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WHY SO MANY LEPTODIRINI (COLEOPTERA, LEIODIDAE) IN ROMANIA?

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Abstract — Leptodirini are Cholevine beetles (Coleoptera Leiodidae) with many cave-dwelling representatives. Fifty-two species have been described to date from the two main karstic regions of Romania, the Western and the Southern Carpathians. The group's distribution in the northern hemisphere and high concentration of species in the Mediterranean region can be explained in terms of present and past events, which also account for the unexpected richness of this group in Romania.

Key words: Beetles, Leptodirini, Romania, Europe, biogeography, statistical analyses

INTRODUCTION

The Leptodirini Lacordaire belong to the Cholevinae (formerly named Leptodirinae or Bathysciinae) and include beetles of the family Leiodidae (Newton, 1998; Perreau, 2000). Cholevinae show a mixture of archaic, plesiomorphic, and derivated traits, together with ultra-specialized, autapomorphic features (Giachino et al., 1998). This mixture of new and old features is also due to the presence in the group of species with different degrees of adaptation to the underground life, from endogean to highly adapted hypogean taxa. More than 30% of the cave beetles in the world belong to this sub-family (Juberthie and Decu, 1998). The tribe Leptodirini comprises seven sub-tribes, 176 genera, and 794 species [for reference, we used the list of Perreau (2000), to which we added some more taxa described by the following authors: Casale, Giachino and Jalžić, 2000; Ćurčić and Brajković, 2002a, 2002b; Ćurčić et al., 2004; Moldovan, 2007). Most species are troglobitic, belonging to 121 genera, while 33 genera have endogean and subterranean (not strictly cave-adapted) species and only 22 genera are epigean. The vast majority of the detritivorous and saprophagous cave beetles of Europe are included in this group, with species adapted to different habitats, feeding on organic matter more or less decomposed, deposited on the substrate (walls and flowstones inside caves), or stored in underground deposits.

Distributed mostly in Europe, the Leptodirini have representatives in North America, the Middle East, and Central and East Asia; a mono-specific genus is also mentioned from South America, but its validity is under question (Perreau, 2000). The distribution of the tribe in Europe is for the most part limited to the southern

half of the continent, the Mediterranean region and non-Mediterranean countries such as Austria, Great Britain, Slovakia, the Czech Republic, and Romania. With its geographic position in Eastern Europe, Romania is very rich in subterranean faunas for a non-Mediterranean country. As a first step in explaining Romania's remarkable richness in cave invertebrates (including Leptodirini), we offer a biogeographic analysis of genera and species in Europe. The historical biogeography and ecology of this group are also discussed in an attempt to explain the present-day situation.

MATERIALS AND METHODS

The distribution of European Leptodirini was analyzed using Perreau's (2000) catalog of Leiodidae, but adding some new data from the Balkans and Romania. For Romania, the new up-dated species list published by Moldovan (2007) was used, in addition to the list published by Decu (1964).

Maps published by Rögl and Steiniger (1984), Steiniger and Rögl (1985), and Popov et al. (2004) were consulted in considering the historical biogeography of the Leptodirini.

Statistical analyses and graphic representation of data were accomplished with the aid of XLSTAT software, version 2007.6. Correlation dendrograms were constructed using similarities such as common genera or common taxa (species and sub-species) for each combination of two countries, the Pearson correlation and unweighted pair-group being employed in both cases (genera and species). For the MDS (multi-dimensional scaling) analysis, the dissimilarities matrix of common genera was transformed to their coordinates in a two-dimensional space. Dissimilarities are considered as continuous and giving exact information to be reproduced as closely as possible. In the polynomial sub-model used here, the distances obtained in representation space must correspond as closely as possible to those observed in the initial matrix using a near second-degree polynomial relationship. The MDS algorithms aim to reduce the difference between the disparity matrix of the models and the distance matrix obtained in the representation configuration. The difference is measured through stress, in our case Kruskal's stress (2):

$$\sigma_2 = \sqrt{\frac{\sum_{i<j} w_{ii}(D_{ij} - d_{ij})^2}{\sum_{i<j} w_{ij}(d_{ij} - \overline{d})^2}}$$

where D_{ij} is the disparity between individuals i and j, d_{ij} is the Euclidean distance on the representation for the same individuals, w_{ij} is weight of the ij proximity (whose value is 1 by default), and $\overline{d}$ is the average of distances on the representation.

RESULTS AND DISCUSSION

The general distribution of Leptodirini genera in Europe is shown in Fig. 1 from which their concentration in the northern part of the Mediterranean region is evi-

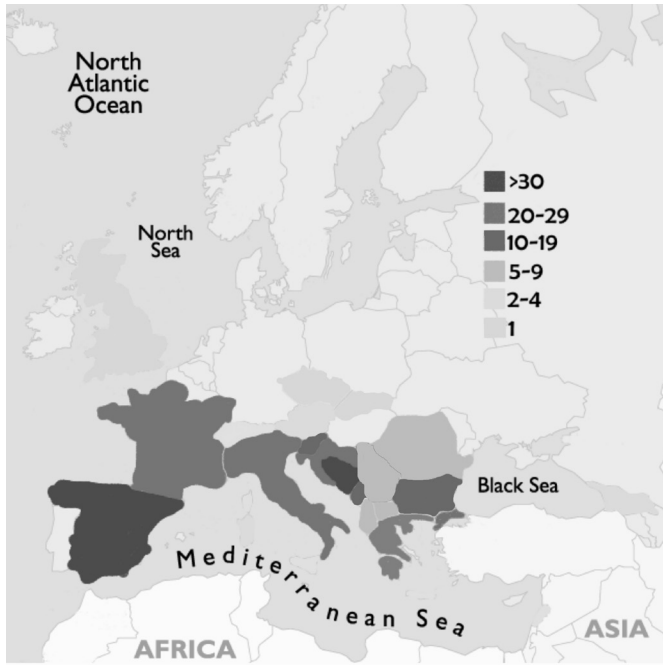

Fig. 1. Distribution of Leptodirini genera in Europe.

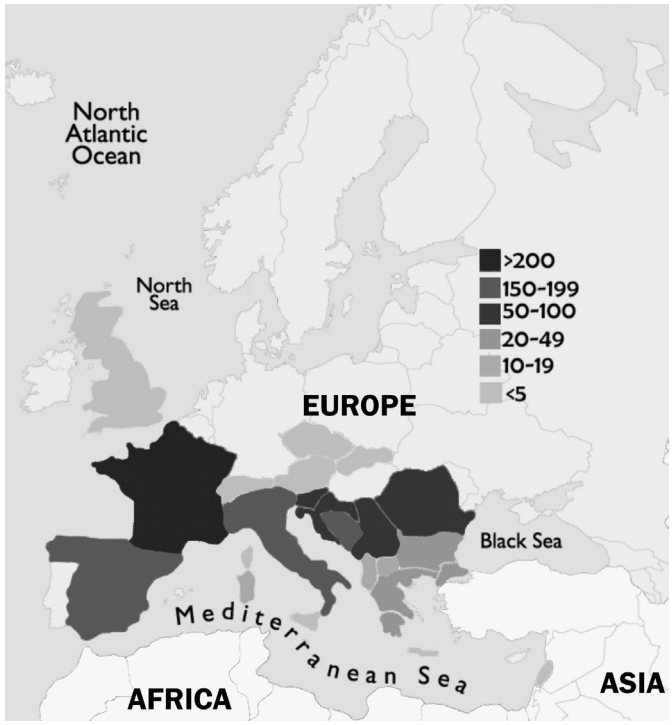

Fig. 2. Distribution of Leptodirini lower taxa (species and subspecies) in Europe.

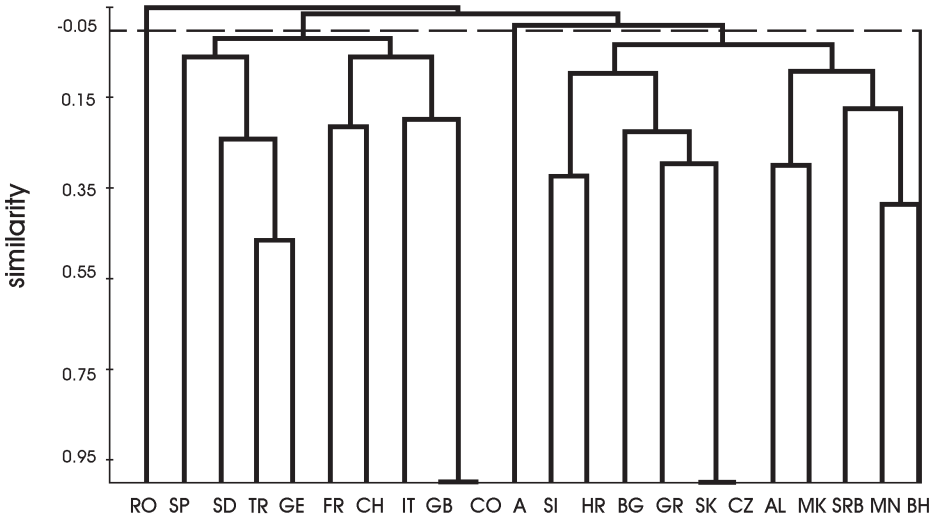

Fig. 3. Dendrogram of European countries based on Leptodirini genera held in common.

dent. The countries with the highest number of genera are Spain (31) and Bosnia-Herzegovina (31). There are also many genera in Croatia (29), Italy (23), France (20), Montenegro (13), Bulgaria (12), and Greece (11). Figure 2 presents the representation of lower taxa and emphasizes the species richness of this group in Romania. The distribution of lower taxa is not identical with that of genera, since the countries with the most lower taxa are France (214), Spain (188), Italy (175), Bosnia-Herzegovina (160), and Slovenia (54). Romania has few genera (eight), but many lower taxa (102).

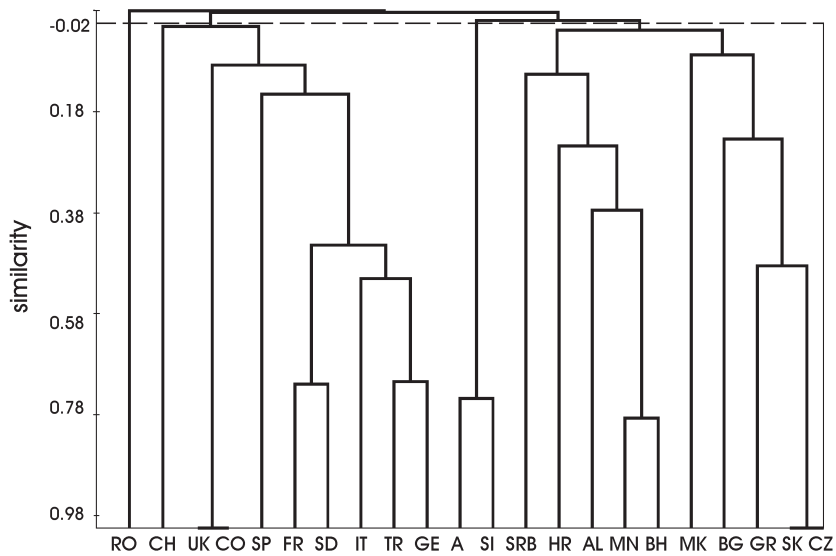

Fig. 4. Dendrogram of European countries based on Leptodirini species held in common.

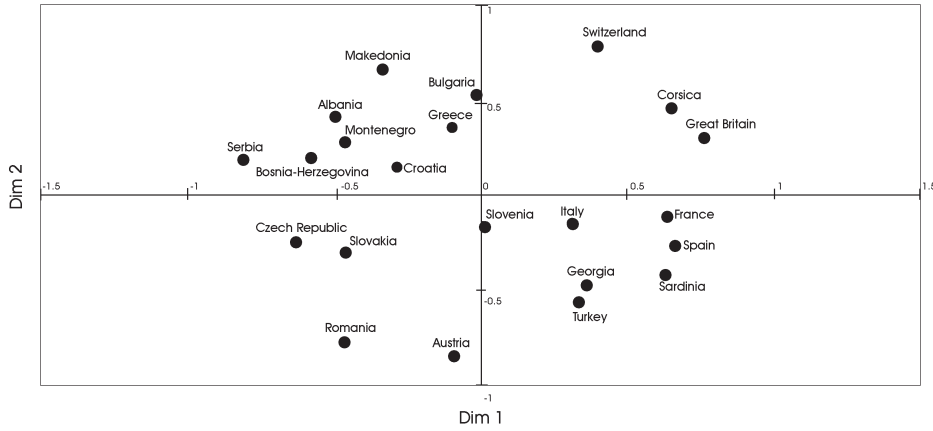

Fig. 5. MDS representation of European countries based on dissimilarities in Leptodirini genera [Kruskal's stress (2) = 0.753].

It is certain that a high number of taxa of any rank in some countries can also result from more active collecting and describing by specialists, but generally it reflects the real situation of species distribution in Europe.

Similarities/dissimilarities between European countries (including Georgia) in terms of Leptodirini genera or lower taxa held in common were also analyzed.

The dendrogram of genera (Fig. 3) is divided into three main groups. One is represented by the Balkan countries (Albania, Macedonia, Serbia, Montenegro, Bosnia-Herzegovina, Croatia, Bulgaria, and Greece) and also includes Slovenia, Slovakia, and the Czech Republic. The presence of the endogean genus *Bathyscia* accounts for inclusion of the last two countries in the dendrogram. Also present in Bulgaria, Greece, Montenegro, Bosnia, Slovenia, and Croatia, this genus might have a more general distribution in the Carpathians. The areas where *Bathyscia* is present may be the remnants of a once larger distribution in the Balkans and the Carpathians and are presumably also the result of a more recent vicariant process of speciation. Austria is externally attached to this group, next to Slovenia. The second group in the dendrogram is represented by northwestern Mediterranean countries/islands such as France, Spain, Italy, Sardinia, Corsica, and others like Turkey, Switzerland, Great Britain, and Georgia. Turkey and Georgia are the only countries linked at a relatively significant level. The third group is represented by Romania, with its eight

Table 1. Endemics in European Leptodirini.

Type of endemism	No. of taxa	%
Endemic taxa in Europe	1153	99
Genera with endemic species	176	100
Endemic species in caves	585	74
Endemic taxa in one cave (locality)	414	36
Endemic species in the Balkans	257	22

endemic genera, none present in other regions or countries. Excepting Turkey and Georgia, none of the groups or sub-groups is linked at a significant level from the statistical point of view. This can be attributed by the high level of endemism characterizing both genus and species levels.

Countries with species held in common form four main groups in the dendrogram on Fig. 4. The first group is represented by the Balkan countries, including Slovakia and the Czech Republic. Significantly linked from the statistical point of view, Slovenia and Austria form the second group. The third group includes all countries except Romania, which forms the fourth group in the dendrogram owing to its 52 endemic species. Within the third group, two sub-groups are linked at a significant level. These are France-Spain and Turkey-Georgia-Italy. The other countries/islands in the group are Switzerland, Great Britain, Corsica, and Sardinia.

Separation of countries is evident only for Romania, Corsica, Switzerland, Britain, the Czech Republic, Slovakia, and Austria in the two-dimensional space of the MDS (Fig. 5). These have few genera, in most cases a single endemic one. The exception is Romania, which has eight endemic genera. Another cloud, which is more or less continuously distributed from the upper-left to lower-right quadrants of the graphic representation, includes all other European Mediterranean countries and Georgia.

As can be seen in all these graphic representations, one of the main characteristics of the group is that many taxa are endemic for one geographic region or even one cave. Table 1 presents the situation of endemism within the tribe Leptodirini, most taxa being distributed exclusively in Europe.

The distribution of Leptodirini in Europe is the result of paleoclimatic history and geology at the regional level. There are two hypotheses explaining processes of subterranean colonization during glacial-interglacial episodes. The first postulates gradual colonization of the underground compartment due to climatic restrictions, while the second holds that colonization of subterranean habitats occurred as soon as these became available (which means long before glacial-interglacial periods), without climatic constraints. By the same taken, these climatic variations were not necessarily causes of extinction for presumably once existing northern cave popula-

Table 2. Genera of Leptodirini in Romania.

Geographical unit	Genus	No. of species	No. of troglobionts
Eastern Carpathians	0	0	0
Southern Carpathians	*Banatiola*	1	1
	Mehadiella	1	0
	Sophrochaeta	17	14
	Closania	2	2
	Tismanella	2	2
Western Carpathians	*Drimeotus*	21	19
	Pholeuon	7	7
	Protopholeuon	1	1
TOTAL	8	52	46

tions, but climate and vegetation represented barriers to colonization by ancestors of the cave fauna. Arguments are to be sought in the distribution of cave species and absence of post-glacial colonization by pre-adapted cave species. Can the 21 taxa living in ice caves be proof of their adaptability to low temperatures?

The biogeographic history of the tribe Leptodirini begins in the Paleozoic. Dispersal, vicariance, and extinction have shaped the distribution of Leptodirini, and three successive stages can be established in the space-time evolution of this group (Moldovan and Rajka, 2007):

1. Dispersal from a center of origin in the present area(s). According to Vailati (1988) and Giachino and Vailati (1998), the ancestral family Oricatopidae inhabited the southern part of the Gondwana supercontinent. Descending from this family, ancestors of the Leptodirini and other tribes migrated at the end of the Paleozoic to what is now the south of Eurasia on the microplates that broke off from Gondwana. Thus, Eurasia was colonized by ancestors of the Leptodirini 120–150 My ago. Later, 50-65 My ago, the group dispersed from the northeast, moving through southern Central Asia to eastern Eurasia and then westward, along the Mediterranean basin. Epigean individuals successively migrated at the surface, and they were probably pre-adapted to, constant low temperatures and high humidity.

2. Dispersal, vicariance, and extinction in the present area(s). 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, and some species colonized the Apennine, Jura, Carpathian, Rhodopes, Taurus, and

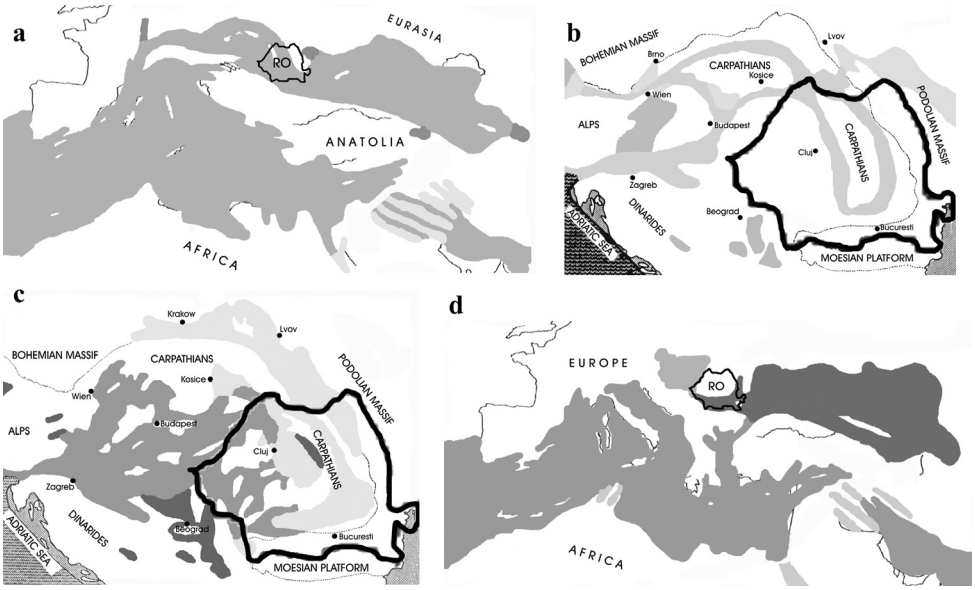

Fig. 6. Paleogeographic maps of Europe (after Rögl and Steiniger, 1984, modified) showing the evolution of continental realms (white) separated by marine realms (dark gray) and evaporitic basins or fluvio-terrestrial areas (light gray): a. Early Miocene (20 – 19 My); b. Early Miocene (19 – 18.5 My); c. Middle Miocene (16.8 – 13 My); d. Late Miocene (12 – 11 My).

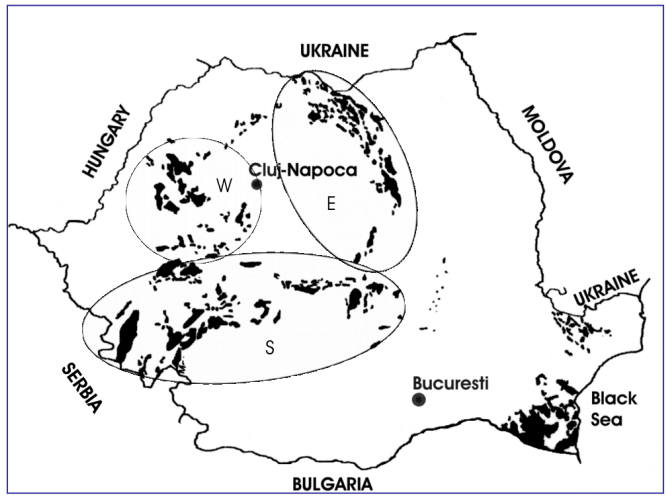

Fig. 7. Map of Romania with the three mountain units, western (W), southern (S) and eastern (E).

Caucasus Mountains and Mediterranean inlands (Giachino et al., 1998) (Fig. 6). A large and continuous distribution area of epigean and probably endogean ancestors of Leptodirini that migrated from the east was then fragmented, even before colonization of the subterranean domain. New paleogeographic data on evolution of the Paratethys from Late Eocene to Pliocene times were published recently (Rögl and Steiniger, 1984; Steininger and Rögl, 1985; Popov et al., 2004), and it appears that paleoconfiguration of the Paratethys shaped distribution of the Leptodirini in Europe.

3. Colonization and speciation in the subterranean domain. The third stage is represented by colonization and speciation in the subterranean domain. Two scenarios have been proposed to explain the mechanisms of underground colonization by epigean and endogean representatives of various faunal groups (Holsinger, 2000, 2005): the climatic-relict and the adaptive-shift models.

A possible common ancestor of the Carpathian Leptodirini could be *Bathyscia* or some genus (genera) that became extinct long ago. For subterranean fauna, a unique feature of the Carpathians with their continuous range from Serbia to Slovakia is that they form patches of limestone at lower altitude. Karst can be associated with islands of limestone separated by non-karstic rocks, which act as natural barriers to migration of subterranean organisms. Each area represents an island for 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. The above-mentioned features explain fragmentation of the initial range of surface ancestors of cave animals and speciation processes. It also explains the high number of genera and species in a country at 45° North latitude, such as Romania.

In Romania, only 2% of the country is represented by soluble rocks, mostly lime-

stone (Onac and Cocean, 1996), and the altitude for cave distribution is generally low, with 27% of karstic rocks at altitudes below 500 m and 47% up to 1000 m a.s.l. (Bleahu and Rusu, 1965). In non-Mediterranean countries or regions with larger karstic areas but higher altitudes (such as Austria, Switzerland, and the Alps), the Leptodirini are poorer in cave species in general.

The Romanian Carpathians are divided into three geographical units: western, southern, and eastern (Fig. 7). The last unit has few caves and no representative of the Leptodirini. More than half of the karst surface of the country belongs to the western unit (the Apuseni Mountains), where only 10% of the inventoried caves have been biologically investigated. The southern unit has about 15% of the surface covered by karst and the same percentage of investigated caves as the western unit.

The Romanian Leptodirini are represented by eight genera, seven sub-genera, 52 species, and 50 sub-species, the last two categories composed of one epigean, 10 endogean, and 91 strictly cavernicolous taxa. Differences in the number of genera and species between the two main karstic regions of Romania (western and southern) can be attributed to their different paleogeography and geology (Fig. 6). The highest degree of speciation is in the Apuseni Mountains, with 69 taxa belonging to the endemic genera *Drimeotus*, *Pholeuon*, and *Protopholeuon*. These species inhabit caves and the MSS. More genera but fewer species are found in the Southern Carpathians. They include the epigean monospecific *Mehadiella* and 34 taxa of subterranean genera *Banatiola*, *Sophrochaeta, Closania,* and *Tismanella*.

CONCLUSIONS

The distribution of Leptodirini in Europe can be explained in terms of paleogeographic events beginning with the Early Miocene and by regional geology. The newly emerged continental realms allowed colonization of surface ancestors of Leptodirini originating from Asia, while later evolution of the Paratethys shaped the distribution of populations and promoted speciation processes. Extinction was also important in areas where changes in marine realms were extremely dynamic during the Miocene.

In the general distribution of Leptodirini in Europe, Romania has a distinct position, not sharing common genera with other European or Carpathian countries, but being extremely rich in cave taxa for a non-Mediterranean country. Proposed explanations are linked with the paleogeography of Europe and the Carpathians, or with incomplete biospeleological investigations in the Romanian Carpathians (Moldovan et al., 2005; Moldovan and Rajka, 2007).

The Carpathians were for a long time isolated from the Dinarids, which are considered the place of origin for ancestors of species inhabiting present-day Romanian caves (Jeannel, 1931; Decu and Negrea, 1969; Moldovan and Rajka, 2007). Species, (probably epigean or endogean) also present in other Carpathian countries either will be found in the future or else became extinct.

There is an obvious need for more investigations, taxonomical revisions, and cla-

distic analyses, which will help us to understand the paleogeographic and paleoclimatic evolution of Europe since the beginning of the Miocene, especially at regional or local levels. Further cladistic analysis may answer the question as to whether or not there was a center of origin for all Leptodirini, although this is a challenging task for the future. For the moment, we reviewed the presence/absence of taxa in the Mediterranean basin as a first step in explaining the richness of Leptodirini in the Romanian Carpathians.

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