Mediterranean Speleobiology

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Haasia Stenopodium
Ph. Teo Delić

Underground life and ecology of subterranean habitats

Two centuries ago a discovery of a blind beetle with elongated legs and unusual morphology settled a milestone in our perception of life underground. It was until then that people were unaware that life of any form is possible underground. This discovery and the scientific description of the slender-necked beetle, *Leptodirus hochenwartii* Schmidt, 1832, set up a whole new biological discipline – speleobiology – the biology of subterranean habitats. From the famous tourist cave – Postojnska jama in Slovenia, where it was first found, the wave of discoveries of specialized subterranean animals started to spread. At first it set out over the Western Balkan's Dinaric Karst, and was, hereafter, transferred to other mountainous areas in Europe. By the second part of the 19th Century, all larger mountain ranges in Europe, including Pyrenees, Jura, Rhodopes, etc., already had first discoveries of their own, specialized cave-adapted fauna.

Throughout the globe, subterranean animals share similar traits - lack of eyes and pigments, and elongated antennae and appendages. Morphological changes, often referred to as troglomorphies, most likely developed as an adaptive response to the ecological constraints of subterranean habitats. However, it is not only the caves, where these specialized animals, also known as troglobionts or stygobionts (bound to terrestrial and water habitats, respectively), can be found. They are known from a variety of air- or water-filled shallow subterranean habitats, including seepage springs, epikarst, hyporheic, scree slopes, soil, etc. The only thing that separates caves from other types of subterranean habitats are their dimensions, enabling us to enter. Different subterranean habitats share the same characteristics. The first and probably the most notable difference, when compared to surface habitats, is the absence of light. Because of this no plant can survive in the subterranean domain. As there is no photosynthesis, the availability of nutrients is reduced. The subterranean habitats are fully dependent (of course exceptions exist) on nutrients from the surface, penetrating with sinking rivers, water drips, occasional visitors (bats, crickets, etc.). Both, the temperature and humidity tend to be constant, with humidity kept at a high level. As a result, combined effects of previously mentioned habitat characteristics, sum up in dramatic

Blind and depigmented representatives of specialized subterranean fauna, the so-called troglobionts: a) The first discovered and scientifically described subterranean animal, *Leptodirus hochenwartii*; b) Subterranean diplopod *Haasia stenopodium;* c) A cave amphipod with extremely elongated antennae and appendages, *Niphargus croaticus*, and d) fiercely appearing appendages, pedipalps, forming a death trap in harvestmen *Travunia* sp . Ph. Teo Delić morphological changes notable in subterranean animals.

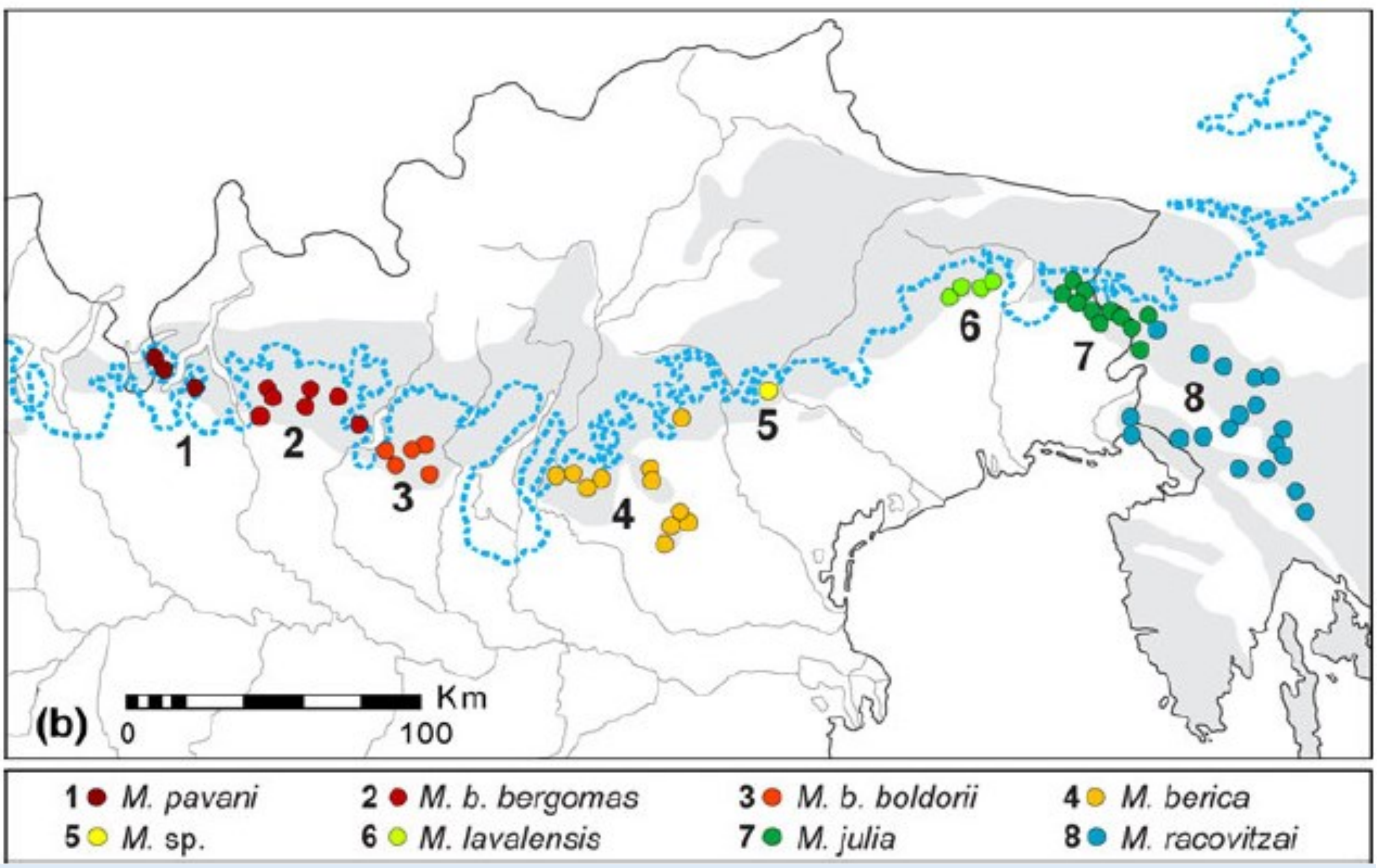
Hotspots of subterranean biodiversity

A large body of data, containing information on species inventories and distributions of troglobionts has been published in the last two centuries. Inclusion of publication records with accurately defined positions of subterranean sites into carefully managed databases, in combination with the usage of computational resources, revealed the spatial patterns present in European subterranean fauna. Due to prevailing characteristic of subterranean domain - its invisibility, the patterns became known much later when compared to surface biodiversity patterns. Once established, they enabled setting the hypotheses and testing the possible mechanism and processes behind the eye catching patterns.

Compared to other continents, Europe bears the richest subterranean fauna. More than half of the global hotspots of subterranean biodiversity, defined by either 25 troglobionts or stygobionts, are found in Europe. One can easily attribute this discrepancy to the relatively long tradition of subterranean research in Europe. However, it seems that for some groups (subterranean beetles, amphipods, springtails), despite additional research efforts in other continents, Europe remains the richest continent. The pattern remains the same also due to the fact that the new species, even genera, are being described not only from unexplored, but also from well explored and biodiversity rich karst areas, i.e Dinarides, Pyrenees or Italian Prealps.

On the continental scale, the difference in species richness is notable. Obvious patterns demonstrate that the number of subterranean species declines northwards and southwards from the so-called “mid latitude biodiversity ridge”, comprising a system of North Mediterranean mountainous chains - Pyrenees, Alps and Dinarides. These mountainous regions bear the highest concentration of subterranean biodiversity hotspots in the world. The reasons for establishment of the “ridge” are manifold, and are largely driven by three environmental factor classes, packed within energy, heterogeneity and history. They include a wide variety of factors like temperature, precipitation, number and size of caves in the area, availability and connectivity of karst landscapes, historical climatic and paleogeographic events.

Probably one of the best documented and vividly imaginable factors, which largely contributed to the existing patterns,



The extent of Last Glacial Maximum, approximately 21.000 years ago, limited the distribution of many subterranean taxa, including subterranean freshwater isopod genus *Monolistra,* to the areas south of Alps. Redrawn from *Stoch & Galassi, 2010* (Still have to get copyright, in process).

are Pleistocene climatic oscillations (2.58 - 0.01 Ma). Temperature decline and glacier coverage, associated with permafrost, which extended as far as to the southern Alpine valleys, decimated subterranean fauna north of the Alps.

Zooming in the specific area exposes sub-patterns that can largely differ from the general ones, revealing the existence of hotspots within the hotspots. In the case of the Dinaric Karst, the analysis of species richness in subterranean beetles and amphipods exposed the existence of the two embodied peaks of species richness. One in the northern part of the region, spreading in southern Slovenia, and the other one in the south, in southeastern Herzegovina, Croatian Dalmatia and western Montenegro. A relatively large share of subterranean amphipods and beetles in Dinarides, 23 and 31 percent, respectively, are the so-called single site endemics. Known from a single locality only, they are the real, narrowly distributed endemics.

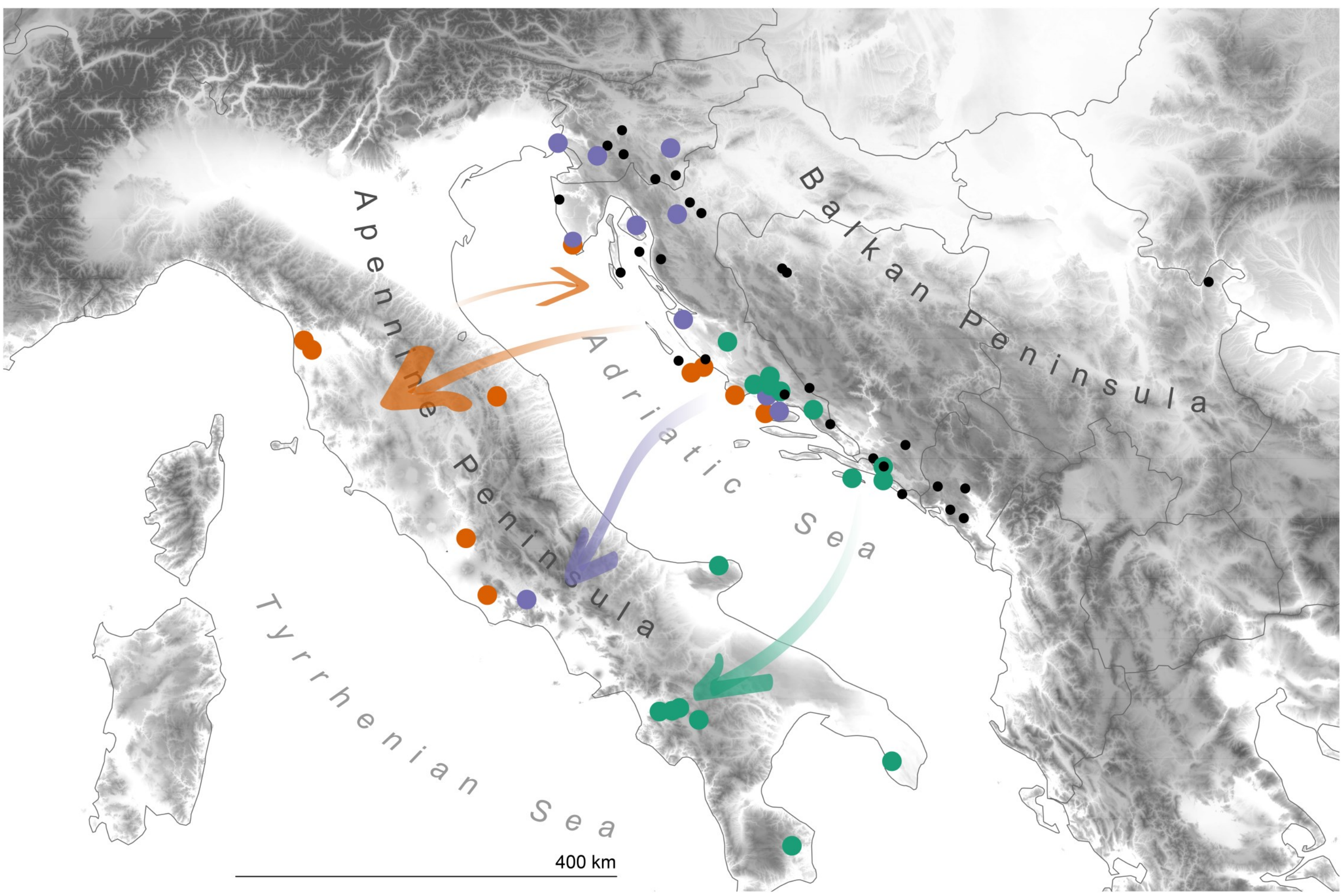
Evolution (speciation) in the Mediterranean karst area

A large mark on the subterranean fauna of the Mediterranean area was left by the paleogeographic events in the wider Mediterranean region. The whole region itself has a rather complicated history, which is in more detail described in the “Geomorphology of the Mediterranean area” section. For someone who is not familiar with the paleogeographic history of Europe, it is essential to understand that, historically, the continent functioned as a group of islands bound to the tectonic plates. In addition, nowadays mountain ranges were, back in the time, largely shallow seas with lagoons, similar to those that can be found in the tropics. Depending on the movement of the tectonic plates, their interactions triggered raising of mountainous ranges in the north of Mediterranean or disintegration of the existing lands, seas or continental lakes. Such events are well documented in geology or geography, but can be tracked down even in the natural histories of subterranean animals.

Paleogeographical changes largely affected natural histories of many subterranean taxa, including: a) the only subterranean freshwater clam, genus *Congeria*, and the only subterranean freshwater serpulid, *Marifugia cavatica*; b) representatives of collembolan genus *Verhoeffiella*, distributed in remote karst areas throughout Europe (Jakupica, Dianrides, Prealps, southern Catalonia and Cordillera Cantabrica); c) continental radiation of subterranean trechini beetles (photo of *Velebitaphaenops giganteus*) and, d) freshwater isopod genus *Monolistra.* Ph. Teo Delić

Some of the most remarkable subterranean species from the Dinaric Karst represent the only subterranean representatives of otherwise marine, freshwater or historically widespread freshwater taxa: i an ii) The only subterranean representatives of predominantly marine polychetes and cnidarians, cave serpulid *Marifugia cavatica* and cave cnidarian *Velkovrhia enigmatica;* iii) the only known subterranean clams, three closely related *Congeria* species (*C. kusceri*, *C. jalzici* and *C. mulaomerovici*), whose relatives were widespread in surface freshwaters during the Miocene (23.03 - 5.33 Ma); iv) the only subterranean sponge in the world, *Eunapius subterraneus*, and v) the top predator in the Dinaric caves and the only true subterranean vertebrate in Europe - the proteus, "humanfish" or olm, *Proteus anguinus*. Natural histories of these unique taxa, including their distributions and habitats, were largely affected by the paleographic changes in Mediterranean area.

Both, terrestrial and aquatic subterranean taxa, were largely affected by desiccation of the Mediterranean Sea during the so-called Messinian Salinity Crisis (MSC, 5.96 - 5.33 Ma), triggered by the closure of Gibraltar strait. Temporal connection between the European and African land masses enabled exchange of some faunal elements, including some of the subterranean diplopods and trechini beetles, nowadays present in North Africa and the Pyrenees. Presumably, the MSC triggered proliferation in some of the most species richest terrestrial subterranean genera, including beetle genus *Duvalius* and the springtail genus *Verhoeffiella/Heteromurus.* In aquatic subterranean fauna, desiccation of the Adriatic Sea enabled at least two crustacean groups, amphipods (genus *Niphargus)* and isopods (genus *Monolistra)*, to disperse over otherwise impermeable barrier, sea. Most of the dispersal pathways led from the Dinarides to the Apennines, however, the vice versa events were also enabled. An imprint of these events can be noted even in ecological preferences of



Desiccation of the Mediterranean Sea, including the Adriatic Sea, during Messinian Salinity Crisis (5.96 – 5.33 Ma) enabled establishment of dispersal pathways over temporal land-bridges connecting the Dinarides (Balkan Peninsula) and Apennine Peninsula (and vice versa). The major pathways of the three major clades of "transadriatic" representatives of the subterranean freshwater genus *Niphargus* are represented in orange, purple and green (redrawn from Delić et al. 2020) closely related sister species of “transadriatic” crustaceans, distributed on the opposite sides of the Adriatic Sea, who are living in brackish waters. In addition, regression and transgression cycles caused establishment of special types of caves, the so-called anchialine caves. Such caves are found all around the Mediterranean Sea. They are characterized by the existence of salinity clines, caused by the input of freshwater into otherwise marine cave environments, and are distinguished by their specialized and highly endemic fauna.

Although most of the presented patterns and processes were connected to origins of subterranean life through physical changes in environments, this is, by far, not the only way that natural histories of subterranean animals are affected. A large part of these highly specialized taxa originated through the processes of ecological speciation, implying differential use of environmental resources, changes in behavior connected to predator avoidance, etc. Some of probably most demonstrative cases of ecological speciation in caves include species rich communities of closely related subterranean amphipods of the genus *Niphargus* or highly specialized filter-feeding, the so-called hygropetricolous beetles. Unfortunately, due to repetitive historical oversimplification of subterranean habitats, the ecological aspect of speciation in the subterranean domain has been neglected for years. However, with the raising awareness that the processes operating in the subterranean domain are identical to the ones operating in the surface habitats, we are setting the stage for future challenges and development of ecological studies within the subterranean domain.

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