

IN MEMORY OF EMIL G. RACOVITZA (1868–1947) – HIS IDEAS REVERBERATE IN OUR SCIENTIFIC RESEARCH

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Abstract. The ideas of E. G. Racovitza which led to the development of biospelaology (biospeology, is the term used by Racovitza and adopted here) are reviewed. We emphasize the important research programme named *Biospeologica* which allowed to implement practical investigations on the subterranean animals due to enthusiastic cooperative work of many scientists. It leads to the exploration of many caves and other hypogean habitats. It is stressed out that the aim of Racovitza's efforts was to stimulate scientists to contribute with their research to the development of an encyclopedic view of the "Natural History of the Subterranean Domain". Examples from our own research reflect such ideas. We adopted Racovitza's views on the phylogenetic systematics, on the way to identify the relict aspect displayed by many subterranean animal groups. Also it is pointed out the importance of Racovitza's ideas for reconstruction of the dynamic dispersion of homogeneous phylogenetic animal lineages in time and space. Such ideas help us to develop biogeographic scenarios which are important for understanding earth's history. It is confirmed this way that the ambitious programme of Racovitza, became during the time a real research tradition that merits being pursued by young naturalists interested in solving exciting problems related to the origin and evolution of the subterranean domain and its ecosystems.

Key words: Racovitza's Biospeology, phylogenetic systematics, the subterranean domain, relict fauna, biogeographic patterns, *Biospeologica* – research tradition.

1. INTRODUCTION

15 November 2018 marks 150 years since the birthday of EMIL G. RACOVITZA, an extraordinary scientist. The brief presentation which follows will demonstrate the impact of the scientific ideas of Racovitza on our own research.

EMIL G. RACOVITZA was a man with huge sensitivity for the observation and description of the natural environment. His intellectual qualities led him to important discoveries in both marine and continental domains. Racovitza was a passionate researcher of the marine faunas, a fine observer of the Antarctic animals and an active investigator of the subterranean organisms. One of his main achievements was the development of a modern approach to the study of biological

aspects related to speology (the term used by Racovitza for what is now named speleology). His intensive investigations related to this latter area opened a modern direction of research in natural sciences, the *Biospeology*.

During the exploration of the Spanish Cueva del Drach on the Spanish island Majorca in 1904, Emil G. Racovitza sampled an unpigmented and blind isopod. He described this wonderful crustacean a year later as *Typhlocirolana moraguesi*, n.g, n.sp. (RACOVITZA, 1905). From this surprising discovery Racovitza proceeded to a critical analysis of the available scientific information on the cavernicolous animals and published in 1907 a remarkable document *Essai sur les problèmes biospéologiques* (translated in English 2006 by DAVID C. CULVER AND OANA T. MOLDOVAN).

RACOVITZA (1907a) in his famous *Essay* argued that cave animals are represented by “old forms (which) are not rare in the subterranean environment and often are relicts of a group nowadays disappeared from the region that had before a much wider distribution.” (RACOVITZA 1907a, p. 472 / English version CULVER & MOLDOVAN, 2006, p. 175). Therefore Racovitza proposed to start intensive investigations not only on this kind of animal but on various aspects of cave environments which should allow a better view of the natural history of the subterranean domain. His idea was to start with monographic descriptions of such animals, to try to reconstruct their origin and their phylogenetic position within homogeneous taxa and finally to follow their geographic distribution during the time. Within this approach it was proposed to combine comparative morphology with a more exact taxonomy leading to phylogentic reconstructions for whole groups from which the relicts still existing in caves were the last survivors. His approach therefore was evolutionary and historicist. The reconstruction of the way such animal lineages spread during the time on or under the earth represented an important goal of the biogeographic research within the framework of the new research direction named by Racovitza as biospeology (RACOVITZA, 1907a). It was clear that detailed research along these directions needed a lot of effort for sampling the subterranean, mainly cave animals and much scientific cooperation between scientists in order to get information from experts on the various organismic groups. Racovitza conceived this cooperative research project as a kind of association where each researcher could participate on a free-will basis. Racovitza named this association and its programme “The enterprise *Biospeologica*” (RACOVITZA, 1926a). Participants were asked that their issued publications dealing with material collected by any member of the association should be also considered, and by extension catalogued, as a scientific contribution of *Biospeologica*. In order to get comparable results Racovitza wrote in 1913 a booklet (Fig. 1) giving instructions to his collaborators on the way to sample cave fauna (RACOVITZA, 1913). Additionally, Racovitza proposed a model for description for the animals and the caves under study (RACOVITZA, 1913). A first presentation of the notable success of *Biospeologica* was made in 1926 (RACOVITZA, 1926a). In this report it was also stressed out that the aim of *Biospeologica* was to produce an encyclopedic view on the “Natural history of the subterranean domain” and this was partly achieved due to the

contribution of the whole group of naturalists. It was also emphasized (RACOVITZA, 1926a, p. 48), that an important success of this scientific enterprise was the discovery of a high number of “living fossils” due to in-depth phylogenetical studies. In fact it was meant that the studies on relict species living in caves was an innovative aspect of biospeology. To the metaphoric way to express the interest in troglobiotic animals RACOVITZA (1926b) added another vivid expression, the subterranean domain should be compared to a natural museum filled with many relicts. From here emerged the normal scientific interest for questions on their origin, using phylogenetic and geographic information but also the way such animals evolved adaptations to the subterranean environment during long periods of time.

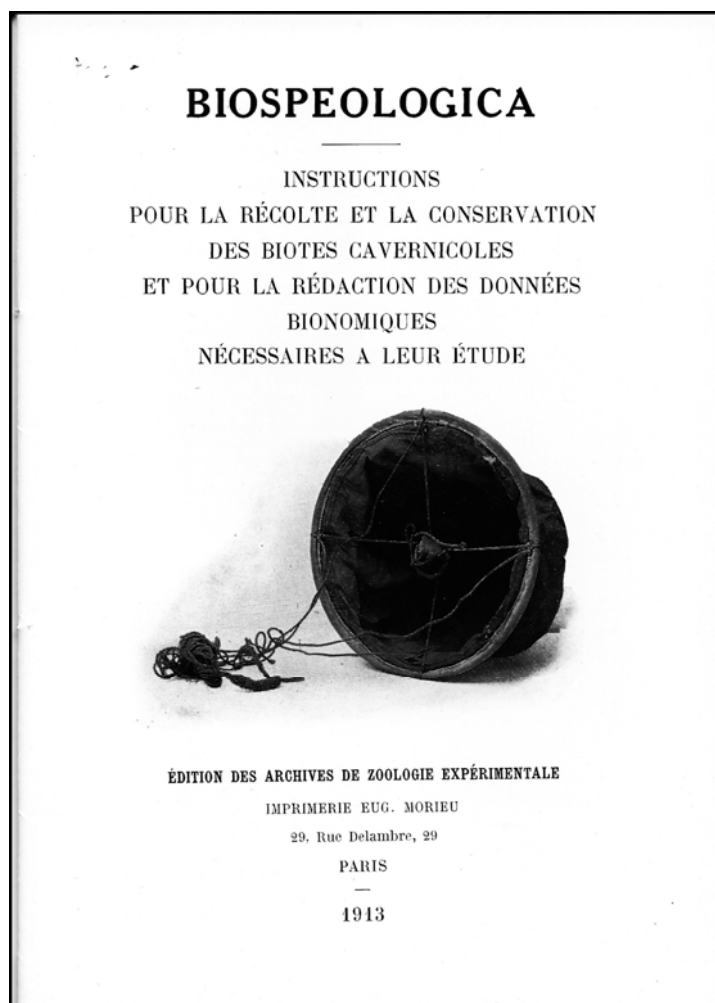


Fig. 1. Cover page of the booklet *Biospeologica* dealing with instructions for sampling and studying methods for troglobiotic animals (from RACOVITZA 1913).

It is *a factum* that naturalists who had the chance to see *in situ* typical subterranean dwelling animals, blind, unpigmented remain impressed by their aesthetics. They also ask questions of how such organisms came to live in an apparently constraining environment, the dark and oligotrophic caves. Here we illustrate as an example of an exclusively hypogean dwelling crustacean (Fig. 2), the quasi-limpid isopod *Stenasellus virei boui* Magniez. When observed moving in its aquatic habitat such animals made on us a huge impression. Immediately came to our mind some of the basic questions asked by Racovitza in his *Essay* at the beginning of last century (RACOVITZA 1907a), namely what is the origin of such animals, to which phylogenetic lineages they belong, what is their history, why we see nowadays in subterranean habitats relicts of animal lineages once flourishing at the surface of the earth.

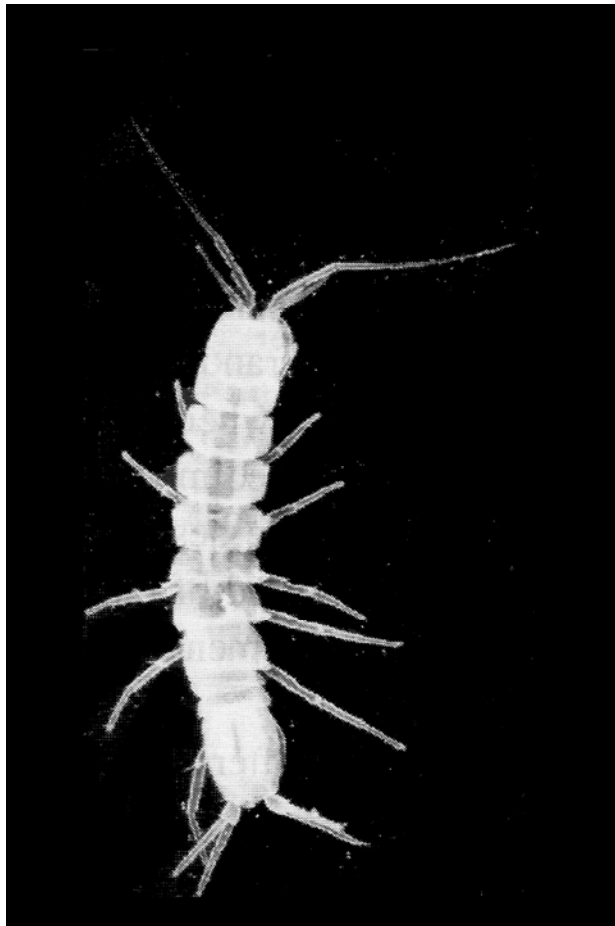


Fig. 2. *Stenasellus virei boui* Magniez, adult specimen about 6 mm length (from ROUCH & DANIELOPOL 1999).

As young scientists we were advised by our mentors Professors Radu Codreanu, Traian Orghidan, Constantin Motaş, and Margareta Dumitrescu, to follow the example of Racovitza's way of thinking and working. Our scientific careers started at the Institute of Speology "EMIL RACOVITZA", in Bucharest, about 50 years ago (for the senior author of this contribution, still earlier) and continued there during a notable numbers of years. We benefited in this institute from an important intellectual atmosphere and we assimilated effectively many of the ideas and the style of working of Racovitza. We observe now, when we completed more-or-less our scientific career, that the spirit of EMIL G. RACOVITZA is imprinted in many ways in how we perceive nature and in the practical mode we have described aspects of natural history of various animal groups for which we accumulated expertise during the years. Below we give some examples which reflect or are directly inspired by the science of EMIL G. RACOVITZA. The senior author (I.G.T.) of this contribution will present information on phylogenetical systematics applied to various groups of Crustacea following an approach, first proposed by EMIL G. RACOVITZA. Examples of the way one can recognise stygobiotic relicts of old terrestrial isopods groups will be also briefly discussed. Dan L. Danielopol (D.L.D.) will present the way in which the spirit of *Biospeologica* reverberates in the research of subterranean dwelling Ostracoda, when cooperating with various zoologists, palaeontologists and hydrogeologists. Finally, Ilinca Juvara-Balş (I.J.-B.) offers an example of the interest of RACOVITZA's ideas when studying the geographic distribution of edaphic Acari (mites).

Additionally we offer excerpts from the publications of EMIL G. RACOVITZA in a section Notes (N). They should exemplify arguments discussed in our text. In this way we hope our readers will get a better feeling for the clarity and aesthetic expression of Racovitza's ideas as a necessary cultural goal, the improvement of our view on a special part of Nature.

Professor Constantin Motaş once commented that the best honour that scientists can offer to their mentors is to continue to develop research within the pathways laid by their idols. We hope that our demonstration will be sufficiently persuasive in order to convince other naturalists to continue within this line of scientific activity.

2. RACOVITZA, FORERUNNER OF THE PHYLOGENETIC SYSTEMATICS

Present day systematics uses as its conceptual background principles of phylogenetic classification, known also as cladistics. This approach uses inferred evolutionary relationships hierarchically built after looking at each step to the most probable ancestor of members belonging to the same taxonomic group. The entomologist Willi Hennig is nowadays considered the founder of this research direction, that he promoted during 1950–1975, especially through his influential

book *Grundzge einer Theorie der phylogenetischen Systematik* (HENNIG, 1950). However we have to point out that EMIL G. RACOVITZA, at the beginning of the 20th century promoted similar ideas.

RACOVITZA (1908; N1) considered that a sound classification needs to be based on natural (parental) relationships of animals. Later on it was argued (RACOVITZA, 1912; N7, N8) that the main aim of taxonomy should be to reach for a given animal group a classification which should reflect phylogenetic relationships. Moreover for RACOVITZA (1925; N17; 1926a; N18) taxonomy should be nothing more than applied phylogeny. To achieve such a taxonomic programme Racovitza considered it necessary to examine for each morphological trait its special history as a reflection of its phylogentic trajectory (N4, N5). In fact already in 1910, Racovitza had already pointed out the need, when building phylogenies for taxonomic purposes, to avoid information derived from the traits displaying convergence and parallel evolution (N6). With other words only morphologic traits which reflect ancestor-descendant filiations should be used for natural classifications.

Following the ideas of EMIL G. RACOVITZA mentioned above we completed three series of investigations on the phylogeny of Crustacea which lead us to propose revised taxonomies. The first one dealt with a special group, the Isopoda Oniscidea (TABACARU & DANIELOPOL, 1996a, 1996b), the second one explored the phylogenetic relationships of the whole group of Isopoda (TABACARU & DANIELOPOL, 1999) and finally we reviewed the main group of the Crustacea, the Malacostraca (TABACARU & DANIELOPOL, 2011, 2012). The phylogenetic taxonomies for these crustacean groups are innovative, as we recognized more homogenous phyletic groups for which we proposed new taxonomic units. Below a brief presentation of the main results offered by the analysis of the three crustacean groups:

For the phylogeny of the suborder Oniscidea we selected 43 morphological traits exempt from the disturbing aspects of the potential origin by convergence or parallel evolution (TABACARU & DANIELOPOL, 1996a, 1996b). We followed in this way Racovitza's ideas of the way to complete phylogenetic systematics exposed in his 1910 monographic study on the aquatic Isopoda (RACOVITZA, 1910). We continued with a cladistical analysis of the selected traits obtaining a cladogram (Fig. 3) which demonstrates the monophyly of the Oniscidea and confirms the dichotomy of the group as proposed by VANDEL (1943) between the Infra-order Tylomorpha Vandel, 1943 and the Infra-order Ligiamorpha Vandel 1943. Within the Infra-order Ligiamorpha we proposed a dichotomy between the Super-section Diplochaeta Vandel, 1957 and a new Super-section, Orthogonopoda Tabacaru & Danielopol, 1996. This latter taxonomic unit was intended to better express the complicated relationships between three groups considered sections, Microchaeta Schmalzfuss, 1989, Synochaeta Legrand, 1945 and Crinochaeta Legrand, 1940. We offered a new phylogenetic solution to the debatable relationships between the three isopod sections, namely we documented that Synochaeta is a sister group

with the Microchaeta and Crinochaeta in our view is the sister group of the two former groups. Earlier studies considered Synochaeta being phylogenetically directly related to Crinochaeta.

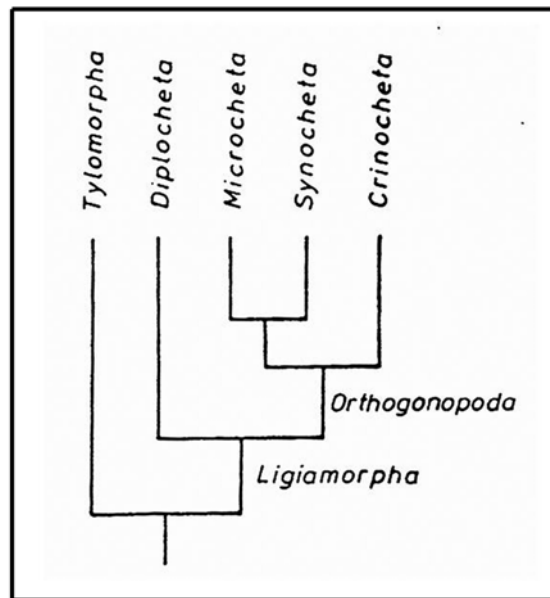


Fig. 3. Cladogram depicting the phylogeny of the Suborder Oniscidea as proposed by Tabacaru and Danielopol (from TABACARU & DANIELOPOL 1996).

For the reconstruction of the phylogenetic relations within the Order Isopoda TABACARU & DANIELOPOL (1999) selected 75 morphologic traits with which we performed the cladistical analysis. We considered for comparative purposes the orders Amphipoda and Tanaidacea as outgroups of the Isopoda. This allowed us to document the cohesion of the Isopoda as a monophyletic group and within this latter we could further analyse the ingroup relationships (Fig. 4). In our phylogenetic analysis it appeared that the orders Amphipoda and Isopoda, considered by many specialists sister groups, are not directly related. Also interesting was that the Microcerberidae, an aquatic hypogean group, formerly considered as a family of the suborder Aselloidea, represents *de facto* a higher phylogenetic unit that we named suborder Microcerberoidea. We considered this latter a sister group of the Aselloidea. We showed also that the enigmatic hypogean group Calabozoidea is not closely related to the Aselloidea previously thought to be the sister group of this latter suborder, but displays closer phylogenetic affinities with the Oniscidea (Fig. 4). Another innovative aspect of our study was to confirm an opinion proposed by RACOVITZA (1923) that the tail fan of the Isopoda is a derived morphologic trait and not a primitive one, as considered by many isopodologists.

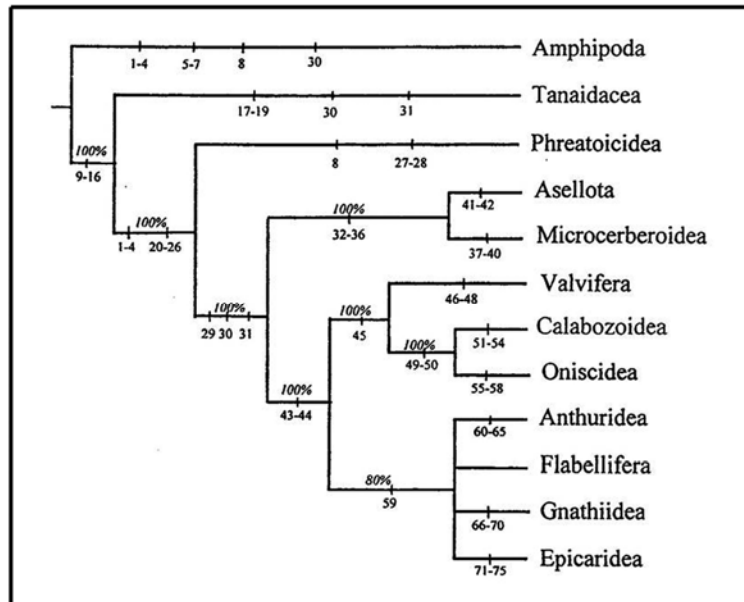


Fig. 4. Cladogram depicting the phylogenetic relationships of the major groups of the order Isopoda, using the 50% Majority Rule algorithm on a matrix of 75 morphologic characters. The numbers on the cladogram belong to the morphologic traits in the matrix; additionally are displayed the percentage of contribution for each morphologic trait to the proposed cladistic solution (from TABACARU & DANIELOPOL 1999).

Coming to the study of the Class Malacostraca we reviewed first the numerous contradictory opinions on the phylogenetic relationships existing between the different orders (TABACARU & DANIELOPOL, 2011). Using 68 morphologic characters we completed a phylogenetic analysis (TABACARU & DANIELOPOL, 2012). The results of this latter study were synthetically expressed by a cladogram (here Fig. 5) which offers new insights into the relationships existing between the major crustacean groups. One of the important conclusion was that the Syncarida does not represent a monophylum because Bathynellacea, nowadays an exclusively dwelling aquatic hypogean dwelling group, split early from the main trunk of the Malacostraca phylogenetic tree. This important crustacean group appears by its basal phylogenetic position to be a very old taxon of the subclass Eumalacostraca. This idea was first proposed by SERBAN (1972) in a remarkable monographic study on the morphology of the crustacean group *Bathynella* Vejdovsky. The style of carcinological studies made by our former colleague at the Institute for Speology, in Bucharest, was also inspired by the basic principles of EMIL G. RACOVITZA discussed here as basis for phylogenetic systematics. The conclusion of SERBAN (1972) was that *Bathynella* represents the type of a new superorder he named Podophallocarida belonging to the subclass Eumalacostraca.

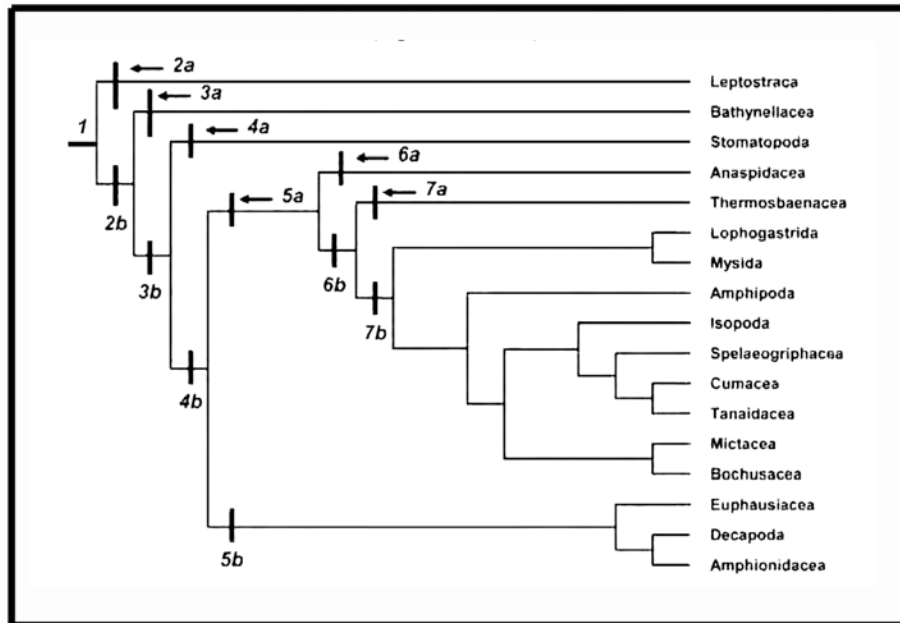


Fig. 5. Cladogram depicting the phylogenetic relationships of the major taxonomic groups of the Class Malacostraca, as proposed by Tabacaru and Danielopol (from Tabacaru & Danielopol 2012). Numbers refer to the following taxa: 1 – Class Malacostraca Latreille, 1802; 2a – Subclass Phylocarida Packard, 1879; 2b – Subclass Eumalacostraca Grobben, 1892; 3a – Infraclass Podophallocarida Serban, 1972; 3b – Infraclass Cephalothoracarida Tabacaru & Danielopol, 2012; 4a – Cohort Hoplocarida Calman, 1904; 4b – Cohort Caridoida Hessler, 1983; 5a – Subcohort Syneocarida Tabacaru & Danielopol, 2012; 5b – Subcohort Eucarida Calman, 1904; 6a – Infracohort Syncarida Packard, 1885; 6b – Infracohort Neocarida Ax, 1999; 7a – Superorder Pancarida Siewing, 1958; 7b – Superorder Peracarida Calman, 1904 (from TABACARU & DANIELOPOL 2012).

Many carcinologists who dealt with the phylogeny and systematics of Malacostraca remained sceptical about Serban's proposal. However our phylogenetic study (TABACARU & DANIELOPOL, 2011, 2012) confirms that Bathynellacea, as a group, is not closely related to the Anaspidacea forming together the order Syncarida. As a logical consequence one can adopt for Bathynellacea views similar to those of Eugen Serban. In our phylogenetic scheme (TABACARU & DANIELOPOL, 2012) we attributed to the Podophallocarida the taxonomic status of an infraclass, representing the sister group of the rest of the Eumalacostraca which belong to the infraclass Cephalothoracarida Tabacaru and Danielopol, 2012. This solution would support not only the efforts for documentation of SERBAN (1972) but also the visionary idea of Racovitza who repeatedly argued (as we stress out below) that the subterranean environment is full of very old animal groups which disappeared at the surface of the earth but continue their evolution within hypogean habitats.

3. THE PROBLEM OF THE RELICT SUBTERRANEAN FAUNA

Research on terrestrial Isopoda, a crustacean group especially well studied by EMIL G. RACOVITZA, was done by one of us (Ionel G. Tabacaru). He followed the ideas and the methodological approach proposed by RACOVITZA (N8, N9, N12–N16). The information of this latter (RACOVITZA, 1920b, 1923), helped for working in laboratory, namely on how to dissect and prepare the material for microscopy studies and finally how to describe and illustrate the material at hand (RACOVITZA, 1907b, 1908, 1912, 1930). The repeated arguments offered by RACOVITZA stressing the importance of troglobites for evolutionary biology (RACOVITZA 1907a, 1908, 1926a, 1926b) had an enormous effect on the way I.G.T. developed his own research on Isopoda during the time. It is now well established as noted by VANDEL (1960) that EMIL G. RACOVITZA opened a new era for Isopoda studies. In the special case of I.G.T. research it is only after the assimilation of Racovitza's information mentioned above that he could describe from Romanian caves a series of blind and unpigmented species, typical troglobites, that can be considered relicts (TABACARU, 1963, 1970, 1973a, 1973b, 1993a, 1993b, 1994; TABACARU & GIURGINCA, 2003). Below several such examples:

The genus *Biharoniscus* Tabacaru, 1963, displays two species *B. racovitzai* Tabacaru, 1963 and *B. fericeus* Tabacaru, 1973 endemics for the caves existing in the Apuseni Mountains, in Romania. This genus belongs to the tribe Oritoniscini Tabacaru, 1993 which do not display in the Carpathians epigeal representatives.

The genus *Thaumatonicellus* Tabacaru, 1973 is characterized by unique morphological traits. Because of the strongly divergent morphology when compared to other related taxa it was necessary to erect a new subfamily Thaumatonicellinae Tabacaru, 1973. The species of this later taxon have disjunct geographic distributions, namely one species is known from a cave in the Meridional Carpathians, *T. orghidani* Tabacaru, 1973, while the second one occurs (KARAMAN, BEDEK & HORVATOVIC, 2009) in an Istrian cave (Croatia), *T. speluncaae* Karaman, Bedek & Horvatovic.

The species *Caucasonethes vandeli* Tabacaru, 1993, described from a cave in Dobrogea, Romania, belongs to the genus *Caucasonethes* Verhoeff, 1932, known for many years through only one species, *C. borutzkyi* Verhoeff, 1932. This latter species was collected by the biospeologist E.V. Borutzky in two caves from Transcaucasia, at the time in the Soviet Union. This genus belongs to the Typlotricholygioidini Rioja, 1959 which, as VANDEL (1965) documented, contains a series of genera morphologically very similar. They display primitive morphological traits and a Mesogean geographic distribution, as the species are dispersed from the Caucasian caves to the Pacific coast of North America. Such a vast transatlantic distribution can be explained, as was done by RENÉ JEANNEL (1942, 1943) through the theory of continental translation developed by Alfred Wegener and now verified by the plate tectonics theory.

The species *Kithironiscus dobrogicus* Tabacaru & Giurginca, 2003, discovered in the boreholes made around the Movile cave in Dobrogea, belongs to the genus

Kithironiscus Schmalfuss, 1995. Until our discovery in Dobrogea, this genus was known through only one species from a cave in the Kithira Island, south from the Peloponnese, in Greece. *K. dobrogicus* represents the northernmost member of the family Scleropactidae. Other taxa belonging to this latter family display a dominant Gondwanian distribution.

These examples confirm the ideas of RACOVITZA (1907a, 1908, 1926a, 1926b) that caves harbour endemic taxa which through their present disjunct geographic distribution have to be considered relicts of old taxonomic groups N2). In past times isopod taxa, to which nowadays belong species with a relict distribution, displayed at the surface of the earth ranges notably extended to biogeographic areas. Therefore, with this type of documentation one has the feeling that investigations of stygobites, as RACOVITZA (1913; N10) suggested, offer useful evidence for scenarios explaining earth history.

4. THE SPIRIT OF *BIO SPEOLOGICA* REFLECTED IN OSTRACODA RESEARCH

The scientific progress related to biological research of organisms living in caves after the 1907 publication of the Racovitza's *Essai sur les problèmes biospéologiques* is really impressive. In his 1926 report on *Biospeologica* activities RACOVITZA (1926a) mentioned that within about 20 years since the start of this project, 52 publications were issued and seven more were in preparation. Several hundred of species, most of them previously unknown were described. This impressive scientific progress in the knowledge of subterranean fauna is partly due to the clear proposals Racovitza made in the working programme for the so-called enterprise *Biospeologica*. However looking to the list of animal groups studied in the annex to the *Biospeologica* report (RACOVITZA 1926a) we notice that from the more than 50 publications only one dealt with Ostracoda (PARIS, 1920). In this short publication six species were recorded from which only the half of them were typical subterranean dwelling crustaceans and only two species were scientifically new. This poor diversity of ostracods recorded during this research programme is surprising, especially when compared to the high species diversity recorded for other animal groups, namely about 60 species of isopods and about 200 insect Coleoptera, most of them new taxa. RACOVITZA already in his *Essay* (1907a) had already noted that some animal groups are poorly represented in the cave fauna. As a consequence the effort to find these groups is particularly high. One of the explanations Racovitza offered is that caves represent only a window accessible to man on the subterranean habitable space and therefore the optimal environment of such apparently rare animals lays somewhere else within the subsurface earth domain. Intensive exploration over time of the subterranean domain over large parts of the earth have confirmed Racovitza's supposition.

Considering the diversity of the Ostracoda in subterranean waters we assisted after 1920 to an increased interest for their study which led to the discovery of a huge number of new species. A large part of them were not cavernicoles but just

inhabitants of other types of subsurface biotopes. For instance many ostracod species occur in the alluvial sediments along rivers and streams, the habitat named by ORGHIDAN (1959) *hyporheic biotope*. Other species live in the alluvial sediments of riverine valleys. Constantin Motas named this subterranean aquatic environment the *phreatic habitat*, as the groundwater of such type of habitat is accessible mainly through various types of wells. The complex study of the phreatic habitats and their organisms was named *Phreatobiology* by MOTAS (1962).

In addition the minute spaces in karstified rocks which do not necessarily have access to caves represent a special habitat with a high number of new species. The calcrete systems in the Pilbara (Western Australia) investigated by William Humphreys and colleagues (reviews *inter alia* in HUMPHREYS 2012, 2017) represent a good example for the ideas of Racovitza that in extra cave systems abundant populations and high species diversity occur. In the compendium *Stygofauna Mundi* (BOTOSANEANU, 1986) there is a world-list of 413 ostracod species, from which 222 stygobites were non-marine subterranean inhabitants was presented by DANIELOPOL & HARTMANN (1986). The number of stygobiotic species has certainly increased during the last 30 years, for instance KARANOVIC (2007) produced a monographic study about the Pilbara (Western Australia) ostracods in which 84 species were described, species not known at the time of the *Stygofauna Mundi* project.

One of us (D.L.D.) was involved since 1963 in the description of new subsurface dwelling ostracod species. His main interest was to understand their origin and historical distribution over time and in space. For such studies the adoption of ideas exposed in the *Biospeologica* programme by RACOVITZA (1913; N10) and repeated with more details in RACOVITZA (1926a; N18, N19) were extremely useful. The advantage of studies on the origin and distribution of ostracod groups with stygobiotic taxa, in context of the *Biospeologica* framework mentioned above, is the possibility to integrate also information extracted from fossil species related to the living ones. In this way one can for ostracod taxa to build, with a better reliability, scenarios for the history of a given phylogenetic lineage. Here an example with the non-marine ostracod group, *Kovalevskiella*, which belongs to the subfamily Timiriaseviinae Mandelstam.

The first ostracod species described by D.L.D. was a troglobiotic species *Cordocythere phreaticola* from Vadu Crisului cave in Romania (DANIELOPOL, 1965). The species was supposed at the time to have affinities with species belonging to *Gomphocythere* Sars from Africa and *Cytheridella* Daday from South America. It was also speculated that the unique species of the new genus could be a relict of a pre-Quaternary ostracod group which preferred warm climate. No precise time for the period when epigeic taxa related to *Kovalevskiella* colonised subterranean habitats could be advanced during the 1960-ies as the whole status of ostracodology related to such topics was in its infancy.

A reanalysis of the data in the 1970ies showed that the troglobiotic species were closely related to a fossil species, *Kovalevskiella turianensis* Klein described from Upper Pliocene sediments in Azerbaijan (KLEIN, 1963), therefore *C. phreaticola*

was transferred to the genus *Kovalevskiella* (COLIN & DANIELOPOL, 1978). Continuing the comparative study of Recent dwelling Timiriaseviinae with fossil related taxa allowed to COLIN & DANIELOPOL (1980) to recognise a phylogenetic lineage within the subfamily Timiriaseviinae Mandelstam which was named the *Kovalevskiella* Group. Beside *Kovalevskiella* Klein two other fossil genera were attributed to this phylogenetic lineage: *Rosacythere* Colin 1980 and *Frambocythere* Colin 1980. In a more recent study (GIDO *et al.*, 2007) we improved the systematics of the subfamily Timiriaseviinae using principles of phylogenetic systematics as proposed by Racovitza to the participants of the *Biospeologica* programme (RACOVITZA, 1926a). The solution issued from the phylogenetic analysis is presented as a cladogram in Figure 6. One should note as an important result of this phylogenetic analysis the well-structured super-clade named the complex *Kovalevskiella-Abrotocythere*. Here several lineages are represented by fossil and by Recent living species, namely the lineages *Kovalevskiella* and the lineage *Abrotocythere*, each with their sister lineages *Frambocythere* and *Dolekiella*. All these lineages have beside the fossil species also Recent taxa, these latter living exclusively in subterranean aquatic habitats (GIDO *et al.*, 2007). Research of our colleague Jean-Paul Colin and co-authors showed that the more basal taxon within the clade *Kovalevskiella* was *Rosacythere*, a taxon with Mesozoic species. The oldest *Rosacythere* taxon was found in Middle Jurassic (Bajocian) sediments from the southern part of the Paris Basin, the others being mainly known as Cretaceous (Aptian-Cenomanian) species recorded in south-western and central Europe (COLIN & CARBONEL, 1996; CABRAL & COLIN 1998; PIPIK *et al.* 2008) as well as in Africa, Chad (COLIN & DÉPÊCHE 1997).

Frambocythere Colin is a species rich taxon (11 fossil species from which one has six subspecies); additionally there is one troglotrophic living species (GIDO *et al.* 2007; SMITH *et al.* 2012). Representatives of this genus were reported in Western Europe, i.e. southern France, northern Spain, southern Belgium, in Asia, Iran, central India, south-western China (Fig. 7) and in Africa, Chad and Zaire (COLIN & DÉPÊCHE, 1997).

Most of the species were found in Upper Cretaceous (Maastrichtian) and in Palaeogene (Palaeocene-Eocene) deposits. Jean-Paul Colin, Yvette Tambareau, Robin Whatley and their colleagues were the main contributors to the documentation of *Frambocythere* taxa (review in SMITH *et al.* 2012). It was an enormous surprise when Robin J. Smith showed us in 2011 during the European Ostracod Meeting in Graz, a Timiriaseviinae species from a cave in South Korea which resembles morphologically to a fossil *Frambocythere*. One year later this living troglotite ostracod was described as *Frambocythere relictata* new species and documented for its close affinities with *Frambocythere* gr. *tumiensis* (Helmdach, 1978), from Palaeocene (Thanetian) deposits of the Paris Basin (SMITH *et al.*, 2012). The living species from Japan has to be considered as both a phylogenetic and an ecologic relict, following the definitions of these terms by GRANCOLAS *et al.* (2014). The argument for a phylogenetic relict of the troglotrophic species is given by the discrepancy between the numerous fossil taxa and the unique living representative.

The geographic relictual aspect of *Frambocythere relict* is clearly visible on the map of Figure 7. One sees the punctual localisation of this troglobiont compared to the large areal occupied during time by the *Frambocythere* taxa now extinct.

On our phylogenetic tree (Fig. 6) the sister group to the Group *Kovalevskiella* is a clade we named Group *Abrotocythere*, this one being dichotomously branched in two lineages, namely *Abrotocythere* Zhao with two fossil species of Oligocene-Miocene age, from the the Guizhou province, South-western China, and *Dolekiella* Gido, Artheau, Colin, Danielopol & Marmonier from the Roussillon, southern France (GIDO *et al.*, 2007). The latter genus was erected for a stygobiotic species *Dolekiella europaea* (GIDO *et al.*, 2007).

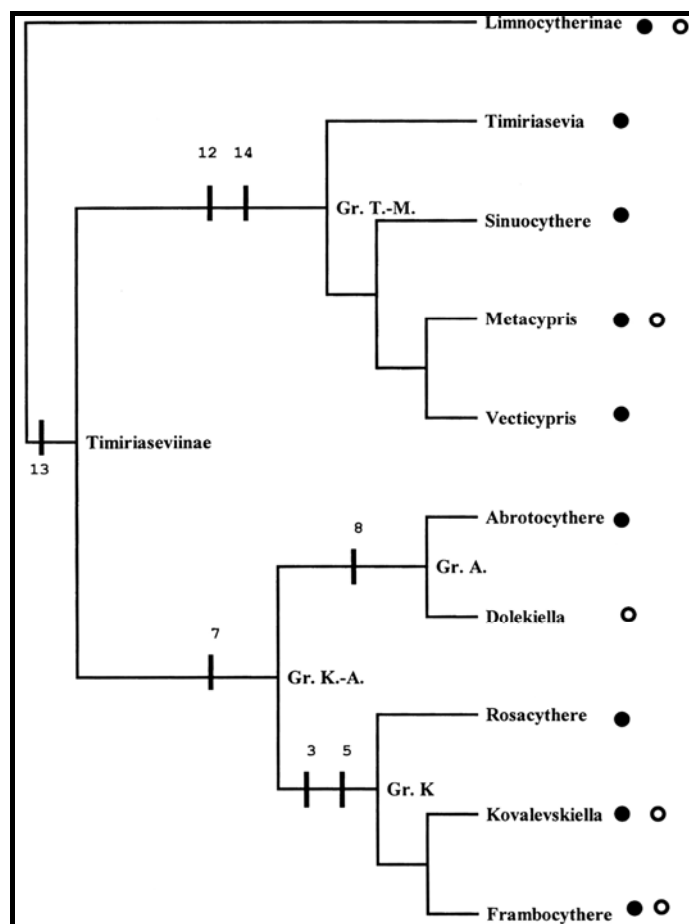


Fig. 6. Phylogenetic tree of the tribe Timiriaseviini Mandelstam (Ingroup), based on the analysis of morphological traits of the valves (Outgroup Limnocytheridae Sars. Bars, synapomorphic traits, numbers relate to the character traits in the matrix published in GIDO *et al.* 2007, Table I; open circles, living species; full circles, fossil species; Gr T. – M. Group *Timiriasevia – Metacypris*, Gr. K. – A. Group *Kovalevskiella-Abrotocythere*, Gr. A. Group *Abrotocythere*, Gr. K. Group *Kovalevskiella* (from GIDO *et al.* 2007, expanded with data from SMITH *et al.* 2012).

In the clade *Abrotocythere* one can see a remarkable segregation in time and space between the fossil species and the Recent stygobiotic one (Fig. 7). In the case of *Abrotocythere* group we have in Eastern Asia two Tertiary (Eocene/Oligocene) species and in Western Europe a living stygobiotic one, belonging to the genus *Dolekiella*. The logical interpretation of this strongly segregated record is to adopt the relict model in its geographic variant as defined by GRANDCOLAS *et al.* (2014). These latter specialists define a geographical relict as a taxon which displays nowadays a restricted area, remnant from a larger distributional area.

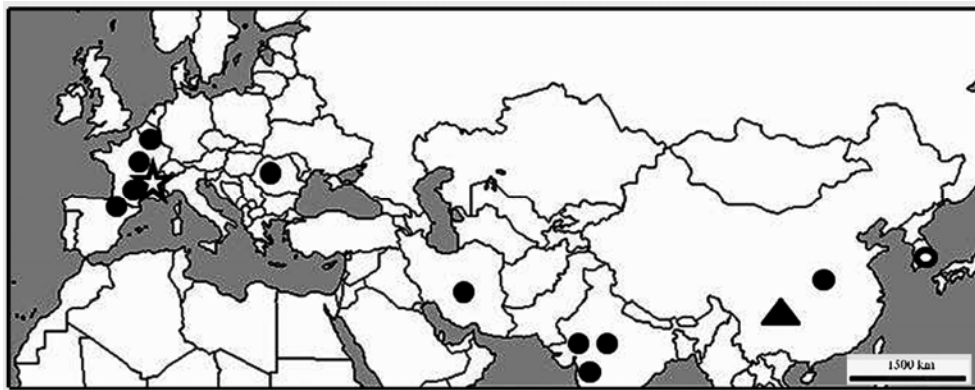


Fig. 7. Geographic distributions of representatives of *Frambocythere*, *Abrotocythere* and *Dolekiella*; black dots, fossil *Frambocythere* representatives; white dot, living *Frambocythere relictica*; black triangle, fossil *Abrotocythere* representatives; white star, living *Dolekiella europaea* (compiled from various bibliographic sources, see text).

Dolekiella europaea is not only a geographic relict but also an old relict belonging to the super-clade *Kovalevskiella-Abrotocythere*. One has to note that between the *Abrotocythere* species dated as Eocene/Oligocene and the Recent *Dolekiella* a laps of about 40 Ma years exist.

The late Jean-Paul Colin pointed out in GIDO *et al.* (2007) that during Middle Jurassic lagoonal carbonates were karstified in the Grands Causses, southern France, therefore Timiriaseviinae species which are known in this region, could already migrate into the hypogean realm.

Continuing the review of the Timiriaseviinae we turn now again to the genus *Kovalevskiella*. One can integrate into this genus two other fossil species, *K. prima* (Carbonnel & Ritzkowski 1969) from Oligocene (Melanienton) sediments south from Kassel, in Germany and *K. caudata* (Lutz 1965) from Upper Miocene/Lower Pliocene deposits (obere Suesswassermolasse/Torton) in southern Germany, near Regensburg (Fig. 8). This latter species was discovered in Lower Miocene (Aquitainian) deposits from south-western France, Aquitaine and in northern Spain, the Ebro valley (CARBONEL *et al.* 1986; MURELAGA *et al.* 1997, here Fig. 8). Additionally Pliocene and Quaternary species of *Kovalevskiella* have been described

from sites located in Eastern and South-eastern Europe as well as from sites around the Asian part of the Caspian and the Black Sea dated as Upper Miocene/Lower Pliocene and Lower Pleistocene, Apsheronian (review in DANIELOPOL 1980; other information in VEKUA, 1975; MOSTAFAWI, 1994; OLTEANU, 1995; KRSTIC, 2006; here Fig 8).

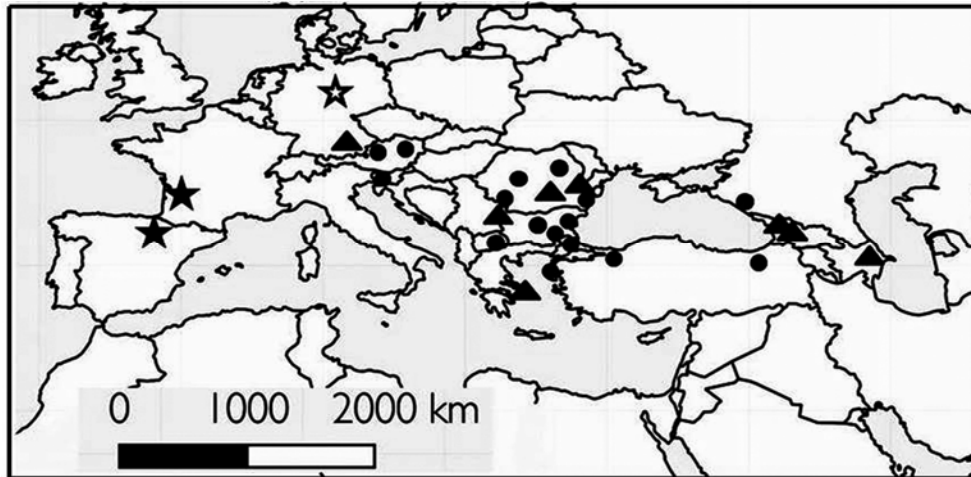


Fig. 8. Geographic distribution of representatives of *Kovalevskiella* Klein. Black dots, living stygobiotic taxa; stars and triangle fossil taxa; white star *K. prima* (Oligocene); black star, *K. caudata* (Miocene); black triangle Pliocene and Quaternary *Kovalevskiella* (compiled from various bibliographic sources, see text).

The nowadays living *Kovalevskiella* species are restricted to the Central and Eastern Europe (Fig. 8) and various sites around the Black Sea (DANIELOPOL 1970; CARBONEL *et al.* 1986. KARANOVIC (2003) described a new species of *Kovalevskiella* from Lesvos Island, in Greece. Recent new sites were mentioned in Bulgaria (KENDEROV & APOSTOLOV 2012), in Slovenia (MORI *et al.* 2012), in Turkey Rezovo valley near Bulgaria (ÖZULUĞ & YALTALIER (2008) and in the Zakaryia province (YAVUZATMACA *et al.* 2018). *Kovalevskiella* was collected from springs located in Zemolen Mountains, N-E Hungary by Dr. Z. Gido (unpublished, pers. Communication to D.L.D.).

It is remarkable that in the western part of Europe (north and central part of Italy, western part of Germany, whole France and Belgium) despite intensive programmes dealing with sampling groundwater fauna, including ostracods, *Kovalevskiella* was not found. For this result we used information from KEMPF (1997); MEISCH (2000); MEISCH *et al.* (1989); PIERI *et al.* (2015), unpublished information from various data bases kept by the following colleagues: P. Marmonier and Claude Meisch, their data base for the *Pascalis European Project* with data from France and Italy; Angel Baltanàs and Sanda Iepure unpublished data of living species in Spain; Maria Cristina Cabral on Recent ostracods in Portugal.

Here we hypothesize that the colonisation of subsurface habitats in the Central and the Eastern Europe (for this latter we include also the Balkans and the sites around the Black Sea) occurred repeatedly during the later Neogene, namely from the Upper Miocene/Pliocene to the beginning of the Quaternary. This supposition is based on the discontinuous distribution of *Kovalevskiella* visible in Figure 8. The model of repeated and implicit independent colonisation of subterranean habitats by epigeal populations of widely distributed species was recently reviewed by DANIELOPOL & ROUCH (2012). One should also see an excellent demonstration in KONEC *et al.* (2015). These authors used as example the isopod *Asellus aquaticus* (L) from which independent populations colonised in Romania and Slovenia subsurface habitats and further evolved there troglomorphic traits leading to new species.

The brief review of data presented above allow us to consider the living *Kovalevskiella* geographical relicts because their distribution area is more restricted than those of the whole geographic area on which the ostracod species spread during the Lower Oligocene to the beginning of the Quaternary (Apsheronian) time.

Combining the information of both Recent and fossil *Kovalevskiella* lead us to demonstrate a more subtle scenario for the way we have to consider the living ostracod species of this group as relicts. Taking in consideration that probably this ostracod group became extinct in surface water habitats after the beginning of the Pleistocene, the present day *Kovalevskiella* appears as a young relict lineage of the Timiriaseviinae.

At the end of this report on the *Kovalevskiella* lineage presented above it is instructive to compare the initial phase of the research on the systematics of the Timiriaseviinae ostracods, including the speculative scenario on the origin and affinities of *Kovalevskiella*, proposed by DANIELOPOL (1965), with the present day image of this ostracod group which emerged through a long and patient work as predicted by Racovitza in his visionary programme *Biospeologica*.

In 1965 the taxonomic description and the possible phylogenetic affinities of *Kovalevskiella* were deduced from simple comparative morphology related to the biogeographic information on the various species. Nowadays we know that *Gomphocythere* and *Cytheridella* with their geographic distribution and ecological preferences in Africa and South America have no direct relation to *Kovalevskiella* (DANIELOPOL *et al.* 2018). The former two genera belong to the tribe Cytheridellini Danielopol & Martens and *Kovalevskiella* belongs to the tribe Timiriaseviini Mandelstam. The accumulation of information from comparative morphology, phylogenetic systematics, micropalaeontology and biogeography data completed in the spirit of *Biospeologica* allowed development of an intuitive approximation of the time and the geographic area for migration of the epigeal *Kovalevskiella* into the groundwater. It allowed also to define the status for the living species of *Kovalevskiella* as a young relict group. These interesting data were obtained through a long cooperation and intensive communication between colleagues who from time-to-time became associated in the so called “Working group for studies on the

Evolution of Timiriaseviinae”. An unpublished report exists of the first meeting of this group in 1996 at the Laboratoire Souterrain, C.N.R.S. at Moulis, France (PIERRE CARBONEL unpubl.).

The data presented above points out to the actuality of the metaphorical idea of RACOVITZA (1926b), namely that the caves and by extrapolation the entire subterranean domain represent a museum containing diverse relict species, belonging to lineages of different ages and different histories. Racovitza used for such relict species the term “Living Fossils”. Even if in previous scientific contributions D.L.D. defended this term (e.g. DANIELOPOL, 1980 and/or in a lecture delivered to the 16-th International Symposium of Biospeleology, Verona 2002) it appears now that the term “Relict” has a more precise explanatory meaning than the former one and therefore we use it here. The three empirically documented examples of relict ostracod groups presented above corroborate once more Racovitza’s vision on the interest for the investigation of the subterranean environment and its fauna. But more than this, as in the case of an art museum, it appears that the diverse relict organisms need environmental protection in order to avoid as far as possible species extinctions. In this respect DANIELOPOL (1996, 1998) and DANIELOPOL *et al.* (2009) reiterated the proposal that for stygobiotic species having an important scientific value, a programme of fauna protection with selection of well-defined sites as nature reserves should be realised. Nothing new with such proposals! EMIL G. RACOVITZA once again was a forerunner of this moral duty of naturalists (RACOVITZA, 1937).

5. THE WAY OF PRESENTATION BIOGEOGRAPHIC DISTRIBUTIONS OF FAUNA

EMIL. G. RACOVITZA (1926a; N19) considered the species as a morphological, historical and geographical unity. He insists on the need to study the history of morphological transformations and homogenous lineages as well as their geographical dispersion as opposed to biogeographical studies of heterogeneous groups. The analysis of the morphological characters must be done very thoroughly in order to reach biogeographical and phylogenetical conclusions.

Ilinca Juvara-Bals started the study of the family Parasitidae, edaphic predatory mites, by the end of 1960. This family was not thoroughly investigated in Romania; it was like no man’s land.

We focused the research on the genus *Pergamasus* Berlese 1903 common in soil and leaf litter of karstic region. This genus meanwhile was separated in three subgenera: *Triadogamasus* Athis-Henriot 1971, *Thenargamasus* Athias-Henriot 1971 and *Pergamasus* (sensu stricto) Berlese 1903. We decided to investigate mainly *Pergamasus* (sensu stricto) with *P. alpinus* species-group, *P. crassipes* species-group and *P. beklemishevi* species-group (JUVARA-BALS, 1976).

Romania is a very interesting biogeographical region as mentioned by JEANNEL (1930), DECOU and NEGREA (1969), TABACARU (1970a, 1970b) for

coleopterans, isopods, diplopods. The same was observed with *Pergamasus* which are edaphic mites with limited dispersion. After 10 years of investigations I reached (JUVARA-BALS 1976; here Fig. 9) at the following results:

(1) The *P. alpinus* species group has not been recorded in Romania. It is well dispersed in Central Europe: Austria (ATHIAS-HENRIOT 1967), Slovenia (JUVARA-BALS unpublished).

(2) The *P. athiasae* species-group is a monotypic group represented by the species *P. athiasae* Juvara-Bals 1970 which we described from Southern Carpathians (Bucegi, Fagaras, Piatra Craiului Mountains). This species is a homogeneous lineage with plesiomorphic characters which seems to be endemic in this region (Fig. 9).

(3) The *P. beklemishevi* species-group have an East-European distribution. In Romania it is represented by five species: *P. tuberopalpus* Juvara-Bals 1976 endemic in north of the Carpathians (Gutâi Mountains), *P. kelemeneus* Athias-Henriot 1967 characteristic for the Eastern Carpathians, *P. adinae* Juvara-Bals 1970 widespread in the north of the Eastern Carpathians (Rodna Mountains) and once sampled from Slovakia (Fig. 9).

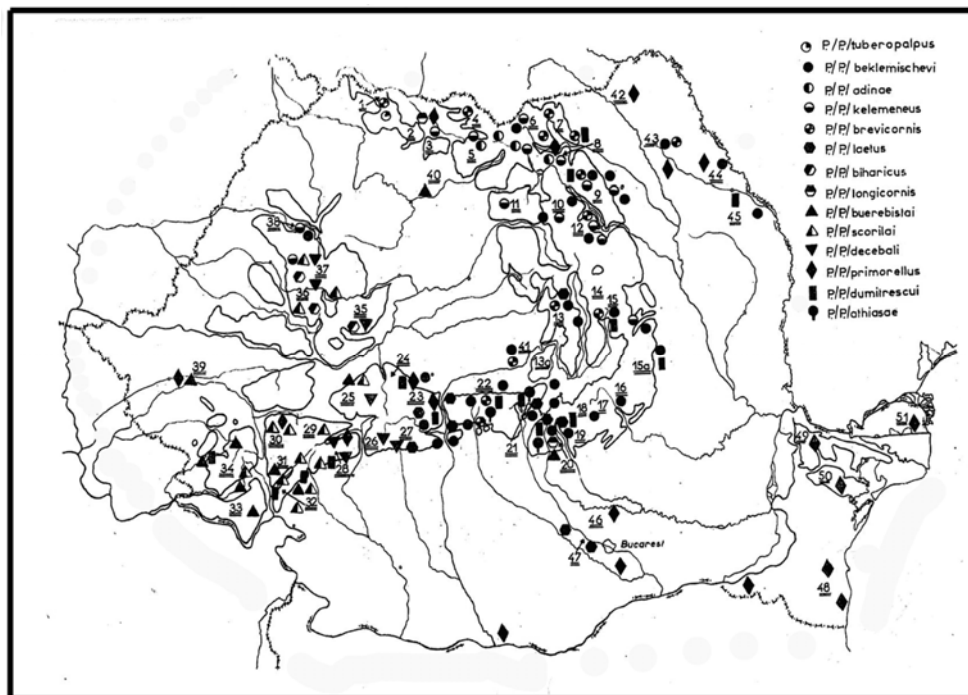


Fig. 9. Distribution of the species of the genus *Pergamasus* Berlese 1903 s.s. in Romania; numbers refers to sites where mites were sampled (cf. Table 3 in JUVARA-BALS 1976; present figure from JUVARA-BALS 1976, modified).

P. brevicornis (Berlese, 1904) is common in the Eastern Carpathians of Romania, Poland (MICHERDZINSKI 1969; WITALINSKI 1971), Slovakia (KAMILA HRUSOVA pers. communication to I.J.-B.) was not recorded beyond the Olt Valley.

P. beklemischevi, north European species, described from Ural Mountains, is widespread in the Eastern Carpathians, and the forests soil of the Moldavian Plateau. Some sporadic populations were sampled from the other side of the Olt Valley (Lotru and Cibin Mountains) and from the north boarder of Western Carpathians (Vadu Depression). This boreal lineage colonized the Eastern Carpathians later. However the geographical area of this species is based on incomplete research of its dispersion particularly in the Russian Federation and the Ukraine.

P. beklemishevi species-group is representative for the Western (Poland) and Eastern Carpathians. KAMILA HRUSOVA (pers. communication to I.J.-B.) confirmed the distribution of this group also in Slovakia. We can suppose that the origin of this east-European species-group can be the Bohemian Massif and the dispersion of the taxa in the Southern Carpathians was stopped by the barrier of the Olt Valley (JEANNEL 1930; DECOU & NEGREA 1969).

The species included in *P. crassipes* species-group were very difficult to identify. BHATTACHARYYA (1963) reviewing *P. crassipes* (L) Berlese and *P. longicornis* Berlese 1906 in the Berlese Collection arrived at the conclusion that there are “sympatric species which can be distinguished by a number of morphological characters”. W. KARG (1993) considered *P. crassipes* a species with high variability of its characters. The situation was similar to those mentioned by RACOVITZA (1908: p. 243; N3) for *Metoponorthus pruinosus* Br. and for *Asellus aquaticus* L. (1919: p. 33; N11). ATHIAS-HENRIOT (1967) described several new species from the east and central of Europe close to *P. crassipes* (L.) and established new morphological features important in the identification of these taxa. The species recorded from Romania were close to *P. crassipes* and different from those described by ATHIAS-HENRIOT (1967). After studying the morphological characters of *P. crassipes*, from France and Spain (ATHIAS-HENRIOT Collection, deposited at the Museum of Natural History, Geneva), I realized that “*P. crassipes*” from Romania was a mixed up of different species. I identified *P. longicornis* Berlese 1906, *P. primorellus* Athias-Henriot 1967 and I described five new species: *P. biharicus* Juvara-Bals 1973, *P. buerebistai* Juvara-Bals 1973, *P. decebali* Juvara-Bals 1973, *P. dumitrescui* Juvara-Bals 1970, *P. laetus* Juvara-Bals 1970, *P. scorilai* Juvara-Bals 1973. The species are very close to *P. crassipes* and the former identification didn't take into account all the morphological characters.

The geographical distribution of the species included in *P. crassipes* species-group is very interesting and we try to explain it in comparison with the known distribution of the edaphic Coleoptera, Diplopoda and Isopoda (JEANNEL 1930; DECOU and NEGREA 1969; TABACARU 1970a, 1970b). In their publications these authors recognised four provinces delimited by natural barriers: 1 – The Eastern and Southern Carpathians up to the Olt Valley; 2 – The Southern Carpathians

between the Olt Valley and the Timis-Cerna corridor; 3 – Western Carpathians south from the Mures river (Banat Mountains); 4 – Western Carpathians north of the Mures river (Apuseni Mountains). All the provinces were the result of the upheaval of the Carpathians during the Eocene and Miocene periods, when this mountain system was surrounded by the Paratethys sea.

P. longicornis was recorded from Northern and Central Europe, from Great Britain, North America and South Africa (ATHIAS-HENRIOT 1967). KARG (1993) considered this latter species as a synonym of *P. crassipes*. I have found it only in the north of Carpathian Mountains. Nowadays many ecological studies, in Romania, continue with identifications following KARG (1993) so that we can't know the precise geographical distribution of this species and thus can be confused with *P. crassipes*.

P. laetus was found in the Southern Carpathians (Bucegi, Piatra Craiului, Fagaras Mountains) but also in some oak forests around Bucharest. These forests were the remainder of the Codru Vlasiei forest which extends from the Southern Carpathians to the Danube. The geographical distribution of this species, similar with those of *P. athiasae*, is stopped by the Olt Valley an important barrier in the dispersion of different taxa. I am not able to explain their origin yet.

P. primorellus described from Hungary was found also in Austria (ATHIAS-HENRIOT, 1967), Eastern Germany and Slovenia (JUVARA-BALS unpublished). In Romania it is a common species in alluvial forests along the rivers and in the soil of low altitude forests (Dobrogea, Moldavia).

P. dumitrscui have been recorded from different localities along the Carpathian Mountains, with the exception of Apuseni Mountains. The morphological characters of this species are close to those of *P. pinguicrus* Athias-Henriot 1967 described from Eastern Alps (Styria) and identified also in Slovenia (JUVARA-BALS unpublished). I presume that the origin of *P. primorellus* and *P. pinguicrus* was in the Eastern Alps. From there, along the Dinaric Alps, they colonized the Southern Carpathians. *P. dumitrscui* could be a subspecies as a result of the dispersal of *P. pinguicrus* into new areal followed by an allopatric speciation.

The Southern Carpathians from the Olt valley to the Danube were an important center of dispersion and a "hot spot" of speciation. I have identified the species *P. decebali* and *P. scorilai* from the biogeographical province situated between the Olt river and the corridor Timis-Cerna. *P. buerebistai* has been recorded from Banat Mountainss which is considered a different biogeographical province (Fig. 9). We decided to study the variability of the morphological characters of *P. decebali*, *P. scorilai*, *P. buerebistai*, from different populations, and compare them with those of *P. crassipes* from France and so we arrived at the conclusion that the new taxa were valid species (JUVARA-BALS, 1976).

Pergamasus biharicus is endemic in the Trascau and Bihor Mountains which belong to the Western Carpathians north of the Mures river. This geographical

region, Apuseni Mountains, was also colonized in the north, from the Eastern Carpathians, by *P. kelemeneus* and *P. beklemishevi* and from the Southern Carpathians by *P. scorilai* and *P. decebali* (Fig. 9).

The province from the Eastern and Southern Carpathians limited in the south by the Olt Valley was probably colonized by Bohemian and boreal lineages. In the other provinces the dispersal of fauna was episodic and seems to have occurred from the territory of North Aegeis during the Miocene (see also JEANNEL 1942, 1943 for the palaeogeographic concept of the “Égéide septentrionale”) and secondary from the Dinaric Alps or from the Balkan Mountains in the Pleistocene. Incomplete studies about the *Pergamasus* genus in Eastern and Southern Europe made us only to presume the origin of its species existing in Romania. KAMILA HRUSOVA (pers. communication to I.J.-B.) started the molecular research of *P. crassipes* in Slovakia and tries to identify the validity of the species found in her material.

Another study was done (JUVARA-BALS, 2008), on the genus *Holoparasitus* Oudemans, edaphic mites, confirming the pertinence of Racovitza theories (as expressed *inter alia* in RACOVITZA, 1928) This latter insisted on the importance of a serious morphological analysis of the species characters, of their geographical distribution in order to understand the history of the homogeneous lineages (see here N20).

We (I.J.-B.) had the opportunity to study a rich material of this genus, deposited in the Collection of the Museum of Natural History of Geneva. We described fourteen new species and identified *H. mallorcae* Juvara-Bals 1975 from new localities (JUVARA-BALS, 2008). The mites were collected from southern Spain (*H. mallorcae*; *H. lunae* Juvara-Bals 2008; *H. malleus* Juvara-Bals 2008); Morocco (*H. mahnerti* Juvara-Bals 2008, *H. vaucheri* Juvara-Bals 2008, *H. rifensis* Juvara-Bals 2008, *H. franzi* Juvara-Bals 2008); Algeria (*H. variabilis* Juvara-Bals 2008, *H. algersensis* Juvara-Bals 2008, *H. singularis* Juvara-Bals 2008); the Balearic (*H. mallorcae*, *H. eivissa* Juvara-Bals 2008); the Canary (*H. canariensis* Juvara-Bals 2008, *H. anaga* Juvara-Bals 2008, *H. lapalma* Juvara-Bals 2008 and Madeira (*H. giganteus* Juvara-Bals 2008) Islands. (Fig. 10). All these species were included in the *Holoparasitus mallorcae* species-group (JUVARA-BALS, 2008). This presumably monophyletic species-group comprised two different lineages which are separated by some well visible morphological characters (JUVARA-BALS 2008). The species *H. eivissa*, *H. algersensis*, *H. singularis* are included into one lineage. The species forming the other lineage possess several types of endogynia which characterize four different other lineages. These latter aspects are further developed in JUVARA-BALS (2008) as the aim of the present contribution is not to discuss about all the differences between the lineages of the species from the *H. mallorcae* species-group. These species, in partim, are the result of allopatric speciation during the formation of the West Mediterranean Basin in the Miocene period. For example the distribution of *H. rifensis* (Rif Mountains–Morocco) and *H. malleus* (south eastern

Spain-near Malaga) is correlated with the palaeogeographical presence of Bético-Rifan Massif during the late Oligocene and the early Miocene. This massif was later integrated in the Africa-Rif Mountains and the South of Spain.

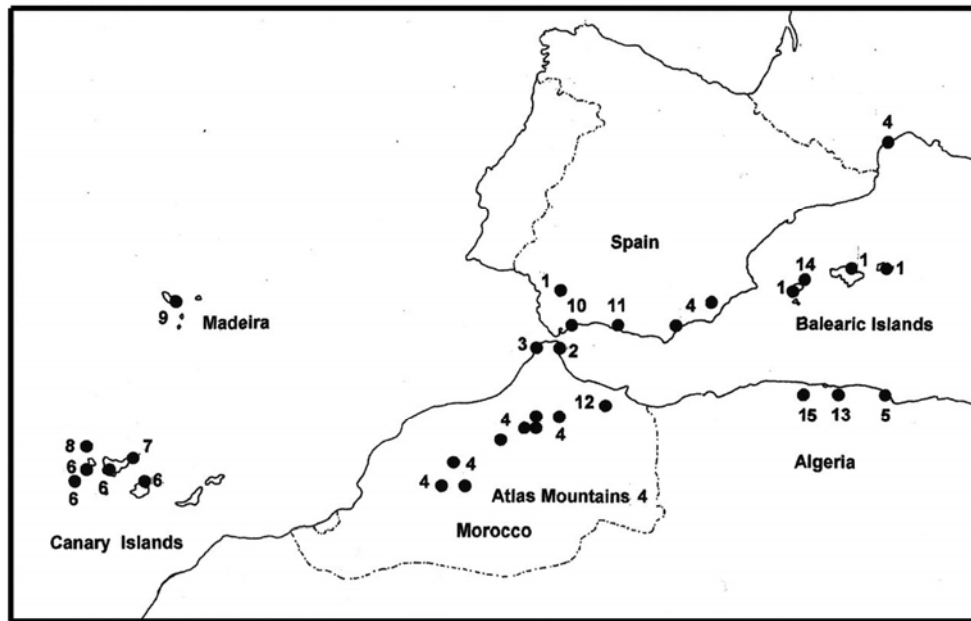


Fig. 10. Distribution of the *Holoparasitus mallorcae* species-group. 1 – *H. mallorcae* Juvara-Bals; 2 – *H. mahnerti* Juvara Bals; 3 – *H. vaucheri*; 4 – *H. franzi* Juvara-Bals; 5 – *H. variabilis* Juvara-Bals; 6 – *H. canariensis* Juvara Bals; 7 – *H. anaga* Juvara-Bals; 8 – *H. lapalma* Juvara-Bals; 9 – *H. giganteus* Juvara-Bals; 10 – *H. lunae* Juvara-Bals; 11 – *H. malleus* Juvara-Bals; 12 – *H. rifensis* Juvara Bals; 13 – *H. algiersensis* Juvara-Bals; 14 – *H. eivissa* Juvara-Bals; 15 – *H. singularis* Juvara-Bals (from JUVARA-BALS 2008).

The presence of *H. canariensis*, *H. anaga* and *H. lapalma* in the volcanic Archipelago of Canary is the consequence of successive colonization of the islands from east to west. The distribution of these taxa is connected to the laurasilva habitat. The intra-island, allopatric speciation of *H. anaga* in the Tenerife is very interesting. The palaeo-islands Anaga in the northeast, Teno in the west and Roque del Conde in the south became attached by volcanic activity. We identified two species on the island *H. canariensis* in the northwest and centre of the island and *H. anaga* in the northeast endemic to the Anaga Mountains. *H. mallorcae* species-group needs more faunistic data and molecular analyses to explain the phylogenetical relation between all the homogeneous lineages.

We have presented here only a summary of what we have achieved guided by the scientific work of Emil G. Racovitza and also by that of René Jeannel.

6. A FINAL STANCE – THE RESEARCH TRADITION INITIATED BY EMIL G. RACOVITZA SHOULD BE CONTINUED

The aim of this essay was to document that the research programme named by EMIL G. RACOVITZA *Biospeologica*, with its main goal to build a solid “Natural history of the subterranean domain” became a success.

The present essay offered as arguments our own positive perception of how important were Racovitza’s ideas and how much of our own scientific research profited from his various publications. One can view nowadays Racovitza contributions as a successful research tradition. Larry Laudan in his book *Progress and its problems* considers that “a research tradition provides a set of guidelines for the development of scientific theories” and the success of such a research tradition, has to be gauged against the degree of completion and/or success of the proposed programme (LAUDAN 1977). Here we showed examples of successful research inspired by Racovitza’s ideas and/or by his empirical way to solve specific goals within the proposed research programme.

The 150th anniversary of the birth of EMIL G. RACOVITZA is an opportunity to remind the question he addressed in the official discourse for his election at the Romanian Academy (RACOVITZA, 1926b): “The subterranean domain appears as a true museum of relicts and the question is why this domain is more prone for this as compared to many others? An answer would request many developments...” (Transl. from Romanian, D.L.D., N21).

The question Emil G. Racovitza addressed 92 years ago at the Romanian Academy, mentioned above, is still relevant. This should motivate a new generation of scientists to consider *Biospeology/Biospeleology* as an exciting scientific domain. In this way the research tradition launched by this illustrious personality will be profitably continued.

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Notes (N)

N1 – E.G. RACOVITZA (1908, p. 240–241): J’ai poussé fort loin l’analyse des caractères, car mon but n’est pas de dresser un simple catalogue de cavernicoles, mais d’aboutir à des conclusions biogéographiques. Ces études biogéographiques, si importantes par la répercussion qu’elles ont sur la paléogéographie et sur la phylogénie, ne peuvent pourtant être tentées si on n’a pas à sa disposition une bonne classification. Or une «bonne» classification doit être *naturelle*, c’est-à-dire se baser sur la parenté réelle des animaux, et de plus l’hierarchie de ses diverses catégories taxonomiques doit être établie de façon que toutes les catégories de même nom soient strictement équivalentes.

N2 – E.G. RACOVITZA (1908, p. 241): Dans le domaine souterrain, et je l’ai montré par plusieurs exemples frappants, on retrouve encore nombreuses les formes archaïques, véritables jalons de colonisations anciens de types qui ont disparu sans laisser traces dans le monde épigé.

N3 – E.G. RACOVITZA (1908, p.243): Enfin j’attire l’attention sur les espèces qualifiées ubiquistes ou cosmopolites. On s’est contenté jusqu’à présent de les examiner superficiellement et de les considérer comme invariables dans les différentes localités de leur aire immense de dispersion. Ce peut être vrai pour les cas de dispersion dus à l’homme. Mais il est des cas où la dispersion fut certainement naturelle et alors cette invariabilité ne peut être admise qu’après enquête approfondie. Ce que j’ai trouvé pour *Metoponorthus pruinosus* Br. fait penser que ces espèces ubiquistes sont constituées, en réalité, par un complexe de formes locales parfaitement définies.

N4 – E.G. RACOVITZA (1910, p. 632–633): Il est donc nécessaire d’examiner les caractères taxonomiques du groupe du point de vue de leur histoire et de leur signification phylogénétique pour arriver à une compréhension exacte de leur classification. Il est donc nécessaire d’examiner l’histoire particulière de chaque caractère.

N5 – E.G. RACOVITZA (1910, p. 637): Les caractères des espèces devront être groupés aussi en caractères de filiation et caractères d’adaptation. De plus, on doit les hiérarchiser suivant leur ancienneté relative et le rôle qu’ils jouent dans la biologie de chaque forme. Ce n’est qu’ensuite qu’on peut établir une classification réellement « naturelle ».

N6 – E.G. RACOVITZA (1910, p.707): Ces cas de parallélisme et de convergence sont plus fréquents qu’on ne pense. Beaucoup, j’ai presque envie de dire “la plupart” des caractères employés dans la systématique actuelle sont des semblables caractères d’évolution parallèle ou de convergence, et non des caractères de filiation, les seuls pouvant servir à établir des classifications naturelles.

N7 – E.G. RACOVITZA (1912, p. 204): Le but principal des études taxonomiques, le seul qui m’intéresse d’ailleurs, c’est, d’après moi, la classification naturelle des animaux, c’est-à-dire une classification qui reflète aussi exactement que possible la parenté réelle des diverses lignées animales. Comprise de cette manière, la taxonomie devient une des branches de la biologie générale, car elle fournit le matériel pour l’étude des lois et modalités de l’évolution.

N8 – E.G. RACOVITZA (1912, p. 207–208): Fixer par des diagnoses les limites des espèces, grouper ensuite les espèces par lignées, et distribuer ces lignées en catégories hiérarchisées suivant la distance historique qui les sépare du tronc commun, c’est la tâche primordiale que doit se proposer le taxonomiste moderne. Le point de départ est donc l’espèce, l’unité taxonomique par excellence.

N9 – E.G. RACOVITZA (1912, p. 208): Pour qu’il y ait subdivision des lignées, donc spéciation, un isolement quelconque est indispensable mais suffisant. La différenciation morphologique est une suite fatale de l’isolement. Une colonie qui s’isole, qui évoluera derechef indépendamment des autres, c’est un facteur nouveau qui s’introduit dans l’histoire du globe. Ces prémisses une fois admises, la conclusion sera que la définition de l’espèce en tant qu’unité taxonomique ne pourra être autre que «Une colonie isolée de consanguins».

N10 – E.G. RACOVITZA (1913, p. 2): Le but que se propose *Biospeologica* n'est pas, en effet, la détermination pure et simple des Biotes cavernicoles, même si cette détermination aboutissait à la description de formes nouvelles! Les collaborateurs de *Biospeologica* s'efforcent de constituer une «Histoire naturelle du Domaine souterrain» dans le sens le plus large et le plus scientifique de ce terme. Il faut donc que matériel et renseignement qui l'accompagnent, sont suffisants pour permettre l'étude des questions de phylogénie et de distribution géographique minutieuse; il faut qu'ils puissent servir aussi bien à la solution des questions de paléogéographie qui intéressent les souches, qu'à l'étude des adaptations spéciales et des transformations morphologiques et éthologiques des Biotes cavernicoles actuels.

N11 – E.G. RACOVITZA (1919, p.33): *Asellus aquaticus* auctorum est un mythe, une grave erreur taxonomique et non une espèce. Sous ce nom consacré par de nombreux lustres, se cache un mélange de formes disparates, d'origine diverse et de valeur taxonomique multiple.

N12 – E.G. RACOVITZA (1920a, p.62–63): D'autre part, la taxonomie est, pour qui veut réfléchir, une des disciplines biologiques les plus synthétiques. Le taxonomiste qui se propose de faire œuvre scientifique doit utiliser tous les résultats des autres disciplines qui s'occupent des êtres vivants. Il doit tenir compte, pour arriver à ses fins, de tous les caractères des biotes, qu'ils soient morphologiques, anatomiques, histologiques, ontogéniques, physiologiques, écologiques, éthologiques, en un mot: quels qu'ils soient, que leur découverte soit due à l'observation ou à l'expérimentation; car pour les caractères, seule vaut la distinction entre ceux qui sont utilisables et ceux qui ne le sont pas; il doit s'efforcer de situer, aussi exactement que possible, son espèce dans l'espace comme dans le temps, car l'espèce est une entité essentiellement historique.

N13 – E.G. RACOVITZA (1923, p. 83): Dès le début de mes études j'ai conçu la zoologie comme une science historique, ce qui m'a singulièrement facilité la compréhension des morphologies animales.

N14 – E.G. RACOVITZA (1923, p. 83–84): Il ne suffit pas de trouver l'origine et l'explication d'une structure; il faut, pour en tirer le maximum de bénéfice scientifique, l'étudier comparativement dans les diverses lignées homogènes...

N15 – E.G. RACOVITZA (1923, p. 88): Les questions de morphologie comparée doivent être d'abord étudiées isolément dans des lignées homogènes et sans idées préconçues; la comparaison des résultats obtenus permettra une généralisation, applicable seulement au groupe dont font partie ces lignées, hypothèse de travail ou première approximation qui doit être vérifiée sur les autres lignées du groupe et modifiée s'il y a lieu. Ces «hypothèses de groupes» peuvent maintenant être comparées entre elles pour donner lieu à des «hypothèses de groupes supérieurs et ainsi de suite, de proche en proche.

N16 – E.G. RACOVITZA (1923, p. 88): Néanmoins la seule manière prudente et sûre d'activer la marche des découvertes morphologiques est de s'adresser d'abord aux lignées les moins spécialisées, qui risquent d'être aussi celles ayant le mieux conservé les traces de l'organisation primitive.

N17 – E.G. RACOVITZA (1925, p. 617): que la taxonomie ne puisse être autre chose que de la *phylogénie appliqué*, qu'elle soit par conséquent l'une des sciences les plus synthétiques de la biologie, je le soutiens depuis longtemps.

N18 – E.G. RACOVITZA (1926a, p. 42–43): Cette incursion en Taxonomie me donna aussi la conviction qu'il n'est d'autre Taxonomie possible que celle basée sur la phylogénie et sur la répartition géographique, qu'il est impossible de situer une espèce correctement dans la classification des êtres sans connaître son origine dans le temps et son extension dans l'espace. *Taxonomie ne peut être que phylogénie appliquée.*

N19 – E.G. RACOVITZA (1926a, p. 48): Concevoir l'espèce comme un «phénomène purement actuel» est certainement une grave erreur. L'espèce doit être considérée comme une entité aussi bien morphologique, qu'historique et géographique. La taxonomie ne peut être autre chose que de la phylogénie appliquée. La définition d'une espèce doit contenir la synthèse de ses caractères morphologiques, de sa distribution géographique et de sa généalogie; il est impossible autrement de situer correctement cette entité biologique dans le système, et de s'en servir, sans inévitables erreurs pour les études spéciales ou les généralisations.

N20 – E.G. RACOVITZA (1928, p. VIII): Un matériel plus abondant, et une phylogénie plus détaillée, apporteront certainement des modifications à cette «Histoire des Trechinae» de JEANNEL; elle offre néanmoins un bon exemple de l'efficacité de la méthode qu'il a suivie, par l'aisance avec laquelle dans son exposé se superpose les phénomènes morphologiques et paléogéographiques, par l'aspect cohérent qu'y prennent les succession de ces phénomènes dans le temps et dans l'espace. Ces résultats très satisfaisants pour l'esprit ne peuvent être obtenus par l'étude de la biopaléogéographie des très grands groupes hétérogènes, errement qui se pratique encore hélas! généralement. Seules les histoires détaillées du plus grand nombre possible de lignées homogènes peuvent procurer les matériaux nécessaires aux généralisations biogéographiques fécondes

N21 – E.G. RACOVITZA (1926b, reprinted 1964, p. 529): Domeniul subteran se dezvoltă ca un adevărat muzeu de relicte și înțrbararea se pune de ce acest domeniu e mai favorizat în această privință decât multe din celelalte? Răspunsul ar cere lungi dezvoltări...

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