ANIMALS

Zoltán Varga

Zoogeographical units and basic concepts

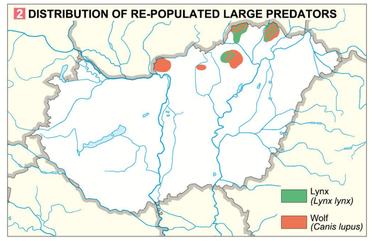
The geographical distribution of biota shows some predictable regularities. Different sciences provide the knowledge necessary to reveal the repetitive patterns in ranges which can lead to a set of generalisations which in turn provide a scientific framework for the biogeographical understanding of our fauna. Since the geography of ranges has been influenced both by direct ecological factors and the evolutionary history of organisms the discipline of *biogeography* has an intermediate position between the geo- and bio-sciences encompassing ecology, paleoecology, evolutionary biology, climatology, historical geology and paleogeography.

According to the traditional zoogeographical method the continental areas are hierarchically subdivided into realms, regions, sub-regions, districts, etc. based on the classical work of the evolutionist A.R. Wallace (1876), a contemporary of Charles Darwin. Following this subdivision, the inner, Pannonian part of the Carpathian Basin was designated as the *Middle Danube faunal district* 1. Although this subdivision and its cartographic representation is quite instructive, it has the deficiency that the regional boundary lines will tend to diverge more and more in the cases of different zootaxa as the scale of analysis becomes finer. As a consequence, we can only follow such subdivisions when looking at a large spatial scale. We therefore have to search for more objective partitions using modern statistical methods which consider the phylogenetic differences between the major groupings. Another approach is the characterisation and grouping of ranges according to horizontal *(zonobiomes)* or vertical *(orobiomes)* vegetation zonality *(faunal types, faunal elements)*. A recent direction of research is *phylogeography*, i.e. the survey of the evolutionary dynamics of ranges in connection with speciation processes using molecular genetic and genomic markers.

The fauna of any region consists of set of species with different ranges of distribution. The species with biogeographically similar ranges, i.e. faunal elements can be grouped into faunal types. Historically, the size and shape of areas served as the principle for grouping. More recently, it has been replaced by the concept of *core areas* (de Lattin, 1967), since the stationary and expansive areas, belonging to the same core area, show a continuous transition between both extremes. In the first step the species with regionally limited areas will be considered and grouped according to their overlapping territories. In the second step the more widely distributed, mostly polytypic species will be considered and the core areas of their subspecies will be compared with the core areas of the more stationary species. The same method can be applied also for monophyletic groups of allo- or parapatric species. These core areas can independently be identified by genetic markers, e.g. mitochondrial or plastid DNA haplotypes, which therefore are the objective characteristica of each chorological unit, i.e. *faunal type*. Based on these genetic markers the spatio-temporal dynamics of population expansion from core areas can also be traced. The proportions of faunal types can be employed quantitatively to characterise the different biogeographical regions and elucidate the underlying processes of faunal composition.

The zoogeographical position of the Carpathian Basin

The zoogeographical position of the Carpathian Basin is mostly influenced by orographical and bioclimatic factors. On one hand the basin is almost completely surrounded by high mountains. These function as barriers but also as filter-corridors for the dynamics of different faunal types. Due to the isolation of the basin, its populations have often become differentiated from those which populate the surrounding areas outside the Carpathians. On the other hand our region has a transitional position between the Central European nemoral zone and the continental forest steppe belt. It also shows, however, some sub-Mediterranean and sub-Atlantic influences. The synergy of climatic and orographic factors often results here in some 'deviations' from the general zonality of the vegetation, being typical for Pannonian landscapes. They often have several historically conditioned 'individual' traits in the mosaic-like pattern of assembled vegetation units.



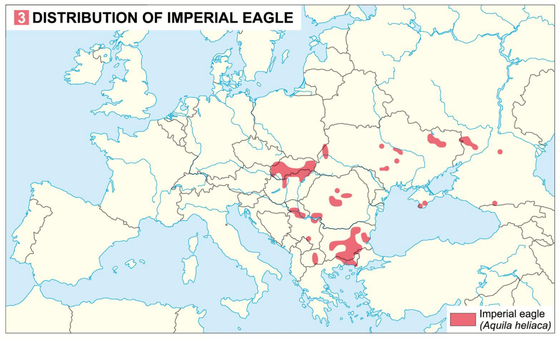
Another important biogeographical feature of the Carpathian Basin is the multiplicity of faunal types. The ranges of distribution of species connected with different core areas often overlap here. Although the majority of the fauna comprises widely distributed species, these are not the most characteristic animals of the region. Some of them, such as the European Bison, have become extinct whilst others, for example the large predators, Wolf 2 and Lynx, became rare or endangered. Recently however, these have received protection and are beginning to re-populate some areas to the extent of becoming regionally frequent.

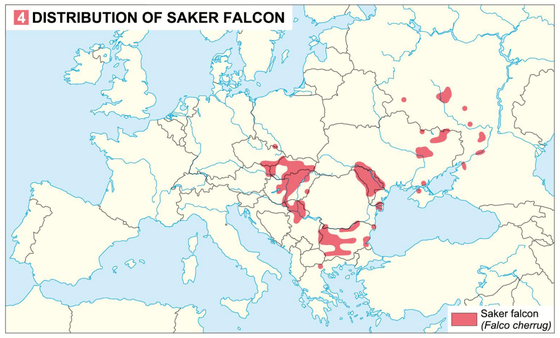
In most groups, about or more than half of the constituent species have a wide Euro-Siberian or European range. Their distribution covers most parts of the temperate zone though the delimitation of their ranges may differ. The distribution of some species is set by summer isotherms ('thermophilous' species), while others, such as the Atlantic and Atlanto-Mediterranean species, are limited by low winter temperatures. Because the environmental restrictions operating at the edges of species' ranges do not form sharp boundaries we find that the eastern-northeastern boundaries of Atlantic species often overlap with the western-southwestern borders of continental species. As a consequence of the transitional situation of the Carpathian Basin, numerous species here reach their western or northwestern range limits (for example many of the typical steppic or forest-steppic faunal elements). These often represent the iconic species of the Pannonian biogeographical region and have often acquired the status of 'flagship' species for nature conservation. Examples are the Great Bustard *(Otis tarda)*, the Imperial Eagle *(Aquila heliaca)* 3, the Saker Falcon *(Falco cherrug)* 4 and the Red-legged Falcon *(Falco vespertinus)* 5.

Some other, more frequent species, such as the Souslic *(Citellus citellus)* and the Hamster *(Cricetus cricetus)*, are highly important as the prey of raptors or as indicator species of habitat quality. Other biologically important species of high nature conservation status have significant populations in the wetland and/or riverine habitats of the Carpathian Basin. These include the Great White Egret and Little Egret *(Egretta alba, E. garzetta)*, the Black Stork *(Ciconia nigra)* and the Corncrake *(Crex crex)*. Unfortunately another, the Aquatic Warbler *(Acrocephalus paludicola)*, has virtually vanished in recent years. Generally, it is widely distributed species which represent the majority of the fauna in the more mobile groups (e.g. birds, dragonflies, butterflies etc.), but these also constitute about half of the species in the more sedentary groups (land snails, myriopods, diplopods, ground beetles etc.). These species belong to the so-called 'basic fauna' which is typical of a larger biotic zone, for example, the Central European nemoral belt or Boreal taiga zone.

The other main group of faunal types consists of less widespread species with restricted regional distributions. These sets of species amount to only 5-15% of the whole faunal assemblage but they clearly signify different bio-climatic (e.g. atlantic, mediterranean, steppic, etc.) influences. In the Carpathian Basin these species are often those typical of the surrounding regions' – the Alpine, Carpathian, Balkanic, etc. – faunal elements. In other cases they show connections with more distant areas, as for example the turano-eremic species with the semi-desert zone 6. Their occurrence is regularly linked to locally or regionally relevant ecological factors, such as orography, substrate, micro-climate, etc. as seen with rupicolous, halophilic or peatland species. These discrete areas providing special conditions tend to be associated with intra- or extrazonal vegetation formations and occur mostly in colline, hilly peri-Pannonian areas.

The Carpathian Basin was populated after the last (Würm/Weichsel) glaciation from different core areas – partly from those which closely surrounded the basin and partly from more distant refugia. During this phase of postglacial recolonisation, some West (Illyrian) and East Balkanic (Moesian) areas, but also the Southern and Eastern Carpathians played an important role. The marginal, 'peri-Pannonian' areas would have witnessed complex scenes of fluctuating species range dynamics with the different faunal components often overlapping one another in space and time 7. As a consequence, the highest diversity of faunal types is most characteristic of some marginal areas of the basin. For instance, the peri-Alpine belt is the area of co-occurrence of East Alpine (Noric), West Balkanic (Illyrian) and Pannonian elements. Some hilly parts of Southern Transdanubia (Mecsek, Villány Hills) are characterised by the co-occurrence of West Balkanic and sub-Mediterranean species. A multiple overlap can be observed in the Apuşeni (West Transylvanian) Mts. where, besides numerous endemic species, the Pannonian, Dacian, East Balkanic and South Carpathian species are also present. Another confluence of different faunal elements is the Aggtelek and Slovak Karst, at the borderline of the Carpathians and Pannonian Basin, typified by the regional accumulation of Boreo-montane, Carpathian, Pannonian, sub-Mediterranean and even Xeromontane species. A similar multiplicity of faunal types is more or less present in the Transdanubian and North Hungarian Ranges, e.g. in the Balaton Uplands and Vértes Mts. but also in the Bükk and Tokaj (Zemplén) Mts. with some sub-Mediterranean and more continental influence. In the lowlands some marginal areas show the highest species diversity, as



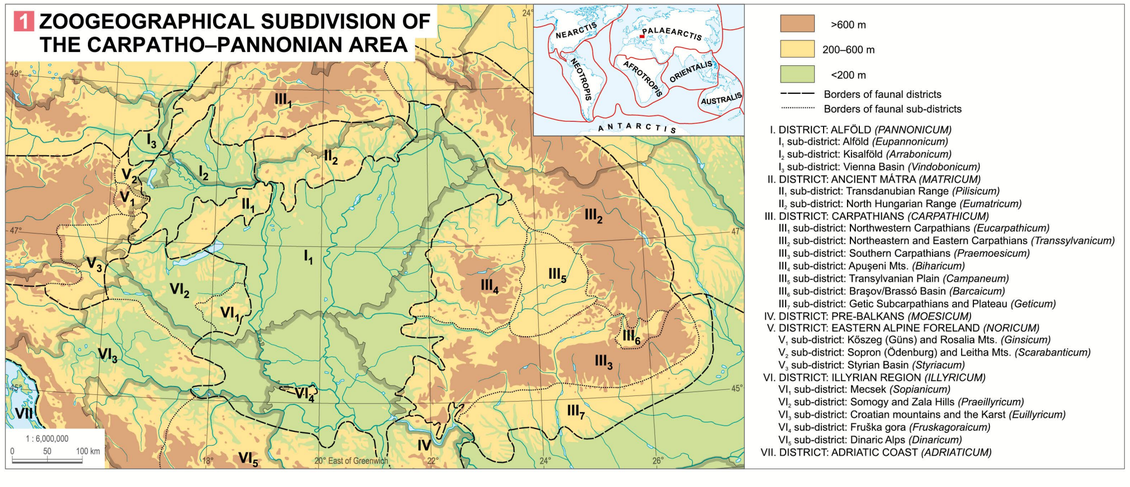


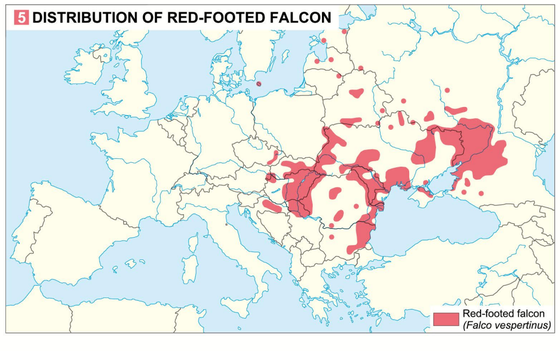
Distribution of the birds of prey of the Carpathian Basin

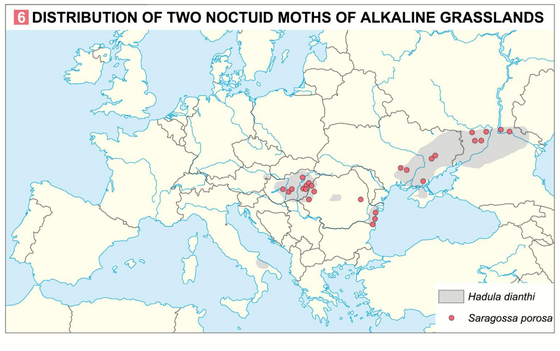
The Imperial Eagle *(Aquila heliaca) is a southern continental species distributed from Southeastern Europe to Southern Siberia and Mongolia* 3*. Its sister species (Aquila adalberti) occurs in the Iberian peninsula. It is considered a character species of the forest steppe zone but also of the grassland-forest mosaic landscape in the Carpathian Basin. Significant breeding populations in Europe occur only in the Southeastern European table-land (Ukraine) and the Carpathian Basin.*

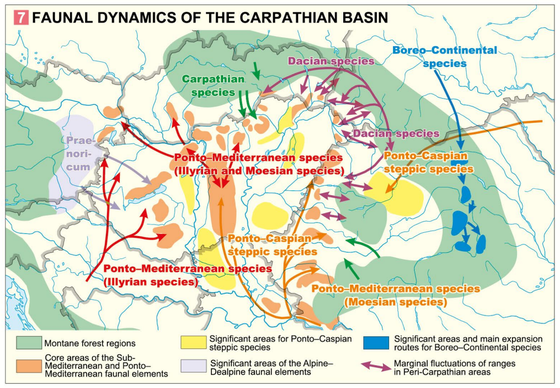
The Saker Falcon *(Falco cherrug) is another characteristic southern continental raptor species of the Carpathian Basin. Its range is similar to that of the former species and it is also typical and indicative species of the forest steppe zone. The strength of its populations greatly depends upon the density of its favourite prey animals, the souslic and other rodent species of grasslands. Its most important European breeding populations are in the Carpathian Basin and in the Ukrainian part of Eastern Europe* 4*. Beyond its intrinsic biological and ecological value the Saker Falcon is an emblematic bird with great importance as a flagship species for nature conservation.*

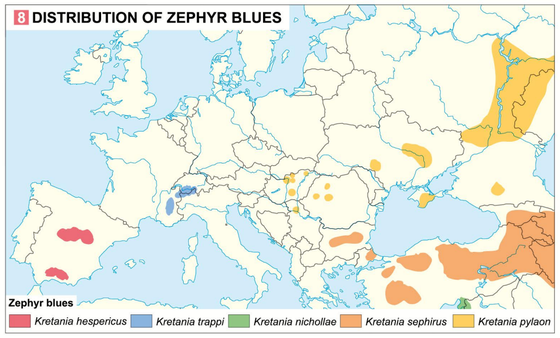
The ***Red-footed Falcon*** *(Falco vespertinus) is a trans-Palearctic, East European, East Asiatic species with a disjunct range* 5*. It is most frequent in the forest-steppe belt, but is more widespread than this zone. The colonies breeding in the Carpathian Basin belong to the most significant populations of the species globally. This small falcon is considered to be one of the most typical birds of the Pannonian landscape.*











the valley of the river Dráva (Illyrian influence) and the Upper Tisza Plain (fluctuation area of the Praecarpathicum). The inner parts of the basin, e.g. the loess ridges and the saline bottomlands exhibit an express continental influence. The loess grasslands

1 *The Hungarian ground beetle (Carabus hungaricus)*

are marked by the presence of continental steppic species such as the bush-cricket *Gampsocleis glabra* or the Cossid moth *Paracossulus thrips.* Other loess steppic species have a Ponto-Pannonian distribution. Examples of these include the oil beetle *Meloe variegatus*, the flower chafer *Protaetia ungarica*, the monophagous longhorn beetle *Pilemia tigrina* (and its food-plant, *Anchusa barrelieri*) and the steppic weevil *Minyops costalis*. Some character species of the saline areas, like the grasshopper *Epacromius coeruleipes* and the tiny Geometrid moth *Narraga tessularia*, however, signify a more distant biogeographical connection, that with the Turano-Iranian semi-deserts. The sandy grasslands also have some southern continental elements like the grasshopper *Stenobothrus fischeri* and the Hungarian Ground beetle *(Carabus hungaricus)* 1.

The Hungarian ground beetle *(Carabus hungaricus)* 1 *is a widely distributed steppic species, subdivided into several subspecies from Southeastern Europe to Southern Siberia. These are geographically separated and also genetically differentiated from the populations distributed east of the Carpathians. The nominotypic subspecies was described by* Johann Christian Fabricius *as early as the end of the 18th century from specimens obtained from Hungary. It reaches the western border of its distribution in the Vienna Basin and Southern Moravia showing a Pannonian biogeographical character. Its most important habitats are sandy grasslands (e.g. Nyírség, Kiskunság, sandy grasslands of the Kisalföld) but significant populations also occur on some of the dolomitic plateaus of Transdanubia.*

Endemic Taxa and Autochthonous Evolution in the Carpathian Basin

The level of endemism generally correlates with the geological age of the refugia where relict taxa have evolved or survived. The Carpathian Basin belongs to the geologically young areas of Europe. Its relief developed under the influence of the Alpine orogenesis and by retreat of the Paratethys and the Pannonian inland sea. Moreover, the phylogeography of some freshwater invertebrates (e.g. Neritidae snails) is clearly connected with the evolution of the Ponto-Pannonian water basin and of the Danube catchment area. In addition, there are several terrestrial groups with a considerable proportion of endemic species. In the case of land snails, Soós (1943) showed that the proportion of endemic species is unexpectedly high (about 29%, a level which is more characteristic of insular faunas). Even higher proportions of endemic species were found in earthworms (Lumbricidae, >40%) and in some soil arthropods. The ranges of distribution of these endemics are often extremely narrow, e.g. the huge (60-80 cm!) Lumbricids (*Octodrilus* spp.) of the Apuşeni Mts., or the allopatric endemic *Dendrobaena* species in the Carpathians. Their core areas (Illyrian, Dacian, Apuşeni Mts.) clearly coincide with the younger Tertiary land masses within and near the Carpathian Basin.

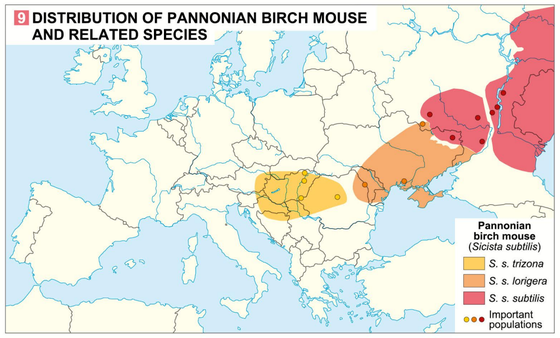
Most endemic species are narrow specialists, inhabiting extreme habitats like thermal springs, karstic caves and karstic springs. Several endemic troglobionta have been described in gastropods, pseudo-scorpions, harvestmen, spiders and springtails, often occurring within a single or a few caves of the karstic mountains. The tiny water snail *Bythiospaeum hungaricum* for example occurs in just two isolated caves of the Mecsek Mts. while another, *Bythinella pannonica*, is more widespread in karstic springs of North Hungary and adjacent parts of Slovakia. Some troglobiotic Diplopods are also restricted to the karstic parts of the Mecsek Mts. Other species are typical for the karstic areas in the North of the Carpathian Basin, like the Amphipod, *Niphargus tatrensis* (in several slightly differentiated populations in different mountains) or the Isopod, *Mesoniscus graniger* occurring in the caves of the Aggtelek and Slovak Karst. It often co-occurs with the blind Carabid species *Duvalius hungaricus.* Many more endemic species of troglobiotic ground beetle occur in the caves of Transylvania and Banat.

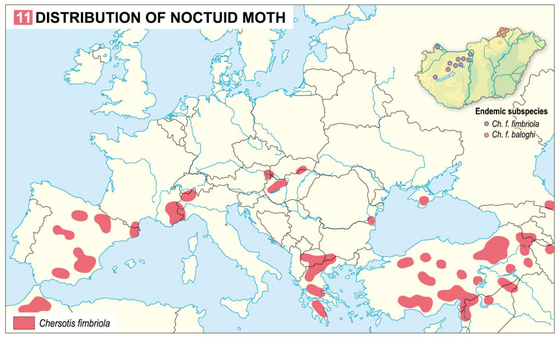
A number of earthworms, millipedes, centipedes and woodlice can be considered as holo-endemic species of the Apuşeni Mts. High levels of endemism were also observed in insects of springs and smaller streamlets, such as stoneflies (Plecoptera) and caddisflies (Trichoptera). The isolated Apuşeni Mts. is known as a core area of endemic species including *Leuctra transsylvanica, Nemoura hamata* (Plecoptera) and *Plectrocnemia kisbelai* (Trichoptera). Some endemic species of soil fauna including various Diplopoda (e.g. *Entomobielzia gaetica, Karpathophilon dacicus*) and Isopoda (e.g. *Hyloniscus transsylvanicus, Protracheoniscus politus*) are indicative of glacial forest refugia in Transylvania. Endemic species occur also in flightless insects such as some genera of bush-crickets *(Isophya, Poecilimon, Pholidoptera)*, grasshoppers *(Miramella, Odontopodisma, Pseudopodisma, Podismopsis)* and ground beetles (e.g. large species of the subgenus *Morphocarabus*, mostly in the Eastern and Southern Carpathians.

2 *Pannonian Zephyr Blue or Steppic Blue of the Fôt hills (Kretania pylaon)*

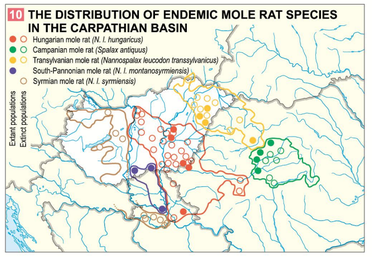
The steppic ***Kretania Blues*** *(Kretania pylaon and related species) comprise a species group which is widely distributed from the arid mountains of Central Asia to the Southern Alps (K. trappi) and the Iberian peninsula (K. hespericus)* 8*. They are represented by genetically differentiated populations on the Balkan peninsula (K. sephirus) and in the Carpathian Basin (K. pylaon kovacsi, K. pylaon uhryki, K. pylaon proximus). The latter populations* 2 *show close contacts with the steppic nominotypic subspecies K. pylaon pylaon. These Blue butterflies are food plant specialists, the larvae feeding on Astragalus species (Astragalus exscapus, A. dasyanthus, A. monspessulanus).*

In the mobile insect groups the proportion of endemism is rather low. Several endemic Macrolepidoptera subspecies of the Carpathians belong to the genera *Erebia* and *Glacies.* A few endemic taxa are only widespread in the Carpathians such as *Erebia epiphron transsylvanica*, *Glacies canaliculata schwingenschussi* while others are confined to the Eastern and Southern Carpathians *(Erebia manto traianus)* or to the Southern Carpathians, often with Balkanic connections (e.g. *Erebia neleus neleus*, *Coenonympha rhodopensis schmidtii*). All these data clearly demonstrate that the





3 *Hungarian mole rat (Nannospalax hungaricus) from Southeastern Hungary*



The lesser ***Mole Rats*** *(Nannospalax species) originated in the mountain grasslands of the Balkan peninsula. In the Carpathian Basin four endemic species of Nannospalax have evolved in adaptation to the climatically different regions of the basin* 10*. The Transylvanian-East Pannonian species (N. transsylvanicus) has the strongest (though vulnerable) populations while the Central and Southern Pannonian species (N. hungaricus* 3*, N. montanosyrmiensis) are critically threatened, and the westernmost species (N. syrmiensis) is probably already extinct. The large Transylvanian species Spalax antiquus has an Eastern European steppic affinity and is critically threatened.*

Carpathians, especially the eastern and southern parts, together with the mountains of Western Transylvania should be considered core areas for the survival and autochthonous evolution of many invertebrate groups.

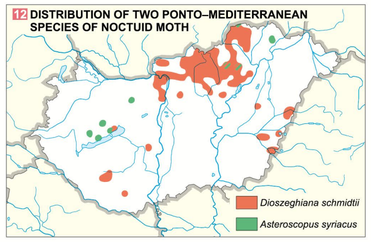
A few endemic species do also occur, however, in the inner, lowland or colline parts of the Carpathian Basin. Examples of these are *Kovacsia kovacsi*, an endemic snail of the Körös river valley, the widely distributed bush-cricket, *Isophya costata*, occurring in tall grass steppic and mesophilous meadows, the tiny oil beetle *Hycleus tenerus* in sandy grasslands, and several micro-moths of the Coleophoridae with flightless females and halophilous larval food plants, for example *Coleophora hungarica* and *C. peisoniella*. Endemic subspecies of *Geometridae* and *Noctuidae* evolved as peripheric isolates of turano-eremic species from the late-glacial, *kryoxerotic* periods, e.g. *Narraga tessularia kasyi, Saragossa porosa kenderesensis* (on food plants: *Artemisia santonicum* and *A. pontica*) and *Hadula dianthi hungarica* (on *Gypsophila muralis*). Some endemic taxa in the sandy areas of the Pannonian lowland are specialised predators or parasitoids, for instance the spider, *Dictyna szaboi* or the pompilid wasp, *Cryptocheilus szabopatayi.*

In some other different taxonomical groups typical Pannonian endemic species/subpecies have also been described. In such cases, recent molecular studies have been able to reveal significant genetic diffferentiation, e.g. in the Pannonian Zephyr Blue *(Kretania pylaon)* 8 2 and closely related allopatric taxa.

Allopatric genetic differentiation and speciation has also been discovered in the Pannonian subterranean Rodents (mole rats, subg. *Nannospalax*). These allopatric populations are also evolutionarily and biologically significant units for conservation (see: *boxes*).

In steppic species a general rule of genetic differentiation was found in connection with the Carpathians as both an orographic and a genetic barrier. The Pannonian Birch mouse was until recently considered a separate species *(Sicista trizona)* – significantly differentiated as it is from the Boreal Birch mouse *(S. betulina)* and the Steppic birch mouse *(S. subtilis)*. Even within the Carpathian Basin some differentiation was found between the Pannonian and Transylvanian populations 9.

Some trends of sub-speciation are also seen in xerothermic species of the lower altitude, hilly parts of the Carpathian Basin with Mediterranean, mostly with Balkanic and West Asiatic connections, for example the moths, *Apamea sicula tallosi* in warm-humid alluvial areas, *Dioszeghyana schmidtii schmidtii* 4 and *Asteroscopus syriacus decipulae* 12 in Pannonian xerothermic oak forests, *Polymixis rufocincta isolata* in the Villány Hills, *Chersotis fimbriola fimbriola*, *Euxoa vitta vitta*, *E. hastifera pomazensis* and *Cucullia mixta lorica* in the dolomitic areas of the Transdanubian Range and *Chersotis fimbriola baloghi* in the Aggtelek Karst 11. The cutworm owlet moth species *(Chersotis fimbriola)* was originally described from the hilly re-



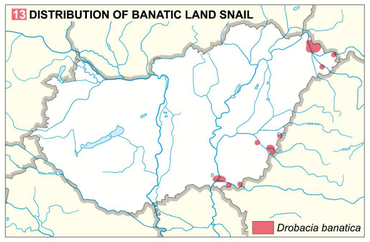
4 *Turkey-oak Owlet (Dioszeghyana schmidtii schmidtii)*

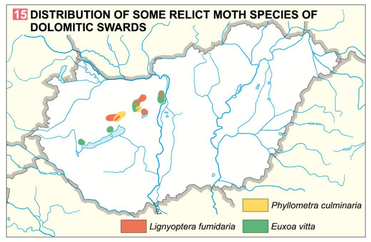
gion near Buda. A Hungarian population, associated with dolomitic rupicolous swards, therefore represents the nominotypic subspecies of this, mostly Mediterranean, xeromontane polytypic species. (Its northernmost population is of another subspecies described from the Aggtelek and Slovak Karst and endemic to the region. Other subspecies are scattered from the Atlas Mountains to the Transcaspian Kopet Dagh mountains.) The same area, the Buda Mountains, are known as typical localities of other xerothermic species, such as the cutworm moth, *Euxoa vitta*, the Pannonian Winter looper, *Erannis ankeraria*, and the spectacular Jolas Blue, *Jolana jolas.*

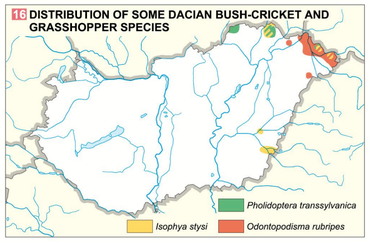
Relict species in the Carpathian Basin

The largest part of the Carpathian Basin was covered in the younger Tertiary by the Pannonian inland sea, and later by the Pannonian lake which gradually shrank due to geotectonic processes and fluvial accumulation. Therefore it was supposed that the origin of some species is connected with these inland sea/lake periods. Recent molecular surveys on the species groups *Theodoxus danubialis, Th. prevostianus* supported this hypothesis. The ancient form of *Th. prevostianus* appeared in the Carpathian Basin at the end of the Pliocene, irradiated and differentiated to isolated populations in different springs, and also to the predecessor of the more widely distributed *Th. danubialis*. The endemic snail of thermal springs at the eastern margin of the Pannonian Basin (Băile Felix near Oradea/Nagyvárad), *Melanopsis parreysi* also has a younger Tertiary origin.

Most relict species, however, do not belong to phylogenetically ancient groups. These are biogeographical relicts which have only relatively recently become isolated from the populations living in neighbouring or even distant areas. In a few cases fossils can also demonstrate the presence of some species in the Carpathian Basin. The Helicid snail, *Drobacia banatica* 13 5, for example is known from the Pliocene. In fishes and amphibians the molecular evidence suggests that some species or genetically differentiated



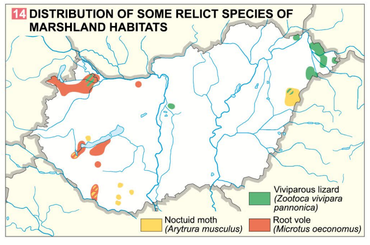




populations of species survived the Quaternary glaciations within or immediately near to the Carpathian Basin. However, in most groups, for example reptiles and mammals, the species comprising the present fauna of the Carpathian Basin appeared here only in the Upper Pleistocene or even after the last glaciation.

In the Carpatho-Pannonian area species that can be considered as glacial relicts are those which are mostly or exclusively distributed at the arctic-boreal latitudes and/or at the subalpine-alpine levels of the high mountains. Isolated occurrences are to be found in peat bog habitats. These glacial relucts include species such as certain caddisflies with larvae that develop in cushions of peat moss *(Sphagnum)*, for example *Oligotricha striata* and *Rhadicoleptus alpestris* and some food plant specialist butterflies like the Cranberry Fritillary *(Boloria aquilonaris,* food plant: *Oxycoccos quadripetala)*. Some other species, which are now mostly distributed in the arid high mountains or plateaux of Central Asia, are also relicts of the cold *(kryoxerotic)* climatic phases of the younger Pleistocene. These occur either on steep loess escarpments or in xeric rupicolous habitats and include the alpine land snail, *Oligolimax annularis*, in a calcareous rocky habitat in the Bükk Mts. and the Geometrid moth species, *Phyllometra culminaria* and *Lignyoptera fumidaria,* on dolomitic plateaux in Transdanubia 15.

Some other species can be connected with the humid-temperate phases of the Quaternary. They occur in areas and habitats with a buffered meso- and micro-climate in Southeastern Europe and, with a huge disjunction, in Pacific East Asia, as for example the Freyer's Purple Emperor (Apatura metis), the Metelka's Tiger Moth *(Rhyparioides metelkana)* or the giant owlet moth *Arytrura musculus* 14. Most thermophilous species, however, populated the xerothermic habitats of the Carpathian Basin only during the thermic optima of the Post-glacial period, as the typical species of the lanuginose oak scrub forests. Species such as the Buprestid beetle, *Kisanthobia ariasi*, the longhorn beetle,

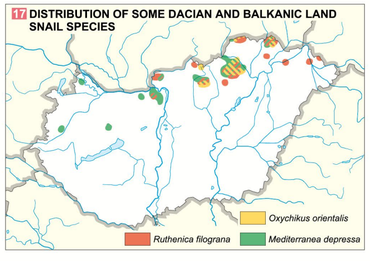


Deroplia genei, the weevil, *Camptorrhinus statua*, the Pannonian Winter looper, *Erannis ankeraria,* the owlet moths *Asteroscopus syriaca decipulae* 12 and *Dioszeghyana schmidtii*, and the Hungarian Buff-tip *Phalera bucephaloides* are representative of this assemblage. Other, food plant specialist southern species are connected to rupicolous grasslands or grassland-scrub mosaics like the Mountain White, *Pieris ergane (Aethionema saxatile)*, the Pannonian Anomalous Blue, *Polyommatus admetus (Onobrychis arenaria)* and the large Jolas Blue, *Jolana jolas (Colutea arborescens)* and the Purple Owlet *Pyrrhia purpurina (Dictamnus albus)*. Another characteristic group of Pannonian species is made up of the typical beetles of lowland steppic grasslands like the phytophagous Geotrupid, *Lethrus apterus,* known for its special parental care, the large Oil beetles, *Meloe tuccius*, *M. decorus* and *M. rugosus*, some Darkling beetles such as *Probaticus subrugosus* and *Blaps abbreviata,* the food-plant specialist longhorn beetles *Cardoria scutellata* and *Pilemia hirsutula*, the flightless weevils *Thamiocolus nubeculosus* and *Brachycerus foveicollis,* etc. The historical processes of the population of the Carpathian Basin can be uncovered through the survey of the distribution of less mobile groups consisting of numerous relict-like species such as Lumbricids, Oribatids, Diplopods from which the ranges of numerous species is connected with peri-Pannonian core areas. Such species comprise for example the East Alpine, Illyrian and Moesian faunal elements. Most Illyrian species occur in the broad-leaved forests of the Dinaric Mountains and adjacent colline and lowland areas (Illyrian beech and oak-hornbeam forests) and expand to Southern and Western Transdanubia ('Praeillyricum'). These include organisms such as the land snails, *Helicigona illyrica* and *Trichia erjaveci,* the millipedes, *Mastigona bosniense* and *Brachydesmus attemsi* but also some flightless Orthoptera species like *Isophya modesta* and *Odontopodisma schmidtii.* There are also some Illyrian species in the freshwater fauna of the Dráva-Sava waterway system, such as the snail, *Amphimelania holandri*, the caddisflies, *Chaetopteryx rugulosa, Platyphylax frauenfeldi* and the large dragonfly, *Cordulegaster heros.*

Carpathian species and *subspecies* are known mostly in those groups for which the Carpathians or some parts of the Carpathians were recognised as discrete core areas of speciation. Such groups are best exemplified by some land snails (the genera *Cochlodina, Spelaeodiscus, Trichia, Vestia*), ground beetles (Carabidae, e.g. *Morphocarabus* spp.) and certain high-mountain genera of moths *(Glacies)* and butterflies (*Erebia*, but only as subspecies in latter case). Carpathian endemic species have also been described in some insect groups of high mountain springs and streamlets like *Pedicia* spp. (Diptera) or *Leuctra* and *Isoperla* spp. (Plecoptera). The influences of the Carpathians are significant in the North Hungarian Range. Characteristic difference was observed between the Tokaj (Zemplén) Mts. on the one hand, and the limestone plateau of the Bükk Mts. and the Aggtelek Karst on the other. The biotic contact of the Tokaj (Zemplén) Mts. with the Carpathians is obviously post-glacial only, and can be characterised by the presence of species which are either typical of the montane forest belts of the Carpathians (e.g. land snails: *Bielzia coerulans*, *Vestia gulo* and ground-beetles: *Abax schueppeli, Carabus obsoletus*, *C. zawadszkyi*) or are widely dispersed in northern Central Europe. The Bükk Mts. with its old Dinaric connections in the Tertiary, has an insular character, however. Its Carpathian and Dealpine elements are isolated relicts (e.g. land snails: *Spelaeodiscus triaria*, *Phenacolimax annularis,* the Geometrid moth *Entephria cyanata gerennae*). In the Aggtelek Karst, with ancient connections to the northern Carpathians, the immediate transition to the higher limestone plateaus of Slovakia is combined with the occurrence of Carpathian (land snails: *B. coerulans*, *Cochlodina cerata, Trichia unidentata;* ground-beetles: *Carabus obsoletus*, *C. zawadszkyi*, *A. schueppeli*) and boreal species at low altitudes, influenced by the meso-climatic and geomorphological features of this area. Some influences of the Northwestern and the Eastern Carpathians are to be observed at the northeastern marginal areas of the Alföld, i.e. along the upper course of the river Tisza and its tributaries (e.g. the land gastropods, *Vitrea diaphana*, *B. coerulans*, *Balea stabilis*, *Perforatella dibothrion* and *P. vicina*).

5 *Banat Land Snail (Drobacia banatica)*

The *Dacian species* can also be considered Carpathian species in the wider sense. We should, however, distinguish these because in many cases their core areas are to be found strictly speaking not in the Carpathian chain but either in the mountains of the Banat or in the Apuşeni Mts. Furthermore, these species, for example, the land snail, *Drobacia banatica* 5, the bush-cricket, *Pholidoptera transsylvanica* 16 6, the flightless grasshoppers, *Odontopodisma rubripes* 16 and *Zubovskia banatica* and the Transylvanian Ground beetle, *Carabus hampei*, mostly occur at the montane-colline level, or descend to the surrounding lowlands. The general term 'Carpathian' could also be misleading if applied to those species which are mostly restricted to some parts of the Eastern or Southern Car-



6 *Transylvanian bush-cricket (Holidoptera transsylvanica)*

pathians (e.g. the *Alopia* land snails of calcareous rupicolous habitats in the Eastern Carpathians). In Hungary, the Dacian species, as flightless Orthoptera 16 and land snails 17 are restricted either to northeastern parts of the North Hungarian Range *(Balea stabilis)*, or to the eastern-northeastern marginal areas of the Alföld with a cool-humid continental climate (bush-crickets: *Leptophyes discoidalis, Odontopodisma rubripes*) or they occur in both areas (land snails: *Lozekia transsylvanica, Perforatella dibothryon*, bush-crickets: *Isophya stysi, Pholidoptera transsylvanica*) 16.

The *East Balkanic (Moesian) species* survived the glaciations in the eastern part of the Balkan peninsula and expanded to the Carpathian Basin crossing the Southern Carpathians and the mountains of the Banat. The most expansive species advanced northwards at the western edge of the Apuşeni Mts. and reached the eastern-northeastern edges of the Alföld, the Upper Tisza region and the eastern part of the North Hungarian Range. Some land snails have this type of range, such as *Laciniaria plicata, Mediterranea depressa, Monacha carthusiana* and *Vitrea inopinata,* etc. 17. Similar patterns of distribution have also been found in Oribatid mites occurring near to the Bátorliget nature reserve and this demonstrates the connection of the northeastern region of the Alföld with the East Balkanic forest refugia.

Alpine and *arctic-alpine species* occur nearly exclusively above the timberline, at the alpine-subnival levels in the Alps, Carpathians and high mountains of the Balkans. However, in exceptional cases, they can survive as glacial relicts in micro-climatically extreme habitats such as peat-bogs or deep ravines. Such species are known on the one side from the hilly regions at the eastern periphery of the Alps (Praenoricum) to the Bakony Mts. (e.g. the flightless grasshopper, *Miramella alpina,* the Geometrid moths *Perizoma didymata* and *Euphya scripturata* and the Alpine newt *Ichthyosaura alpestris* 7) and on the other side in the sub-Carpathian highest parts of the North Hungarian Range (e.g. the caddisflies *Drusus discolor* and *Melampophylax nepos* in the *Bükk* mountains, the land snail, *Vertigo alpestris* in the Tokaji-Zempléni mountains and the Alpine newt in both ranges).

7 *Alpine newt (Ichthyosaura alpestris)*

Historical biogeography and phylogeography

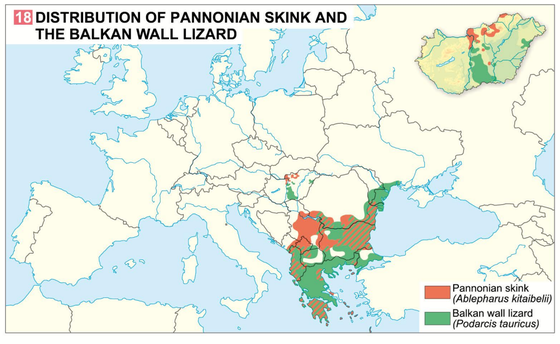
The Carpathian Basin belongs to the regions of Europe with the highest biodiversity. Not only is it currently characterised by a climatically transitional position, but this was also the case during the younger Quaternary glacial-interglacial cycles. While the lowlands were mostly covered by a cold-continental tundro-steppe (the so-called mammoth steppe) during the last glacial maximum (LGM) with scarce intermediate patches of coniferous and cold resistant deciduous trees and some marshy-boggy vegetation, the climatically more buffered hilly areas to the southwest and southeast supported cool-temperate forest or forest-steppe refuges which could have – at least in the milder climatic periods – some continuity with the Balkanic core areas of arboreal vegetation. On the southern slopes and foothills of the Transdanubian and North Hungarian Range some thermo-xerophilous elements were able to survive during cold and cool-humid climatic phases of the Quaternary period and they served post-glacially as sources for their dispersal. Thus, many thermophilous elements probably populated the Carpathian Basin postglacially not only by long-distance colonisation from southern 'classical' glacial refuges, but also from numerous meso- or microclimatically favourable sites, lying at the fluctuating margins of the Mediterranean refugial areas and periglacial belts. The biostratigraphical structure of the Hungarian young Pleistocene, often characterised by a coexistence of forest and non-forest faunal elements has given evidence demonstrating the transitional character of this region during the whole span of the Quaternary period. Thus, the Carpathian Basin and surrounding areas were biogeographically transitional with much overlap of different faunal types and the potential to function as 'melting pots' of genetic diversity.

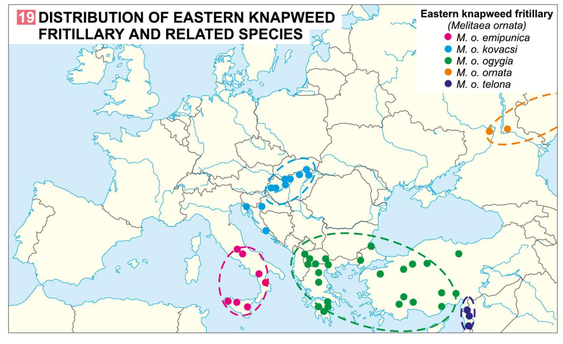
8 *Balkan wall lizard (Podarcis tauricus)*

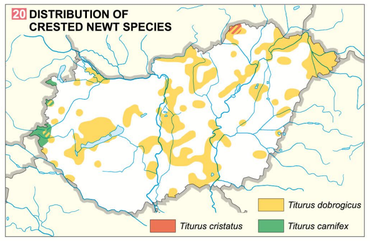
Dispersal from North Balkanic core areas was exhibited by several thermophilous reptiles. In these species the Southern Balkanic populations proved stationary. The Pannonian populations of the Scincid lizard *Ablepharus kitaibeli fitzingeri* 18 belong to the same genetic group as the northern Balkanic ones, and they are separated both from the nominotypic race *(A. kitaibeli kitaibeli)* on the Aegean Islands and also from the populations of Asia Minor *(A. chernovi)*. Similarly, the Hungarian populations of the Balkan wall lizard *(Podarcis tauricus)* 8 belong to a widely distributed Northeast Balkanic genetic group, separated both from the Dalmatian and from West and South Balkanic demes of this species 18. Although they have similar biogeographical origins, they co-occur only exceptionally due to their preferences for different substrates.

9 *Caspian whipsnake (Dolichophis caspius)*

A Balkanic phylogeographic connection was also demonstrated in the Caspian whipsnake *(Dolichophis caspius)* 9, expanding northwards at the western side of the Danube and showing a considerable level of variation despite the strict isolation of the Southern Transdanubian (Villány Hills) and Central Hungarian (Paks, Buda Mts.) populations. A Southern Italian genetic connection was shown in the polytypic Eastern knapweed fritillary *(Melitaea ornata)* which has a disjunct steppic range 19. The isolated food plant *(Cirsium pannonicum)* specialist population of Central and







Northern Hungary *(Melitaea ornata kovacsi)* is closely related to the Southern Italian subspecies *(M. ornata emipunica)*.

Other food plant specialist steppic species also show strong genetic differentiation, like the Zephyr Blue *(Kretania pylaon)* 8 2, associated with *Astragalus* species (in Hungary *A. exscapus* and *A. dasyanthus*, and in Transylvania also *A. monspessulanus*) and the Transylvanian Blue *(Pseudophilotes bavius hungaricus)* which feeds on *Salvia nutans.* Recent research has unraveled that some flightless steppic beetles (e.g. the weevils, *Centricnemus leucogrammus* and *Polydrusus inustus*) show a genetic split between the Pannonian populations and those East-European ones outside of the Carpathian Basin. A parallel pattern of genetic differentiation is also known in some Rodents such as the Souclic *(Spermophilus citellus)* and the Hamster *(Cricetus cricetus)*.

Several surveys have shown that, from a population genetic perspective, the Carpathian Basin is a peculiar focal area. The overlap of demes from different geographical origins has been observed in numerous monophyletic species groups or polytypic species. Such a case was described in the Crested Newt species group (*Triturus cristatus* agg.), where the inner part of the Carpathian Basin and the lower Danube valley is populated by *Triturus dobrogicus*, while the northern part of the Carpatho-Pannonian area belongs to the range of *T. cristatus* and the pre-alpine stripe to the area of *T. carnifex* 20.

A somewhat similar situation was described in the Discoglossid toads *Bombina* spp. 21 which have expanded from Black Sea (Red-bellied toad *B. bombina*) and Balkanic (Yellow-bellied toad *B. variegata*) refugia and formed some hybrid populations in the contact zones in Southern Transdanubia, and northeastern margin of the Alföld. The genetic composition of these hybrid belts is rather complex, since the expansion of *B. variegata* to the Carpathian Basin has proceeded from different refugia: to Southern Transdanubia from the West Balkanic core area, while to Northeast Hungary from the Southern Carpathians. Significant peri-Carpathian refugia have been demonstrated also in two cold-tolerant boreo-montane reptiles, the Viviparous lizard *(Zootoca vivipara)* and the Adder *(Vipera berus)*. From the smaller vipers (*Acridophaga* subg.) several allopatric taxa of the *Vipera ursinii* superspecies occur in Southeastern Europe, including within the Carpathian Basin. The endemic *V. ursinii rakosiensis* 10 occurring in West and Central Hungary but also in the Transylvanian Basin, is one of the most threatened zootaxa of the Carpathian Basin 22.

10 *Rákos Meadow Viper (Vipera ursinii rakosiensis)*

A significant contribution of some Carpatho-Pannonian core areas has been shown in the post-glacial re-population of Europe by several mammals, including the Brown bear *(Ursus arctos)*, Roe deer *(Capreolus capreolus)*, Bank vole *(Clethrionomys glareolus)* and Common shrew *(Sorex areneus)*, etc.

Refugia in the Carpathian Basin have been shown to have been used in several species. In such cases the populations are subdivided into two or more evolutionarily significant units. The Transdanubian vs. Transylvanian populations of the Dusky Large Blue *(Maculinea nausithous)* belong to two different European population groups. The pre-Alpine populations are closely related to the Slovenian-Croatian ones, whilst the demes of the Transylvanian Basin show links with the populations of the East European meadow steppes. Genetic differentiation has also beeen found in populations of the Woodland Ringlet *(Erebia medusa)* from the Carpathian Basin and surrounding areas. The Transdanubian populations are connected with those of the Slovenian Karst and have a locally isolated race in the Vértes Mountains. The range of the Northeast Carpathian population (Tokaj/Zemplén Mts., Aggtelek Karst) has extended to the Bükk Mts. in recent decades. Multiplicity of genetic core areas was demonstrated also in the Clouded Apollo *(Parnassius mnemosyne)* in Southeastern Europ 24 11. The mtDNA haplotype network provided strong evidence concerning the existence of two Balkan lineages, which probably formed a 'zone of admixture' in the Transdanubian and North Hungarian Range. Unique haplotypes were, however, also recognised in the North Hungarian Range. One of the mitochondrial haplotypes has expanded from the Carpathian Basin to northern Central Europe while the south-eastern (Körös region) and Transylvanian populations have exclusively eastern Balkanic connections.

11 *Clouded Apollo (Parnassius mnemosyne)*

The bank vole *(Clethrionomys glareolus) is a cold tolerant European nemoral species with a nearly continuous distribution from Southern Europe to the Boreal zone. Its populations exhibit a strong genetic subdivision* 23 *which is connected with survival in several isolated Upper Pleistocene refugia. According to the fossil evidence, the bank vole was able to survive the last glaciation in the Carpathian Basin. This evidence is further supported by a distinct Carpathian mitochondrial haplotype, widely distributed in Eastern Central Europe. However, postglacially also the West Balkanic and the East European demes of this species could expand to the Carpathian Basin, therefore two or even three haplotypes can be found in some populations.*

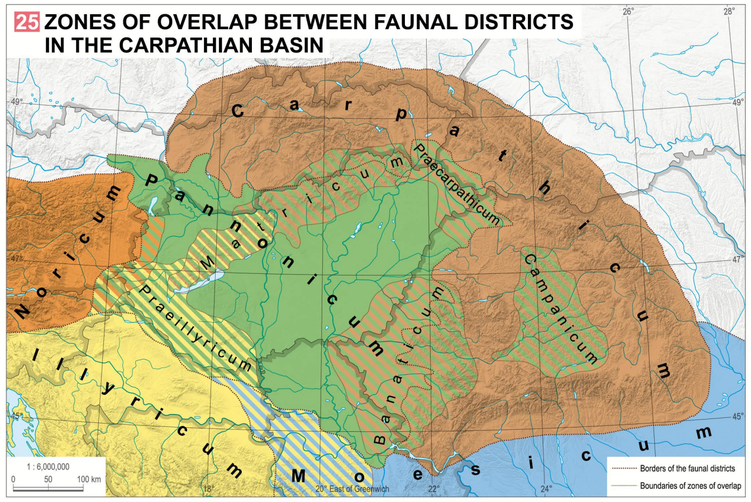
Short review of the zoogeographical regionalisation of the Carpathian Basin

Regionalisation has traditionally been a basic aim of zoogeographical surveys, although it was recognised that the boundaries of regions would only be snapshots of a dynamic process. The commonsense relativity of zoogeographical regionalisation is a pratical necessity in such a typically transitional area as the Carpathian Basin, especially given that this transitional character has been in evidence throughout the whole Quaternary period. It would be plausible to consider the mountainous regions as the Carpathicum – where boreal and Carpathian species predominate. The other large unit, where species of xerothermic oak forests and forest steppe prevail, should be called the Pannonicum. These two contrasting areas, however, in reality often overlap in response to the local particularities in orographic, edaphic and meso- and micro-climatic conditions. Furthermore, these factors fluctuated continuously during the Quaternary glacial-interglacial cycles. By way of example, those Carpathian land snail species which today occur in cold, deep gorges or ravines with a northern aspect, were present during the last glaciation, according to fossil evidence, on karstic plateaus which are currently occupied by xerothermic Pannonian habitats supporting sub-Mediterranean and Ponto-Pannonian species. This illustrates how climatic changes induce not only large-scale shifts in ranges but also small-scale switching of habitats which may be proportionally more relevant to more mobile and more sessile groups of animals respectively.

As a consequence, the zoogeographical boundaries do not always coincide exactly in relation to each of the taxonomic groups considered. The North Hungarian Range is considered, for example, as an impoverished periphery of the Carpathicum with regards to land snails, mayflies, stoneflies and caddisflies but for mobile animals or, as we have seen, certain insects closely associated with particular vegetation types or special food plants, it is best understood as part of the Pannonicum due to the presence of numerous sub-Mediterranean or Ponto-Pannonian species. Similar issues apply in the western-southwestern peripheries of the Carpathian Basin where in the composition of the fauna Pannonian, East Alpine (Noric) and West Balkanic (Illyrian) species overlap. Especially strong West and East Balkanic (Illyrian and Moesian) influences were found in land snails (see: Praeillyricum and Banaticum) where the transitional areas have cumulatively high numbers of species. In more mobile insect groups, however, the ranges of numerous West Balkanic species reach the Transdanubian Range.

Therefore, we should only consider the lower units of zoogeographic regionalisation as simplifications. They are useful in framing our broad understanding but in order to better reflect the important transitional dimension of the Carpathian basin's zoogeography we modify the traditional regional subdivision of the map (Mócz ár 1967, based on Dudich 1952) with the addition of zones which show the principal areas of overlapping influences 25.

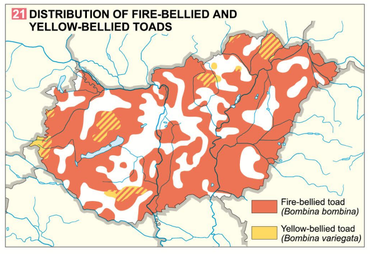
The Clouded Apollo *(Parnassius mnemosyne)* 11 *is distributed in the Carpathian Basin mostly in hilly and mountainous areas. Its main habitats are sun-penetrated deciduous forests with rich geophytic undergrowth (food plants are Corydalis spp.). Figure* 24 *shows the main core areas and directions of post-glacial dispersal. Red and orange colours are connected with the peri-Alpine refugia, the blue, green and violet colors with the West and East Balkanic core areas. The size of circles on the map is correlated with sample size and the colouring of the sectors in circles shows the diversity of mitochondrial haplotypes in populations. The accessory figure shows the mitochondrial haplotypes and their connections. The larger circles are the main haplotypes and the radially located smaller ones the derived variations which originated with single or a few mutations (nucleotide substitutions). It is evident that a mixture of haplotypes has proceeded in several populations but 'in situ' changes also have taken place (see: 'star-like' orientation of minor haplotypes). N.B. in the Carpathian Basin both processes have occurred!*

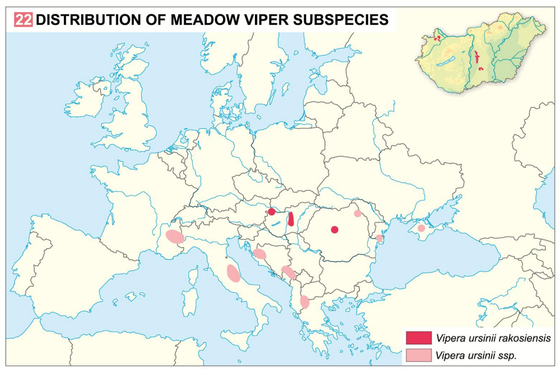


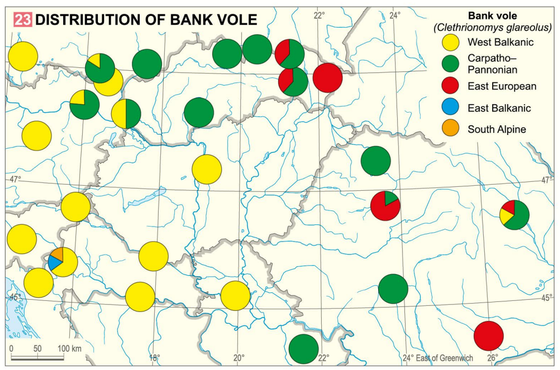
Diversity of the fauna of Hungary

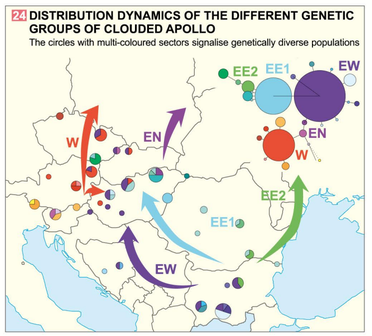
The concept of diversity is applicable for all kinds of systems which consist of differentiable elements and can be characterised both by the number and relative frequency of these elements. In this case the differentiable elements are animal species, and the first stage is to estimate the their gross numbers in Hungary. We counted here only native species since survey of domesticated animals belongs to the science of animal husbandry.

It should be stated in advance that the species numbers here 26 are provided only as a preliminary orientation. There are numerous taxa of animals for which we cannot give more exact species numbers, due to their tiny size, or cryptic way of life, for example. We should recognise that the scientific description of species is far from complete in many groups of animals, and our knowledge on animal assemblages is also insufficient in many areas and habitats. The Nematodes provide a good example of this uncertainity (between ten and hundred thousands) despite their huge potential medical and agricultural importance. The estimation of numbers of insect species is also rather difficult. The figures in different references vary widely between ten and thirty million, of which only about one-one and half million species have been scientifically described. Even in the best known groups we do not have a complete catalogue of described species. The numbers of species are reasonably exact only in those groups for which we have modern catalogues or check lists on the world, European or Hungarian fauna (e.g. mammals, birds, reptiles, butterflies and larger moths, etc.).









26 DIVERSITY OF THE FAUNA IN HUNGARY

Animal taxa	Scientific name	Species numbers (described)	
		on Earth	in Hungary
Insects	Insecta	>1 million	~35,000
Crayfishes	Crustacea	~150,000	~380
Arthropods total sum	***Arthropoda***	***>1,5 million***	***~45,000***
Other Invertebrates	***Invertebrata varia***	***>300,000***	***~3,000***
Fishes	Pisces	~35,000	89
Amphibians	Amphibia	~10,000	18
Reptiles	Reptilia	~12,000	16
Birds	Aves	~10,500	365
Mammals	Mammalia	~5,500	83
Vertebrata total sum	***Vertebrata***	***~73,000***	***~560***

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English translation by
Zoltán Bálint, Endre Dobos, Gábor Gercsák, Krisztián Klima, Krisztina Labancz, Györgyné Laczkó, Dénes Lóczy, Richard William McIntosh, Erika Michéli, Brigitta Palotás, László Pásztor, András Schmidt, Péter Szabó, Tamás Telbisz, Eszter Tímár, Gábor Timár, László Tóth, Zoltán Varga

English translation revised by
Iain Coulthard, Gábor Gercsák, Daniel Kibirige, Richard William McIntosh, Robin Lee Nagano, Philip Sansum

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Authors
Szilvia Ádám
†László Alföldi
Réka Aszalós
György Babolcsai
Zoltán Barina
Dénes Bartha
Judit Bartholy
Zsombor Bartos-Elekes
Teodóra Bata
Ákos Bede-Fazekas
Zita Bihari
Marianna Biró
Attila Borhidi
János Bölöni
Károly Brezsnyánszky
Tamás Budai
Szabolcs Czigány
Bálint Czúcz
István Csepregi
János Csiky
Péter Csima
Péter Csorba
Gábor Csüllög
István Dancza
Laura Dobor
Endre Dobos
Szabolcs Fábián
Tamás Fancsik
Edit Farkas
Sándor Farkas
István Fazekas
†Gábor Fekete
Zita Ferenczi
László Fodor
Nándor Fodor
Sándor Frisnyák
Gyula Gábris
Nóra Gál
Attila Galsa
†Judit Gerhátné Kerényi
Gizella Gombárné Forgács
László Gyalog
János Haas
László Haszpra László
Katalin Homokiné Ujváry
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Enikő Magyari
Ákos Malatinszky
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Erika Michéli
Gábor Mikesy
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†András Nagymarosy
Gábor Négyesi
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Anna Solt
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Árpád Szentiványi
Gábor Szepessy
Gabriella Szépszó
Péter Szilassi
Ferenc Szmorad
Teodóra Szőcs
Gergely Szövényi
Erzsébet Szurdoki
Ágnes Tahy
László Tamás
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Viktor Tiborcz
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Gábor Varga
György Varga
Zoltán Varga
Mária Vasvári
József Vatai
Zsuzsanna Vikor
András Vojtkó
Tünde Andrea Zagyva
László Zilahi-Sebess
Zita Zsembery

Chief cartographers
Norbert Agárdi
Zoltán Keresztesi
Fanni Koczó
Anikó Kovács
Gáspár Mezei
Zsombor Nemerkényi
Renáta Szabó

Contributors to cartography
Gergely Bagaméri
Éva Balázs
Ádám Barancsuk
Zsanett Butor
Anna Gertheis
Zoltán Gulyás
Réka Kiss
Csaba Szigeti
József Sziládi
Zsuzsanna Veszely

Technical staff
Margit Laczkó
Árpád Magyar
István Poór

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