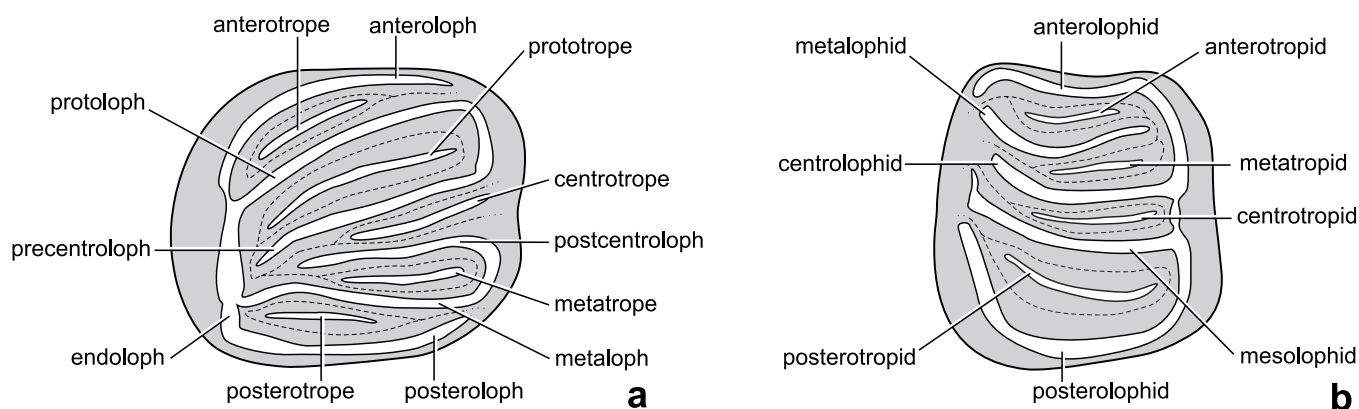
Introduction

The genus *Glis* is predominantly a European radiation of large-sized glirids, with but two surviving species: the edible dormouse (*G. glis*) of Europe and western Turkey, and the Iranian fat dormouse (*G. persicus*) from the southern rim of the Caspian Sea (Rossolimo et al. 2001, Kryštufek 2010, Kryštufek et al. 2021). Among the living genera within the family Gliridae, the fat dormice are the most ancient. The genus is believed to have arisen in the middle Oligocene, some 30 Ma, when no other living genera of glirids had yet emerged (Ünay 1989, de Bruijn 1998). Furthermore, fat dormice still retain some features that are primitive among all glirids, to the extent that the living *Glis* are often used to illustrate a morphologically generalized forest-dwelling glirid. They possess a massive skull with a deep rostrum, small auditory bullae, and a primitively high mandible lacking an angular foramen, the features characterizing the ancestral morphotype of Gliridae (Vianey-Liaud 1974, Rossolimo et al. 2001). In living *Glis*, however, these primitive features are combined with a set of derived craniodental characters, which suggest a rather crownward position of the fat dormice in morphology-based phylogenies (Wahlert et al. 1993), and serve to distinguish the representatives of the genus in the

fossil record. With nine to ten currently recognized extinct species, the fossil record of *Glis* is sparse. Prior to the second half of the Pliocene, they are always rare components of fossil vertebrate faunas. Some species are known only from the type material, and many more only from a handful of isolated teeth. Here, I summarize what is known of the fossil record, evolution and origin of edible dormice, the genus *Glis*.

Material and methods

For this review, the morphological data for most taxa were taken from published figures and descriptions. The specimens of *Glis glis*, *G. complicatus*, *G. minor*, *G. sackdillingensis* and *G. vallesiensis* were studied from original specimens in the collections of the Zoological Museum of the Russian Academy of Sciences, St. Petersburg, Russia; Naturhistorisches Museum Wien, Austria; and the National Museum of Natural History, National Academy of Sciences of Ukraine, Kyiv, Ukraine. The higher-level systematics of living glirids follow Montgelard et al. (2003), and the dental nomenclature (Text-fig. 1) follows Sinitsa and Nesin (2018). The



Text-fig. 1. Terminology used for upper (a) and lower (d) teeth of Gliridae.

timescale and stratigraphic frameworks follow Speijer et al. (2020) for the Paleogene, and Raffi et al. (2020) for the Neogene. The reference levels and values of the mammal-based chronological zones follow Speijer et al. (2020) and Raffi et al. (2020) for the Paleogene (MP) and Neogene/Quaternary (MN/MQ), respectively.

Abbreviations

P/p	premolars
M/m	molars
Ma	million years
ELMA	European land mammal ages

Craniodental defining features of the genus *Glis*

Cranial

The skull is massive, with a deep and elongated rostrum, moderately widened, myomorphous zygomatic arches, relatively large infraorbital foramen transmitting the anterior medial portion of the masseter muscle, dorsoventrally expansive braincase, and relatively small auditory bullae. The mandible is generalized and deep, the coronoid and angular processes are large, the angular foramen is absent. The most phylogenetically relevant cranial characters of the genus include (Wahlert et al. 1993): the posterodorsal process and incisive foramen of the premaxilla are short, the jugal is in contact with the lacrimal, the postpalatine spine is weak, the optic foramen is dorsal to M3, the parietal contacts the alisphenoid, the stapedia artery and stapedia foramen are lacking, the dorsal portion of the mastoid region is only slightly inflated, the anteriormost part of the masseteric fossa of the mandible is shifted anteriorly to the level the p4–m1 embrasure or slightly posterior to it.

Knowledge of the cranial anatomy of extinct *Glis* is severely limited by the scarcity of fossil material. A few incomplete skulls have been reported from the Pleistocene of Sackdilling Cave, but these await a description. Known mandibles of *G. minor*, *G. sackdillingensis* (Heller 1930, Kowalski 1956), and early Late Miocene *G. vallesiensis* (pers. obs.) are very similar in morphology to those of the living species.

Dental

The incisors are massive and covered with smooth enamel, the lower incisor enamel is primitive, having uniserial Hunter-Schreger bands almost parallel to the occlusal surface. The cheek teeth are moderately high-crowned, with a flattened occlusal surface (more concave in primitive forms). The premolars are molariform and complex. The ridges of the occlusal surface are roughly transversal, in cross-section, the ridges are swollen, symmetrical and V-shaped. The valleys between them are narrow and trenchant in the bottom. The number of extra ridges is reduced, and the main ridges are mostly isolated. In the upper cheek teeth, the precentroloph, anterotrope and posterotrope are strong, and the postcentroloph is small to absent. The protoloph and metaloph are slightly oblique, bent anteriorly and subparallel. In the lower cheek teeth, the pairs anterolophid and metalophid, centrolophid and metaconid, and mesolophid and entoconid are disconnected. The centrolophid does not reach the lingual edge of the occlusal surface. The anterotropid and posterotropid on the molars are rather prominent. The latter tends to be confluent lingually with the posterolophid.

Systematic palaeontology

Order Rodentia BOWDICH, 1821
Family Gliridae MUIRHEAD, 1819
Subfamily Glirinae MUIRHEAD, 1819

Genus *Glis* BRISSON, 1762

***Glis glis* (LINNAEUS, 1766)**

Text-fig. 2a, b

Synonyms. *Glis esculentus* BLUMENBACH, 1779: 79, *Glis vulgaris* OKEN, 1816: 868 (nomen nudum), *Myoxus giglis* CUVIER, 1832: 444, *Myoxus avellanus* OWEN, 1845: 25, *Glis italicus* BARRETT-HAMILTON, 1898: 424, *Glis insularis* BARRETT-HAMILTON, 1899: 228.

Type locality. “Southern Carniola in Slovenia”, as emended by Violani and Zava (1995: 111).

Characteristics. Large species of the genus (the condylobasal length of adult specimens is 32.8–43.0 mm, the M2 length is 1.68–2.33 mm, the total length of upper tooth row is 6.4–8.7 mm). The posterodorsal process of the premaxilla is nearly equal or only slightly wider than the posterior extent of the nasal. The cheek teeth have a flattened occlusal surface with massive and transversal ridges. The extra ridges are shortened, represented by the anterotrope and posterotrope in the upper molars, and the anterotropid and posterotropid in the lower molars; the upper and lower premolars lack the extra ridges, except for the posterotrope and posterotropid, respectively. The postcentroloph in the upper cheek teeth is also missing. The P4 is three-rooted, trapezoid in occlusal outlines, about 30 % smaller than M1. The anteroloph and, in most cases, the metaloph and posteroloph are free. The precentroloph and posterotrope are fused with the paracone and metacone, respectively, and do not extend onto the lingual half of the occlusal surface. The M1 and M2 have seven ridges. The anteroloph, anterotrope, protoloph and precentroloph are invariably free. The metaloph and posteroloph, as well as the latter and posterotrope can be connected labially. The M3 is roundly triangular, nearly as long as wide. The protoloph, metaloph and posteroloph are fused lingually. The precentroloph is extensive and may reach the lingual border of the occlusal surface. Like the upper premolar, the p4 is approximately 30 % smaller than m1. The crown is trapeziform. The ridges vary in quantity from five to six. The anterolophid and metalophid are fused at their ends. The mesolophid and posterolophid are fused lingually. The centrolophid and posterolophid are present in most p4s. The m1 and m2 have seven ridges. The anterolophid, metalophid, mesolophid and posterolophid are transversal and long. The anterolophid and metalophid, as well as the mesolophid and posterolophid, are lingually connected. The anterotropid, centrolophid and posterolophid are about one and a half times shorter than the main ridges. The posterotropid tends to fuse with the entoconid. The subtriangular m3 is similar to the m1 and m2 in the configuration of the occlusal surface.

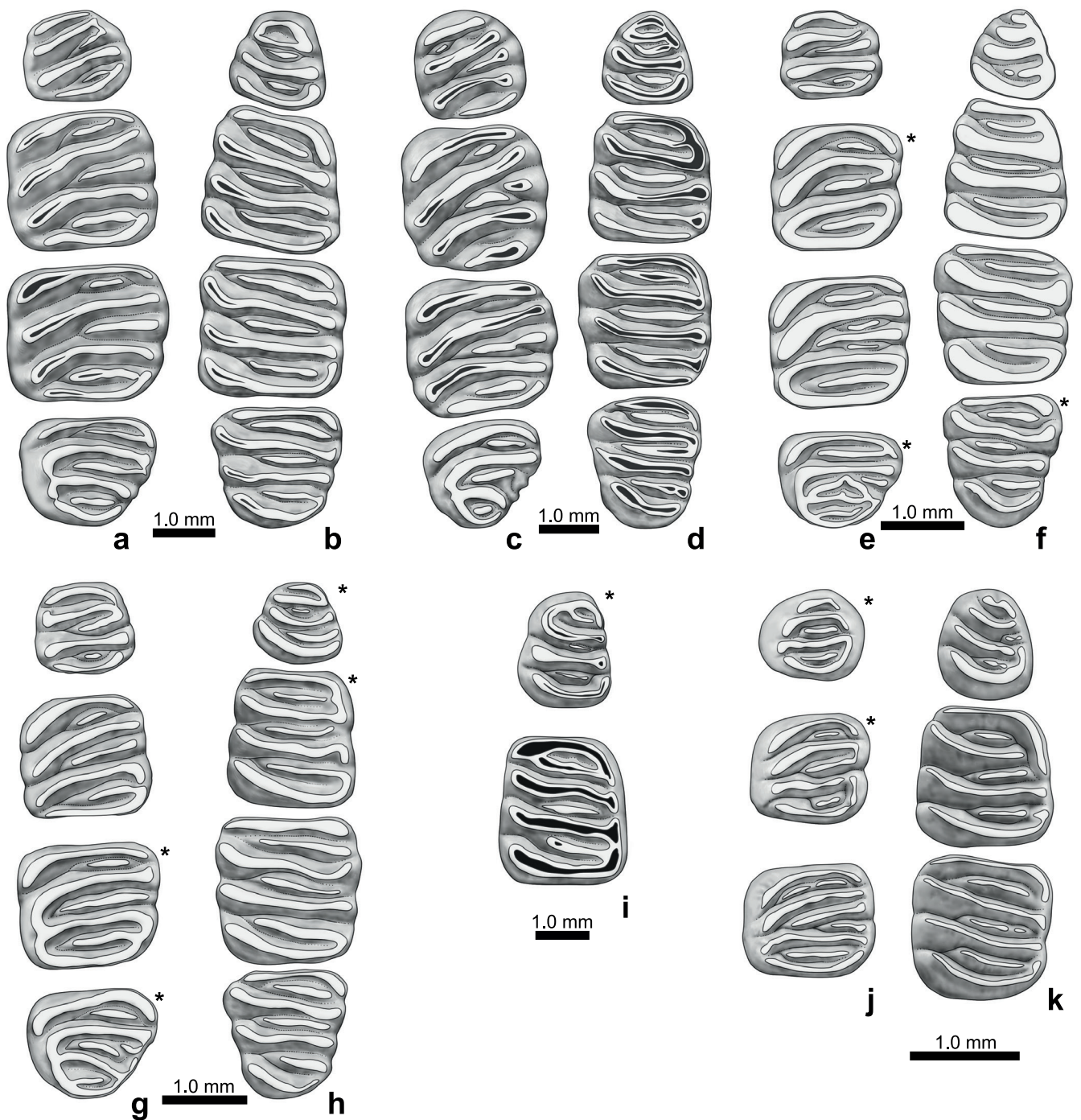
Distribution. The past distribution of *G. glis* coincides well with the present area of the species. The fossil and subfossil remains are reported from a plethora of Early Pleistocene (early Calabrian, early Biharian, MQ 1) to Holocene localities in Austria (Sankt Margarethen, Gudenushöhle, Schusterlucke, Nixloch), Belgium (Scladina Cave, Trou du Frontal), Bulgaria (Varshets, Kozarnika B1 and B2, Varbeshnitsa, Bacho Kiro, Filipovska Cave-2, Morovitsa 11-9 and 8-1, Mecha Cave 1 and 2, Magura Cave, Temnata Cave-V, Cave 16, Borikovska Cave, Bosnek 1, Cave 15-II, Raziska-Rz-0, Kastrakly), Croatia (Krapina, Veternica), Czech Republic (Chlum 7B, Dobrkovice-2), France (Fage à Noailles, Vaufray, La Chaise, Lazaret-de-Nice, Baume Moula-Quercy, Arcy-sur-Cure, Hortus, Combe Grenal, Garenne, Espeche, Rond-du-Barry, Rochedane), Germany (Bilzingsleben, Weimar-Ehringsdorf, Burgtonna, Osteifel volcanoes, Wannenköpfe volcanoes, Fuchsloch near Sigmansbrunn, Kemathenhöhle, Süssenborn), Greece (Loutra Almopias Cave, Ravine of Vulnarakis), Hungary (Nagyharsányhegy-6, Solymár, Süttő-6, Kalman-Lambrecht Cave-layer V, Rejteck-1), Italy (Averla Cave,

Boscochiesanova, Campo dei Fiori, Cengelle-I, Covoloni del Broion Cave, Fontana Marella Cave, Ghiacciaia Cave, Grotta Breuil, Grotta Cala, Grotta del Broion, Grotta del Cere, Grotta del Principe, lower levels, Grotta della Serratura, Grotta di Castelcivita, Grotta di Scario-level A, Grotta Maggiore di S. Bernardino, Grotta Mino re di S. Bernardino, Grotta Paglicci-inner levels, Grotta San Agostino, Grotta San Leonardo, Grotta su Guanu, Mezzena Rockshelter, Moncucco Torinese, Montorio, Praia a Mare, San Giovanni di Duino, Sossano-2 and 5, Spessa-2, Tagliente Rockshelter, Tina Cave, Torre in Pietra, upper levels, Zovencedo), Moldova (Brînzești-1, Buzdugeni-1), Poland (Dziadowa Skała Cave, Oblazowa Cave-1, Berkowa Cave, Babie Nogi, Biśnik Cave, Komarowa Cave, Zegar Cave, Krucza Skała Rock-shelter, Shelter in Podlesice near Kroczyce 1, Deszczowa Cave), Romania (Brașov, Sândominic-I, Caves 10 and 13 in the Lupșa Valley, Cave in the Parului Valley, Dealul Burzău, Cioarei Cave), Russia (Ilovaisky Kordon, Zhiguli Caves), Serbia (Vrelska Cave, Smolučka Cave), Slovenia (Potočka zijalka), Spain (Ermitons Cave, Arbreda Cave, Erralla Cave), South Ossetia (Kudaro, Talyng-Leget Cave), Switzerland (Cotencher, Bildstock, Kesslerloch, Schweizersbild, Ettingen, Birseck-Azilian), and Ukraine (Nizhnee Krivche, Devichiy Skaly, Malaja Ugolka, Snyakovo) (Hescheler 1906, Rutot 1910, Soergel 1919, Méhely 1914, Stehlin 1918, Sarasin and Stehlin 1924, von Mandach 1930, Dubois and Stehlin 1933, Kormos 1933a, 1933b, 1937, Kretzoi 1941, 1965, Pasa 1947, Brunner 1954, Heller 1955, Gromov 1957, Malez 1963, 1970, Bartolomei 1964, 1970, 1977, Fejfar 1965, Chaline 1969, 1972, 1980, Jánossy 1969a, 1986, Wehrli 1969, Bartolomei and Pasa 1970, Lozan 1970–1971, Bartolomei et al. 1974, 1977, Martini et al. 1974, Kahlke 1975, 1978, Mourer-Chauvire et al. 1975, Radulescu and Samson 1975, 1992, Rakovec 1975, Rabeder 1977, von Koenigswald 1978, 1995, Gautier and Heinzelin 1980, Agajanian 1981, Heinrich 1981, Madeyska 1981, Alcalde Gurt 1982, 1986, 1987, Jurcsák et al. 1982, 1984, Kowalski and Nadachowski 1982, Nadachowski 1982, 1989, 1990, Paunesco et al. 1982, Baryshnikov and Baranova 1983, Clot 1984, Cordy 1984, Kotsakis 1984, 2003, Popov 1984, 1986, 1989, 2018, Peman 1985, Baryshnikov et al. 1986, Bastin et al. 1986, Terzea 1987, Vigne 1987, Brunet-Lecomte 1988, 1989, Radulescu 1989, 1995, Heinrich 1990, Maul 1990, 1994, van Kolfschoten 1990, von Koenigswald and Tobien 1990, Sala 1990, Bon et al. 1991, Dimitrijević 1991, 1996, Marković and Pavlović 1991, Nagel and Rabeder 1991, Vigne and Marinval-Vigne 1991, Brunet-Lecomte et al. 1992, 1994, 1996, van Kolfschoten and Roth 1993, Marquet 1993, Burgehele et al. 1994, Ferrandini and Salotti 1995, Jeannet 1995, Koliadimou and Koufos 1995, Hír 1997, Tatarinov 2000, Boev 2006, Kalthoff et al. 2007, Bona et al. 2008, Nadachowski et al. 2009, Stefaniak et al. 2009, Krokhmal' and Rekovets 2010, Pazonyi et al. 2014, Horáček et al. 2016, Vasileiadou and Sylvestrou 2022).

***Glis persicus* (ERXLEBEN, 1777)**

Text-fig. 2c, d

Synonyms. *Myoxus glis caspius* SATUNIN, 1905: 55, *Glis glis petrucii* GOODWIN, 1939: 1.



Text-fig. 2. Upper (a, c, e, g, j) and lower (b, d, f, h, i, k) cheek teeth of *G. glis*, Recent, Bulgaria (a, b), *G. persicus*, Recent, Iran (c, d), *G. sackdillingensis*, Early Pleistocene, Kamyk (e, f), *G. minor*, Early Pliocene, Podlisice (g, h), *G. major*, Early Miocene, Oschiri (i), *G. apertus*, Early Miocene, Weissenburg 6 (j, k). Modified from Kryštufek et al. (2021), Kowalski (1963), de Bruijn and Rümke (1974), Mayr (1979). Asterisked specimens are inverted to facilitate comparison.

Type locality. Gilan Province, Iran (Lay 1967: 193, Kryštufek et al. 2021).

Characteristics. Size is large (the condylobasal length of adult specimens is 35.4–44.6 mm, the M2 length is 1.90–2.35 mm, the total length of upper tooth row is 7.3–8.4 mm). The posterodorsal process of the premaxilla is considerably wider than the posterior extent of the nasal. Except for having larger cheek teeth, the dental morphology of *G. persicus* appears to be closely similar to that *G. glis*, slightly differing in having a more rounded P4 and posteriorly tapered M3.

Distribution. The species is not known from the fossil record.

Glis sackdillingensis (HELLER, 1930)

Text-fig. 2e, f

Synonyms. *Glis antiquus* KORMOS, 1930.

Type locality. Sackdilling Cave, Germany; Pleistocene (probably Early; see Kowalski 2001 for details).

Characteristics. Medium to large species of the genus, about 10 % smaller in average than the recent *G. glis* (the M2 length is 1.50–1.87 mm, length of lower dentition is 5.73 mm). The cheek teeth morphology is identical to that of the latter, except for having the prototrope and centrotrope of M2 and M3, weaker posteroloph of P4, and more isolated p4 anterolophid and posterolophid.

Comments. I follow de Bruijn and van der Meulen (1975) in regarding *Glis antiquus* described by Kormos (1930) from the Early Pleistocene (early Biharian) karstic locality Betfia-II (Püspökfördő) in Romania as a junior synonym of *G. sackdillingensis*.

Distribution. Middle Pliocene (Piacenzian, early Villanyian, MN 16) to the Middle Pleistocene (early Toringian, MQ 1) of Austria (Deutsch-Altenburg D-A 2A, 2C1 and 4B), Bulgaria (Verbeshnitsa Cave, Varshets), Croatia (Razvodje, Podumci-1, Tatinja Draga), Czech Republic (Mokrá-1, Mladeč, Chlum 4S, 4K7, 4C6 and 4C7), France (Mont-Hélène, Mas Rambault 2, Grand Serre, Montoussé-5), Germany (Hohensülzen near Worms, Gundersheim, Sackdilling Cave, Schambach near Treuchtlingen, Schernfeld, Untermassfeld), Greece (Tourkobounia-1 and 2, Kaiafa), Hungary (Villány-3 and 5, Osztramos-2, 3 and 8, Újlaki-Hegy, Somssich-Hegy, Kövesvár, Tarkó 2–16, Uppony-1, Vértesszőlős), Italy (Monte La Mesa, Palena), Poland (Kadzielnia-1, Przymilowice, Kielniki 1–3, Kamyk, Żabia Cave, Zalesiaki-IA, Kozi Grzbiet-2), Romania (Betfia-II, VII and X), Slovakia (Kolíňany-1–2, Včeláre 3, 5, 4E and 6), Slovenia (Črni Kal 3, Velika Pirešica), Switzerland (Vue-des-Alpes), and Ukraine (Chortkiv) (Heller 1930, 1960, Kormos 1930, 1931, 1933a, 1934, Kretzoi 1941, 1956, Kowalski 1958, 1960b, 1963, 1990, 2001, Dehm 1962, Jánossy 1962, 1963, 1969b, 1976, 1986, Heller 1962, Kretzoi and Vértes 1965a, b, Storch et al. 1973, de Bruijn and van der Meulen 1975, Jánossy and Kordos 1976, Fejfar and Heinrich 1983, Fejfar and Horáček 1983, Kretzoi 1941, 1956, von Koenigswald 1977, 1995b, Horáček and Ložek 1984, 1988, Malez and Rabeder 1984, Aguilar et al. 1986, van der Meulen and van Kolfshoten 1986, Carls and Rabeder 1988, Popov 1988, Jánossy and Topál 1990, von Koenigswald and Tobien 1990, Maul 1990, Aguilar et al. 1993, Bolliger et al. 1993, Daoud 1993, Paunović and Rabeder 1996, Terzea 1996, Masini et al. 1998, Stadnik 2010, Aguilar and Michaux 2011, Striczky and Pazonyi 2014, Horáček et al. 2016).

***Glis minor* KOWALSKI, 1956**

Text-fig. 2g, h

Type locality. Podlesice, Poland; Early Pliocene, early Zanclean, early Ruscinian ELMA, MN 14.

Characteristics. Size medium (the M2 length is 1.42–1.71 mm). The cheek teeth have a slightly concave occlusal surface and weak to moderately developed extra ridges. The two-rooted P4 is rounded, bearing six to seven ridges. The precentroloph and posteroloph are strong in most specimens. The M1 is simple, with seven ridges arranged as in *G. glis*.

Most M2 are similar to the M1, the geologically older specimens retain the prototrope and postcentroloph. The M3 possesses eight to nine ridges. The lower cheek teeth are essentially the same as in *G. glis*. About 20 % of m3 lack the centrolophid.

Distribution. Late Miocene (Tortonian – Messinian, early Vallesian – late Turolian ELMA, MN 9) to Early Pleistocene (Calabrian, early Biharian ELMA, MQ 1) of Austria (Richardhof-Golfplatz, Richardhof-Wald, Götzendorf, Kohfidisch), Bulgaria (Muselievo), Czech Republic (Suchomasty, Vitošov), France (Plä-de-la Ville, Lo Fournas-4, Lissieu, Les Valerots, Vallonet, Perpignan, Celleneuve), Germany (Dorn-Dürkheim 1, Hambach 11, Sondershausen, Wölfersheim, Gundersheim), Greece (Maramena, Komanos 1 low, Notio 1, Lava 2), Hungary (Rudabánya, Beremend 14, Osztramos-7, 9 and 10, Csarnóta 2), Italy (Moncucco Torinese, Rivoli Veronese, Steglio Basin), Moldova (Lucești, Novaya Andriashevka), Poland (Bełchatów A, Podlesice, Ewa Cave 3, Pańska Góra, Raciszyn 1, Węże 1, Rębielice Królewskie 1A, Mała Cave), Romania (Betfia-XIII), Russia (Kabakova Balka), Serbia (Sibnica 1, 2 and 4, Riđake), Slovakia (Ivanovce), and Ukraine (Goryshya Vynanka) (Kormos 1938, Kowalski 1960a, 1997, Sulimski 1964, Mein and Michaux 1970, Chaline 1972, Jánossy 1973, 1986, Sulimski et al. 1979, Bachmayer and Wilson 1983, Chaline et al. 1985, Bachelet et al. 1990, Fejfar and Storch 1990, Daoud 1993, Paronuzzi 1994, Sala et al. 1994, Daxner-Höck 1995, 2005, Vangengeim et al. 1995, Mörs et al. 1998, Tatarinov 2000, Dahlmann 2001, Mörs 2002, Kotsakis 2003, Popov 2014, 2018, Sabol et al. 2004, Čermák et al. 2007, Daxner-Höck and Höck 2009, 2015, Nadachowski et al. 2009, Krokmal' and Rekovets 2010, Marković and Milivojević 2010, Hellmund and Ziegler 2012, Colombero et al. 2014, Marković et al. 2016, Mészáros et al. 2016, Pazonyi et al. 2016).

***Glis major* DE BRUIJN et RÜMKE, 1974**

Text-fig. 2i

Type locality. Oschiri road cut, Northern Sardinia, Italy; Early Miocene, middle Burdigalian, early Orleanian ELMA, MN 3.

Characteristics. The largest species of the genus, p4 and m1, are 15 % to 20 % larger than those of extant *G. glis* (1.86 and 2.50 mm in length respectively). The p4 is molariform, complex, and only slightly smaller than the m1. The p4 crown is anteroposteriorly elongated and angular. The occlusal surface has strong anterolophid, centrolophid, mesolophid and posterolophid. The anterolophid and metalophid are labially fused. The anterotrope is present and connected to the middle part of the anterolophid. The centrotrope and posterotrope are approximately two times shorter and narrower than the main ridges. The m1 closely resembles the m1s of the geologically younger Late Neogene and Pleistocene species of the genus, including *G. glis*.

Distribution. Known only from the type locality (de Bruijn and Rümke 1974).

***Glis apertus* MAYR, 1979**

Text-fig. 2j, k

Type locality. Weissenburg 6, Germany; Early Miocene, early Aquitanian, early Agenian ELMA, MN 2.

Characteristics. Small species. The occlusal surface of cheek teeth is slightly concave. The ridge pattern is simplified, in a way similar to that in derived species of the genus. The P4 is three-rooted, ellipsoidal, with anteroloph, protoloph and metaloph lingually confluent. The precentroloph and posterotrope are long and isolated. The M1 and M2 possess seven to eight ridges: the four main ridges, strong precentroloph that tends to extend onto the lingual side of the occlusal surface, equally long anterotrope and posterotrope, and variably present postcentroloph. The lingual arms of the anteroloph, protoloph and metaloph end free; the precentroloph, in turn, is connected to the paracone. The structure of a single-rooted p4 is essentially the same as in *G. glis*, with well-developed and partially fused anterolophid and metalophid, mesolophid and posterolophid, shortened centrolophid, and a posterotropid between them. The lower molars show this pattern, but the metalophid is mostly isolated, and the anterior valley is occupied by a strong anterotropid.

Distribution. Known only from the type locality (Mayr 1979).

***Glis vallesiensis* AGUSTÍ, 1981**

Text-fig. 3a, b

Type locality. Ballestar, Spain; Late Miocene, early Tortonian, early Vallesian ELMA, MN 9.

Characteristics. Large species, approaching in size the smallest specimens of *G. glis* (the M2 length is 1.80–1.81 mm), morphologically similar to *G. minor*. The occlusal surface of M1–2 and m1–2 is slightly concave. The P4 precentroloph is long, the M1 and M2 often retain the prototrope and postcentroloph. The mesolophid and posterolophid of m1 and m2 are separated, the m3 lacks a centrolophid.

The P4 is large, almost as wide as M1. The trapezoidal crown has six ridges, of which the anteroloph, precentroloph, posteroloph and a small posterotrope are free; and the protoloph and metaloph are in contact lingually. The M1 and M2 have six to eight ridges. The main ridges, the anteroloph, protoloph, precentroloph, metaloph and posteroloph are free when unworn. Some specimens demonstrate a weak postcentroloph. Three extra ridges are rudimentary and variably present. Among them, the anterotrope and prototrope are the weakest, and posterotrope is the strongest crest. The M3 is triangular with a somewhat irregular ridge pattern of the talon. The anterotrope is long and strong. The p4 with roundly triangular outlines and five to six ridges are reminiscent of those in the geologically younger *Glis* species. The posterolophid and mesolophid are separated, the centrolophid is small to absent. The m1 and m2 mostly bear seven ridges: long anterolophid, metalophid, mesolophid and posterolophid, and shortened anterotropid,

centrotropid and posterotropid. The ridges are mainly free, except the pairs anterolophid-metalophid and posterolophid-posterotropid, which show a tendency to form lingual connections. The m3 is triangular occlusally and similar to m2, but shows no distinct centrolophid.

Comments. *Glis vallesiensis* is a rare taxon with a patchy fossil record, reported from the geographically restricted early Late Miocene sites in Spain, central and eastern Europe. The assignment of eastern European *Glis* materials to *G. vallesiensis* was questioned by Daxner-Höck and Höck (2009, 2015), who argued that the specimens from Bełchatów A (Poland) and Grytsiv (Ukraine) appear to be closer to *G. minor* than to the typical *G. vallesiensis* from Ballestar and Can Petit. The two species are different in size and the absence of centrotropid on m3 of *G. vallesiensis*, which occurs in nine out of the eleven m3s of *G. minor* from the type locality Podlesice (Daoud 1993). Based on these criteria, I suggest reattributing the population from Bełchatów A to *G. minor*, as proposed by Daxner-Höck and Höck (2009, 2015), but retaining that from Grytsiv in *G. vallesiensis*.

Distribution. Late Miocene (early Tortonian, early Vallesian, MN 9) of Spain (Ballestar, Can Petit, La Bastida), Germany (Petersbuch 14), Poland (Opole 2), Hungary (Felsotárkány 3/2 and 3/10), and Ukraine (Grytsiv) (Kowalski 1967, Agustí 1981, Bolliger and Rummel 1994, Nesin and Kowalski 1997, Hír and Kókay 2010).

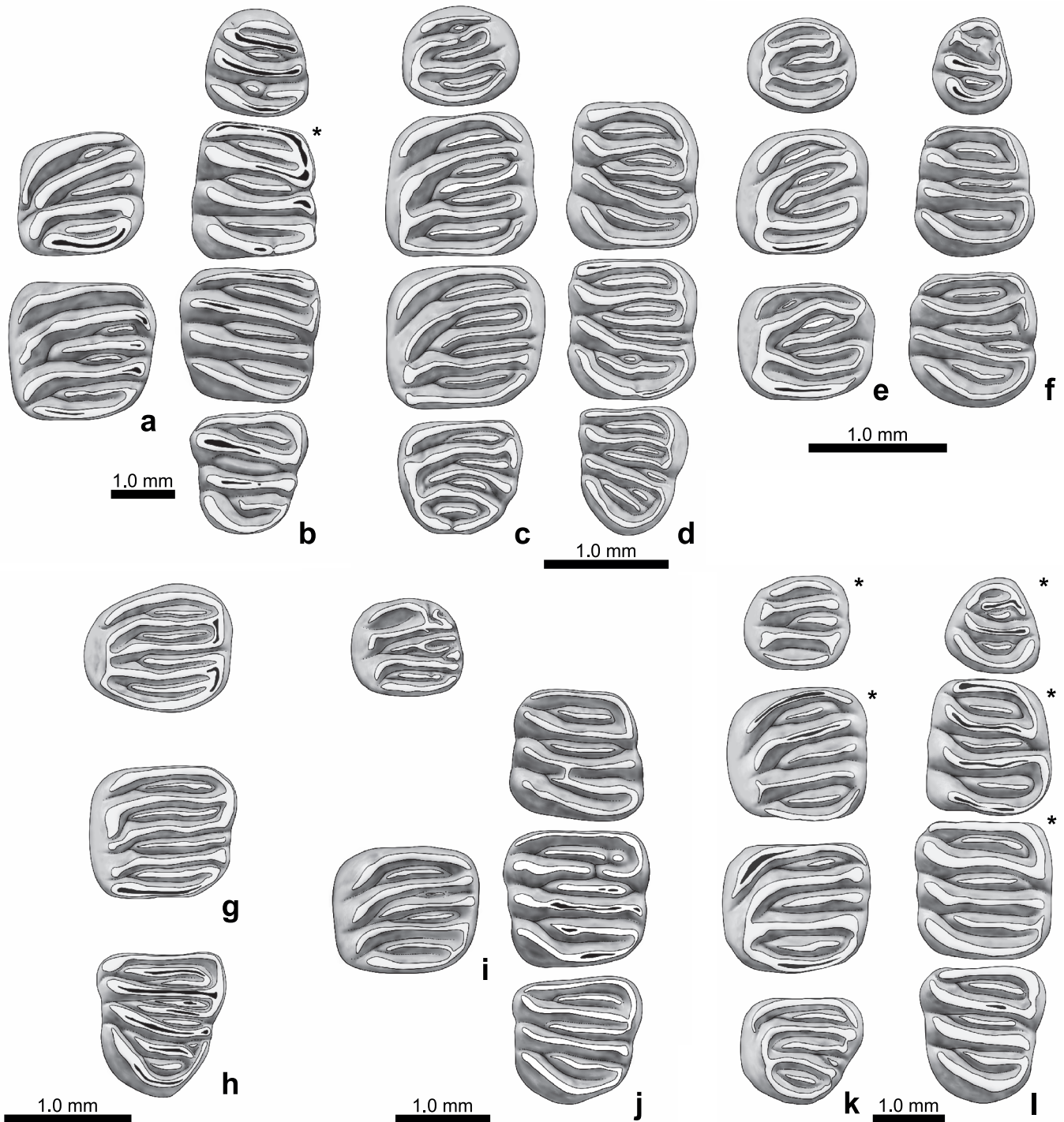
***Glis galitopouli* VAN DER MEULEN et DE BRUIJN, 1982**

Text-fig. 3c, d

Type locality. Aliveri, isle of Euboea (Evia), Greece; Early Miocene, Burdigalian, early Orleanian ELMA, MN 4.

Characteristics. Small species of the genus (M1 length varies from 1.08 to 1.27 mm, an estimated average length of upper dentition is 4.20 mm), with relatively high-crowned cheek teeth bearing the postcentroloph, well-developed extra ridges, including the prototrope, centrotropid, metatropid and up to two posterotropids on the concave occlusal surface. The occlusal surface of M3 and m3 is rather flat.

An oval and three-rooted P4 possesses six to seven ridges. The anteroloph is either isolated or connected to the lingual end of the protoloph. The protoloph, metaloph and posteroloph are labially connected. The extra ridges include anterotrope and posterotrope. The M1 and M2 are virtually identical in size and morphology. There are nine ridges. The protoloph and metaloph, as well as the metaloph and posteroloph, are lingually connected in most specimens. The labial connection between the metaloph and posteroloph is observable in about half of the specimens. The anteroloph is mostly free. The precentroloph is connected to the protoloph, and the postcentroloph is isolated. There are the anterotrope, prototrope and posterotrope on M1 and M2. The occlusal surface of M3 is similar to that of M1 and M2 in the quantity and arrangement of ridges. The protoloph, metaloph and anteroloph are connected lingually. The anteroloph is isolated in most specimens. The labial end of the prototrope is free, the anterotrope is connected to the paracone. The p4



Text-fig. 3. Upper (a, c, e, g, i, k) and lower (b, d, f, h, j, l) cheek teeth of *G. vallesiensis*, Late Miocene, Ballestar, La Bastida, and Grytsiv (a, b), *G. galitopouli*, Early Miocene, Aliveri (c, d), “*G.*” *guerbuezi*, middle Oligocene, Kocayarma (e, f), *G. transversus*, Early Miocene, Harami 1 (g, h), *G. complicatus*, Early Miocene, Oberdorf 3 and 4 (i, j), *G. mihevci*, Middle to Late Pleistocene, Velika Pirešica and Črni Kal 2, 4 (k, l). Modified from Agustí (1981), Nesin and Kowalski (1997), van der Meulen and de Bruijn (1982), Ünay (1989, 1994), de Bruijn (1998), Aguilar and Michaux (2011). Asterisked specimens are inverted to facilitate comparison.

is trapezoidal. Its occlusal surface is formed by six to eight ridges. The anterolophid and metalophid are connected both lingually and labially. The labial arms of mesolophid and posterolophid are fused. The extra ridges are represented by a strong posterotropid, weaker anterotropid and occasionally present centrotropid. The m1 and m2 are rectangular in outline, with nine to ten ridges. The only irregular ridge is a second posterotropid, present in one m2 from Aliveri. The anterolophid, metalophid and centrolophid, as well as the mesolophid and posterolophid, are connected lingually. The

extra ridges are always isolated. The m3 crown is triangular in occlusal outline. The number of ridges varies between eight to ten. The second posterotropid is frequent; the centrotropid and metatropid are rudimentary.

Distribution. The species has been reported from the Early Miocene (middle to late Burdigalian, early – middle Orleanian, MN 3–4) of Greece (Aliveri, Karydia), Turkey (Bornova 183, Keseköy, Sabuncubeli), and Switzerland (Mittlerer Hegengraben) (van der Meulen and de Bruijn

1982, Ünay 1994, Kálin 1997, Doukas 2003, de Bruijn et al. 2006, Bilgin et al. 2019).

“*Glis*” *guerbuezi* ÜNAY 1989

Text-fig. 3c–f

Type locality. Kocayarma, Turkey; middle Oligocene, late Rupelian, early Arvernian ELMA, MP 25.

Characteristics. The smallest (the M2 length is 0.84–0.95 mm) and morphologically the most primitive species of the genus. The cheek teeth have a slightly concave to almost flat occlusal surface. The protoloph, metaloph and posteroloph on P4–M3 are connected lingually. The occlusal outlines of P4 are oval; the ridge pattern is represented by connected anteroloph, protoloph, metaloph, posteroloph, precentroloph and occasionally, a rudimentary postcentroloph. The M1 and M2 have eight to nine ridges: an isolated or labially confluent with the paracone anteroloph, protoloph, metaloph, posteroloph, long precentroloph and postcentroloph, and weak anterotrope and prototrope. The posterotrope is rare. The metaloph of M2 is bent posteriorly and oriented obliquely relative to the protoloph. The protoloph, metaloph and posteroloph are fused lingually. The sub-oval p4 bears the four main ridges, a diminutive centrolophid, and a strong posterotropid. The m1–2 has four main ridges, a long centrolophid, and moderately developed anterotropid and posterotropid. Some specimens possess an additional centrotropid. The anterior and posterior valleys are opened labially.

Comments. The attribution of the species to the genus *Glis* is ambiguous, and has been doubted by several authors (Vianey-Liaud 2004, Lu et al. 2021). Indeed, the species does not possess the definitive dental features of *Glis*, and its assignment to the genus is based primarily on the characteristic V-shaped cross-section of loph and lophids, with extra ridges comparable in width and height to the main ones (Ünay 1989). However, the main ridges of its upper teeth are often connected and converged lingually, but not isolated, nor subparallel as in *Glis*. Additionally, most M1 and M2 of *G. guerbuezi* lack the posterotrope, found in all unambiguous members of the genus, indicating its phylogenetic affinities with more basal glirid taxa. The results of the phylogenetic analysis by Lu et al. (2021) suggest a closer relationship between *G. guerbuezi* and the genus *Microdyromys* than to any of the remaining species of *Glis*. Although this hypothesis is the most parsimonious interpretation of all the available evidence, the species also lacks several diagnostic features of *Microdyromys*, such as an irregular inner wall and lingually fused anteroloph and protoloph in M1–2, which, in turn, make the attribution of *G. guerbuezi* to *Microdyromys* dubious. Therefore, here I conservatively place *G. guerbuezi* among fat dormice, with a query, awaiting definitive evidence that will unravel the phylogenetic placement of the species within the glirids.

Distribution. Middle Oligocene, late Rupelian, early Arvernian of Turkey (Kocayarma and Kavakdere) (Ünay 1989).

***Glis transversus* ÜNAY, 1994**

Text-fig. 3g, h

Type locality. Harami 1, Turkey; Early Miocene, early Burdigalian, late Agenian ELMA, MN 2.

Characteristics. Small species (the M2 length is 1.07–1.09 mm). The occlusal surface of cheek teeth is slightly concave; the ridge pattern is complex, with strong and long extra ridges, constantly present prototrope of M1–2, and narrow valleys. In upper molars, the extra ridges are subparallel and reach the lingual border separately; the prototrope is the longest extra ridge. The medial wall of the upper cheek teeth is crenulated. The p4 has two roots.

The P4 is very large, close to the molars in size, and possesses three roots. There are eight long ridges on the occlusal surface. The anterotrope and prototrope are isolated. The anteroloph, postcentroloph and posterotrope are free at their lingual end. The protoloph and precentroloph are connected both lingually and labially, as are the metaloph and posteroloph. The M2 is reminiscent of P4 in the structure of the occlusal surface, with nine well-developed, and virtually straight, transversal ridges. The extra ridges are only slightly weaker than the main ones. The p4, as the upper premolar, is molariform and large. The trapezoidal occlusal surface bears eleven ridges, including four main ridges, the centrolophid, metatropid, centrotropid, posterotropid, and up to two ridges in the anterior valley. The m3 crown is more nearly triangular, as seen occlusally. It has twelve ridges: the lingually joined anterolophid, metalophid and centrolophid; and isolated mesolophid and posterolophid with somewhat shortened extra ridges between them. The centrolophid is also short. The anterior and posterior valleys possess two anterotropids and posterotropids respectively.

Distribution. The species is represented by seven specimens from the type locality Harami 1, Turkey (Ünay 1994).

***Glis complicatus* DE BRUIJN, 1998**

Text-fig. 3i, j

Type locality. Oberdorf 4, Austria; Early Miocene, late Burdigalian, middle Orleanian ELMA, MN 4.

Emended diagnosis. Medium-sized species, similar to *G. minor* in dimensions and cheek teeth morphology. Differs from *G. minor* in having a postcentroloph in all M1–2 and most P4. Further differs from *G. apertus* in being larger and having labially isolated protoloph and precentroloph, as well as a well-developed prototrope of M1–2, and non-confluent mesolophid and posterolophid of m1–2 and m3.

Characteristics. Size medium, the M2 length is 1.47–1.53 mm. The P4 is two-rooted, with lingually isolated protoloph and metaloph, constantly present precentroloph, frequent postcentroloph, and occasional antero- and posterotrope. The protoloph and metaloph are isolated in M1–2; the pre- and postcentroloph, antero- and posterotrope are invariably present; most specimens show

a short prototrope. The molariform p4 has four isolated main ridges, solitary centrolophid, as well as the antero- and posterotropid. The m1 and m2 are similar in occlusal pattern; the four main ridges are isolated labially; there are somewhat weaker centrolophid and posterotropid. In one of the two m3s, the mesolophid is lingually confluent with the posterolophid, and the posterotropid ends free lingually.

Comments. Rich Early Miocene small mammal communities of Oberdorf 3 and Oberdorf 4 fossil localities in Western Styrian Basin, Austria (Daxner-Höck 1998), yielded twenty-one isolated cheek teeth of a member of the genus *Glis*, morphologically similar to *G. minor*. Based on these specimens, de Bruijn (1998) described a new subspecies of *G. minor*, *G. m. complicatus*, noting that (de Bruijn 1998: 110) “The material from Oberdorf occupies an intermediate position between *G. apertus* and *G. minor* in many respects, but is closer to *minor*”.

In my opinion, *G. complicatus* differs so markedly from *G. minor* that it seems necessary to regard it as a full species. Although it resembles *G. minor* more nearly than any of the other species, it differs from it by the presence of the posterior centroloph in all M1–2 and in most P4. The morphological disparity between the taxa is further accentuated by an approximately 5.5 My gap separating *G. complicatus* and the oldest undoubted record of *G. minor*.

Distribution. Known from the type locality Oberdorf 4 and Oberdorf 3 (de Bruijn 1998).

***Glis mihevcii* AGUILAR et MICHAUX, 2011**

Text-fig. 3k, l

Synonyms. *Glis percoi* AGUILAR et MICHAUX, 2011.

Type locality. Velika Pirešica, Slovenia; Pleistocene (either Middle or Late), late Biharian – Toringian ELMA, MQ 1–2.

Characteristics. Large-sized *Glis*, slightly smaller than living *G. glis* (M2 length is 1.88–2.11 mm). Cheek teeth are morphologically indistinguishable from those of *G. glis*, but have lingually confluent protoloph, metaloph and posteroloph in about a half of M1 and M2.

Comments. Aguilar and Michaux (2011) described two new species of the genus *Glis* based on abundant materials (more than one thousand specimens) from the Pleistocene karstic localities Velika Pirešica, Črni Kal Quarry, Sežana and Bestažovca in central and southwestern Slovenia. The two species, *G. mihevcii* and *G. percoi*, are very similar in size and dental morphology; the only distinction between the taxa reported by the authors is a slightly smaller size of *G. percoi*. The taxa are considered here as conspecific, and the senior synonym of the two, based on page priority, is *G. mihevcii*.

Distribution. Pleistocene of Velika Pirešica, Črni Kal 2, 4, Sežana, and Bestažovca localities, all Slovenia (Aguilar et al. 1998, 2001, Aguilar and Michaux 2011).

The origin and evolutionary history of the genus *Glis*

Origin

Fat dormice have traditionally been viewed as a European group. That view has been questioned by findings stemming from the growing Anatolian and Greek late Paleogene and early Neogene records that reveal supposedly the oldest representatives of the genus, a mouse-sized “*Glis*” *guerbuezi* from the middle Oligocene, some 30 Ma, of Turkey (Ünay 1989). The basal phylogenetic position of “*G.*” *guerbuezi* is congruent with recent molecular divergence dates that estimate the modern Glirinae genera *Glis* and *Glirulus* to have diverged from each other around 25–29.5 Ma (Montgelard et al. 2003, Nunome et al. 2007). The exact ancestry of the genus remains controversial. Certain attempts to decipher the origin of *Glis* are hampered by the incomplete nature of the available fossil data and the lack of adequately preserved cranial remains. The glirines are united by several morphological characters, such as transverse Hunter-Schreger bands in the portio interna of the enamel in lower molars, the lower incisors with a thick prism-free outer layer of the portio externa, a short lateral pterygoid process, reduced pterygoid fossa, and a non-perforated angular process (von Koenigswald 1995a, Storch 1995). Despite providing a morphological characteristic of the subfamily, these conditions are certainly plesiomorphic, hence cannot be considered phylogenetically informative.

The origin of *Glis* is most often sought among the Paleogene early glirid genus *Gliravus*, a cluster of three to ten species of primitive glirids known from the Eocene and Oligocene of western Europe (Mayr 1979, Daams 1981). Daams and de Bruijn (1995a) placed *Gliravus* as a common ancestor of several fossil and extant dormouse genera, including *Glirudinus*, *Muscardinus* and *Glis*. Other workers viewed the origin of *Glis* from the Oligocene *Bransatoglis* and *Paraglis* (Chaline and Mein 1979). A third alternative hypothesis has been recently proposed by Freudenthal and Martín-Suárez (2013). The authors restricted the extinct *Glis* to include only the late Neogene and Pleistocene taxa deriving from the Oligo-Miocene species of *Microdyromys*. This view was partially supported by the results of the most recent and only phylogeny of extinct glirines using numerical methods (Lu et al. 2021), which reconstructed a paraphyletic *Microdyromys* in a basal position relative to a clade containing, among other glirids traditionally arranged within Glirinae and Bransatoglirinae, the representatives of *Glis*.

The dental evidence is rather equivocal in deciphering the origin of *Glis*. The problem is further complicated by an unclear status of the purported earliest member of the genus, the Oligocene “*G.*” *guerbuezi*. In terms of cranial morphology, however, the living fat dormice retain a generalized facial skull and mandible, characterized by a primitively deep, slightly downcurved rostrum, strong zygomatic arches, and a massive mandible with a deep body and a well-developed angular process, lacking the angular foramen. Based on these, the structural ancestor of *Glis* can be depicted as a form descended from gliravines.

This would imply, however, that a purported transition from a protrogomorphous condition, documented for Gliravinae (Vianey-Liaud 1974), to the myomorphous one in *Glis* occurred in the early stages of the evolution of the genus. Alternatively, the early *Glis* could retain their cranial morphology from members of *Microdyromys*, whose skull, unfortunately, remains undescribed. This, together with the lack of cranial data for early members of *Glis*, represents the main obstacle in deciphering the origin of the genus.

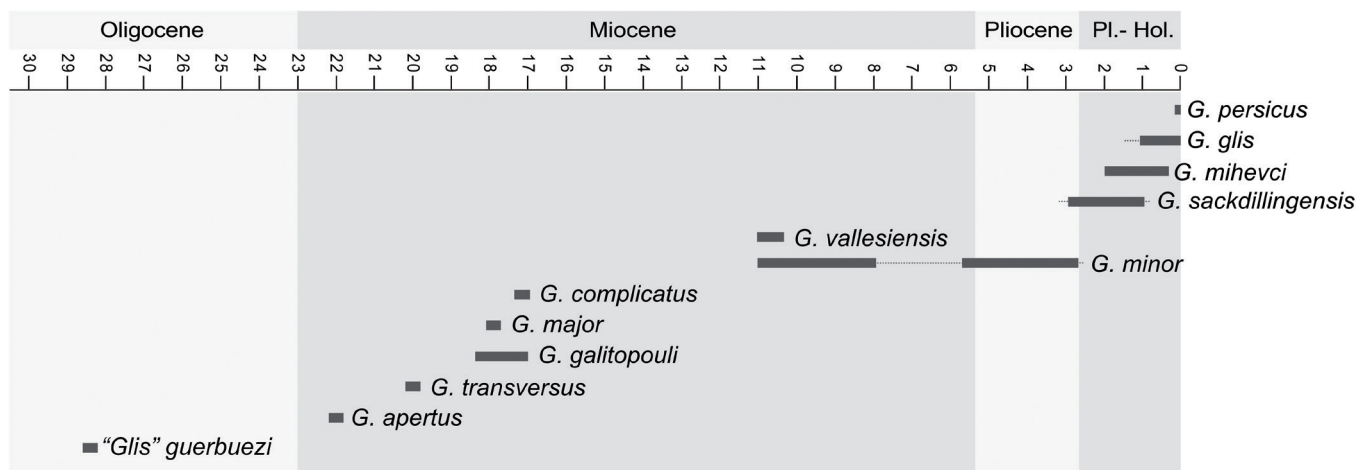
Evolutionary history

As stated above, the fat dormice fossil record begins with a small and morphologically generalized form, “*G.*” *guerbuezi* in the middle Oligocene of Turkey (Text-figs 4–6). Besides retaining a suite of dental characters that are generally considered primitive for the family and similar to those inferred for the basal glirids, such as the lingual connection of the protoloph, metaloph and posteroloph on P4–M3, and convergent protoloph and metaloph on P4–M2 with well-developed pre- and posterotrope, “*G.*” *guerbuezi* is also characterized by firmly swollen, V-shaped in cross-section ridges orientated rather transversal relative to the long axis of the teeth, conditions that are inherited by all known members of the genus (Text-fig. 3g–h). In this and various other ways (e.g., small size, rounded P4, well-developed anterotrope, centrotrope and posterotrope of the lower molars, as well as relatively early appearance in the fossil record), “*G.*” *guerbuezi* is sufficiently primitive to be ancestral to all later species of *Glis*. On the other hand, the very primitive morphology of “*G.*” *guerbuezi* makes its attribution to the genus doubtful (Vianey-Liaud 2004, Lu et al. 2021), which, however, is a common problem in the interpretation of a morphologically generalized, potentially basal form.

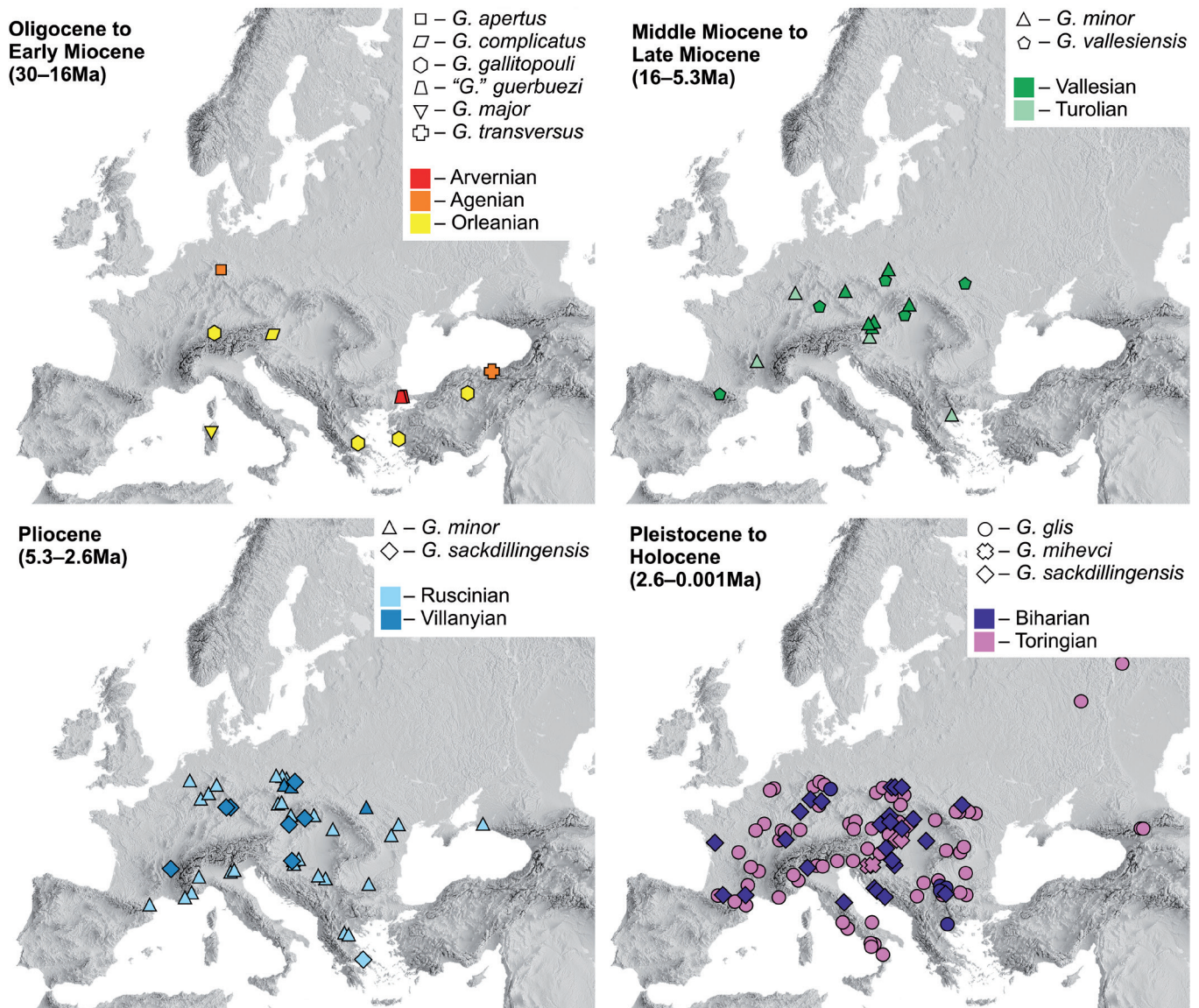
After a long gap spanning approximately 5.5 Ma, *Glis* *apertus*, the first unequivocal representative of the genus, appeared in the fossil record (Mayr 1979). Although it is known only by a handful of teeth from a single fossil site, Weissenburg 6 in Germany, the species possesses a definitive dental morphology of *Glis*, with non-confluent anteroloph, protoloph and metaloph on the upper, and metalophid, mesolophid and posterolophid on the lower

molars respectively (Text-fig. 6). Yet, it retains well-developed extra ridges in the central valley and paraconepre-centroloph connection of P4–M3, a plesiomorphic condition of basal glirids. When described, the species was placed as a transitional form between a purported ancestral glirid (the genus *Gliravus*) and more advanced species of *Glis* (Mayr 1979). Despite the subsequent discovery of even more primitive “*G.*” *guerbuezi*, the Early Miocene *G. apertus* is still widely regarded as a transitional species leading to the living fat dormice.

By the second part of the Early Miocene (late Aagenian – early Orléanian), the genus experienced its maximum diversity and morphological disparity, and reached its maximum body size (Text-figs 4–6). During this time interval, traditionally associated with a long and stable warm period between the late Oligocene cooling and mid-Miocene climatic optimum, at least four species of the genus had emerged: *G. complicatus*, *G. galitopouli*, *G. major* and *G. transversus* (de Bruijn and Rümke 1974, van der Meulen and de Bruijn 1982, Ünay 1994, de Bruijn 1998). The high diversity of Early Miocene *Glis* further supports the view that the Early Miocene was a time of diversification for the genus rather than a time of origin. The rapid diversification of the Early Miocene *Glis* is also reflected by the increasing geographical distribution of the genus. Its representatives are reported from western Asia, southeastern and central Europe, and even the central Mediterranean region (de Bruijn and Rümke 1974). In the Early Miocene Sardinia, the stem *Glis* experienced insular gigantism and evolved into *G. major*, the largest known species, about 15 % to 20 % larger than the living edible dormouse and almost twice the size of contemporaneous members of the genus (Text-fig. 6). Apart from the large size and somewhat too molariform p4, *G. major* possesses a dental pattern seen in geologically younger taxa (Text-fig. 2). In contrast, two other Early Miocene species are known from southern Europe, *G. transversus* and *G. galitopouli*, reveal an unusual combination of primitive features, such as the retention of extra ridges, labially connected protolophs, metalophs and posterolophs, as well as lingually connected precentrolophs and postcentrolophs in upper cheek teeth, and remarkably advanced traits (van der Meulen and de Bruijn 1982, Ünay 1994). Both species possess very long,



Text-fig. 4. Temporal ranges for *Glis* species.



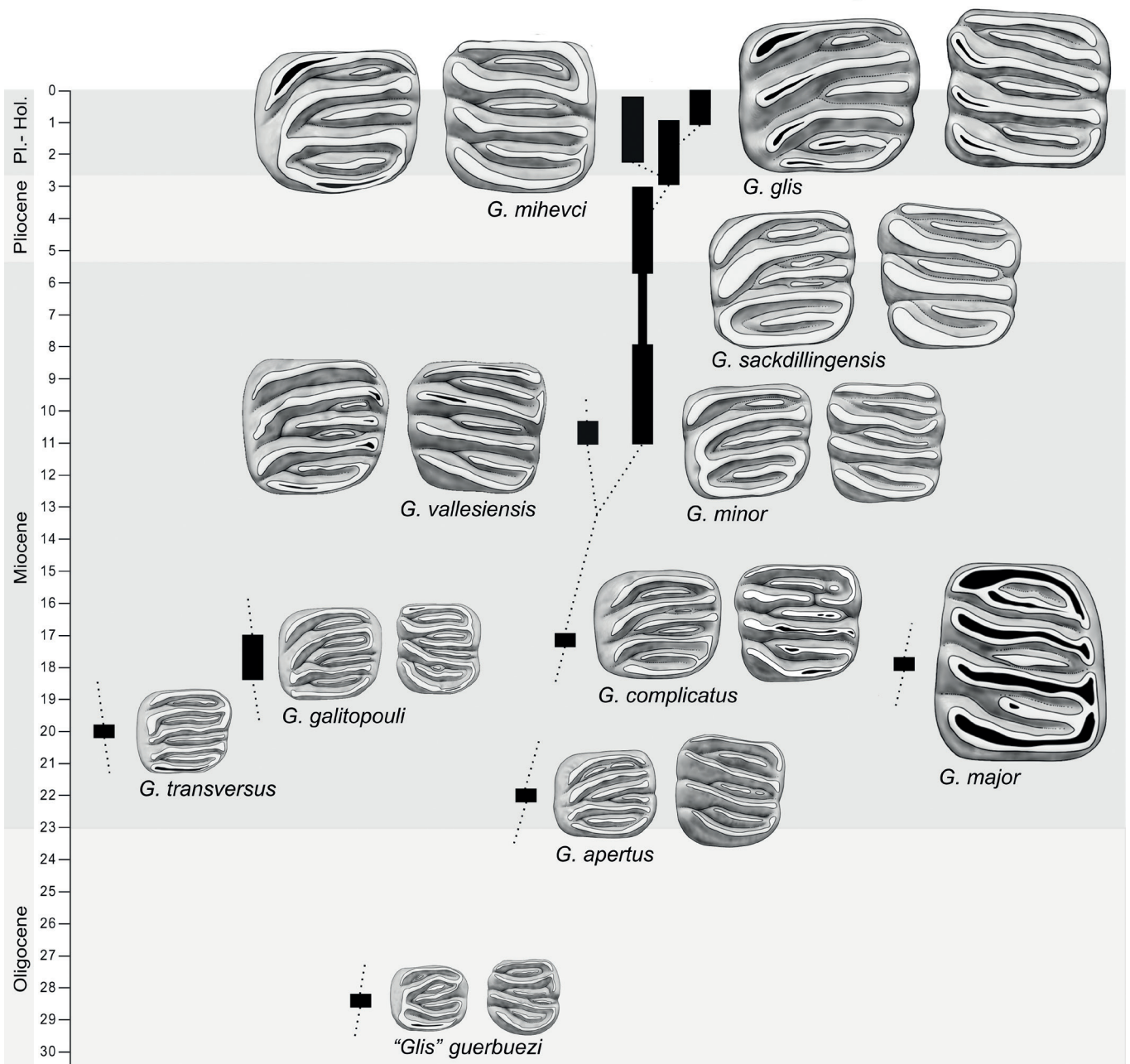
Text-fig. 5. Geographic distribution of fossil *Glis*.

transversal anterotrope, prototrope, posterotrope, pre- and postcentrolophs, anterotropid, centrolophid, centrotropid and posterotropid, exceeding in these respects all other members of the genus. Such a morphology indicates *G. transversus* and *G. gallitopouli* to be early offshoots of the stem *Glis*, too specialized to be considered ancestral to any later taxa (Text-fig. 6).

The early Late Miocene fossil record of Austria, the Czech Republic and Hungary documents the first occurrence of *G. minor* (Daxner-Höck 2005, Daxner-Höck and Höck 2009, 2015). The specimens, albeit somewhat smaller, demonstrate a rather derived morphology seen in typical representatives of *G. minor*. The species was a rather successful glirid, and persisted into the earliest Pleistocene. As such, *G. minor* represents the longest-lived dormouse, spanning around eight million years (Text-fig. 4, 6). The latest Miocene materials of *G. minor* from Greece (Daxner-Höck 1995) predates the Pliocene flourishing of the species, whose descendants dispersed westwards and eastwards across most of Europe (Text-fig. 5). The second Late Miocene species, *G. vallesiensis*, is close to *G. minor*, and despite some morphological and size differences, could be conspecific

with this species. Outside of the early Late Miocene Spain, *G. vallesiensis* is known from several localities in central and eastern Europe (Kowalski 1967, Agustí 1981, Bolliger and Rummel 1994, Nesin and Kowalski 1997, Hír and Kóckay 2010). The late Neogene *Glis*, although well documented by numerous findings in some local faunas, maintain a relatively low diversity, never having more than two co-occurring species in any biochron (Text-figs 4–6). This apparent difference with the Early Miocene members of the genus probably reflects the fact that the late Neogene forms were largely restricted to a rather specialized forest-dwelling lifestyle of the living species, while a diversity of Early Miocene taxa filled a variety of ecological niches.

The Plio-Pleistocene history of the genus *Glis* is associated with what is believed to be a single phylogenetic lineage, deriving from *G. minor* and leading to *G. glis* and *G. persicus*. Alongside a gradual increase in size, the morphological evolution within the lineage is evidenced by a tendency towards more heavily built, straightened and transversal lochs on flattened occlusal surfaces, weaker anterotrope and rudimentary accessory ridges, including prototrope, centrotrope and postcentroloph (Text-fig. 6).



Text-fig. 6. Temporally-calibrated size and morphology variation of M2 and m2 (m1 in case of *G. major*) in selected species of *Glis*. Dashed lines indicate implied phylogenetic relationships.

Through a transitional *G. sackdillingensis*, known from the Middle Pliocene, the extant species emerged in the Early or Middle Pleistocene. By the middle Early Pleistocene time, the recent species *G. glis* had presumably appeared in Greece and Bulgaria (Koliadimou and Koufos 1995, Popov 2018), and by the Middle Pleistocene in Austria, Bulgaria, the Czech Republic, Germany, Hungary, Poland and Romania (Kowalski 2001). Thus, the south European record seems to predate the central European ones, suggesting a northwestward dispersal of this form (Text-fig. 5). These conclusions about the palaeobiogeographic history of edible dormouse should be treated cautiously, considering that precise relationships among the extant *Glis* species and its predecessors, such as *G. sackdillingensis*, are not firmly established, and further studies focused on the relationships within the genus will likely alter and refine the current palaeobiogeographic conclusions.

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