

HISTORICAL BIOGEOGRAPHY OF SUBTERRANEAN BEETLES – “PLATO’S CAVE” OR SCIENTIFIC EVIDENCE?

ZGODOVINSKA BIOGEOGRAFIJA PODZEMELJSKIH HROŠČEV – »PLATONOVA JAMA« ALI ZNANSTVENI DOKAZ?

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Abstract

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Oana Teodora Moldovan & Géza Rajka: Historical biogeography of subterranean beetles – “Plato’s cave” or scientific evidence?

The last two decades were particularly prolific in historical biogeography because of new information introduced from other sciences, such as paleogeography, by the development of quantitative methods and by molecular phylogeny. Subterranean beetles represent an excellent object of study for historical biogeography because they are the group with the best representation in the subterranean domain. In addition, species have reduced mobility, display different degrees of adaptations to life in caves and many specialists work on this group. Three processes have shaped the present distribution of the tribe Leptodirini (Coleoptera Cholevinae) in the world: dispersal, vicariance, and extinction. Therefore, three successive stages can be established in the space-time evolution of Leptodirini: (1) dispersal from a center of origin in the present area(s); (2) dispersal, extinction and vicariance among the present area(s); and (3) colonization and speciation in the subterranean domain. The Romanian Leptodirini, especially those from Western Carpathians is examined with respect to these processes. Their pattern of distribution in different massifs and at different altitudes is discussed, with possible explanations from a historical biogeographic point of view.

Key words: Historical biogeography, cave beetles, Leptodirini, Romania.

Izvleček

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Oana Teodora Moldovan & Géza Rajka: Zgodovinska biogeografija podzemeljskih hroščev – jama »Platonova« ali znanstveni dokaz?

Zadnji dve desetletji sta bili za historično biogeografijo še posebej bogati, predvsem zaradi številnih novih informacij in dognanj paleogeografije, razvoja kvantitativnih metod ter molekularne filogenije. Podzemeljski hrošči so odličen model za proučevanje historične biogeografije, saj spadajo v tisto skupino organizmov, ki je v podzemlju najpogosteje zastopana. Hrošči iz podzemlja imajo zmanjšano mobilnost, razvili so številne načine prilagoditev na življenje v tem habitatu. S to skupino organizmov se ukvarjajo številni raziskovalci po svetu. Na trenutno razširjenost vrst rodu Leptodirini (Coleoptera Cholevinae) so vplivali trije procesi: disperzija, vikarianca in izumiranje. V prostorsko-časovnem razvoju Leptodirinov se lahko pojavijo tri zaporedne faze: (1) razširjanje iz izvornega mesta na sedanje/a poročje/a, (2) razširjanje, izumrtje in vikarianca med sedanjimi območji, ter (3) kolonizacija in speciacija v podzemeljskih habitatih. S tega vidika smo proučevali Leptodirine iz Romunije, s poudarkom na vrstah iz zahodnih Karpatov. V prispevku je opisan vzorec razširjenosti hroščev v različnih gorskih predelih ter na različnih nadmorskih višinah. V razpravo smo z vidika historične biogeografije vključili tudi verjetno interpretacijo.

Ključne besede: zgodovinska biogeografija, speleobiologija, Leptodirini, Romunija.

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INTRODUCTION

The Greek philosopher, Plato (428-348 BC), in his book, *The Republic*, tells about Socrates teaching lessons of wisdom. One of these is about human beings kept in a cave with one source of artificial light coming from behind. The idea of the allegory is that we might have a wrong perception about what is reality, or, that most people live in a world of ignorance because they rely only on their narrow experiences and rely on their own truths. Another possible interpretation of Plato's allegory is that we might be wrong if we consider concepts and perceived objects on the same level. Historical biogeography is a science based on concepts and suppositions and there is no direct evidence available in the attempt to build credible scenarios about past and present animal distributions. However, development of this science on circumstantial evidence ensures better understanding of the objects under study.

Biogeography studies geographic distribution of organisms. This simple definition describes an extremely complex science. Geology, geography and various branches of biology define a discipline that is continuously developing. The Swiss botanist de Candolle (1820) was the first to speak about ecological and historical biogeography as separate branches of biogeography. They differ mainly in what concerns spatial and temporal scales. Historical biogeography reports on evolutionary processes over millions of years, mostly on a global scale (Crisci 2001). Pleistocene glaciations are sometimes collectively considered a separate or intermediary branch between historical and ecological biogeography. The last two decades were particularly prolific in papers on historical biogeography due largely to new information introduced from other sciences, such as paleogeography, by the development of quantitative methods (Morrone &

Crisci 1995) and by the development of molecular phylogeny.

Morrone & Crisci (1995) and Crisci (2001) define the biogeographic processes that modify the spatial distribution of taxa and recognize nine basic approaches to historical biogeography: (1) Identification of the centers of origin, or the existence of "Eden" where different lineages of all living beings moved from by dispersal to the present areas; (2) Panbiogeography, which plots the distribution of different taxa on maps, connecting their distribution areas together with lines; (3) Phylogenetic biogeography and (4) Cladistic biogeography, both assuming correspondence between taxonomic relationships and area relationships; (5) Parsimony analysis of endemism that classifies areas by their shared taxa; (6) Event-based methods; (7) Phylogeography; (8) Ancestral areas; and (9) Experimental biogeography.

The evolution of subterranean animals is a process that can be presumed but not directly proven. The origin, migration and colonization of the subterranean realm can be explained by a multitude of arguments and indirect evidences which support or falsify the proposed hypotheses. The role of historical biogeography is to explain the way subterranean animals gain their present distribution, using available data from biology and other sciences. Through this process, we can gain a new insight into the mechanisms of colonization that have affected some of the extreme areas or habitats which exist in the subterranean domain. Chronologically, the history of a taxonomic group (like the beetles), or of a phyletic lineage must begin with its origin. To understand present distribution patterns and why some areas were colonized and others were not, we must first establish temporal and spatial reference points.

SUBTERRANEAN COLEOPTERA EXAMPLES IN HISTORICAL BIOGEOGRAPHY

There are several reasons why subterranean beetles represent an excellent object of study for historical biogeography:

1. They are the best represented group in the subterranean karst environment or domain, with many species inhabiting caves and the mesovoid shallow substratum (also called MSS, see Juberthie *et al.* 1980);
2. Most species are terrestrial and therefore have reduced mobility; and while they are not limited to limestone/karst areas, most taxa inhabit caves;
3. A group whose representatives that display different degrees of adaptations to life in caves. Some of

the lines have endogean and hypogean species, of which the last is more or less adapted to subterranean environment.

4. They are a well known group, with many specialists studying various aspects of their biology, including taxonomy, adaptations, behavior and molecular phylogeny.

Two families encompass most of the world's subterranean beetles, the Trechinae (predator Carabidae) and the Cholevinae (detritivorous and saprophagous Leiodidae). Our example is from one of the best represented subterranean tribe of Cholevinae, the Leptodirini (for-

mer Bathysciini). According to ecological biogeography, Leptodirini are presently distributed in caves, MSS, and other dark and humid habitats, such as litter and moss, mostly in the Palearctic region.

For historical biogeography the life of the tribe Leptodirini begins in the Paleozoic. The present distribution of Leptodirini can only be explained through Wegener’s theory of continent drift and the dispersal, vicariance and extinction processes. Dispersal was the main concept in biogeography before Wegener and it explains the area of a population by the mechanisms of migration and crossing over geographical barriers. Extinction means the death of local populations, species or even supraspecific taxa, and its role in biogeography has not always been recognized. Vicariance represents the splitting of an ancestral population into several subpopulations, which will later evolve into species through isolation. These three processes have shaped the present distribution of Leptodirini, and three successive stages can be established in the space-time evolution of this group:

I. Dispersal from a center of origin in the present area(s);

II. Dispersal, vicariance, and extinction among the present area(s);

III. Colonization and speciation in the subterranean domain.

I. According to Giachino & Vailati (1998) the ancestral family of Oricatopidae inhabited the southern part of the Gondwana supercontinent (Fig. 1). Descending from this family, ancestors of Leptodirini and other tribes migrated at the end of Paleozoic to the what is now the south of Eurasia on the microplates that broke off from Gondwana. Thus, Eurasia was colonized by the ancestors of Leptodirini 120–150 Ma ago. More recently, 50–65 Ma ago, the group dispersed from northeast, through the central south of Asia, up to eastern Eurasia and then toward the west, along the Mediterranean basin. Epigeal individuals successively migrated at the surface, and they were probably pre-adapted to low, constant temperatures and high humidity. Jeannel & Leleup (1952) provide excellent examples for preadapted ancestors of pselaphid beetles, after studying high altitude (2000–2900 m) beetles on Mount Kivu (Congo). At this level, the species are exclusively humic inhabitants, deepened at few centimeters in humus, where proper conditions, such as constant temperature (10°C) and high humidity, are fulfilled. They also described a species with similar adaptations to those inhabiting caves, and also found deeper, under the humus.

II. The second phase of evolution of the group probably happened before the Miocene, and possibly in the late Oligocene. The dispersal of beetles was from Asia, along

the Miocene Alpine chain, whose remains are the Cantabric chain, Pyrenees, Central French Massif, Alps, Dinarides, Balkans, Pindus chain, Peloponnesus chain, and Pontic Alps. Afterwards, some species colonized the Apennines, Jura, Carpathians, Rodops, Taurus, Caucasus and Mediterranean inlands (Giachino *et al.* 1998). Due to major geological and geographical transformations of the landscape, extinction and vicariance alternated during the next periods. A large and continuous distribution area of epigeal and probably endogean ancestors of Leptodirini that migrated from east was then fragmented, even before the colonization of the subterranean domain. New paleogeographic data about the evolution of the Paratethys from Late Eocene to Pliocene has been recently published (Steininger & Rögl 1985, Popov *et al.* 2004), and it appears that paleogeographic configuration of the Paratethys shaped the distribution of Leptodirini in Europe.

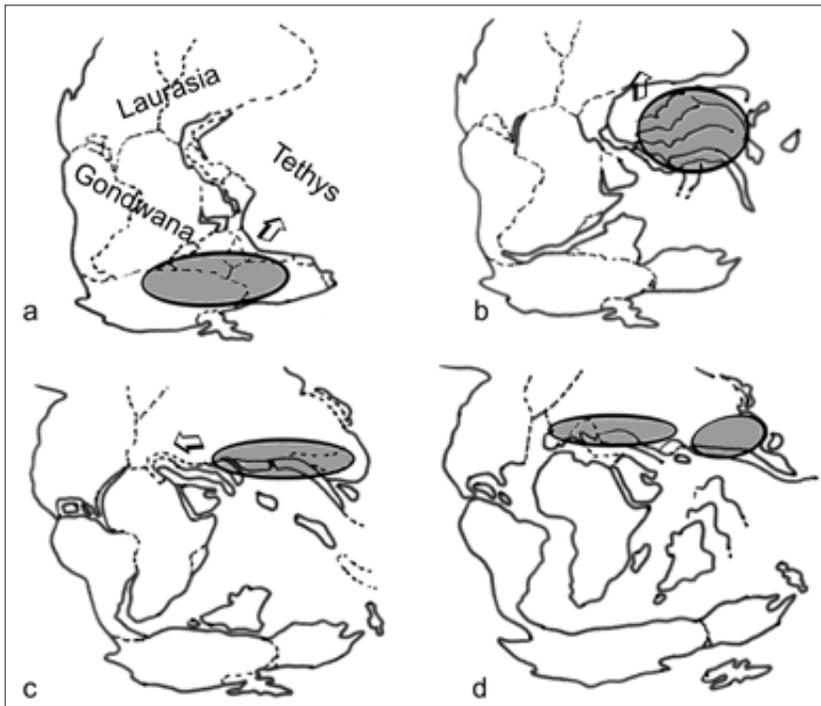


Fig. 1: Historical biogeography of ancestors of Leptodirini, which migrated from Gondwana (a) together with continental microplates (b), up to Eurasia (c), from there dispersed west to the Mediterranean region (d) (modified from Giachino *et al.* 1998): areas covered by Leptodirini are represented by grey ellipses.

III. The third stage is represented by colonization and speciation in the subterranean domain. Two scenarios were proposed for explaining the mechanisms of underground colonization by epigeal and endogean representatives of various groups of fauna (Holsinger 2000, 2005):

(1) The climatic-relict model, in which preadapted or adapted animals were “forced” or constrained by climatic fluctuations to find refuge in caves. The best documented are the Pleistocene glacial-interglacial periods. Eventually, surface ancestors of these successful colonizers went extinct. This model not only fits temperate climate regions, but also any region that has previously sustained drastic climatic changes.

(2) The adaptive-shift model is mostly applied to lava tubes and tropical karst regions. Proposed by Howarth (1981), it explains the active colonization by preadapted ancestors and exploitation of new and empty niches to avoid competition. In this model, adaptation to the new environment does not depend on physical isolation from surface ancestors, as is necessary in the previous model.

In our opinion, colonization of the subterranean domain is an active process, as is the case of empty niche colonization anywhere on Earth. Climatic changes have made important contributions in shaping the distribution areas and breaking off gene flow with surface relatives. Climatic changes can also interrupt energetic flow between surface and subterranean environments, leading to extinction of populations on one or both sides. This apparently happened in parts of the world directly affected by or covered by Pleistocene glaciers.

Bellés (1991) enumerates three reasons for cave colonization:

1. Survival, when external stress determines animals to find refuge in caves;
2. Opportunism or colonization of an empty space;
3. Convenience or escaping surface competition which uses the same trophic resources.

Peck (1980), Vailati (1988) and Juberthie (1988) proposed scenarios for cave colonization by beetles in the family Leiodidae from North America and Europe. Juberthie’s model uses complex data from studies on the ecology, ethology, genetics, tectonics, paleoclimate and geology of species from the *Speonomus delarouzei* complex (Leiodidae: Cholevinae: Leptodirini). These species inhabit the MSS and caves on Mount Canigou in the French Pyrenees. The history of this complex begins with the first glacial period (2.3 Ma), when high altitude species separated from those at low altitude in the Mediterranean climate. The two species, *S. brucki*

and respectively *S. delarouzei* are characterized by different mating behavior, by reproductive isolation and by genetic distance. There are also differences in fecundity and egg development speed at different temperatures. Thus, depression of temperature during glaciation selected cold resistant genotypes at 1000 m altitude, where annual mean temperature in caves is today 8-10°C, while *S. delarouzei* remained at low altitude at temperatures of 14°C. During glacial periods, the forest belt displaced several hundred meters downslope on Mount Canigou and was replaced by steppe vegetation. Cracks, voids, MSS and even caves formed during these periods, while filling happened during interglacial periods. At altitudes between 500 and 1000 m two other species, *S. emiliae* and *S. charlottae*, inhabit subterranean habitats. *S. emiliae* lives in the MSS at 720 m altitude and is presumed to be the ancestor of *S. brucki*, and probably populated caves and MSS at different altitudes. *S. emiliae* migrated together with the forests during glacial periods through cracks and MSS down to the present altitude. The isolation of this species and *S. brucki*, which formed a population at high altitude, happened by infilling of the MSS and related cracks and crevices. Similar mechanism acted in a previous period for separating *S. charlottae* from ancestors of *S. brucki*.

By comparing cuticular hydrocarbons (pheromones that act at short distance or by contact) of species of the *S. delarouzei* complex, Moldovan (1997) and Moldovan *et al.* (2003) obtained a different composition in the mountain species *S. brucki* and the Mediterranean species, *S. delarouzei*: shorter chains in the first one and longer in the second. *S. emiliae*, at an intermediate altitude, displays a mixture of short and long molecules in the cuticular hydrocarbon cocktail. The result can be explained by temperature influence on cuticular hydrocarbon composition. A small variation in temperature can change hydrocarbon composition even from the first generation (Toolson *et al.* 1990). For subterranean beetles, adaptation to a new climate can rapidly change the pheromone composition, thus representing an important mechanism of isolation that acts prior to mating. Climate changed the distribution of populations on the slope of Canigou Mountain through migrations of ancestral populations. Consequently, composition in cuticular hydrocarbons changed and preceded genetic mutations. Hydrocarbon changes become stable if climate is maintained over long periods of time, eventually causing isolation of populations and genetic mutations. Therefore, speciation of subterranean inhabitants can occur without the existence of physical barriers as proposed in Juberthie’s model.

REFERENCE MARKS IN HISTORICAL BIOGEOGRAPHY OF ROMANIAN LEPTODIRINI

With its geographic position in eastern Europe, Romania is very rich in subterranean fauna for a non-Mediterranean country. This is due to the special features defined as follows (Moldovan *et al.* 2005):

1. The geographic position of the country, with climatic and fauna influences from various regions;
2. The reduced total surface of limestone; karst areas are distributed along the Carpathians and in Dobrogea, covering only 2% of the surface of Romania (Onac & Cocean 1996);
3. The high number of caves/surface units; even if the covered surface is so small, the speleological potential is high, with almost 12,000 caves discovered prior to 1989 (Goran 1989);
4. The distribution of caves at low altitude, with 27% of karstic rocks at altitudes below 500 m and 47% up to 1000 m a.s.l. (Bleahu & Rusu 1965);
5. The patchy distribution of limestone, with small outcrops scattered especially in western and southern regions. From an ecological point of view Romanian karst forms small continental islands between non-karstic rocks, which act as natural barriers to migration of subterranean organisms. Each area represents an island to its inhabitants, which in turn leads to isolation and promotes evolution and formation of new species. The discovery of the MSS has added new insights into the availability of subterranean habitats, but it can explain only short distance migrations between geographically close areas.

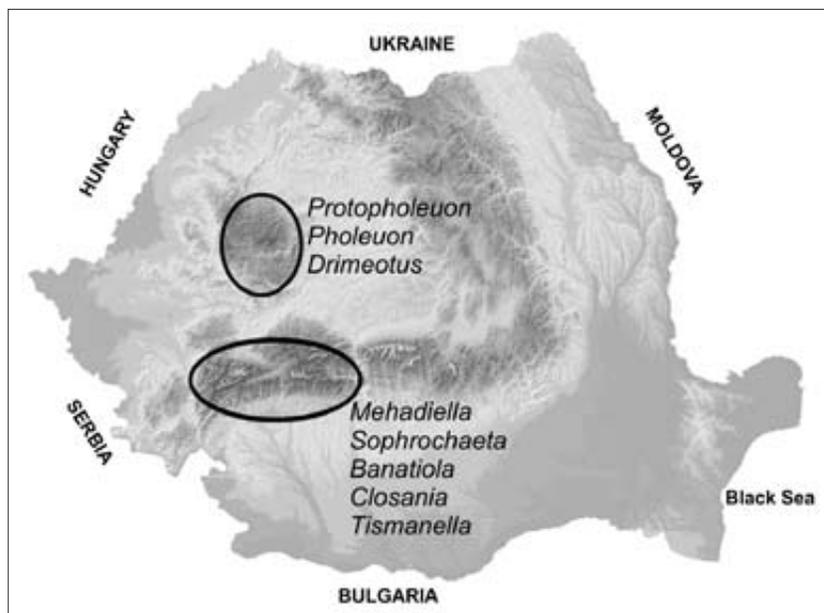


Fig. 2: Genera of Leptodirini distributed in the Western and Southern Carpathians of Romania.

The above-mentioned features explain the fragmentation of the initial distribution area of surface ancestors of cave animals and speciation processes. It also explains the high number of genera and species for a country at 45° northern latitude. Other countries at the same latitude are much poorer in species (e.g., Austria - 2 species, Switzerland - 1 species), even though their limestone areas in these countries are larger.

Romanian Leptodirini is represented by 8 genera and 6 subgenera with 50 species and 46 subspecies, composed of 1 epigeal, 10 endogean and 85 strictly cavernicolous taxa. Concerning the distribution of subterranean beetles, the Romanian Carpathians can be divided in three geographical units: Western, Southern and Eastern Carpathians. The last unit has few caves and no representatives of Leptodirini. More than half of the karst surface of the country belongs to the Western unit (the Apuseni Mountains). This region also has the highest degree of speciation with 63 taxa in the genera *Drimeotus*, *Phloeumon* and *Protophloeon*. These species inhabit caves and the MSS. More genera but fewer species are found in the Southern Carpathians: the epigeal monospecific *Mehadiella*, and the 34 taxa of subterranean *Banatiola*, *Sophrochaeta*, *Closania* and *Tismanella* (Fig. 2).

The origin of Romanian Leptodirini is strictly linked to dispersal of ancestral lineages that inhabited the Alpine Miocene chain and to a Paratethys evolution. Jeanel (1924, 1931) and Decu & Negrea (1969) suggested a Dinaric origin for the Romanian Leptodirini, based on morphological similarities, and especially on features of the male genitalia. This theory explains the colonization of the Apuseni Mountains through the Bohemian massif, and direct colonization of the Southern Carpathians from the Dinarides. Differences between the two phyletic lineages (Western *Drimeotus* and Southern *Sophrochaeta*) justified this hypothesis, which is also supported by new paleogeographic data (Steininger & Rögl 1985, Popov *et al.* 2004). When these different waves of colonization occurred is questionable, because direct Dinarides-Carpathians connection is either very old or too recent.

Migration of Asian ancestors of Cholevinae was not possible until the Upper Oligocene-Early Miocene, when a Dinaric-Pelagonian-

Anatolian landmass was formed, and linked to the rest of Europe by the recurring Slovenian corridor. This was the first connection between the Dinarides and Carpathians and lasted until Lower Badenian (16 Ma) when the Central Paratethys was flooded. It provided the possibility of populating the Southern Carpathians by Dinaric lineages, which was also at the time of Carpathian system development (Fig. 3). In Upper Ottnangian (17-18 Ma), the basin of the Paratethys was profoundly altered and a connection between the Alps and the Carpathians was established. The first Alps-Bohemian Massif-Carpathians connection provided conditions for the Apuseni Mountains colonization through the Bohemian massif. In Lower Badenian (15-16 Ma) a major transgression temporarily interrupted the connection between the Carpathians and the Bohemian Massif. Later, in Middle Badenian (14-15 Ma), the connection was definitively established. A connection between the Dinarides and the Carpathians was also established during the Messinian crisis (5-6 Ma) but cannot explain the processes of Southern Carpathian colonization and speciation. Subterranean beetles are less mobile, even if they can migrate over relatively short distances through the non-calcareous MSS. Supposing that epigeal and edaphobiont forms migrated and colonized this region, it is improbable to admit that adaptation to deep subterranean habitats and speciation could have occurred in such a short period of time.

In conclusion, the Dinaric origin of subterranean Romanian beetles can be explained by a first migration wave of a Dinaride lineage over the Southern Carpathians and a later one through the Bohemian massif of a lineage that colonized the Apuseni Mountains. Both lineages are morphologically linked to Dinaric species, with some peculiar features in the *Drimeotus* western lineage. An additional migration from the southwest during the Messinian crisis also could have been possible but only for species less adapted to caves. The next step in the evolution of the Apuseni beetles was subterranean domain colonization. The processes and mechanisms that could have driven the subterranean colonization were presented in the previous section.

We also analyzed spatial distribution of species and subspecies of the *Drimeotus* phyletic lineage to obtain information which can be corroborated with available taxonomic and molecular data. Romanian Leptodirini offer good material for studying speciation and vicariance processes, because it involves insular distribution, which is different from the large, continuous limestone surfaces such as those of the Dinarides and the Pyrenees, where speciation has occurred in the absence of geographical barriers. The Apuseni Mountains are inhabited by three genera (*Protopholeuon*, *Pholeuon* and *Drimeotus*), belonging to the *Drimeotus* phyletic lineage (Fig. 4).

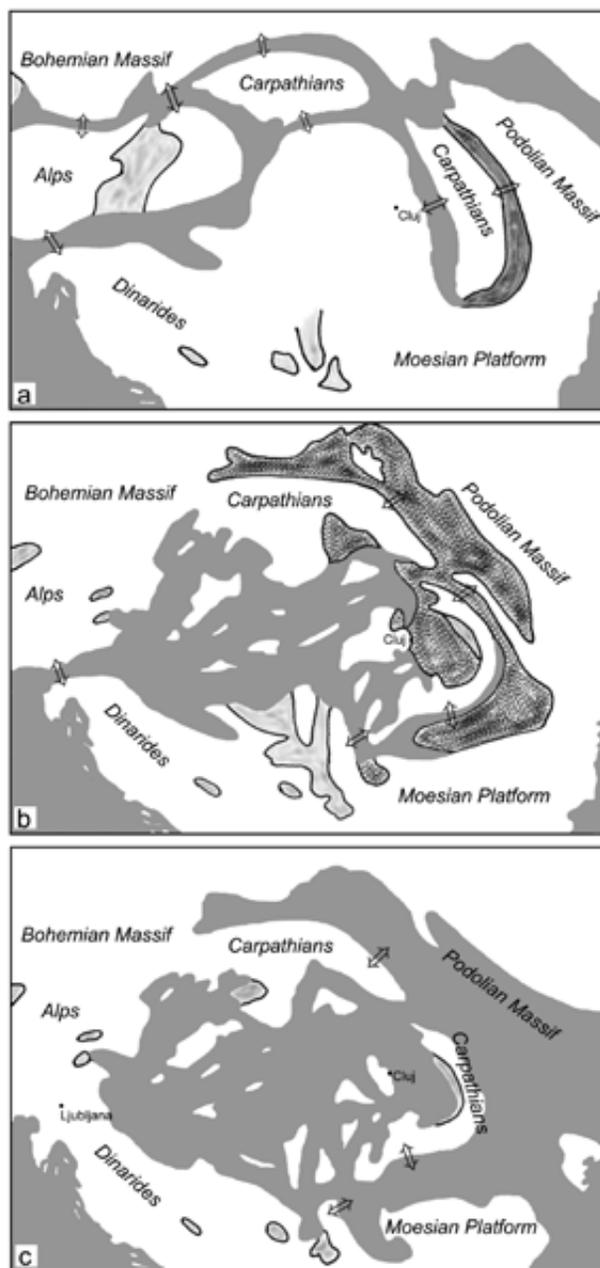


Fig. 3: Evolution of the Paratethys in Upper Ottnangian (a), Middle Badenian (b) and Lower Badenian (c) (Cluj is located in North-Western Romania) (simplified after Rögl & Steininger 1984): grey – marine realms, dark grey – evaporitic basins, light grey – important areas with fluvio-terrestrial sedimentation and/or lignite formation, white – continental realms, \Leftrightarrow – basins narrowed post-sedimentation by tectonic processes.

The lineage is monophyletic (Bucur 2003) and suggests a common ancestor, probably epigeal. *Protopholeuon*, which is monospecific, inhabits the Metaliferi Mountains, while the other two genera have larger distribution. Most species of *Pholeuon* and *Drimeotus* occur in the Pădurea Craiului and the Bihor mountains. *Pholeuon* also

has sub-genera in the Codru-Moma unit, while *Drimeotus* is in the Metaliferi and the Trascau Mountains. Each mountain is inhabited by a different sub-genus. It is possible that future searches will enlarge the distribution of *Drimeotus* also in Codru-Moma. (The first and last specimen of *Drimeotus* in the Metaliferi was found as recently as 2001 in a cave well known for *Protophloeon* and this was after several trapping episodes where *Protophloeon/Drimeotus* ratio was 150/1.)

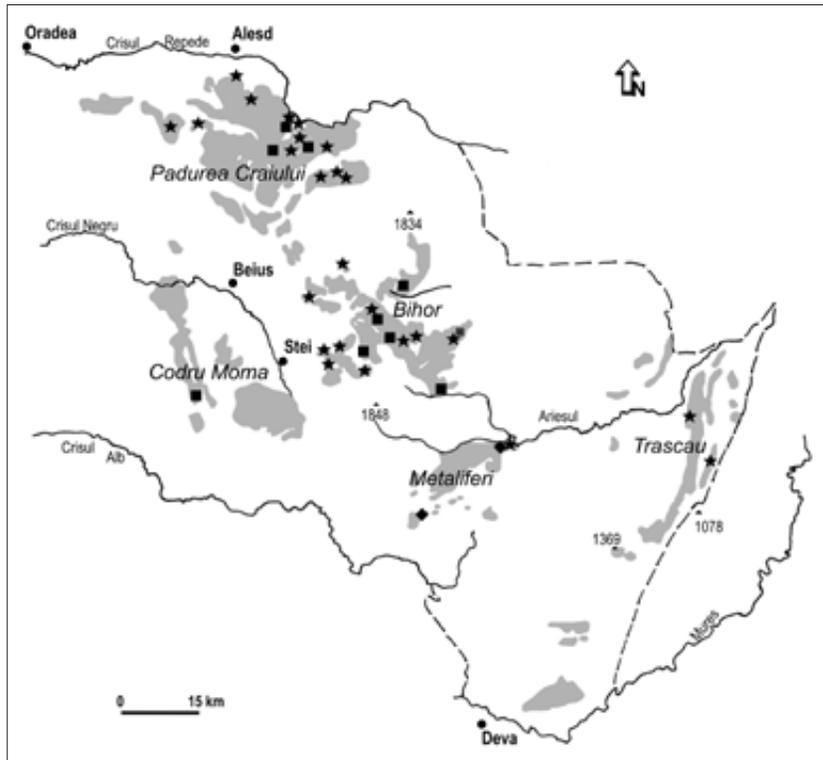


Fig. 4: Distribution of Leptodirini in the Western Carpathians (Apuseni Mountains):

★ - *Drimeotus*, ■ - *Phloeon*, ◆ - *Protophloeon*, grey areas - karst.

Comparing the largest geographical units in the Apuseni, Padurea Craiului and Bihor, the number of species and subspecies of less adapted *Drimeotus* and the more adapted *Phloeon* is different between genera and between units. *Drimeotus* (20 species and 12 subspecies) has higher specific diversity in both units and lower sub-specific diversity than *Phloeon* (6 species and 20 subspecies). This can be explained by the difference in adaptation and different histories of the two genera. *Phloeon*, very adapted, is less mobile and very few individuals were found in MSS or under rocks. Preadapted ancestors of *Phloeon* colonized deep subterranean environment in the entire area and since then small modifications have occurred. Lacking competition, infra-generic differentiation of *Phloeon* is slow. *Drimeotus*, less adapted and relatively mobile between limestone areas, is under

stronger climatic and biologically stronger selective pressures, which explains larger distribution areas and higher specific diversity. There are also differences between the Padurea Craiului and the Bihor *Drimeotus*, with more than two-thirds of the species in the first mountains. In Padurea Craiului the climate is warmer and less humid, with caves at lower altitude than in Bihor. Therefore, migration and gene flow between populations inhabiting different limestone areas or caves are limited and speciation is stronger. The more humid and colder Bihor Mountains allows superficial migrations and gene interchange between geographically close populations.

The altitudinal distribution of Leptodirini was first discussed by Jeannel (1952), who mentioned the presence of the same genus and even same species at the surface at 1500 m altitude, under the rocks at 1000 m, and strictly cavernicolous at 500 m. A sound analysis of the distribution published by Decu (1980) emphasizes the lack of correlation between body size and altitude. We found different results, given in Table 1. For *Drimeotus*, correlation between altitude and body length or relative length of antennae is negative for Padurea Craiului samples, and positive for Bihor samples. An approach that links geography to morphology is the kriging method, which uses a topographic representation of the data sets. Using the Golden Software Surfer 8 we obtained the maps in Fig. 5. As one can see, the vectors define

centers of origin at about 500-700 m altitude. Ancestors of the *Drimeotus* lineage probably inhabited superficial habitats between 500 and 1000 m altitude. Colonizing caves at lower or higher altitude induced body increase, a process explained by lack of competition and/or decrease of temperature. Body growth, as a result of cave colonization, is not only known for subterranean beetles. The *t* test showed no significant difference in body length between populations of Padurea Craiului and Bihor. The same test on the relative length of antennae gives shorter antennae in Bihor than in the Padurea Craiului samples. This can be due to the fact that the higher Bihor Mountains are inhabited by populations less confined to cave, compared to the Padurea Craiului. *Phloeon* has the same tendencies as *Drimeotus*, with a negative correlation of body length and altitude in Padurea Craiului and

a positive correlation in Bihor, and the antennae length decrease with altitude.

Tab. 1: Linear regression (y) and coefficient of determination (R²) at *Drimeotus* (13 populations) and *Pholeuon* (6 populations) from the Padurea Craiului and the Bihor Mountains (Western Carpathians): BL Body length, AL/BL antenna/body lengths ratio.

	Altitude (m)		
	0-499	500-999	> 1000
<i>Drimeotus</i>			
BL	y = -0.0003x + 4.4511 R ² = 0.0096	y = 0.0004x + 4.1025 R ² = 0.2337	y = 0.0007x + 3.5404 R ² = 0.3301
AL/BL	y = -8E-05x + 0.5969 R ² = 0.1077	y = 3E-05x + 0.5327 R ² = 0.0195	y = 0.0001x + 0.4088 R ² = 0.2449
<i>Pholeuon</i>			
BL	y = -0.0001x + 3.9152 R ² = 0.0239	y = 0.0031x + 2.142 R ² = 0.7849	y = 1E-04x + 4.6179 R ² = 0.0150
AL/BL	y = -1E-04x + 0.8619 R ² = 0.2445	y = -0.0002x + 0.9593 R ² = 0.7847	y = -0.0001x + 0.9044 R ² = 0.2529

Mantel's test is a regression in which variables are matrices summarizing pairwise similarities among sample locations. Geographic distance was used as a predictor variable, and morphological features of populations belonging to *Drimeotus* and *Pholeuon*, from the Padurea Craiului Mountains, as dependant distance matrices. For $\alpha = 0.01$, the test gives strong correlation for *Drimeotus* samples (Fig. 6) and no correlation for *Pholeuon*. For the moment, we cannot explain this result, although presumptions can be formulated.

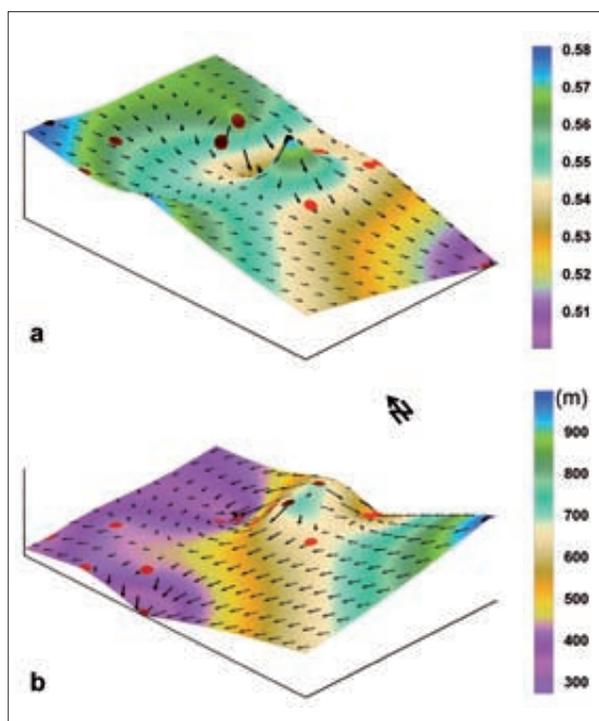


Fig. 5: Antennae relative length (a) and altitude (b) variations in geographical coordinates for 15 populations of *Drimeotus* s. str. (red dots) of Padurea Craiului Mountains, in 3D and vectorial overlaid representations.

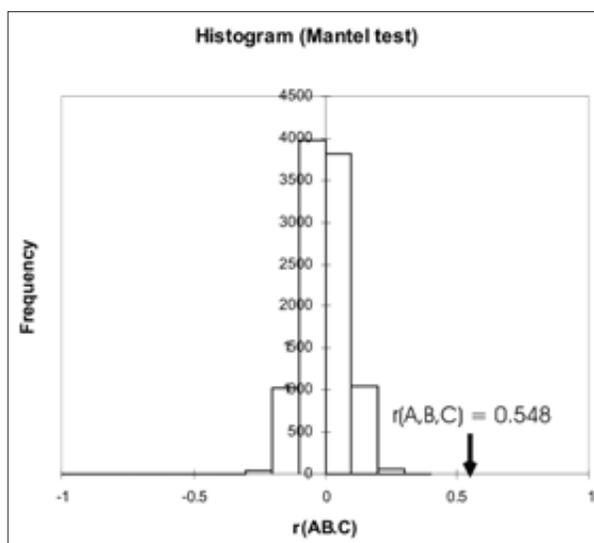


Fig. 6: Histogram representing results of the Mantel test on representatives of *Drimeotus* s. str. from Padurea Craiului.

Mantel's test (XLSTAT 2006.5 software) was also used to correlate geographic distance with morphological features, such as body and relative antennae lengths.

CONCLUSIONS

Plato’s allegory still raises questions in historical biogeography of cave beetles, but new scientific acquisitions will also enhance the chances for a more objective view in explaining the history of one group or another and what shaped their present distribution.

We have only presented few results and further research must take into consideration more populations and the surface of the populated area, as in insular studies. In caves, as well as on oceanic islands, the number of endemics can be related to the size of the area. Studies of Barr (1985) and Culver *et al.* (1973) applied the insular theory of McArthur & Wilson to karst areas, which have the characteristics of continental islands separated by non-calcareous “seas”. Thus, the number of subterranean species is strongly correlated with the surface of the limestone.

The recent interest in biogeographic studies has resulted from conservation necessities, especially in the last

decade. For example, the concept of habitat fragmentation became one of the priority themes of conservation researches. The concept is considered ambiguous, and empirical studies demonstrate a wide variety of direct and indirect effects, even with opposing implications (Haila 2002). The effects of habitat fragmentation are considered extremely dangerous for species and population preservation, and are often mentioned when establishing protection areas for rare and vulnerable species.

From a biospeleological point of view, habitat fragmentation represents one of the main mechanisms that enhanced speciation processes in reduced areas (at least for terrestrial fauna). This idea, different from the conservationist concern, can be extremely useful in solving protection problems. Unfortunately, none of the main contributions in conservation biology mentions caves and cave fauna as examples of survival in small, fragmented areas.

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