A HISTORY OF EUROPEAN MAMMALS

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The comprehensive survey of current information on European mammals provided by this *Atlas* reveals impressive diversity in the distribution and population status of individual species. It raises the questions: What came before, what are the sources of this diversity, and which drivers are responsible for obvious differences between particular species? In many cases, the environmental diversity of our continent and the diverse habitat requirements listed in the species accounts might provide a partial answer. The mammals, our closest relatives, have been for hundreds and thousands of years exposed to diverse interactions with humans and anthropogenic impacts altering the natural condition of our continent at a large scale. Moreover, in a broader perspective, the effects of multiple climatic and geological rearrangements changed the environmental setting of Europe even more radically, and the European mammal fauna has had to evolve in response to these changes.

As in general, history is an indispensable dimension of the present, and many of the phenomena we currently see can be understood only in the light of their histories. The diversity of extant European mammals is no exception. This is why the present chapter was included in the *Atlas*. It is intended to provide a condensed snapshot of the main processes and events which modified the history of European mammals and established deep stepping stones prefiguring the current situation. Yet, prior to reading it, keep in mind a general warning: A peephole into history is essentially biased – the deeper the past the more fragmented and fuzzier the information available. The most reliable information is thus available on alien species recently introduced by humans, so the survey begins just with them.

RECENT INTRODUCTIONS

Undoubtedly, the most precise information on the history of current European mammals is available for those species introduced by humans, which now compose nearly 10% of the extant European mammals (24 species: 10 rodents, 6 ungulates, 5 carnivores, 1 lagomorph, 1 Diprotodontia, and 1 primate). The history of *Ondatra zibethicus* in eastern Europe is perhaps the most complete, as it was documented year by year and serves as a common textbook example. Its expansion started with the release of a few individuals in Dobříš, Central Bohemia, in 1905, and by the 1930s, it already covered most areas of the European mainland. *Ondatra* was introduced essentially as a pet to rewild suburban habitats. Such intentions were probably also behind the release of *Sciurus carolinensis* and *Hydropotes* (both first released around 1875 in the UK), or those of *Callosciurus* spp. (in Italy), *Eutamias sibiricus*, *Tamias*, *Atlantoxerus* (in the Canary Isles), and *Muntiacus*, all taking place during the 20th century. The multiple introductions of *Castor canadensis* in the 20th century (mostly unsuccessful except for Finland), when the Eurasian species was close to extinction, could also fall in this category.

Many of the intentional introductions performed during the first half of the 20th century were novel game animals (*Cervus nippon*, *Odocoileus*, *Axis*, *Ammotragus*, *Sylvilagus*), supplementing multiple alien introductions of native European game mammals (among others the former Mediterranean endemics *Ovis*, *Dama*, and *Oryctolagus*) which had taken place since Roman times. The earliest records of *Herpestes ichnemuon* in Spain are also from Roman times, as it is now clear that it did not spread naturally via the Straits of Gibraltar. Perhaps it was introduced for the same reason as another herpestid, *Urva auropunctata*, introduced into Istria in 1910 as a possible exterminator of viper snakes. The other alien carnivores (*Nyctereutes procyonides*, *Neogale vison*, *Procyon lotor*) and coypu *Myocastor coypus* first appeared in the 1920s–1930s in fur farms (*Nyctereutes* in Russia, the others in Central and Western Europe). Their feral populations mapped in this *Atlas* originate from their release, either intentional or unintentional (since the 1930s for *Nyctereutes* and the 1970s–1980s for the others). The unintentional introduction of *Rattus norvegicus* in the 18th century was similar to the expansion of *Rattus rattus* in the Mediterranean during Roman times, promoted by maritime trade. Also, the sole extant European population of non-human primates (on the Rock of Gibraltar) originated from a recent

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Table 1.1 **A synopsis of range characteristics of the extant European mammals: Numbers of species possessing particular range types. Based on the geographic setting of Europe as dealt with in the Atlas.**

ORDER	ALIEN	NATIVE IN EUROPE												
		MACRORANGES						MICRORANGES						MARINE
		CENTRED IN EUROPE			MARGINAL IN EUROPE, CENTRED IN			ENDEMICS IN						
		EXTENDED BEYOND	MOSTLY IN EUROPE	MEDITERRANEAN	E OF EUROPE	S OF EUROPE	NE OF EUROPE	ISLANDS	IBERIA	APENNINES	BALKANS	ALPS	OTHER	
Eulipotyphla		6	3	2	4		3	4	4	4	3	1	2	
Rodentia	10	19	4	1	14	2	5	3	7	7	15	3	8	
Lagomorpha	1	1	1			1		1	2	1				
Carnivora	5	14			1		3	1	2		1			8
Cetartiodactyla	6	7	1				2		2	1		1		
Primates	1													
Chiroptera		19	6	6	1	4		7	3				1	
Diprotodontia	1													
Total	24	66	15	9	20	7	13	16	20	13	19	5	11	8

introduction, though *Macaca sylvanus* was a resident European species until the Late Pleistocene.

NATIVE SPECIES

By contrast, a study of the history of native clades of European mammals is incomparably more complicated. Already a diversity of range types (Table 1.1) suggests that the taxonomic diversity of European mammals and their distribution patterns cannot entirely be explained by their habitat requirements or behaviour; the past dynamics of individual clades must be taken into account as well. In reality, the current patterns of the extant European fauna have to be looked upon as a direct heritage of a superposition of multiple faunogenetic events. These were driven by diverse global, regional, or local rearrangements, either climatic, paleoenvironmental, or paleogeographic, accompanying the Cenozoic history of Europe, to which each clade responded in a particular way.

When investigating these topics, we currently tend to rely heavily on predictions provided by molecular phylogenetics and molecular phylogeography. Yet, these predictions do not always completely correspond to our quest for the truth. The history of a species might not be identical to the history of a few of its genotypes surviving in the present fauna, and correspondingly, the molecular clock's unresolved misconceptions might sometimes bias the dating of phylogenetic divergences.

Consequently, this brief account of the history of European mammals is essentially based on the European fossil record, which, besides the past of individual clades, informs us about the trends of faunal rearrangements and their contextual settings. This approach is possible because Europe is a classical area of paleontological research, and some of the world's most important sites, illustrating key points in mammalian history and the early roots of mammalian community development, are here (such as the Eocene Messel Pit Fossil Site, Quercy Phosphorites, etc.). Even when we restrict our interest to much younger stages, more or less directly responsible for the present composition of the European mammal fauna, the European fossil record is indeed very rich, which, of course, makes an

overview of that topic a hard task. No wonder Google Scholar reports nearly 200,000 papers on that subject.

In any case, a direct fossil record is available for almost all European mammal genera and, with a varied resolution, for at least 120 (50%) extant European species (15 insectivores, 41 rodents, 29 bats, 4 lagomorphs, 14 carnivores, and 17 ungulates).

Of course, the fossil record is inevitably incomplete and unequal, both in spatial and taxonomic respects. In general, it is much more detailed for small mammals, which often appear in very abundant fossil bone deposits from the pellets of owls and raptors, than for large mammals, whose records are often limited to the remains of single individuals. Combined with rapid radiations in particular clades and time-specific changes in community structure, the fossil record of small mammals presents the most reliable source of information on the terrestrial history of the Late Cenozoic past and its stratigraphic framework (Figure 1.1).

THE MIOCENE ROOTS OF THE CURRENT FAUNA

The deep roots of the contemporary mammal fauna of Europe can be seen in the early Neogene–Miocene (23–5.4 million years ago), when many current genera first appeared. The Early and Middle Miocene fauna of Europe is characterised by greatly diversified communities of a tropical pattern, rich in insectivores (including

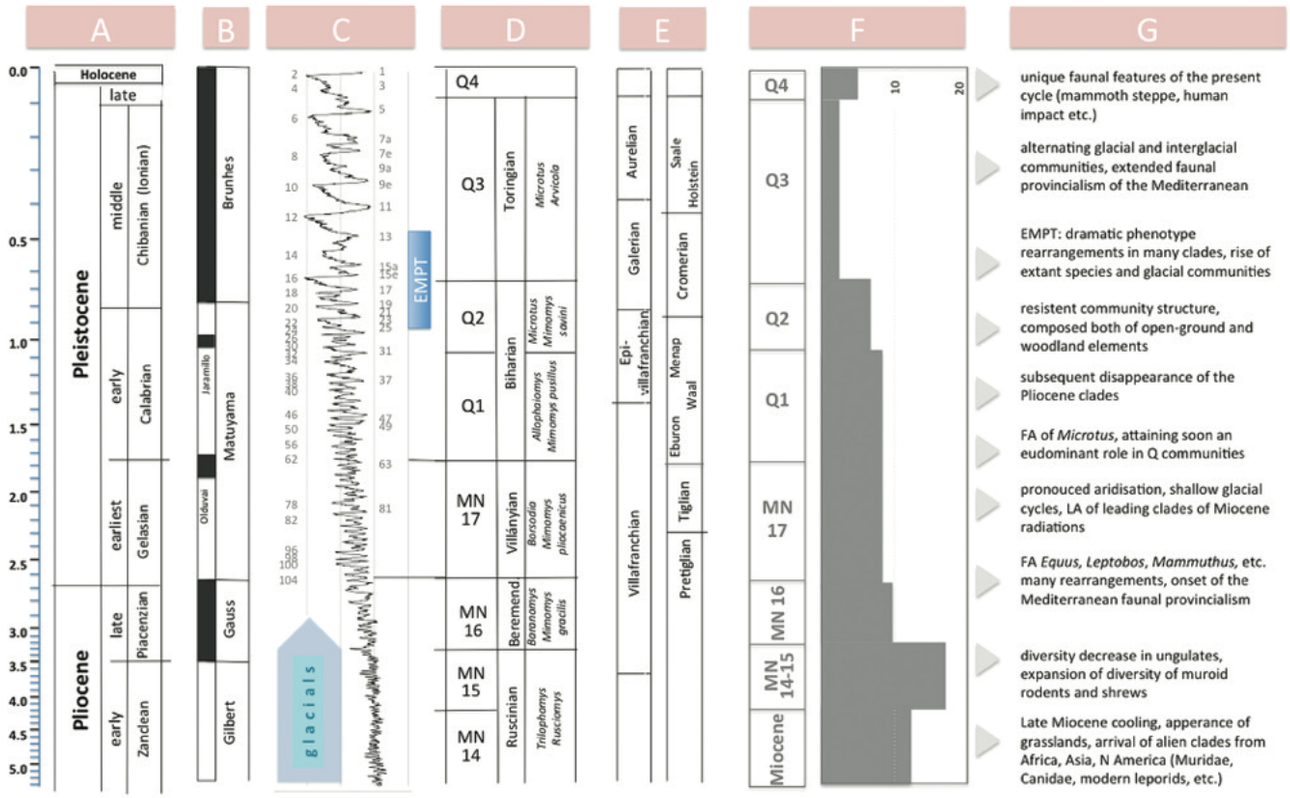

Fig. 1.1 **A stratigraphic framework of the Pliocene and Quaternary history of European mammals. (A) Chronology (scale in millions of years – Ma) and standard subdivisions (referred to stages defined on marine record). (B) Magneto-stratigraphic scale (black, normal; white, reversed polarity stages). (C) Paleotemperature record based on $\delta^{18}O$ variation in benthic marine microfossils (after Liesecki and Raymo, 2005) and sequence of MIS (marine isotopic stages) units of a global climato-stratigraphic scale (1–104). (D) Standard mammalian biostratigraphy – sequence of the Neogene (MN) and Quaternary (Q) mammal biozones, stages of traditional hierarchic biostratigraphy, and index fossil of small mammal communities. (E) The biostratigraphic scales frequently applied in the case of large mammal record (left) and the units alternatively used in diverse (mostly W European) literature (right). (F) Number of extant genera of native European terrestrial non-volant mammals first recorded in particular biozone. (G) Major faunogenetic events. EMPT, Early/Middle Pleistocene transition; FA, First appearances; LA, Last appearances; Q, Quaternary. (Original graphics by I. Horáček.)**

erinaceids, echinosoricins, talpids, dimylids, soricids, etc. – in total about 140 species of 58 genera), rodents (with dominant glirids, sciurids, spalacids, zapodids, and early clades of cricetids), ancient proboscideans and rhinocerotids, tapirs, diverse clades of ruminants (Cervidae, Bovidae, Giraffidae: In total about 70 genera), pliopithecine primates, early clades of mustelids, viverrids, felids, ursids, early lagomorphs and bats with most extant European genera and/or their direct ancestors. Thus, the currently occurring genera *Erinaceus*, *Talpa*, *Atlantoxerus*, *Glis*, *Muscardinus*, *Eliomys*, *Myomimus*, *Spalax*, *Martes*, *Rhinolophus*, *Myotis*, *Eptesicus*, *Pipistrellus*, *Nyctalus*, *Plecotus*, *Miniopterus*, *Tadarida* and direct ancestors of *Genetta* were already present in Europe before the Late Miocene, the stage which brought an essential turnover.

At that time, following global tectonic, paleogeographic, and paleoclimatic rearrangements, the extensive marine basins covering most of central and Eastern Europe disappeared, and the Anatolian and Levantine region opened direct contacts with Asiatic and African biota, which invaded first the Mediterranean and southeast European regions. During the early stage of the Late Miocene (Vallesian, 11–8 million years ago [Ma]) European mammal communities exhibited a vast predominance of woodland elements. The early stage of the Vallesian (MN9 – in terms of the MN-mammalian Neogene zones) is characterised by the first European appearance, via transcontinental expansion from Northern America, of hipparions – the equid genus typical of European communities until the beginning of the Pleistocene. Also, the genus *Castor* first appeared at that stage, accompanying ancient clades of castorids (such as *Trogontherium* and *Steneofiber*), resident in Europe since the early Miocene. The next stage (MN10) was then characterised by the first appearance of Muridae, followed by their rapid radiation, causing a dramatic decline in the role of glirids, the disappearance of diverse clades of early cricetid clades, etc. At this time, the first Hystricidae appeared from an east Asiatic source (similarly to murids), with the earliest record of *Hystrix*, closely resembling the extant *H. cristata*, as well as *Bellatona*, an ancestor of pikas. Among these clades and particularly in cricetid rodents a pronounced hypsodoncy – increasing height of molar teeth – is a common adaptive trend. This trend is visible in several clades of "microtoid cricetids", showing it in combination with further dental adaptations resembling the apomorphies of Arvicolinae. These novelties prefigured the rearrangements that began in the Turolian, the last stage of the Late Miocene (MN11–13, 8–5.4 Ma), and later accompanied the history of European mammals until the present.

During the Late Miocene, the content of atmospheric CO_2 decreased dramatically (from c. 450 to 300 ppm), the temperature in the temperate zone dropped by c. 5° C, and the structure of the vegetation was considerably changed by the mass appearance of C4 plants and the expansion of grasslands habitats. Mammals responded in multiple ways. The fossil record demonstrates a clear increase in tooth height in most clades of large herbivores (establishing among others the direct ancestors of *Cervus* and *Capreolus*), and the influx of novel clades mostly of African (*Orycteropus*, *Pliohyrax*, *Hippopotamus*, *Maremmia*, modern Hyaenini, Gerbillidae, *Paradolichopithecus* and *Theropithecus*), but also Asiatic (*Gazella*, *Macaca* and *Mesopithecus*, a colobine primate) or even North American origin. The latter included leporid genera *Alilepus* and *Hypolagus*, camelids (*Procamelus*), and the family Canidae with *Eucyon*, and perhaps the first appearances of *Canis*, followed in the next stages by *Vulpes* and *Nyctereutes* (surviving in Europe until the early Pleistocene). Among resident European clades, the extant genera *Erinaceus*, *Sorex*, *Apodemus (Sylvaemus)*, *Felis*, *Lynx* or direct ancestors of *Gulo*, *Meles*, or *Lutra* are first reported from that stage. The early species of *Micromys* (reported since then until the Middle Pleistocene, mostly from Mediterranean Europe) were found to represent more likely *Parapodemus*, an extinct sister genus of *Apodemus (Sylvaemus)*.

The Miocene epoch terminated with the Messinian salinity crisis, when the radical uplift of north-west Africa disrupted the connection between the Mediterranean Sea and the Atlantic. This resulted in a nearly complete change of the Mediterranean into an extensive arid to semiarid terrestrial basin that interconnected all Mediterranean regions including the former islands (Murchas–Granada basin, Balearics, Sardinia-Corsica, Maremma, Gargano), inhabited until then by distinct insular endemics. The extensive range expansions of resident clades subsequently colonising the basin (5.7–5.3 Ma) were dramatically disrupted by reflooding 5.3 Ma, rapidly establishing the present appearance of the region. The elements of the Messinian communities isolated by this event, particularly on Mediterranean islands, evolved a plethora of curious local endemics, most of which survived there until being exterminated by human activities in recent historical times. Examples include giant glirids, such as *Hypnomys* and *Eliomys (Eivissia)* on the Balearics, *Leithia* on Malta, *Tyrrhenoglis* on Sardinia, but also several other mammals such as a leporid *Prolagus sardus* on Sardinia. The Balearic endemics further included, e.g. *Myotragus balearicus*, a curious bovid, and a shrew genus *Nesiotites*, whose subrecent remains provided ancient DNA (aDNA) showing convincingly its sister relations to the extant Indian genus

Soriculus, quite distant from the European *Neomys* (and its supposed ancestor – genus *Asoriculus* first recorded in the early Turolian). Among extant island endemics, *Crocidura sicula*, *C. pachyura*, *C. zimmermanni*, and *Myotis nustrale*, are also worth mentioning in these contexts. In any case, the impact of the Messinian event can be traced in several other clades of European mammals, as suggested, for example, by molecular dating of root divergences of the Western Palearctic clades of *Crocidura*, *Talpa*, *Plecotus*, *Meriones* or the *Eliomys quercinus–melanurus* complex. Its sorting effect started multiple divergences within the *Pipistrellus pipistrellus-pygmaeus-hanaki* clade, which has been documented in particular detail.

The climatic history of the Late Turolian was accompanied by increasing seasonality (mean temperature of the coldest month in central Europe was even below 5 °C) and pronounced differences between the Mediterranean and northern regions of Europe, the former being warmer with a less marked seasonality but pronounced aridification. These trends, and regional differences in faunal arrangements associated with them, grew particularly apparent since the beginning of the Pliocene, the stage associated with the disappearance and/or dramatic decline of many Miocene clades.

THE PLIOCENE REARRANGEMENTS

The faunal turnover along the Miocene/Pliocene boundary is particularly well marked in the fossil record of bats. Since the beginning of the Pliocene (MN14), it is characterised, first in Central Europe, by mass multi-species accumulations in cave deposits corresponding to hibernation colonies featuring a predominance of *Myotis* spp. and other vespertilionids, supplemented with a few rhinolophids and *Miniopterus*, all clearly related to extant species (though not identical with them). Those clades incapable of hibernation (megadermatids, hipposiderids, rhinopomatids) disappeared from the European record (except for two early Pliocene records of *Megaderma*). Since the beginning of the Pliocene, the Soricidae became a dominant clade of European insectivores, evolving several novel lineages (including large-sized carnivorous forms *Beremendia*, *Amblycoptus*, *Allosorex*). These were mostly extinct by the Late Pliocene and Early Pleistocene, except for a widely prospering genus *Sorex*, establishing a pattern for modern shrews. *Sorex minutus*, already present in the earliest Pliocene, is a top candidate for the longest-surviving extant species.

Compared to the Turolian, the Pliocene diversity of ungulates decreased dramatically, while the diversity of rodents and lagomorphs increased significantly, the latter with the first appearance of *Ochotona* and *Oryctolagus*. As well as the diversification of murids, novel features of rodent communities included the appearance of modern cricetines (*Allocricetus*), derived clades of hypsodont microtoid cricetids (*Baranomys*, *Trilophomys*, etc.), gerbilids, and the earliest true arvicolids (*Promimomys*). The voles soon became the dominant elements of rodent communities, exhibiting pronounced cladogenetic radiation, particularly since the later stage of the early Pliocene (MN15). The dental rearrangements, common to all clades of that group, included a gradual enlargement of the molar row, a rapid increase in molar height, and the complexity of their occlusal arrangement, all improving the efficiency of grazing. Voles are r-strategists, disposed to rapid adaptive responses, and their abundant representation in the fossil record and the rapid dental rearrangements of particular clades makes them a key reference group for a detailed biostratigraphy of the Pliocene and Pleistocene period.

A period of climatic instability along the early/late Pliocene (MN15/16) boundary brought a period of rewarming accompanied by an expansion of savannah-like habitats in southern Europe. This promoted the arrival of novel immigrants, particularly by the end of this stage and along the MN16/MN17 boundary: *Equus*, *Leptobos*, *Potamochoerus*, *Sus*, *Hyaena*, *Capra*, *Mammuthus*, hunting dog *Lycaon falconeri*, cheetah *Acinonyx pardinensis*, or *Puma pardoides*, ancestor of the extant American genus. The communities of resident Turolian clades (tapirs, hipparions, mastodonts, etc.) enriched with these novel elements, which were particularly frequent in southern Europe, are traditionally termed Villafranchian faunas. The MN16 record of small mammals reveals a dominant contribution of voles with rooted but quite high molars such as several clades of *Mimomys*, the earliest forms of *Clethrionomys* and *Pliomys* (the genus closely related to extant *Dinaromys*, first reported from late MN17 in northern Italy), and the first clade losing their molar roots, *Plioctomys*, ancestor of extant Lemmini of Asiatic origin. Despite the predominant role of the Pliocene clades and novel invaders, various Miocene clades (such as eomyids, uropsillini talpids, etc.) still survived, at least locally. Thus, it seems that at the European scale, the mammal fauna during MN16 (Beremendian or the early Villanyian in terms of classical mammalian biostratigraphy) attained one of the peaks of its diversity. This was particularly attributed to a considerable degree of faunal provincialism: A mosaic of local faunal patterns associated with distinctly pronounced divergences between the faunal history of Iberia, south-west Europe, the Apennine peninsula, and south-east Europe, which

also prefigured deep divergences among some extant clades (e.g. *Erinaceus europaeus-roumanicus-concolor*).

FAUNAL DYNAMICS UNDER RECURRENT CLIMATIC CYCLICITY

The gradual cooling terminating the MN16 stage (until then rather indistinct) exhibited first a well-pronounced climatic cyclicity – an alternation of cold and warm stages (glacials and interglacials) reappearing with a periodicity of c. 41,000 years (ka). Since the beginning of the Quaternary period at 2.6 Ma (starting with the MN17 stage – the Villanyian proper zone), the sedimentary series are marked by the recurrent appearance of loess, indicating the appearance of prolonged glacial conditions – a dry open country with cold winters and arid summers covered by a mosaic of grassland, shrub and savannah-like vegetation. Selection for adaptations to these conditions resulted in a further expansion of arvicolid rodents and their phylogenetic radiation, producing novel clades such as *Pitymimomys*, *Villanyia*, *Ungaromys* (a small-sized Ellobiusini), and *Borsodia* (an ancestor of Lagurini, still with rooted molars), all index fossils of the MN17 stage. At the same time, specialised clades of former radiations, particularly among both talpids and soricids but also in large mammals (see above) disappeared from the fossil record. During the terminal MN17 cycles some *Borsodia* lost the roots of their molars (prefiguring the extant genus *Lagurus*). Simultaneously, the earliest member of the genus *Microtus sensu lato*, characterised by an absence of molar roots, *Allophaiomys deucalion*, first appeared as a rare element.

The disappearance of roots enabling the continuous growing of molar teeth, dramatically increasing the efficiency of grazing grass, promoted these clades, and *Microtus* s.l. in particular, to a dominant role in small mammal communities, the most obvious characteristic of the Quaternary fossil record. An abrupt expansion of early *Microtus* – *Allophaiomys pliocaenicus* throughout the whole Holoarctic, which marks the beginning of the Biharian stage (MN17/Q1 boundary, c. 1.8 Ma), represented one of the most striking faunal events in the Late Cenozoic terrestrial fossil record. A particularly detailed fossil record of that clade illustrates rapid phylogenetic radiation during Q1 (early Biharian) with the subsequent appearance of *Chionomys*, *Alexandromys*, *Lasipodomys*, and *Microtus* s.s. (in the current classification), and independent clades in Iberia (among others, those resembling extant *Arvicola* – *A. jacobea*). There is a pertinent discrepancy in dating these events between the fossil record and the predictions of molecular phylogenetics, which date the divergences among these clades into the deep Pliocene past (4–5 Ma). It might suggest an increased rate of molecular evolution in these clades (similar to e.g. in Lemmini) due to recurrent abundance cycles patterning the population dynamics of these clades: Alternating temporal survival in isolated local populations (promoting locally specific adaptive rearrangements under enlarged genetic drift effects) with strong abundance bursts fixed the particularly successful adaptive efforts, supposedly associated with novel genomic arrangements, by the pan-mixing effects of large-scale abundance maxima. As a result, at a species level, the pace of molecular clocks might rapidly increase. The flexible population dynamics allowing these clades to profit from the climatic and environmental oscillations of the Quaternary period became perhaps one of the key factors promoting their prosperity during their time. Besides *Microtus* and *Lagurus*, it also applied to other clades constituting the communities of the early Pleistocene: *Clethrionomys*, *Pliomys*, *Cricetus*, *Allocricetus*, *Lemmus*, and *Myopus*. It may also include the index clade of shrews, *Sorex runtonensis/araneus* group and *Drepanosorex*, which exhibited a gradual increase in body size during the Biharian, responding perhaps to the disappearance of large-sized genera of the Pliocene radiation in that time. In any case, despite steady regional differences, the Biharian communities are characterised by relatively high species diversity and the simultaneous presence of resident clades demanding not only open and semi-open habitats but also woodland (*Glis*, *Clethrionomys*, *Muscardinus*, *Sciurus*) or wetland habitats (*Desmana*, *Castor*, *Trogontherium*, *Galemys* in Iberia). This community pattern was, to a considerable degree, retained also in the time of the late Biharian, when the fauna is further characterised by the disappearance of ancient elements (such as *Allophaiomys* phenotypes in *Microtus*, a small-sized *Mimomys pusillus*, *Hypolagus*, *Puma pardoides*, etc.) and the appearance of the last offshoot of the genus *Mimomys*, the large-sized *Mimomys savini*. The disappearance of molar roots characterising its transformation to the genus *Arvicola* (dated to 0.65 Ma) is taken as a Biharian/Toringian or Q2/Q3 boundary.

The faunal history of the late Biharian was essentially impacted by a global turnover in the Quaternary history – the Early/Middle Pleistocene Transition (EMPT). During the EMPT, between 0.9 and 0.6 Ma, the regular periodicity of glacial–interglacial cycles (41 thousand years [ka] on average during the Early Pleistocene) changed to 100 ka by a dramatic prolongation and strengthening of the glacial stages. Under the harsh glacial conditions first appearing during the EMPT stage, areas of central and

northern Europe became largely uninhabitable to most of the specialist and woodland elements. Some disappeared from Europe or became extinct (*Acinonyx*, *Lycaon*, *Beremendia*); others survived glacial episodes in isolated refugia in southern Europe, some with northward expansions during interglacial warming stages.

At that time, the non-glaciated regions of middle latitudes were colonised by communities of those clades disposed to evolve adaptations to extreme seasonality and a mosaic of open to semi-open steppe, boreal forest, and tundra habitats dominating during the glacial stages. However, such adaptations reduce the chance to prosper under conditions of warm and humid interglacials with predominating woodland habitats and promote extensive range retreats during interglacial stages.

In short, the EMPT split the European mammal fauna of middle latitudes into two distinct groups of interglacial and glacial elements, both responding to the recurrent glacial-interglacial alternations with expansions or regressions of their ranges. The capacity for this kind of response – orbitally driven range dynamics (ORD) – was made possible by rearrangements of life-trait patterns promoting it (elastic reproduction strategy and abundance dynamics, enlarged spatial dispersal with unconstrained gene flow, reducing tendencies to allopatric speciation, enlarged phenotype variation and behavioural opportunism). Obviously, since the EMPT, these drives have patterned the mammalian clades colonising a major part of the European mainland in an essential way. In any case, the mammal communities of peak glacial and peak interglacial stages differed substantially both in their core elements and energetic structure (grazing herbivores and their predators in glacial communities, corresponding to the pasture-predatory energetic pathway, vs. greatly diversified foraging specialisations in the interglacial communities, corresponding to the detritic pathways of energy assimilation).

The idea of the recurrent alternation of glacial and interglacial faunas, combining survival of their elements in mutually isolated microrefugia with extensive range expansions, acts as a central explanatory paradigm of European historical biogeography, a default model for many phylogeographic studies. Nevertheless, in most European mammals its validity seems to be rather limited. It does not apply to most of the Mediterranean endemic taxa and many clades resident in the southern parts of middle latitudes. Correspondingly, the pertinent differences in core elements of the glacial and interglacial communities, reported from middle and northern latitudes, do not appear in the fossil record from southern Europe. Rather, it indicates that in the Mediterranean region or even in the Balkans the community structure was only marginally affected by glacial–interglacial dynamics. Moreover, contrary to the predictions of the central paradigm, Mediterranean populations of mid-European forms were only rarely confirmed as the real source population for the postglacial northward spread of their mid-European relatives.

In any case, the EMPT brought an essential turnover in the history of the European mammal fauna, and its heritage can be identified in the vast majority of European mammals. The fossil record demonstrates that during the EMPT or early stages of the Middle Pleistocene almost all resident taxa exhibited marked phenotype rearrangements by which their Middle and Late Pleistocene records are, in most instances, directly co-identified with the extant European species (Figure 1.2).

As well as some extinctions (see above), the EMPT faunal rearrangements also included the immigration of several novel elements not previously recorded from Europe. Some of them, such as the large flying squirrel *Petauria voigstedtensis*, the large shrew *Macroneomys brachygnathus*, and the bear *Ursus thibetanus*, show relations to extant clades distributed in northern India, and their European records were mostly restricted to the EMPT period. Yet, most of the novel EMPT immigrants, such as *Sorex minutissimus*, *Pteromys volans*, *Dicrostonyx*, *Myopus schisticolor*, *Colobotis*, *Marmota* – first in Spain and Croatia 0.8 Ma, are inhabitants of boreal forest, steppe or tundra habitats able to survive a pronounced seasonality, and at least some of them reappeared regularly in European glacial communities until the Late Pleistocene. In large mammals (including those in southern Europe) the corresponding trends were expressed also by a general increase in body size. For instance, the gracile *Leptobos* spp. was replaced by a robust bovid, the aurochs *Bos primigenius*, and its sister clade *Bison schotensacki*, considered a direct ancestor of both *Bison bonasus* and European steppe bison *B. priscus*, supposedly an ancestor of the American bison. These forms, as well as Irish elk, *Megaloceros giganteus*, separated from the *Dama* clade at this time and survived in Europe until the end of the last glacial period. During the EMPT, the small-sized *Canis etruscus* was replaced by the large *Canis mosbachensis*, a direct ancestor of *C. lupus*, and forms like *Preovibos priscus*, the direct ancestor of muskox, *Rangifer*, and *Ursus deningeri*, an ancestor of Late Pleistocene cave bears, sister to the *Ursus arctos-maritimus* clade, first appeared in the European fossil record.

Unfortunately, the faunal record of individual Middle Pleistocene interglacials is still too scarce to support any general conclusion and/or a reliable statement on the faunogenetic differences of individual cycles. By contrast,

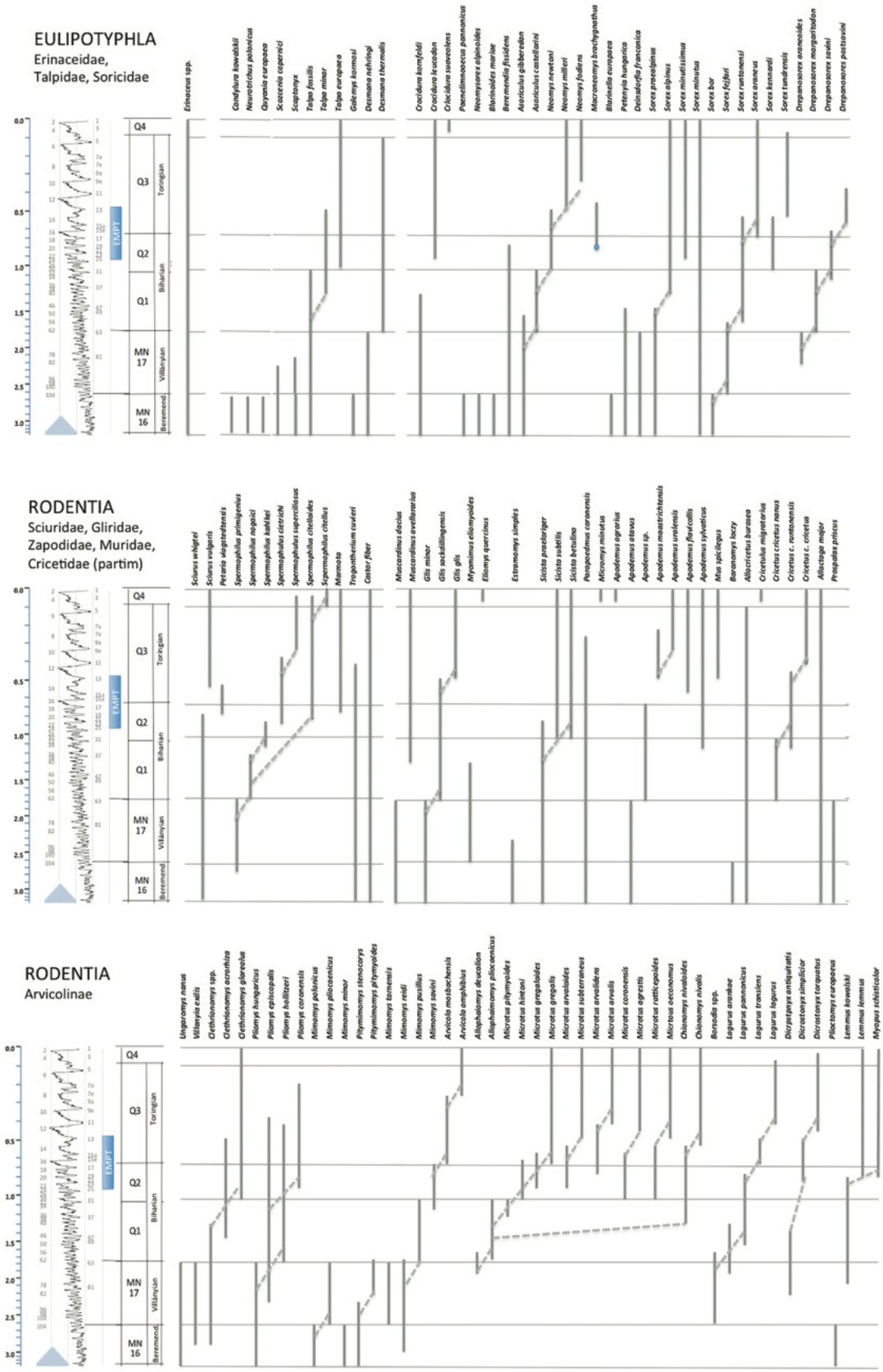

Fig. 1.2 (*Continued*)

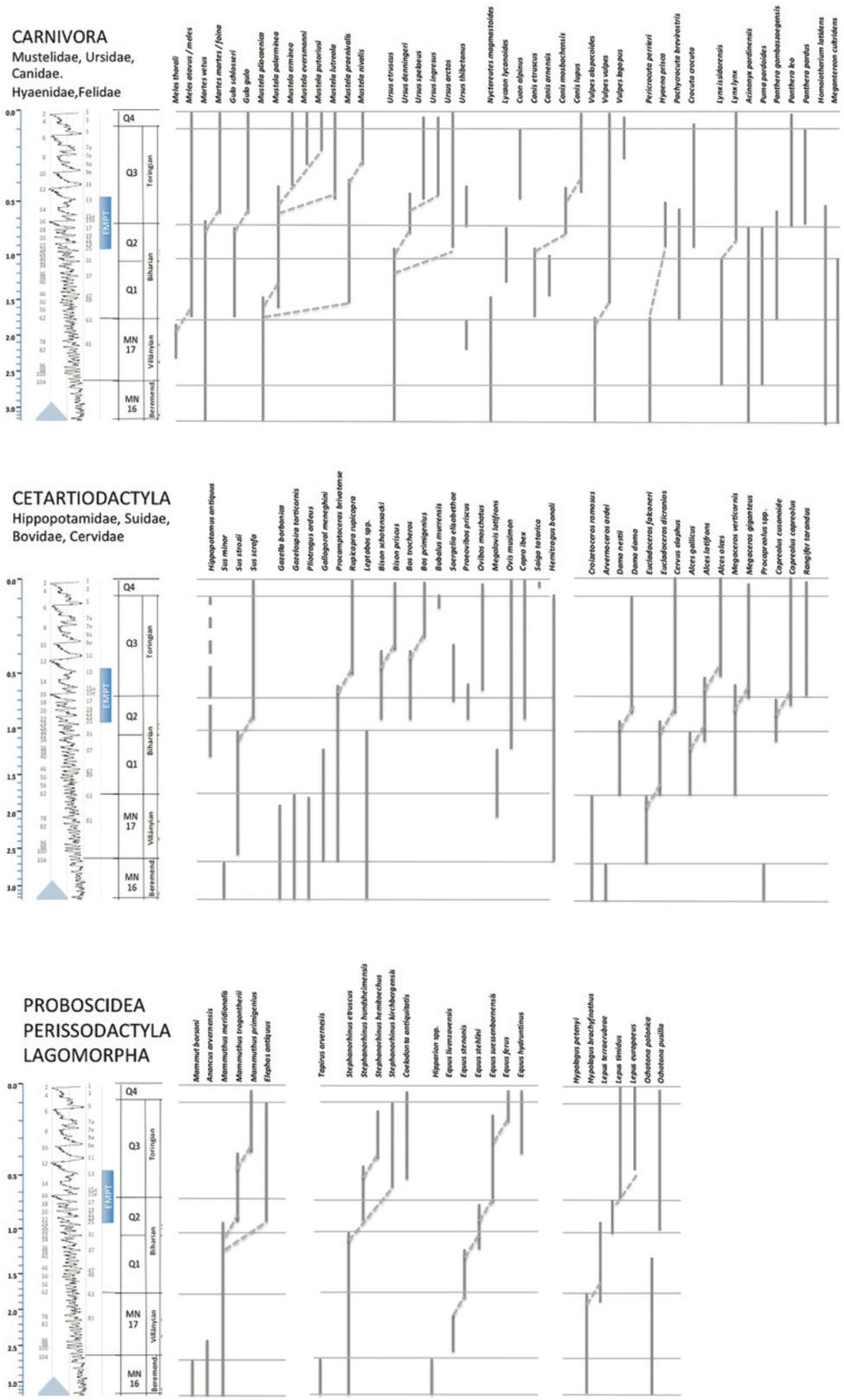

Fig. 1.2 **A synopsis of the putative stratigraphic distribution of selected taxa of terrestrial non-flying mammals composing the fossil record of the European middle latitudes. Note: Dotted lines show phenotype transformations supposedly related to phyletic rearrangements in resident European clades. (Original graphics by I. Horáček.)**

the abundant assemblages of glacial communities available from the whole of middle latitude Europe (including south-west Europe and northern Iberia) show the common structural characteristics and species composition, which was nearly identical throughout the whole Middle to Late Pleistocene period. The core of these assemblages was composed of a few arvicolid species: *Lasiopodomys gregalis*, *Microtus arvalis*, *Dicrostonyx* sp., *Lemmus lemmus*, *Chionomys nivalis*, *Microtus oeconomus* supplemented with *Microtus agrestis*, *Ochotona pusilla*, *Lepus timidus*, *Spermophilus (Colobotis)* and satellite elements of a mosaic distribution (both in a spatial and temporal sense) (*Cricetus cricetus*, *Phodopus sungorus*, *Sorex araneus*, *Clethrionomys glareolus*, *Sicista subtilis*, *Allactaga*, *Lagurus*). The abundant megafauna characterising the glacial communities included *Mammuthus trogontherii-primigenius*, *C. antiquitatis*, *Equus* spp., *Bison priscus*, *Rangifer tarandus*, *Alces alces*, *Panthera leo*, *Crocuta crocuta* or herbivorous bears *Ursus denningeri-spelaeus*, etc. The traditional default hypothesis expects that these glacial elements, identical to extant species, responded to interglacial stages by large-scale range regression, surviving in either northernmost Europe, high alpine habitats, or in extra-European distribution islets (comparable with the current ranges of lemmings, *L. timidus*, *Marmota marmota*, *Rupicapra rupicapra*, *Capra ibex*, *O. pusilla*, etc.). However, the universal validity of that model was recently disproved by detailed aDNA analyses of the dominant element of European glacial communities, traditionally considered identical with extant *L. gregalis*, distributed in northernmost eastern Eurasia and central Asiatic mountains. It was found to represent a distinctly separated species (*Lasiopodomys anglicus*) restricted to Europe for at least the last three cycles, i.e. without direct relations to the extant clades of *L. gregalis* – yet also still without any interglacial record except for the early Holocene, when the species obviously became extinct. This pertinent case illustrates convincingly that the actual history of European mammals might actually proceed in ways differing essentially from traditional textbook models.

UNDER THE HISTORY OF THE PRESENT CLIMATIC CYCLE

The general models of mammalian response to the Quaternary climatic cycles are essentially inferred from a very detailed record of the last cycle (MIS 1–5, in terms of Marine Isotopic Stages [MIS], the global climatostratigraphic scale). Yet, it should be remembered that the present cycle differs substantially from the previous ones in the course of both its glacial stage (Würm in the Alps, Vistulian in the continent) and the present interglacial, the Holocene.

The last interglacial, the Eemian (MIS 5e, Riss/Würm in Alps, Ipswichian in UK, Mikulian in E. Europe, etc.) began 129 ka BP with an abrupt temperature and humidity increase following the maximum of the Saalian glacial (MIS 6). The trend peaked about 125 ka BP when the average temperature was about 2 °C higher than preindustrial Holocene temperatures and nearly the whole of Europe was covered by continuous woodland extending beyond the Arctic circle. Notwithstanding a short cooling episode (c. 120 ka BP), the full interglacial (MIS 5e) lasted to 112 ka BP. The faunal record indicates the vast predominance of woodland elements both among large and small mammals: *Palaeoxodon antiquus*, *Stephanorhinus hemiechinus/kirchbergensis*, *Cervus elaphus*, *Dama dama*, *A. alces*, *B. primigenius*, *Ursus arctos*, *Glis glis*, *Apodemus sylvaticus*, *C. glareolus*, *Microtus subterraneus*, *M. agrestis*, *S. araneus*, *S. minutus*, etc. The absence of some of them from Britain suggests its insular status during the Eemian, not evidenced in earlier stages. Worth mentioning is the appearance of *Hippopotamus amphibius* and *Bubalus murrensis*, both appearing also during previous interglacials and surviving in the Mediterranean region until the end of the Eemian, and *M. sylvanus*, recorded even in the western regions of Central Europe. Some elements demanding warm subxerothermic open habitats became extinct during the Eemian (*Allocricetus bursae*, *Hemitragus bonali*); others survived, probably in Mediterranean microrefugia, some even into the Holocene, e.g. *Pliomys coronensis=lenki* in Iberia.

The late Eemian is then characterised by a sequence of pronounced cooling and warming episodes (MIS 5d, 5b vs. 5c, 5a) terminating with the peak glacial condition of the early Vistulian pleniglacial (MIS 4: 71–57 ka BP). Both in southern Europe and middle latitudes, woodland habitats were gradually replaced by a mosaic of open-ground habitats, yet during MIS 5 the above-mentioned interglacial elements still survived. Anyhow, the members of glacial communities clearly increased their numbers, first those demanding warm or mild steppe environments. This includes the resident European elements (*M. arvalis*, *M. oeconomus*, *Apodemus* spp., *C. cricetus*, etc.) in middle latitudes, *Spermophilus citelloides*, *Lagurus lagurus*, a small-sized *Hystrix vinogradovi* or *S. subtilis* in the Balkans, similarly the Iberian local endemics such as *Microtus cabrerae*, *Microtus duodecimcostatus*, and *Oryctolagus cuniculus.* A regular appearance of *Crocidura* spp. throughout the whole Mediterranean is also notable. During MIS 5b or MIS 4 most of the interglacial elements disappeared from middle latitudes, some becoming extinct (*Palaeoxodon*, *Dicerorhinus*), while the index elements of

glacial communities *L. anglicus*, *Mammuthus primigenius*, *Coelodonta antiquitatis* first (in that cycle) appeared.

The next stage, MIS 3 (56–29 ka BP) was the longest and most characteristic part of the Vistulian glacial. Its paleoclimatic record reveals the repeated effects of pronounced millennial cyclicity (Dansgaard-Oeschger cycles) and the appearance of Heinrich events, the episodes of massive breaking off of large masses of the glacier covering the Northern Atlantic. Both activated the supply of oceanic warm waters into that region which contributed to the relative stability of the continental climate in middle latitudes, resulting in the continuous expansion of steppe/savanna habitats of very high productivity. The final product of that development often called "the mammoth steppe" represented a unique biome spreading throughout the middle latitudes of the whole Palearctic region. Besides a particularly abundant megafauna (mammoths, woolly rhinos, reindeer, European bison, muskox, horses including a hemionid *Equus hydruntinus*, lions, leopards, hyenas, cave bears, etc.) it was inhabited by greatly diversified communities of small mammals composed of the European glacial fauna (dominated by *L. anglicus*, *M. arvalis*, *C. nivalis*, *Alexandromys oeconomus*, *Arvicola amphibius*, etc., including *Dicrostonyx*, *Lemmus*, *Myopus* or *Sorex araneus*, *S. tundrensis*, *S*, *minutissimus*, *Neomys fodiens*, *Mustela erminea*, *M. nivalis*, *M. eversmanni*), with accessory elements of a Central or East Asiatic origin, e.g. *O. pusilla*, *Spermophilus (Colobotis) superciliosus*, *P. sungorus*, *Allactaga major*, *Apodemus uralensis*. During MIS 3, the East Asiatic species *Apodemus agrarius* and *Micromys minutus* first appeared in Europe via large-scale transcontinental range expansions.

Communities of that type have been documented by numerous fossil records from all middle latitude regions of Europe, including western Europe as far as northern Iberia and Britain, which was an integral part of the continent due to a lowered sea level. Though the communities of southern Europe with resident populations of glirids and other diverse habitat specialists were not greatly impacted (except for the invasion of *Eolagurus luteus* in the Balkans), expansion of the mammoth steppe communities extended considerably in the south. This happened particularly in the west of Europe, where a spread of the glacial elements brought the introgressions retained in extant genomes of their sister Iberian endemics (*L. timidus* in *L. granatensis* and *L. castroviejoi*, *M. agrestis* in *M. lavernedi* and *M. rozianus*).

Many glacial elements responded to the quasi-stable conditions lasting throughout MIS 3 with a gradual increase of body size in both the small and large mammals; in some the giant glacial forms were formerly even described as independent glacial species (*Talpa magna*, *Cricetus major*, *Equus germanicus*, *Canis lupus maximus)*.

A radical break in the faunal history came with the late Vistulian peak glacial (MIS 2: 30–14 ka BP), and particularly its coldest stage, the Last Glacial Maximum (LGM, 27–18 ka BP). The highly productive mammoth steppe gradually changed into a mosaic of raw tundra soils covered by sparse grassland vegetation. Those elements of glacial communities intolerant of cold vegetation seasons (*Lagurus*, *Hystrix*, *Marmota*, *S. supercilliosus*, *Phodopus*) disappeared from the mid-European fossil record. At that time, the saiga *Saiga tatarica*, an ungulate perfectly adapted to harsh semi-desert environments with extreme seasonality, first appeared in Europe, while the resident taxa of glacial megafauna exhibited a considerable decline. The woolly rhinoceros became extinct except for a few isolated records in Central Europe. *C. crocuta* disappeared from Europe (the last European record in Italy, 30 ka BP). The cave bear (*Ursus spelaeus* including *Ursus ingressus* – last record 24 ka BP) also became extinct. The resident populations of mammoth and *Dicrostonyx torquatus* were impacted by introgression of their Siberian clades, supposedly better adapted to tundra conditions, and similar replacements have also recently been demonstrated, with the aid of a DNA analyses, for other resident taxa (*M. arvalis*, *M. agrestis*). In general, the fossil record clearly shows that the demise of the mammoth steppe during the LGM was associated with numerous local extinctions and range fragmentation in most European species of all groups. Obviously, this was the main factor responsible for the collapse of the European glacial megafauna, often attributed to humans, who, of course, undoubtedly contributed to it by killing its last remnants.

The LGM has been traditionally given as a *tabula rasa* of paleobiogeographic scenarios. Indeed, with the continental and mountain glaciers reaching their maximum extent during the LGM, most regions of middle latitudes took the appearance of a hostile periglacial desert with sparse patches of tundra on permafrost, uninhabitable for most mammalian species. Yet, in the diversified landscape of central Europe, multiple islets rich in vegetation, liquid water, and suitable microclimatic conditions existed (in sheltered mountain valleys, surfaces of mountain glaciers, or basins of hydrothermal aquifers, e.g. in Pannonia, South Moravia, or in SW Germany), serving as isolated microrefugia where the rarer forms capable of long-term survival in small, isolated populations might occur continuously. Increasing evidence suggests the importance of these refugia not only for most elements of the European glacial fauna but also for some members of the interglacial communities such as *C. glareolus*, *S. araneus*, *M. agrestis*,

and *Sicista betulina*, and/or high mountain endemics such as *Apodemus alpicola*, and *Microtus tatricus*. Such a scenario receives robust indirect support from the immediate appearance of these elements in the mid-European communities of the post-LGM stage. A shallow climatic amelioration, continuing during the following stages of the late Vistulian, enriched the small mammal communities, dominated by *Microtus gregalis*, *D. torquatus*, and *M. arvalis*, with more specialist elements of open habitats probably re-expanding from local refugia (*O. pusilla*, *P. sungorus*, *C. cricetus*, *S. subtilis*, *A. uralensis*, *C. glareolus*, and in rocky areas *C. nivalis)*. Some re-expansion of the mammoth is also evident in this stage, which, like other elements of the glacial megafauna, finally disappeared 12,000 years ago in middle latitudes and the earliest Holocene in the far north. The dramatic warming during the Bölling and Alleröd interstadials (14–15 ka BP) brought a rapid expansion of shrub and tree vegetation (*Juniperus*), radically changing the character of the open steppe. This warming pulse, particularly pronounced in the Mediterranean region, promoted range expansions of those elements demanding warm open or semi-open habitats. This also affected those surviving in the mid-European refugia, which soon became regular components, enriching still-surviving glacial communities: *A. uralensis* and *S. betulina*, soon accompanied by the elements expanding from the Mediterranean refugia: *Apodemus flavicollis* (from south-east Europe), and first in western Europe *A. sylvaticus*, and *E. quercinus*, *Crocidura russula* (from south-west Mediterranean). The mid-European fossil record of that stage also includes forms (supposedly south-eastern immigrants) not recorded here in earlier stages of the Middle and Late Pleistocene (*Crocidura leucodon*, *M. minutus*, *P. pipistrellus*, *A. agrarius*). Similarly, in the large mammal communities, the species relying on semi-open and forest habitats – roe deer, wild boar, moose, brown bear, and beaver – gradually appeared alongside glacial index taxa like horse, reindeer, wolf, and fox.

These trends were partly interrupted by a cold pulse of the young Dryas (12.8–11.7 ka BP), with a temporary re-expansion of glacial features. Compared to previous sections, in which the composition and abundance structure of vertebrate faunas were roughly identical throughout central and western Europe, the Late Glacial–Early Holocene section encounters considerable regional variation in the patterns of both the dispersal of the interglacial elements and the survival of the glacial elements. In the western part of central Europe (e.g. southern Germany) glacial elements (*L. anglicus*, *C. nivalis*, *Dicrostonyx*, *Lemmus*, *Ochotona*) disappeared completely at the beginning of this period, while the proportion of woodland elements (*C. glareolus*, *G. glis*) increased rapidly. In the Carpathian basin and surrounding areas, the core species of the glacial fauna (except for *Lemmus*) contributed regularly to local communities up to the end of the early Holocene.

The strong thermal pulse around 11.7 ka BP, which started the Holocene proper, forced the final stage of deglaciation and a rapid rise of sea level. At that time, Ireland, which until Bölling was covered by a glacial sheet, was already becoming isolated from both Britain and mainland Europe. Thus, apart from a few glacial elements capable of occasional long-distance dispersal during the Bölling–Alleröd stage (*M. giganteus*, *L. timidus*, *M. erminea*), Ireland was not colonised by those terrestrial mammals, such as voles or shrews, otherwise common throughout the whole middle latitudes of Europe. Exceptions to this are those introduced by humans, since the Mesolithic (*S. minutus*, *A. sylvaticus*) to the early Middle Ages (red fox, European badger, pine marten, *R. rattus*, *Mus musculus*, *Sciurus vulgaris*), or more recently (*C. russula*, *S. carolinensis*). By contrast, Britain, glaciated only in northern Scotland, kept a land-bridge connection with Europe until ca 8 ka BP. Thus, its Late Pleistocene/early Holocene faunal history shows no difference from the trends common to the whole middle latitude European mainland.

Compared to the Eemian, the Holocene is often regarded as a relatively dry stage. Indeed, until the middle Holocene, the rapid thermal increase was only partly followed by an increase in precipitation. Thus, in central and south-east Europe, the Early Holocene is characterised by a variegated mosaic of open-ground grasslands, shrubs, and arboreal patches. Also in the Mediterranean, the first millennium of the Holocene was associated with very dry climatic conditions, which delayed reforestation but promoted range expansions of the elements demanding warm open to semi-open xerothermic habitats, soon appearing even in Central Europe. Thus, in Central Europe, an increased representation of the forms requiring arboreal vegetation (*C. glareolus*, *A. flavicollis*, *S. betulina*, *Muscardinus avellanarius*, *M. subterraneus*, *S. vulgaris*) was, particularly in the Pannonian region and Moravia, accompanied by the appearance of south-eastern European elements not previously recorded (*Crocidura suaveolens*, *Rhinolophus hipposideros*, *Mus spicilegus*, *A. agrarius*, *Myotis blythii*, *Miniopterus schreibersii*, *Hypsugo savii*). However, most of these soon disappeared from there, at least by the time of the cold event terminating the early Holocene at 8.2 ka BP.

The increase in precipitation at the beginning of the middle Holocene led to the disappearance of open habitats and the expansion of woodland formations, terminating with the mass expansion of beech throughout Europe 6,000 years ago, a novel phenomenon of the interglacial

vegetation history. The characteristic elements of the Late Pleistocene/early Holocene communities, until then almost continuously distributed throughout Central and Western Europe (*S. betulina*, *A. uralensis*, *M. agrestis*, *A. oeconomus*, *C. cricetus*) underwent extensive retreat and range fragmentations at that time. In contrast, the Mediterranean regions (particularly Iberia) revealed pronounced aridisation tendencies.

At the same time, the history of European mammals became impacted by extensive landscape changes associated with the human Neolithic revolution arising in the Middle East at the beginning of the Holocene and spreading via Anatolia into the Mediterranean region and south-east Europe. Reaching central Europe about 7,000 years ago, it brought extensive deforestation beginning in the lowlands, replacing woodland habitats with a novel biome, a cultural steppe, an open ground formation combined (in contrast to glacial conditions) with a warm climate. In the fossil record, it is well marked by a decreased representation of woodland elements and the reappearance of some elements of glacial communities surviving in local refugia, particularly in Pannonia (*M. arvalis*, *C. cricetus*, *S. citellus*), accompanied by the Mediterranean elements relying on such a habitat, novel in central Europe (see above). Besides domestic ungulates, the Neolithic expansion was also associated with the expansion of commensal mammals, beginning with *M. musculus*, which first appeared around 11 ka BP in the Near East and c. 6 ka BP in South-East and Central Europe, accompanied by domestic cats kept for mouse control.

Mammals also contributed to the post-neolithic rearrangement of the European biota in another way – the abundant herds of domestic sheep accompanying the Neolithic invaders acted, with their thick fur, as mobile seedbanks of the Middle Eastern and Mediterranean archeophytes which nowadays compose about one-third of the European flora.

The dramatic history of human civilisation in the Eastern Mediterranean, expanding with maritime trade since the early Bronze Age (c. 4 ka BP) into the whole Mediterranean, radically changed the history of the European mammal fauna. It almost completely exterminated a diversified spectrum of endemic clades of the Mediterranean islands, replacing them with domestic animals and unintentional introductions of *M. musculus*, *Crocidura gueldenstaedtii* or *R. rattus* (first appearing in Mesopotamia 5 ka BP). Extensive deforestation and large-scale pastures practiced throughout the Mediterranean resulted in a mass spread of the sclerophyllous evergreen macchia-garigue formations replacing the highly diversified original habitat mosaic and reducing the differences in mammal communities between regions.

Thus, in general, the late Holocene history of European mammals has been largely influenced by a plethora of diverse interactions with human civilisation – its economic interests (agriculture, hunting, forestry, industry) and attitudes. In contrast to the mass exterminations impacting almost all species of large mammals during historical times, recent decades have brought considerable changes. Nature conservation and rewilding efforts saved European bison and promoted current re-expansions of some large carnivores, Eurasian beaver, and Eurasian otter and the maintenance of relict populations of some endangered forms like *Spermophilus citellus*, *C. cricetus*, *Lynx pardinus*, and *Galemys pyrenaicus*. The adaptation of wildlife to urbanisation and to human settlements have been other factors influencing the current distribution of many mammals. Some bats, particularly the cave-dwelling species, have adapted to roosting in human-made structures, which is allowing them to extend their ranges into latitudes where the cave microclimate is unsuitable for reproduction (*R. hipposideros*, *R. ferrumequinum*, *Myotis myotis*, *M. blythii*, *M. emarginatus*, *Plecotus austriacus*). In addition, other lithophilous and dendrophilous species show recently established preferences for anthropogenic habitats (*Eptesicus*, *Pipistrellus*, *Nyctalus*). A well-pronounced population increase in most bat species during recent decades, contrasting with a pronounced decline in some of them in the 1970s and '80s, can be further ascribed to global warming, similar to the extensive northward range expansions in some Mediterranean elements, until then absent in middle latitudes, e.g. *Pipistrellus kuhlii*, *H. savii* or *Canis aureus*. Yet, it is very hard to predict whether these trends will continue and/or what will happen even in the immediate future. The varied history of European mammals teaches us that current trends might change quite rapidly. At least for this reason, the population development and distribution status of European mammals remains a hot topic worthy of continuous careful monitoring. An indispensable platform for this task is fortunately available. You hold it in your hands.

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