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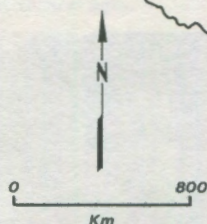
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CHINA

KARST STUDIES IN THE PEOPLE'S REPUBLIC

*Russell W. Graham**
and
*Dennis J. Stanford***



THE SMITHSONIAN INSTITUTION initiated a scientific exchange program with the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) of the People's Republic of China in 1981. The primary thesis of this exchange program has been to investigate the Old World origins of man in the New World. Since northeastern China may have been one of the source areas for human immigrants into the New World during the Pleistocene, Drs. Dennis Stanford (Smithsonian Institution), C. Vance Haynes (University of Arizona), and Russell Graham (Illinois State Museum) visited China. The three scholars from the United States were guests of the IVPP in Beijing (Peking) from July to September, 1982.

This trip gave Graham and Stanford the opportunity to see several caves, as well as to tour the Institute of Karst Research. Since little information about karst research and related speleological activities in China has been available to speleologists in the United States, we believe that it is appropriate to provide a report of our experiences. This report is in no way a definitive statement on karst research in China. It is merely impressions based upon our recent visit.

Much of our information was derived from a tour of the Institute of Karst Research and interviews with the director, Dr. Yuan Daoxian, and his staff. We also benefited from discussions with our Chinese hosts, especially Dr. Hu Chang-kang of the IVPP. Certain information in this report was derived from the following publication: *A Brief Introduction to China's Research in Karst* by Yuan Daoxian, The Institute of Karst Geology, Ministry of Geology, People's Republic of China.†

INSTITUTE OF KARST RESEARCH

The Institute for Karst Research is the central agency for the coordination of all karst-related research in China. Hydrogeologic teams from the Institute are stationed in all provinces of China, but headquarters

†Other recent Chinese publications on karst are noted in *GEO* 10:14—Ed.

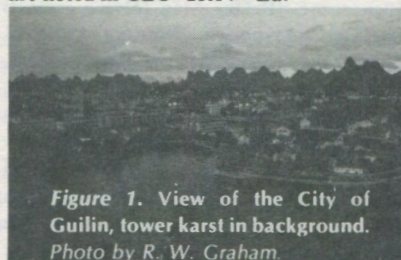


Figure 1. View of the City of Guilin, tower karst in background.
Photo by R. W. Graham.

for the Institute are located in the city of Guilin, Guangxi Province. Guilin is approximately 320 km northeast of Nanjing and 380 km northwest of Guangzhou, the new name for Canton. It seems only fitting that the Institute of Karst Research is nestled within the world-renowned tower karst area of southern China (Fig. 1).

Dr. Yuan Daoxian is the director of the Institute of Karst Research. He has a staff of 240 people, of which 150 are scientists and scientific technicians. At least 60 members of the scientific staff have degrees in the engineering sciences. The following six departments provide the organizational framework for the institute:

- Fundamental theory
- Karst hydrogeology
- Karst engineering
- Prospecting techniques
- Laboratory analyses
- Public information

The department of fundamental theory is concerned with basic theory relating to the various aspects of karst research (*i.e.*, geochemistry, geomorphology, engineering, hydrogeology, etc.). One of the primary theoretical considerations of this department is the mechanisms involved in the formation of karst. This department, like the institute, is not restricted to the study of

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karst in carbonate rocks, but researches karst phenomena associated with any soluble rocks (*i.e.*, evaporites). Theories developed in this department are used to direct the research of the other departments and allied institutes.

The other departments are more concerned with applied studies of karst phenomena than with theoretical issues. The department of karst hydrogeology deals with problems relating to water supply, hydroelectric generation, and water pollution. Reservoirs for water supply have been constructed by damming subterranean streams; for instance, a small dam in a tunnel under the Longwangdang Anticline, Jiangbei County, Szechwan Province, stores 20 million cubic meters of water. Seasonal variation of 10 to 100 times in discharge of subterranean streams is used to generate electricity in South China. The Nandong subterranean stream in the bare karst region of Kaiyuan County, Yunan Province, had a minimum discharge of 0.2 m³/s and a maximum discharge of 20.2 m³/s in 1959. The pollution of water resources by water draining from mining operations is also a major area of investigation for this department.

The department of karst engineering deals with problems encountered during railway construction, development of foundations for buildings, and construction in caves. The principal problem encountered is the cave-in and its prevention or treatment. The karst institute has been involved in the development of land use planning for some cities in karst terrains. Also, many caves have been used as warehouses, manufacturing plants, and air-raid shelters. Five- to eight-story buildings have been constructed in some caves.

Exploration for economic mineral deposits associated with caves and the development of karst is under the jurisdiction of the department of prospecting techniques. Chemical deposits in caves yield economic minerals like phosphorite, niter, gypsum, quartz, and cinnabar. Detrital minerals such as tin, manganese, gold, and quartz are recovered from alluvial deposits in caves. At Gejiu, Yunan Province and He Xian County, Guangxi Province, tin has been mined commercially from caves for many years.

Quantitative and qualitative laboratory analyses for all departments in the karst institute are the responsibility of the department for laboratory analyses. The laboratories are mostly equipped with instruments manufactured in China. A mass spectrometer provides the capabilities for stable isotope analyses; a scintillation counter renders radiocarbon dates; and a microcomputer is used for data storage and analysis.

The function of the department of public information is to coordinate the release of educational information about the research of the institute. This is accomplished by news releases, publications, and symposia. A new museum will be used to exhibit and interpret the scientific work and collections of the institute for the general public and visiting scholars.

Staff members from the Karst Institute have participated in international scientific exchanges with other countries, such as France, Yugoslavia, Australia, and the United States. These exchange programs provide foreign scholars with the opportunities to study karst problems in China, but they also permit Chinese scholars to make scientific observations and conduct research in other karst areas in the World. These exchange programs should facilitate the free exchange of information and ideas amongst karst scientists throughout the World.

PALEONTOLOGY AND ARCHEOLOGY OF CAVES

The caves of China have a tremendous potential for the study of prehistoric Man and his environments. Man has utilized caves in China since at least the middle Pleistocene (≈ 500 ka). Historic data is also preserved in caves in the form of religious carvings and inscriptions. Chinese scientists have been studying cave sites for a long time, but with the advent of new methodologies and technologies, we can look forward to an explosion of information on the archeology and paleontology of caves in China.

The Institute of Karst Research is not actively involved in archeological and paleontological research, but staff members do collect artifacts and fossils during the process of mapping caves for other purposes. Scientists from the Karst Institute also work with colleagues from the Institute of Vertebrate Paleontology and Paleoanthropology and the Institute of Archeology in the analysis of archeological and paleontological sites. The Karst Institute does plan to add a vertebrate paleontologist to its staff in the near future.

One of the most famous archeological/paleontological sites in China is the middle Pleistocene "Peking Man (*Homo erectus*) Site" at Choukoutien. There are at least 23 known fossil localities at Choukoutien, ranging in age from Pliocene to late Pleistocene. The Lower Cave at Choukoutien Locality 1 (Peking Man Site) provided the first record for *Homo erectus* in China and the first evidence for the association of man with fire. The original excavations at the Lower Cave site were conducted in the 1920's and 1930's. Fossils of *Homo erectus* recovered during these excavations were lost

during World War II; events surrounding this loss have provided one of the most intriguing mysteries in paleoanthropology. Casts of the original specimens were preserved in museums in China as well as in those of other countries. In order to recover additional specimens, as well as to learn more about this important site, the IVPP has recently commenced new excavations at the Peking Man Site (Fig. 2).

During our visit, Graham had the opportunity to study Pleistocene vertebrate collections at the IVPP with Dr. Hu Chang-Kang. Examination of vertebrate fossils from the Peking Man Site revealed new information about the accumulation of bones within this cave. Discovery of fossil owl pellets with rodent bones provides evidence that some of the rodents were derived from the predatory habits of owls rather than exclusively from human exploitation of a small mammal source.



Figure 2. New archaeological/paleontological excavations at the "Peking Man Site," the Lower Cave of Locality 1 at Choukoutien. Photo by R. W. Graham.

Choukoutien is also the locality of Upper Cave, which has yielded human bones (*Homo sapiens*) and material cultural remains (artifacts) of the Paleolithic culture. Upper Cave, like Lower Cave, contained the remains of a diverse Pleistocene vertebrate fauna, primarily mammals. Sediments and associated materials from Upper Cave have been radiocarbon dated at approximately 18 ka. Some sediments still remain at the back of Upper Cave, but no new excavations are in progress. The Peking Man Site and Upper Cave are exhibited and interpreted in an excellent museum at Choukoutien.

We also had the opportunity to visit the Zengpi Cave Site, located near the Guilin airport. Zengpi Cave is a rockshelter and, like many archeological sites in China, it contains an *in situ* exhibit of the excavation and an attached museum building. The rockshelter is not enclosed, and the humid

environment at Zengpi has nurtured an abundant growth of algae on the exhibited excavations. It was therefore difficult to observe the stratigraphy of the rockshelter. If radiocarbon dates are accurate, and if the stratigraphic context is certain, then pottery shards from the lower levels (≈ 10 ka) may be some of the oldest pottery in the World. It may take new work at the site to confirm these facts.

Archeologists and paleontologists are actively excavating and analyzing prehistoric cave sites throughout China. Many of these cave sites date to the middle Pleistocene, in direct contrast to the paucity of cave sites of this age in the United States. Middle Pleistocene cave sites in China frequently do not resemble caves, but are usually cave fills left as remnants on topographic high points. New work in China may provide a better understanding of the processes involved in the accumulation and natural preservation of cave sites of various ages.

SPELEOLOGY AND COMMERCIAL CAVES

Thousands of caves have been recorded or mapped in China during the last 20 years. Cave exploration and mapping in China is considered a business and not a sport. Therefore, most cave surveys are conducted by professionals, not laymen. Many caves

have been discovered during hydrogeological and engineering investigations. Mineral exploration in karst terrains has also increased the number of known caves. In addition, archeological and paleontological surveys have contributed to the speleological data base in China. To our knowledge, there has been no attempt to compile a systematic index to the caves of China.

Many commercial caves have been opened to the public. Usually, there is a slight admission fee, and tours are lead by trained guides. The commercial caves of China appear to be very popular with the general public, as indicated by the number of tourists that visit them. Ya Ling Cave, approximately 90 km west of Hangzhou, is fairly typical of most commercial caves that we visited in China. The commercial entrance and exit to Ya Ling Cave have been created by blasting openings into the cave wall and then constructing stone gateways (Fig. 3). The natural entrance of Ya Ling Cave has been closed, but in other commercial caves the natural entrance is still used. Extensive stone walkways and stairs have been constructed along the tour route; side passages that exit from the main chamber are not open to the public.

There are many spectacular speleothems in the cave, and it is quite comparable to many of the commercial caves in the United

States. Speleothems are illuminated by electric lamps of various colors, and the lights are turned off after the tours to guard against the growth of algae. Discussions by the tour leaders appear to focus on the imaginary shapes of the speleothems. Lions, dragons, and pagodas are frequent patterns pointed out by the tour guides.

Karst is an exceptional natural resource for China. It is not only of economic and utilitarian importance, but karst provides aesthetic scenery which adorns many of the landscapes of Chinese art. The further development of karst research in China will undoubtedly contribute to greater insights into the phenomena of this field of science.



Figure 3. Commercial entrance to Ya Ling Cave, Zhejiang Province. Photo by R. W. Graham.

Romero, Aldemaro (1983)—Introgressive Hybridization in the *Astyanax fasciatus* (Pisces: Characidae) Population at La Cueva Chica: *The NSS Bulletin* 45: 81-85

INTROGRESSIVE HYBRIDIZATION IN THE *ASTYANAX FASCIATUS* (PISCES: CHARACIDAE) POPULATION AT LA CUEVA CHICA*

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INTRODUCTION

Hybridization in Fishes

STUDIES OF HYBRIDIZATION have contributed substantially to our understanding of evolutionary mechanisms. Natural and artificial fish hybrids, including intergeneric, have been reported for more than 50 families, mostly freshwater (Hubbs, 1955; Schwartz, 1981). This extensive hybridization apparently is due to the fact that external fertilization is common in these vertebrates (Bianco, 1982; Daget and Moreau, 1981; Hubbs, 1955; Whitmore, 1983).

A review of the literature reveals several generalizations frequently made concerning fish hybrids:

1) The characteristics of hybrids are phenotypically intermediate when com-

SUMMARY

Results of morphological studies on a population of the characid *Astyanax fasciatus* at La Cueva Chica, San Luis de Potosí, Mexico, suggest that the current population is the result of introgression between a blind depigmented population at that cave locality and eyed pigmented fish from a nearby surface population. A synthesis of morphological data with previous breeding, electrophoretic, karyotypic, and behavioral information is made in order to assess how much and in what respects the cave population resembles other natural populations of hybrid fish. Current ideas on the relationship between genetic and phenotypic differentiation of cave populations from their surface ancestor are also discussed.

pared with those of the parents, although the degree of intermediacy has rarely been specified (Bianco, 1982; Hubbs, 1955; Mayden and Burr, 1980; Pethon, 1974);

2) Among hybrids, the sex ratio is skewed toward males (often about 4:1) (Bianco, 1982; Daget and Moreau, 1981; Hubbs, 1955; Pinto, 1982);

3) Hybridization is more likely to occur

when parental population sizes are substantially unequal (Bianco, 1982; Busack and Gall, 1981; Butcher, 1980; Cashner and Jenkins, 1982; Daget and Moreau, 1981; Rakocinski, 1980; Wallace and Ramsey, 1982; Whitmore, 1983);

4) Greater survival of hybrids occurs when the parental species and/or populations are closely related (Cashner and

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Jenkins, 1982; Dauble and Buschbom, 1981; Rakocinski, 1980; Wallis and Beardmore, 1980; Whitmore, 1983);

5) Hybrids are more successful when the environment of the contact zone between the parental populations is intermediate (Hubbs, 1955; Moore, 1977);

6) Hybridization is more likely to take place when overlap occurs both in spawning space and in spawning periods (Bianco, 1982; Dauble and Buschbom, 1981; Hubbs, 1955; Pethon, 1974, 1978, 1981; Rakocinski, 1980; Wallace and Ramsey, 1982).

Hybridization in Cave Animals

Because most related cave species are allopatric (geographically separated), hybrids among cave organisms or between cave and surface populations are rare (Allegrucci, *et al.*, 1982). Although hybridization between surface and cave fish populations has been suspected in at least three cases (*Caecorhamdia urichi* [Endler, 1982, pers. comm.]; *Poecilia spheonops* [Gordon and Rosen, 1962; Walters and Walters, 1965]; and *Lucigobius* spp. [Tomiya, 1936]), the only well-known example is that of the characid *Astyanax fasciatus mexicanus*. This fish can be found as an eyed, pigmented, surface form and as a blind, depigmented, cave form; the latter was initially described by Hubbs and Innes (1936) as a new genus and species, *Anoptichthys jordani*. These forms interbreed under both natural and experimental conditions to produce fertile F₁ hybrids that are phenotypically intermediate and F₂ individuals (after F₁ × F₁) which range from an almost completely blind and depigmented form to an essentially eyed and pigmented one (Peters and Peters, 1973; Sadoglu, 1957). Electrophoretic and karyotypic

studies also indicate that blind cave and eyed surface forms are conspecific (Avisé and Selander, 1972; Kirby, *et al.*, 1977). These forms differ not only in morphology but, also, in behavior: contrary to the behavior of the eyed surface form, the blind cave one does not school, shows no circadian activity rhythm, and is not aggressive (Boucquoy, *et al.*, 1965; Breder, 1942; Breder and Gresser, 1941; Erckens and Weber, 1976). These behavioral differences can be seen among other cave fishes and their surface ancestors (Thinès, 1969).

Despite conspecificity of the cave and surface forms, their strong morphological and behavioral divergences and the phenotypic intermediacy of progenies resulting from crosses between these forms has led all authors concerned to refer to these progenies as hybrids (Breder, 1943; Peters and Peters, 1973; Sadoglu, 1957; Wilkens, 1969).

Hybridization between the surface and the cave populations has been reported for 9 of the approximately 30 caves supporting subterranean populations of *A. fasciatus* in the San Luis de Potosí area of east-central Mexico (Mitchell, *et al.*, 1977).

The first indication that introgression (*i.e.*, stabilization of backcross types) between surface and cave forms was taking place was presented by Breder (1943). He compared specimens of *A. fasciatus* from La Cueva Chica collected from 1936 to 1942, and, based on changes in phenotypic ratios (eyes and pigmentation), he concluded that a recent invasion of eyed and pigmented fish through a subterranean connection with surface waters was changing the genetic structure of the cave population. Further studies support the cave/surface connection hypothesis (Mitchell, *et al.*, 1977).

The aim of this paper is: a) to give further evidence that introgression between cave and surface populations of *A. fasciatus* has occurred at La Cueva Chica, and that it has occurred rapidly in evolutionary time; b) to compare the characteristics observed in this introgressed population with those commonly attributed to hybrid fishes; and c) to discuss the implications of introgression regarding our present knowledge of the evolutionary biology of cave organisms.

MATERIAL AND METHODS

One hundred individuals of *A. fasciatus* were collected during May 1983 in pool II (*sensu* Breder, 1942) of La Cueva Chica. Pool II was chosen for this study because: a) almost all previous information about the morphology of this cave population comes from material collected at that pool (Álvarez, 1946; Breder, 1942, 1943; Hubbs and Innes, 1936); b) this population is comparatively large for that of a cave organism, (Mitchell, *et al.*, 1977); and c) this pool is the most remote of all from the surface, eyed *A. fasciatus* and is isolated from the rest of the pools during the dry season, restricting gene flow.

Norelco red-infrared 125-watt lamps were used for collecting in caves, since preliminary studies had shown that these fish do not react to such light (Romero, *in litt.* a). All fish were randomly caught by netting, and their standard lengths were immediately measured using calipers read to the nearest 0.1 mm. Sex was determined using sexually dimorphic characters described by Álvarez (1946), Kosswig (1964), and Wiley and Collette (1970). To make comparisons with data previously published, I used Breder's (1943) qualitative criteria for eye condition and pigmentation. Immature individuals (< 35

EYE CONDITION (% of the population)					
Year	N	Sunken			
		Blind	Covered	Uncovered	"Normal"
1936	90?*	100	0	0	0
1939	90?*	100	0	0	0
1940	38	85	6	0	9
1942	28	61	4	21	14
1983	100	4	83	9	4

PIGMENTATION (% of the population)						
Year	N	Intermediate				
		None	Little	Moderate	Considerable	Full
1936	90?*	100	0	0	0	0
1939	90?*	100	0	0	0	0
1940	38	90	2	6	2	0
1942	28	53	11	11	0	25
1983	100	0	28	31	37	4

* Estimate drawn from Breder's (1943) comment, "something less than 100."

EYE					
Pigmentation	Normal	Sunken			
		Reduced but external	retina visible	retina not visible	Absent
Full	0	0	0	4	0
Considerable	0	5	18	10	4
Moderate	2	2	18	9	0
Little	2	2	15	9	0
None	0	0	0	0	0

Table 2. (above) Crosstable of distribution of features in the individuals collected in 1983 (N = 100).

Table 1. (left) Phenotypic conditions in the fishes from La Cueva Chica; 1936 to 1942 data from Breder (1943); 1983 data, this paper.

mm) were impossible to sex and were not included in the 100 individuals used for the present study. Fifty four fish were retained for behavioral studies; the rest were returned to the pool.

RESULTS

My results and those of Breder (1943) are presented in Table 1; they suggest that introgression has occurred since 1940. Table 2 shows that none of the 100 individuals collected in 1983 has the morphological attributes of the parental populations (*i.e.*, either totally blind and depigmented or displaying full eyes and pigmentation simultaneously). Table 3 gives the sex ratio of the individuals collected in 1983, plus the sex ratios obtained in previous studies by other authors at this and other localities for cave and surface forms. The hybrid population at La Cueva Chica contains fewer males than females, as is the case for most populations of *A. fasciatus*.

Table 3. Sex ratios for different cave and surface populations of *A. fasciatus*. Data from Mitchell, *et al.* (1977) unless otherwise indicated.

Cave Populations	(male:female)
Cueva Chica**	42:58
Cueva Chica*	3:6
Los Sabinos*	5:5
Pachon	10:12
Pachon*	6:9
Montecillos	5:4
Arroyo	8:7
Curva	6:7
Tigre	9:15
Jos	6:18
Palma seca	6:17
Tinaja	4:20
TOTAL	110:178
Surface Populations	
Tamesi	12:13
Arroyo	11:10
Panuco	8:15
TOTAL	31:38

*After Álvarez, 1946.

**This paper.

DISCUSSION

The identification of F_2 and/or backcross individuals is the basis for assessing introgressive hybridization (Whitmore, 1983). One of the reasons why introgression has been rarely reported in fishes is the difficulty in identifying these hybrid classes (Rakocinski, 1980). However, both the clear-cut morphological differences between the cave and surface forms of *A. fasciatus* and the detailed descriptions of F_2 and backcross generations from breeding studies on this

fish allow hybrid identification and, consequently, introgression assessment. The data in Table 2 show that: a) no parental forms were found in the current hybrid population; and b) most (if not all) individuals collected correspond to the descriptions of the F_2 and backcrossed individuals obtained in the laboratory. These data strongly indicate that the *A. fasciatus* population at La Cueva Chica is the result of introgression.

The data in Table 1 suggest that introgression took place in about 40 years (or less). Lack of hybrids and of eyed, pigmented individuals in the first two collections (1936 and 1939) and the absence of parental forms in the last one (1983) support such a contention. Unfortunately, there is little reliable information on the rate of introgression in natural fish populations. The introgression described here could have taken place long before the last collection (1983). *A. fasciatus* reaches sexual maturity at the age of six months, so it could produce up to two generations per year. Recent data on natural hybrid cichlids on Madagascar, for example, show that introgression can take place in less than 20 years (Daget and Moreau, 1981).

Generalizations on Fish Hybrids

1) *Intermediacy of hybrids.* Experimental studies have shown that hybrids between the blind form from La Cueva Chica and the eyed form from nearby surface populations are not precisely intermediate in their morphological and behavioral features. Wilkens (1969, 1970), for example, showed that eye size and the number of melanophores and their melanin content is slightly skewed to the surface population characteristics in both F_1 and F_2 generations. Boucquoy, *et al.*, (1965) found that F_1 hybrids display a rhythmic pattern of activity similar to that of the surface form, while the F_2 (after test-cross) shows the same arrhythmic time-regulation of activity as does the cave form. Schemmel (1980) showed that the angle of erection for bottom-feeding in F_1 and F_2 generations is closer to that of the surface form. Romero (*in litt.*, a), indicated that the level of photoresponses among natural hybrids is closer to that of surface populations than to that of blind, depigmented *A. fasciatus* from both natural and artificially bred cave populations.

Lack of exact intermediacy for various characteristics in the F_1 and F_2 hybrids of this characid is consistent with recent results of careful studies which suggest that other fish hybrids rarely are exactly intermediate in their characteristics, when compared with their parental populations (Bao and Kallman, 1982; Kerby, 1979; May, *et al.*, 1980; Neff and Smith, 1979; Ross and Cavender, 1981; Sutton, *et al.*, 1981; Wallace and Ramsey, 1982).

2) *Skewed sex ratio.* Table 3 does not provide support for the contention that hybrid populations of fish necessarily display sex ratios skewed toward males. Previous data on sex ratios for other surface and cave populations of *A. fasciatus* (including data for the original blind population of La Cueva Chica) suggest that the sex ratio in most populations, including the current population at La Cueva Chica, is skewed toward females (usually 2:3). A binomial test (95% probability) demonstrated no significant difference between surface and cave populations (excluding La Cueva Chica, 1983 data) and between either of these two sets of data and the 1983 La Cueva Chica data. These results indicate that neither adaptation to the cave environment nor hybridization between surface and cave populations changes the observed sex ratios in these populations.

3) *Disproportionate size of parental populations.* Given the nature of the connection between the cave and surface waters (subterranean and physically impossible to explore), it is difficult to ascertain how frequently and in what numbers surface individuals may invade. The level of introgression may fluctuate through time.

4) *Close relationship of parental species.* Electrophoretic (Avisé and Selander, 1972), karyotypic (Kirby, *et al.*, 1977), and morphologic studies (Hubbs and Innes, 1936; Álvarez, 1946) show that the La Cueva Chica population and the nearby surface population are genetically very similar, and that they differ morphologically only in those characters related to cave-dwelling. This is consistent with the view that close relationship can be considered to be a facilitating factor for rapid introgression.

It has been proposed that there is more genetic than morphological differentiation between related cave and surface species and/or troglitic populations (Culver, 1982 p.95). This is largely based on Barr's (1968) contention that cave adaptation involves considerable reorganization of the genotype, which is, in turn, an application of Mayr's (1970) genetic revolution of the founder principle to the evolution of cave organisms.

5) *Hybrid success and intermediacy of the environment at the contact zone.* Although introgression has taken place in the native environment of one of the parental populations, the intermediate-environment hypothesis cannot be rejected, because: a) eyed, pigmented populations of *A. fasciatus* can be found in many caves not occupied by blind forms in the San Luis de Potosí area (Mitchell, *et al.*, 1977; Romero, *in litt.* b), in the cenotes of Yucatán (Hubbs, 1938), and in a cave in northern Mexico

(Reddell, 1982), and as facultative caver-nicoles in Costa Rica (Romero, 1984a, b); and b) the high adaptability of this fish allows it to survive in many different kinds of environments (Bussing, 1976; López, 1978). In consequence, although La Cueva Chica does not represent an 'intermediate' environment for facilitating introgression, it is clear that caves are not unusual habitats for eyed, pigmented *A. fasciatus*. Mitchell, *et al.*, (1977), also suggested that hybridiza-tion might be favored by availability of abundant food resources.

6) *Overlap in reduced spawning space and spawning periods.* The physically constricted habitat in La Cueva Chica, whose waters are subdivided into several pools (especially during the dry season), facilitates contact among the individuals occupying the pools (Breder, 1942). Although there is little information on spawning behavior of these fish under natural conditions, no strong dif-ferences have been found in laboratory studies other than those related to the lack of vision in the cave form (Breder and Rosen, 1966). As for all characids, fertilization is external in *A. fasciatus*, and crosses between the cave and the surface forms are readily obtained under experimental conditions (Sadoglu, 1979). Even hybrids between cave

A. fasciatus and two other characids (*Ctenobrycon spilurus* and *Moenkhausia oligolepis*) have been reported (Kauffeld, 1954), suggesting that cave *A. fasciatus* display the spawning behavior common to this fish family. The reduced space in La Cueva Chica facilitates close contact be-tween the cave and the surface forms, and, given the apparent lack of any reproductive isolating mechanism between these forms, there is a high probability of hybridization under these conditions. This is further sup-ported by the fact that eight other hybrid cave populations of this fish have been described (Mitchell, *et al.*, 1977).

However, the introgression here de-scribed, as well as the breeding, electro-phoretic, karyotypic, and behavioral studies mentioned above for the *A. fasciatus* population of La Cueva Chica, does not support such a generalization. In fact, all seem to indicate that typical cave features (e.g., blindness, depigmentation, larger number of taste buds, and behavioral modi-fications) can appear before any major dif-ferences in electrophoretic, karyotypic, or reproductive barriers arise between the cave and surface populations. It should not be forgotten that comparative morphological studies of cave and surface populations of

this fish species have shown that no signifi-cant meristic or morphometric differences exist between the forms, except for the cave-dwelling attributes (Álvarez, 1946; Peters and Peters, 1973; Wilkens, 1969). Similar conclusions have been reached when related but ecologically distinct fish species are studied from a genetic viewpoint (Avise and Selander, 1972; Avise, *et al.*, 1975; Bell, *et al.*, 1982). More extensive comparisons among obligatory cave organisms, their sur-face ancestors, and their hybrids will yield additional information about the correla-tion between phenotypic and genetic changes during the evolution of cave adapta-tions.

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TERRESTRIAL CAVERNICOLOUS

THE SUBTERRANEAN DOMAIN consists of four main terrestrial habitats (*i.e.*, soil, networks of microspaces between rock fragments, networks of small fissures, and caves). Of these, it is the cavernicolous habitat which has been the subject of most faunistic studies in Romania. Recent studies have also been concerned with both the edaphic (soil) fauna and with the fauna inhabiting the network of microspaces existing between rock fragments within the layer developed between the edaphic habitat and calcareous or noncalcareous bedrock.

An endemic (native) edaphobitic fauna was discovered in the soil layer containing roots of plants by washing the soil (using the Normand method). This fauna consists primarily of Coleoptera, Isopoda, Diplopoda, Collembola, and Acarina.

Investigations with Barber traps buried in the network of microspaces resulted in the discovery of new endemic taxa, most of which belonged to the Coleoptera (Juberthie, *et al.*, 1981). It is significant that almost all of the strictly subterranean taxa discovered so far in the network of microspaces are restricted to this habitat and have not also been found in caves, as happens in the Pyrenees. In the Carpathian Mountains, the mode of colonization of microspaces appears to be specific to the entire region and is determined by paleoclimatic, hydrologic, and tectonic factors.

According to the new classification of the subterranean domain, the caves and the fissure network, both developed within the bedrock, belong to the deep subterranean, while the soil and the microspace network are classified as the shallow subterranean. The caves, the fissure network, the microspace network, and the soil (particularly the first three) are connected through multiple interrelationships within a unique func-

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SUMMARY

Romania is divided into 5 biospeleological provinces based upon the present distribution of the endemic troglobitic and edaphobitic fauna. Ancestors of this fauna migrated into Romania primarily from the north Aegean region probably at various times during the Tertiary Age. Four paleogeographic barriers—the couloirs of the Danube, Timis-Cerna, Olt, and Mures Rivers—acted to constrain the migration routes and settlement areas, thus producing distinct patterns in the distribution of the cave fauna in the Carpathians. The present day terrestrial troglobitic fauna of Romania consists of 208 known species and subspecies, including 126 Coleoptera, 23 Araneae, 20 Diplopoda, 12 Collembola, 8 Pseudoscorpiones, and 6 Isopoda. More than 97 percent of these troglobitic taxa are endemic, and more than 80 percent are paleotroglobitic.

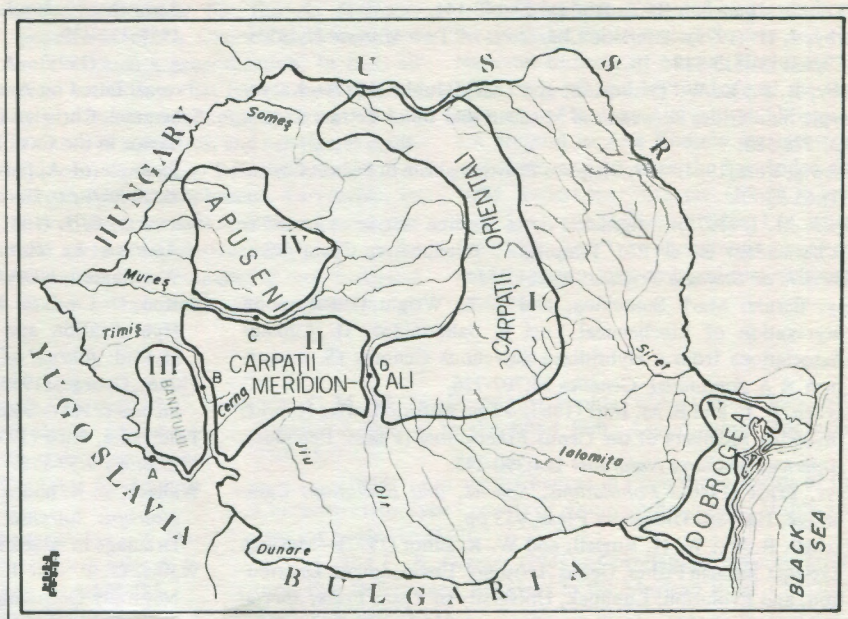


Figure 1. Biospeleological provinces I to V and the main paleogeographical Miocene barriers (interrupted line). Province I: eastern and southern Carpathians up to the Olt River; province II: southern Carpathians between the Olt River and the Timis-Cerna Couloir; province III: western Carpathians south of the Mures River (Banat Mountains); province IV: western Carpathians north of the Mures River (Apuseni Mountains); province V: Dobrogea. (a) Dunare Couloir; (b) Timis-Cerna Couloir; (c) Mures Couloir; (d) Olt Couloir.

tional system. Each of these habitats is characterized by a specific fauna (detectable through abundance criteria) as well as by a fauna also common to the other media.

In this paper, we briefly discuss the distribution of the terrestrial cavernicolous fauna in Romanian caves, with special emphasis on troglobitic species. As for the other ecological categories of cave-dwelling fauna, only a few references will be made to some of the main troglophile, guanophile, or subtroglophile (animals that use caves seasonally for aestivation or hibernation) elements in the Carpathians and in Dobrogea.

THE ORIGIN AND DISTRIBUTION OF THE TROGLOBITIC FAUNA

Figure 1, a map of Romania's biospeleological provinces, defines the province of the eastern and southern Carpathians up to the Olt River (I), the province of the southern Carpathians between the Olt River and the Timis-Cerna Couloir (II), the province of the western Carpathians south of the Mures River (Banat Mountains) (III), the province of the western Carpathians north of the Mures River (Apuseni Mountains) (IV), and the province of Dobrogea (V). These

FAUNA OF ROMANIA

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faunistic regions were first defined and published by Decu in 1967. The five biogeographical provinces were delimited according to the distribution of presumed old endemic troglotic species, 61% of which are coleopterans (provinces II to V) and according to edaphobitic endemisms (province I). These five provinces presumably correspond to paleogeographical provinces of Tertiary isolation. Consequently, studies of

these areas into Romanian territory at various periods during the Tertiary Age. Romania, including the Apuseni Mountains region, is situated at the northern limit of the range of the cavernicolous fauna in general.

The migration of the ancestors of the troglotic and edaphobitic fauna from the south or from the north was dependent on the presence of wooded hills or low mountains (*i.e.*, areas ranging between 200 and

edaphobitic endemisms (Decu, 1967; Decu and Negrea, 1969).

In the eastern and southern Carpathians up to the Olt River (Province I), five troglotic species from the genera *Nesticus* and *Lepthyphantes* (Araneae), and *Romanosoma* (Diplopoda) have been found to date. The ancestors of the troglitic populations of edaphobitic beetles, probably belonging to *Trechus*, *Duvalius* (*Duvalidius*) *procerus* group, and *Duvaliopsis*, migrated from the Bohemian Massif and spread along the Carpathians up to the Olt River at the beginning of the Tertiary Age (probably in the Tortonian). An exception to this is *Duvalius* (*Duvalidius*) *delamarei* Decu, a neotroglitic species that crossed the Olt River and populated caves in the Comarnic Gorges (Stogu Massif).

From the caves of the southern Carpathians between the Olt River and the Timiș-Cerna Couloir (Province II), the only troglitic species of Bohemian origin are the *Duvalius* (*Duvalidius*) *merkli* group, which probably spread into the Carpathians towards the end of the Oligocene and the beginning of the Miocene, through the Tisia calcareous massif (Jeannel, 1931; Decu, 1967). All other cavernicolous forms are probably of Dinarian or east Balkan origin: *Duvalius* (*Duvaliotes*) *budai* group (Coleoptera-Trechinae), and *Sophruchaeta*, *Tismanella*, and *Closania* (Coleoptera-Bathysciinae); *Trachysphaera*, *Trichopolydesmus*, *Dacosoma*, *Typhloiulus*, and *Anthroleucosoma* (Diplopoda); *Neobisium* (Pseudoscorpiones); *Centromerus* and *Troglohyphantes* (Araneae); and *Trichoniscus* and *Haplophthalmus* (Isopoda-Trichoniscidae).

The north-Aegean origin of these taxa, as well as of other taxa from the other remaining biogeographical provinces, is indicated by their affinities and distribution in the Balkan region, particularly in Yugoslavia and Bulgaria. A number of taxa from Balkanian caves, *e.g.* *Duvalius* (*Duvaliotes*) *pilifer* group, and *Rhodopiola* (Coleoptera); *Trachysphaera orghidani* n. ssp. (Tabacaru, in press, a), *Bulgarosoma bureschi* Verhoeff, *B. crucis* Strasser, and *Verhoeffodesmus* (Myriopoda-Diplopoda); *Trichoniscus tenebrarum* Verhoeff, *T. bureschi* Verhoeff, and *Troglocyphoniscus* (Isopoda) are phylogenetically very near to cavernicolous species from Romania, *e.g.* *Duvalius*

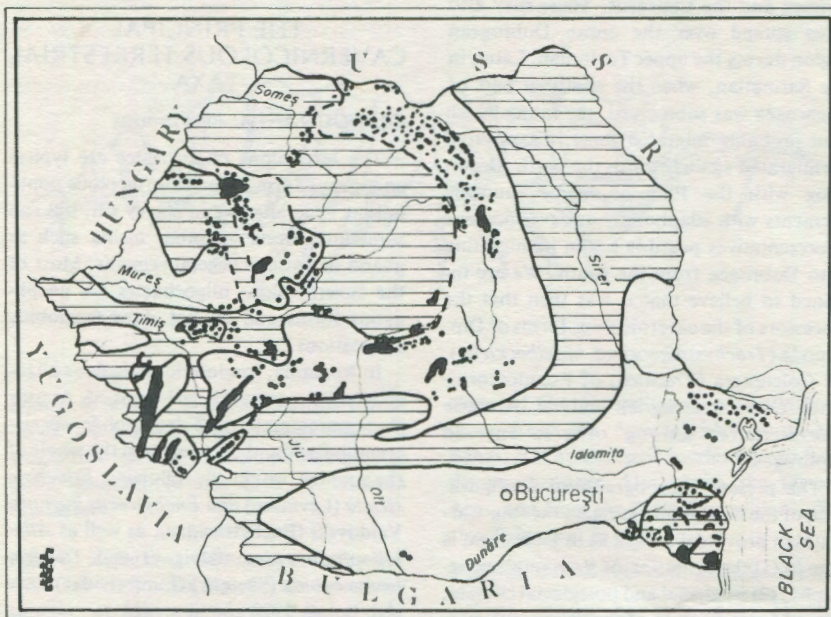


Figure 2. Paleogeographical map of Romania in the upper Tortonian (Miocene). The dark areas represent the present karstic zones, the hatched areas represent the Tortonian Sea.

the troglitic (and edaphobitic) elements have proven to be remarkably important for interpreting Romania's paleogeography. These elements provide evidence for the existence of the main Miocene geographical barriers and (implicitly) for the constraining effects on faunal distribution of many of the antecedent transverse valleys. Moreover, owing to the long time span that has elapsed since their arrival, these troglites represent real biogeographical indicators (Decu and Negrea, 1969).

The ancestors of the Romanian troglitic and edaphobitic fauna were probably derived from faunistic elements established in the northern Aegean region (more precisely, in the Dinarian zone) and on the Bohemian Massif at the beginning of the Paleogene. The ancestors migrated from

1000 m elevation). This migration was not a continuous process; it took place during various geological periods, depending on the paleogeographical situation of the country and on the evolutionary potential of the species.

During the advance of this fauna into the southern and western Carpathians, four paleogeographical barriers played very important roles. These barriers were marine channels which, at that time, filled the couloirs of the (a) Dunăre, (b) Timiș-Cerna, (c) Mureș and (d) Olt where these rivers cut through the Carpathians (Fig. 1). These barrier-basins (some of them beginning with the Eocene, others in the Miocene) isolated four biogeographical provinces (I to IV) evidenced today by the distribution of the fauna showing characteristic troglitic and

(*Duvaliotes*) *budai* and *redtenbacheri* groups, and *Banatiola* (Coleoptera); *Trachysphaera orghidani orghidani* (Tabacaru), *Bulgarosoma ocellatum* Tabacaru, and *Trichopolydesmus* (Diplopoda); *Trichoniscus inferus* Verhoeff and *Haplophthalmus tismanicus* Tabacaru (Isopoda).

The faunistic elements of north-Aegean origin (beetles, spiders, millipedes, centipedes, and isopods) probably colonized the southern Carpathians (Province II) by successive migrations beginning in the Miocene. During these migrations, Romania possessed a tropical-to-subtropical climate that allowed an easy and relatively homogeneous distribution of these elements up to the Olt River. Most of the troglobitic elements found in the area between the Olt River and the Timis-Cerna Couloir are distributed between the Cerna and Jiu rivers (Fig. 1). Beyond the Jiu Valley (which was another important paleogeographical barrier), they occur in smaller numbers—the most eastern troglobitic species being found in caves of the Stogu Vinturarița Massif. The present distribution and composition of the troglobitic elements in this part of the Carpathians parallels the variations registered from the west to the east in epigeal fauna and flora.

In the Banat Mountains (Province III), the troglobitic elements [*Trichopolydesmus* (*Banatodesmus*) *jeanneli* Tabacaru, *Bulgarosoma ocellatum*, and *Lithobius dacicus* Matic (Myriopoda), *Banatiola vandeli* Decu and *Duvalius milleri* (Frivaldszky) (Coleoptera)], are also of probable north-Aegean origin. Their ancestors apparently entered this region in the Miocene, but probably migrated independently of the troglobitic elements from the southern Carpathians. The Miocene (Tortonian) Sea (Fig. 2) that transformed the western and southern Carpathians into an archipelago isolated, through its various barriers, the areas colonized by the ancestors of the troglobitic (and edaphobitic) forms that presumably had recently immigrated from the south.

The Apuseni Mountains (Province IV) are populated by troglobitic elements: *Neobisium* (Pseudoscorpiones); *Nesticus* (Araneae); *Biharoniscus* (Isopoda); *Trachysphaera* and *Typhloiulus* (Diplopoda); *Pholeuon*, *Drimeotus*, and *Duvalius* (*Duvaliotes*) *redtenbacheri* group (Coleoptera); all of north-Aegean origin. However, the ancestors of at least the Coleoptera in the Apuseni Mountains did not migrate through Banat or through the western and southern Carpathians, but through the Tisia region (a massif of Triassic limestone whose sinking, beginning with the Miocene, gave birth to the Panonian Plain). Paleogeographic barriers deflected the migrating fauna away from the Banat region. Similarly,

paleogeographic barriers also kept the Bohemian (northern) elements away from the Apuseni Mountains when they immigrated into the southern Carpathians (Jeannel, 1931; Decu, 1967; Decu and Negrea, 1969). The spread of the ancestors of the troglobitic fauna into the Apuseni Mountains appears to have taken place towards the end of the Oligocene, because at the beginning of the Miocene, terrestrial communication between these mountains and the south terminated with the formation of the Panonian Sea and of the Mureș Couloir.

Troglobitic elements in Dobrogea (Province V) probably also immigrated from the south. From the upper Eocene to the upper Tortonian, Aegean faunistic elements migrated towards the northeast up to the Crimea and the Caucasus. These may also have spread over the entire Dobrogean region during the upper Tortonian. Later, in the Sarmatian, when the southern part of Dobrogea was submerged, the fauna which had probably migrated there, disappeared or migrated again towards the north. Beginning with the Pliocene, some faunistic elements with edaphobitic or cavernicolous representatives possibly began immigrating into Dobrogea from the south. We are inclined to believe that it was then that the ancestors of the cavernicolous forms of Diplopoda (*Trachysphaera* and *Apfelbeckiella*), of Coleoptera (*Trechus*), of Pseudoscorpiones (*Acanthocreagris*) and of Araneae (*Lessertiella*) among others, entered Dobrogea.

The present zoogeographical configuration of the troglobitic fauna, in the four Carpathian provinces as well as in Dobrogea, is due to (1) the evolution of Romania's geography, (2) its glacial and postglacial climate, (3) the karstification of the calcareous massifs (which deprives them of surface water, vegetation, and soil), (4) reduction in dispersal ability among earlier immigrants, as they became more cave adapted and (5) biotic interactions (such as competitive exclusion, prey and host species abundance, and food resources). A steppe climate became dominant in Dobrogea about 3,000 years ago which had important repercussions on the zoogeography of the hygrophilous fauna there.

THE PRINCIPAL CAVERNICOLOUS AQUATIC TAXA

Aquatic species are poorly represented in the caves of Romania and as such are here only briefly mentioned. Among the more interesting troglobitic species recorded so far, we would mention: *Dendrocoelum botosaneanui* del Papa and *D. tismanae* Codreanu and Balcesco (Tricladida); *Haplotaxis bur-*

eschi (Michaelson) (Oligochaeta); *Troglochaetus beranecki* Delachaux (Polychaeta); *Paladilhia transsylvanica* (Rotarides) and *P. leruthi* Boettger (Gastropoda); *Kovalevskiiella phreatica* (Danielopol) (Ostracoda); *Megacyclops reductus propinquus* Pleșa, *Speocyclops troglodytes* Chappuis, *Elaphoidella phreatica* Chappuis, and *Spelaecamptus spelaus* Chappuis (Copepoda); *Parabathynella motasi* Dancău and Șerban and *Bathynella paranatans* Șerban (Bathynellacea); *Microcerberus plesai* Chappuis and Delamare (Isopoda); *Niphargus carpathicus variabilis* Dobrea, Manolache, and Puscariu, *N. andropus* Schellenberg, and *N. longicaudatus maximus* Karaman (Amphipoda).

THE PRINCIPAL CAVERNICOLOUS TERRESTRIAL TAXA

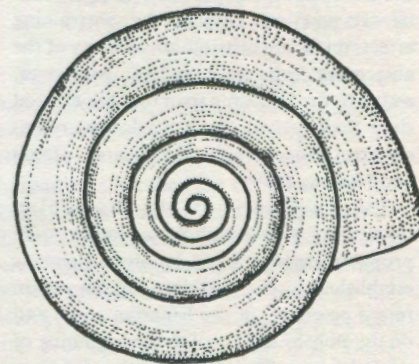
OLIGOCHAETA: Earthworms

The terricolous oligochaetes are typical endogenous forms. The cavernicolous populations generally live in clayey silt, but can sometimes occur in other media such as guano or various vegetal remains. Most of the cavernicolous oligochaetes are geophagous forms and do not show troglobitic adaptations.

In Romania, troglobitic terricolous oligochaetes have not yet been identified. Among the approximately 12 troglophile species commonly found in caves from the whole of the country, we cite the following: *Fridericia striata* (Levinson) and *Enchytraeus bucholzi* Vejdovski (Enchytraeidae), as well as *Allolobophora rosea* (Savigny) and *Dendrobaena rubida* (Savigny) (Lumbricidae). (See also Botea, 1970 and in press.)

GASTROPODA: Gastropods

No terrestrial troglobitic gastropods have been found in Romanian caves. Among the 24 troglophilic species, 4 are more frequent cave inhabitants: *Oxychilus glaber* (Rossmässler) (Fig. 3), *O. depressus* (Sterki), *Spelaodiscus triaria* Rossmässler, and *Troglomitrea argintarii* Negrea and Riedel.



The *Oxychilus* species are widely distributed in central and southeastern Europe, being the most frequently encountered species of gastropods from the caves of Romania, particularly in provinces II and III (Oltenia and Banat). They possess flattened, transparent, reddish-brown shells. *S. triaria* is much smaller (4 to 5.5 mm), with a yellow-brown shell and a horny appearance. It is endemic to Romania and has been found only in the caves of Banat, the northwest of Oltenia, and Transylvania. *T. argintarui*, endemic to northwestern Oltenia, has a thin, whitish or yellowish shell.

In caves, the gastropods live on moist walls, clay, guano, and various other organic remains. (See also Negrea, A., 1966 and in press.)

ISOPODA: Isopods

Terrestrial species of this group of crustaceans are well represented in caves. The troglitic and trogliphilic species belong to the family Trichoniscidae (see figs. 4 and 5). All troglitic species are endemic, blind, and depigmented. Among the most significant are: *Caucasonethes* n. sp. (Tabacaru, in press, b), endemic to Liliecilor Cave (Bat Cave) in Gura Dobrogei; *Trichoniscus* aff. *inferus* Verhoeff, inhabiting many caves in Oltenia; *Haplophthalmus tismanicus* Tabacaru (Fig. 4), found in the cave at the Tismana Monastery; and *Biharoniscus racovitzae* Tabacaru, discovered in the Cîmpeasca Cave (Apuseni Mountains). A trogliphilic species, *Mesoniscus graniger* (Frivaldsky) (Fig. 5), is distributed in many

predators in the caves of Romania.

In Europe, most of the troglitic species belong to the genera *Neobisium*, *Chthonius*, and *Rhonus*. In Romania, most belong to the genus *Neobisium*, e.g. *N. (Blothrhus) closanicus* Dumitrescu and Orghidan, inhabiting several caves from the Motru Basin; *N. (Blothrhus) brevipes* Frivaldszky, from Soroniste Cave and several caves in the Apuseni Mountains; and *N. (Blothrhus) leruthi* Beier (Fig. 6), known also from several caves from the Apuseni Mountains. These three species, together with an additional five species, are considered paleotroglitic. *Acanthocreagris callaticola* Dumitrescu and Orghidan, populating Limanu Cave and *Chthonius vandeli* Dumitrescu and Orghidan, from Liliecilor Cave of Gura Dobrogei, are endemic neotroglites in Dobrogea. Among the trogliphilic species, we mention *N. blothroides* (Tömösvary), endemic to several caves in the Apuseni Mountains. (See also Dumitrescu, et al., in press.)

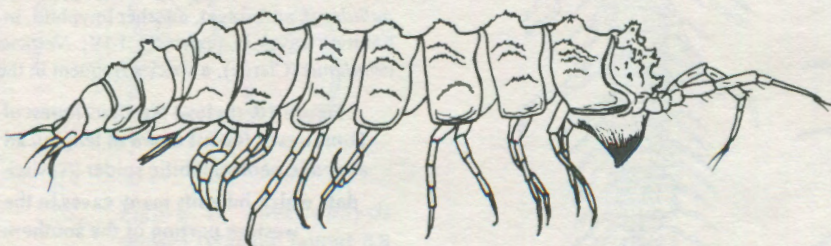


Figure 4. (above) *Haplophthalmus tismanicus* Tbc. (about 2.5 to 3 mm in length), a troglitic species of haplophthalmid isopods, endemic in the cave at Tismana Monastery.

Figure 5. (below) *Mesoniscus graniger* (Friv.) (about 1 cm in length), a trogliphilic species of mesoniscid isopods, widely distributed in the caves of the Carpathian chain, but most frequently found in the Banat and Apuseni mountains.

caves of the Carpathians, particularly in those from the Apuseni Mountains and Banat. It is an endogeic species known from the southeastern Alps, from the Dinaric Alps, and from the Tatra Carpathians. (See also Tabacaru, in press, b.)

PSEUDOSCORPIONES: Pseudoscorpions

This group of arachnids is well represented in caves. Troglitic forms are small, blind, depigmented and, together with opilions, are the most important

OPILIONES: Harvestmen or Daddy-Longlegs

There are no troglitic species of opilions known from Romania. From among those having trogliphilic populations, we cite *Holoscotolemon granulatus* (Roewer) (Fig. 7) and *Paranemastoma sillii* (Herman). The former belongs to the suborder Laniatores and inhabits only caves of the Carpathians, particularly those in northwestern Oltenia. It prefers wet caves, is depigmented, but possesses eyes. *P. sillii* belongs to another suborder, Palpatores, but, unlike *H. granulatus*, it has thin pedipalps and long legs, and the integument is pigmented. It can be found in caves, especially in winter, as it is a main component of the parietal (wall-dwelling) community. It has been reported from the caves of provinces II, III and IV, being more frequently recorded in provinces

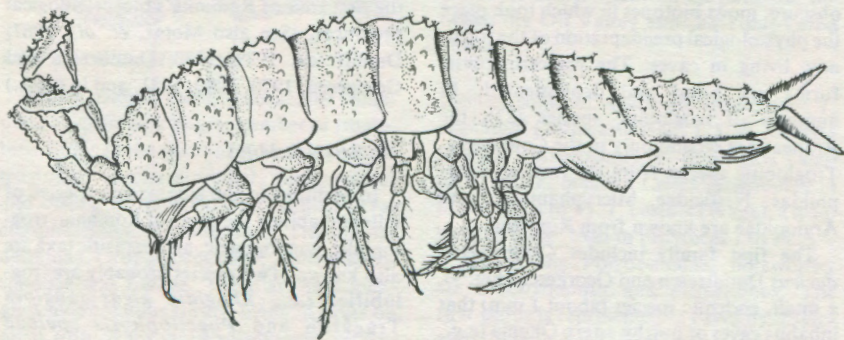
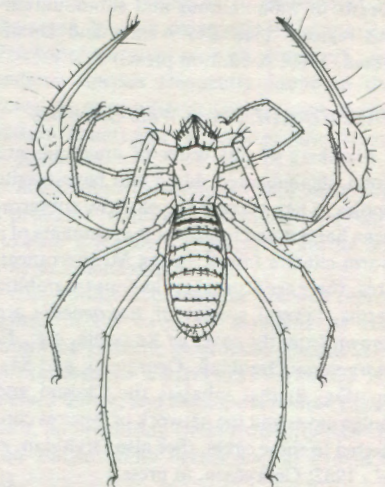


Figure 3. (left) *Oxychilus glaber* (Rossm.), a trogliphilic species of zonitid snails (shell about 14 mm in diameter), commonly found in the caves of Oltenia and Banat (provinces II and III).

Figure 6. *Neobisium leruthi* Beier (about 3.5 to 4.5 mm), a troglitic species of neobisiid pseudoscorpions, endemic in several caves from the Apuseni Mountains.



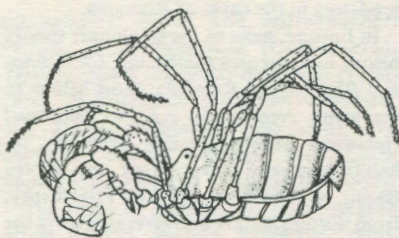
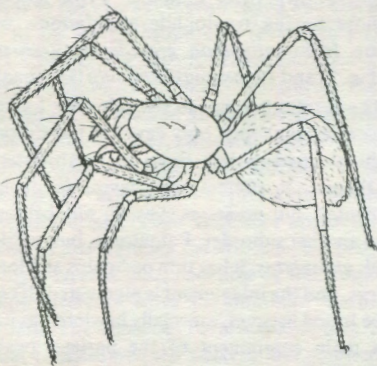


Figure 7. (above) *Holoscotolemon granulatus* (Roewer) (about 4.5 mm in length), a troglomorphic species of erobomastriid opilionids, found in caves throughout the Carpathians, particularly in Province II.

Figure 9. (below) *Centromerus dacicus* Dumitrescu and Georgescu (about 1 mm in length), a troglomorphic species of linyphiid spiders, endemic in caves of northwestern Oltenia (Province II). It is the most interesting species of troglomorphic spiders in Romania. Its cocoon contains 1 or 2 (rarely 3) eggs.

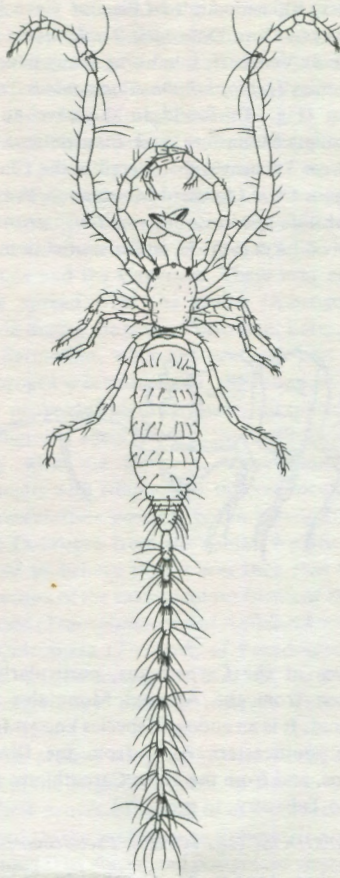


II and III (Oltenia and Banat). Outside of caves, it is found in various biotopes in the forests of mountainous and submountainous regions. (See also Avram and Dumitrescu, 1969; Avram, in press.)

PALPIGRADI: Micro-Whip-Scorpions

Members of this order of arachnids are small, depigmented, blind and have fragile bodies. They occupy the shallow subterranean habitat and represent the remnants of a warm climate fauna. In the Mediterranean area, there are also cavernicolous troglomorphic forms. Several species of *Eukoenenia* are known from the caves of Romania, e.g., *E. margaretae* Orghidan, Georgescu, and Sârbu (Fig. 8) that inhabits the Cloșani and Bulba caves and the network of fissures connected to these caves. (See also Orghidan, *et al.*, 1982; Georgescu, in press.)

Figure 8. (below) *Eukoenenia margaretae* Orghidan, Georgescu, and Sârbu (about 2.5 mm in length), a strictly subterranean species of Koeneniidae, characteristic of the fissures network, found so far only in Cloșani and Bulba caves (Province II), especially at the water surface.



ARANEAE: Spiders

As with other groups of arthropods, the troglomorphic spiders belong to lines adapted to obscure, moist biotopes in which took place the physiological preadaptation of the forms now living in caves. The paleotroglomorphic forms are blind and depigmented. In numbers of troglomorphic species (23), the Araneae are second only to the Coleoptera. Troglomorphic species from the families Linyphiidae, Nesticidae, Micryphantidae, and Argiopidae are known from Romania.

The first family includes *Centromerus dacicus* Dumitrescu and Georgescu (Fig. 9), a small, endemic species (about 1 mm) that inhabits caves of northwestern Oltenia (e.g., Cloșani Cave), *Troglohyphantes herculanus* (Kulczynski), a species endemic in caves of provinces II and III, and *Porrhomma pygmaeum convexum* Westring, inhabiting caves in Oltenia, Hunedora, Banat, and the Apuseni Mountains.

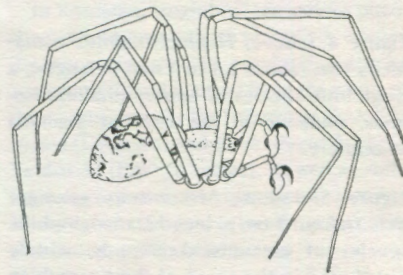
Among the Nesticidae are several species of *Nesticus*, most of which (13) are neotroglomorphic—for example: *N. ionescui* Dumitrescu (Fig. 10), present in many caves from Oltenia; *N. biroi* Kulczynski; endemic in several caves of the Apuseni Mountains; and *N. puteorum* Kulczynski, a species endemic in caves of Province II.

The micryphantid *Lessertiella dobrogica* Dumitrescu and Miller is a neotroglomorphic species endemic in Liliecilor Cave from Gura Dobrogei, which possibly became isolated in the subterranean habitat once the steppe climate became dominant.

The single representative of Argiopidae is *Meta bournetii* Simon, a neotroglomorphic species known only from the caves of Dobrogea.

Besides these troglomorphic species, there also are troglomorphic species found only very rarely outside of caves: e.g., *Lepthyphantes pallidus* (Cambridge), another linyphiid, inhabiting caves in provinces I-IV; *Nesticus cellulanus* (Clerck), a species frequent in the

Figure 10. (below) *Nesticus ionescui* Dumitrescu (about 6 mm in length), an endemic neotroglomorphic spider (Nesticidae) which inhabits many caves in the western portion of the southern Carpathians (Province II).



caves of Oltenia and Banat; and *Meta menardi* (Latreille), an argiopid common in the first four of Romania's biospeleological provinces. (See also Motas, *et al.*, 1967; Dumitrescu, 1979, 1980; Dumitrescu and Georgescu, 1970, 1980, 1981, and in press.)

ACARINA: Mites

In addition to the troglomorphic species of mites inhabiting the caves of Romania, troglomorphic, guanophagic, and parasitic taxa are also known. Two species probably are troglomorphic, i.e., *Rhagidia gigas longipes* Trägårdh and *Poecilophysis spelaea* (Wankel) (Fig. 11), found in a few caves in the Carpathian chain (particularly from the Apuseni Mountains). They are depigmented, blind, and have long appendages. *P. spelaea* occurs only in European caves and under rocks in northern Siberia. The caver-

nicolous populations are probably glacial relicts (Zacharda, 1978).

The troglomorphic-guanophilic species most frequently found are: *Euryparasitus emarginatus* (Koch), *Parasitus niveus* (Wankel), and *Hypoaspis miles* Berlese, belonging to the guano community; a uropodid, *Uroactinia* sp., probably representing a tropical relict and extremely abundant in Adam's Cave in Baile Herculane; *Trichouropoda orbicularis* Koch, also an uropodid and well represented in Adam's Cave and in Gura Ponicevei Cave.

A species common in the caves of all biospeleological provinces is *Ixodes vespertilionis* Koch, an ixodid whose females are parasitic only on bats. (See also Georgescu, 1968; Iavorschi, et al., in press.)

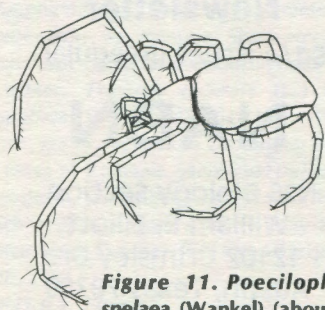
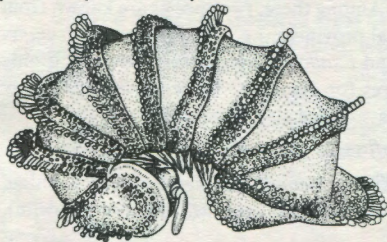


Figure 11. *Poecilophysis spelaea* (Wankel) (about 0.8 to 1.1 mm), a probably troglomorphic species of rhagidiid mite, found in several caves in the Carpathians.

Figure 12. *Trachysphaera orghidani* (Tbc.) (about 4.7 mm in length), a troglomorphic trachysphaerid millipede, endemic in caves in the western portion of the southern Carpathians (Province II).



DIPLOPODA: Millipedes

After Coleoptera and Araneae, the Diplopoda have the next largest number of troglomorphic forms in the caves of Romania. All the troglomorphic species are blind, depigmented, and belong to the following families: Trachysphaeridae, Polydesmidae, Trichopolydesmidae, Orobainosomidae, Anthroleucosomidae and Iulidae. These are saprophagous hygrophilous forms, living in caves on areas with clayey moist substratum, on rotten wood, on patches of old guano, and under stones. All the troglomorphic species found so far are endemic to individual biospeleological provinces of Romania.

Among the Trachysphaeridae, we mention the genus *Trachysphaera* with many

Figure 13. (below, center) *Polydesmus oltenicus* Negr. and Tabc. (about 8.5 mm in length), an endemic troglomorphic species of polydesmid millipede, found in caves in the western portion of the southern Carpathians (Province II).

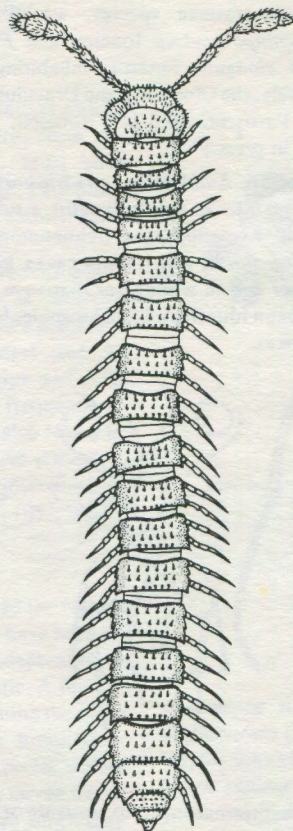
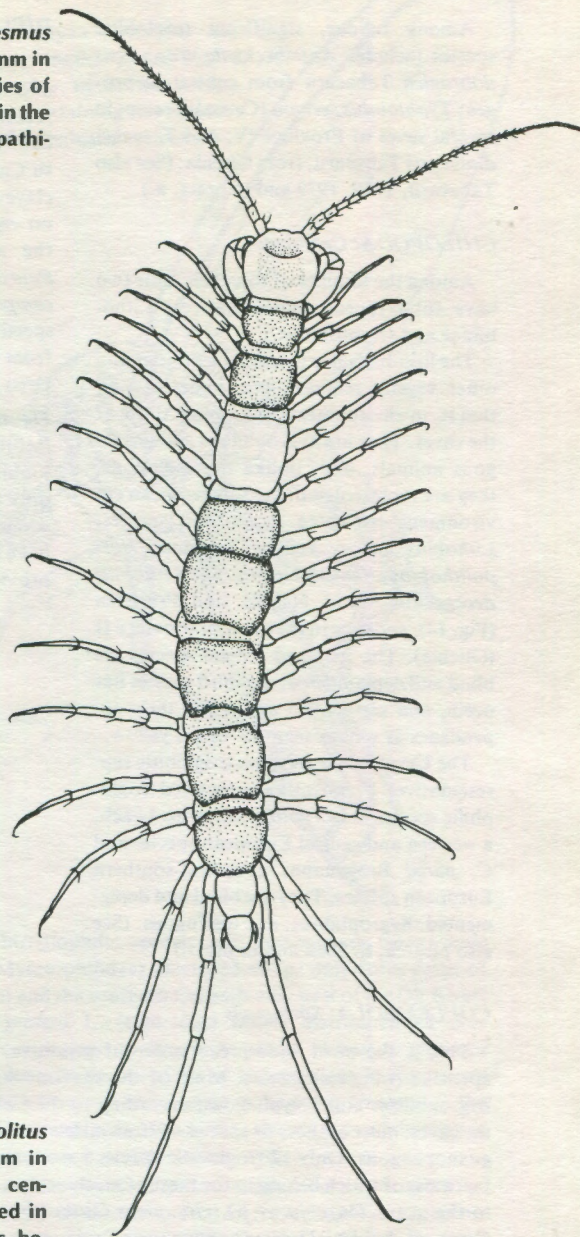


Figure 14. (right) *Lithobius decapolitus* Mat., Negr., and Prun. (12 to 19 mm in length), an endemic neotroglomorphic centipede (Lithobiidae), widely distributed in the caves of the southern Carpathians, between the Olt Valley and the Timiș-Cerna Couloir.



species, some of which are troglomorphic: *T. orghidani* (Tabacaru) (Fig. 12), *T. jonescui* (Brölemann), *T. dobrogica* Tabacaru, and *T. biharica* Ceuca (distributed in provinces II to V). *T. costata* (Waga), a troglomorphic form, lives in provinces I to IV.

Among the Polydesmidae, noteworthy are *Brachydesmus* and *Polydesmus*. The first genus is represented in caves by troglomorphic populations of *B. troglomus* Daday and *B. dadayi frondicola* Verhoeff. *Polydesmus* also includes a neotroglomorphic species with depigmented integument, *P. oltenicus* Negră and Tabacaru (Fig. 13), distributed in caves in Province II.

The Trichopolydesmidae, a group widely

distributed in America, is represented in Romania by two paleotroglomorphic species: *Trichopolydesmus eremitis* Verhoeff, an endemic species frequently found in the caves of northwestern Oltenia and southeastern Banat, and *T. jeanneli*, also found in Banat.

The Orobainosomidae are represented by a probable troglomite, *Orobainosoma hungaricum orientale* Tabacaru, found so far only in provinces II and III.

The Anthroleucosomidae are well represented in the caves of Romania by the following endemic troglomorphic species: *Anthroleucosoma banaticum* Verhoeff, *A. spelaea* Ceuca, and *Dacosoma motasi* Tabacaru, all inhabiting caves from province II; and *Bulgarosoma ocellatum*, in Province III.

Among Iulidae, significant troglotic species include: *Apfelbeckiella trnowensis dobrogica* Tabacaru from central Dobrogea; *Typhloiulus serbani* (Ceuca), present in several caves of Province IV; and *T. mehedintzensis* Tabacaru, from Oltenia. (See also Tabacaru, 1970, 1979 and in press, a.)

CHILOPODA: Centipedes

Among the families of this class, only two have subterranean representatives: Lithobiidae and Cryptopidae.

The lithobiids live in soil, in leaf litter and other vegetal remains, and under stones, that is, in environments resembling those of the caves. They are hygrophilous and lucifugous animals, and, unlike the diplopods, they are represented in the subterranean environment by three troglotic species: *Lithobius dacicus*, endemic in Banat, *Harpolithobius oltenicus* Negrea, and *Lithobius decapolitus* Matic, Negrea, and Prunescu (Fig. 14), endemic in the caves of province II (Oltenia). The first and second species are blind and depigmented; the third species has ocelli, and segments 5 and 6 and their appendages as well as segment 16 are yellow.

The Cryptopidae have no troglotic representatives. Frequently encountered troglitic species are *Cryptops hortensis* Leach, a western and central European species and *C. parisi* Brölemann, a central-southern European species. They are blind and depigmented, hygrophilous, and lucifugous. (See also Negrea, S. 1966 and in press.)

COLLEMBOLA: Springtails

This is the most widespread order of primitive, subterranean, apterous (wingless) insects. Most of the cavernicolous species are hygrophilous and polyphagous; according to their affinities within the caves, most of these 64 species of Collembola are troglitic and guanophagous. Only 12 troglitic species have been discovered so far, most of which belong to the family Onychiuridae, more precisely to the genus *Onychiurus* (*O. closanicus* Gruia [Fig. 15], *O. ancae* Gruia, *O. boldorii* Denis, *O. romanicus* Gruia, etc.).

The families Entomobryidae and Tomoceridae include troglitic elements of the genera *Pseudosinella*, *Heteromurus*, and *Tomocerus*. All are blind, depigmented, and, according to the specialists, are neotroglitic forms.

Among the guanobitic forms (possibly troglitic-guanobitic) of note are *Acherontides spelaea* (Ionescu) and *Mesogastrura ojcoviensis* (Stach), commonly found in caves containing guano in Oltenia and Banat. They are both depigmented, the latter also being blind. (See also Gruia, 1969 and in press.)



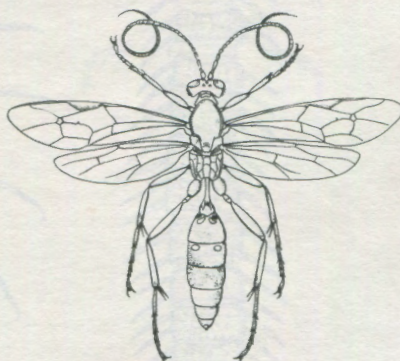
Figure 15. (left) *Onychiurus closanicus* Gruia (about 1.2 to 1.8 mm), an endemic troglitic species of onychiurid Collembola, found in caves between the Jiu and Cerna valleys.

Figure 17. *Triphosa sabaudiata* (Dup.) (about 4 cm), a subtroglyphic species of geometrid moths, common in the caves of Romania, both in winter and summer.

DIPLURA: Diplurians

These depigmented, blind, hygrophilous, and apterygote forms are frequently recorded in caves, although their favorite habitat is the soil and its direct annexes (sensu Cassagnau, 1961). In caves, they live on clayey areas or moist humus, under stones, on vegetal remains, and on guano. Among the subterranean species, we mention *Paurocampa spelaea* Ionescu and *Plusiocampa elongata* Ionescu, inhabiting, respectively, the Glod Cave and Dracului Cave from Paroşeni. (See also Ionescu, 1955; Decu, in press.)

Figure 16. *Amblyteles quadripunctorius* (Müll.) (16 to 20 mm in length), a subtroglyphic hymenopteran (Ichneumonidae), only females of which enter caves, both in summer and in winter, for diapause. They have been found in all five biospeleological provinces.



THYSANURA: Bristletails

This is another group of apterygote insects uncommon in caves and found only at the entrances. Most often encountered are two species of Machilidae, i.e.: *Trigoniophthalmus banaticus* Verhoeff and *T. alternatus* Silvestri, two subtroglyphic forms which go underground and hibernate in October or November, leaving the caves in March. (See also Motaş, et al., 1967; Holinger, in press.)

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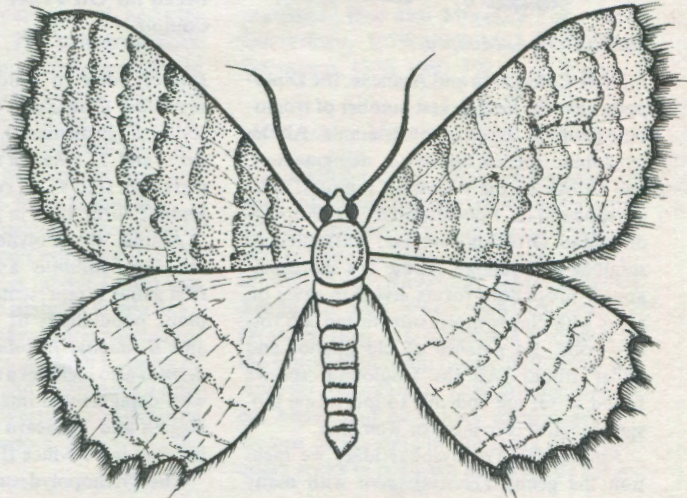
NSS Biology Section,
William R. Elliott
12102 Grimsley Dr.
Austin, Texas 78759

HYMENOPTERA: Sawflies, Ichneumons, Chalcids, Ants, Wasps, and Bees

Like the Thysanura, these are represented in the subterranean media solely by subtroglyphic forms (populations that enter caves to aestivate or hibernate). Among these, two species are known from all the five biospeleological provinces, i.e.: *Amblyteles quadripunctorius* (Müller) (Fig. 16) and *Exallonyx longicornis* (Nees). It is only the females that enter caves for diapause. These species are widely distributed in European caves. (See also Decu and Decu, 1961.)

TRICHOPTERA: Caddisflies

Three species of caddisflies, *Stenophylax permistus* McLachlan, *Micropterna nycterobia* McLachlan, and *M. testacea* (Gmelin),



distributed in the Palearctic Zone, enter moist and cold caves (in summer) for diapause, where they remain from May until September. The individuals entering caves are subtroglaphiles which aestivate. *S. permistus* and *M. nycterobia* occur in caves in provinces I to IV, particularly in caves from provinces II and III; *M. testacea* has been found only in caves from Province IV. No subtroglaphile caddisfly (nor any dipteran or mycetophilid) has been found in Dobrogea, because of the semi-arid steppe climate which began in that region at the end of the lower Quaternary. (See also Botoșăneanu, 1966.)

LEPIDOPTERA: Moths and Butterflies

The moths, too, have several cavernicolous representatives which, together with Trichoptera, Diptera, and Hymenoptera, form the principal components of the parietal community. Most subtroglaphilic species enter caves to aestivate or hibernate. Like other subtroglaphilic cavernicolous organisms, they do not show troglomorphic adaptations.

Among the most frequently encountered species of subtroglaphilic Lepidoptera, we mention *Scoliopteryx libatrix* (L.), a holarctic species distributed in caves throughout Romania and more abundant in winter. *Triphosa dubitata* (L.) (palearctic species) and *T. sabaudiata* (Duponchel) (Fig. 17), distributed in Europe and Asia Minor, are two species of Lepidoptera also found very frequently in the caves of Romania. *Acrolepia pulicariae* Klimesch, also found in Yugoslavia, is another moth present in Romanian caves (Oltenia), which aestivates from April to May and begins its hibernation in September or October. (See also Căpușe and Georgescu, 1963; Motaș et al., 1967.)

DIPTERA: Flies

Cave-dwelling species of flies belong to the parietal, to the vegetal remains, and to the guano communities. Although they have been inhabiting caves for a very long time, they do not show adaptations to cave life, and none of them may be considered troglotitic. A few are troglaphiles, but most of them are subtroglaphiles. Among the more frequently found troglaphilic forms in the caves of Romania is *Speolepta leptogaster* Winnertz (Bolithophilidae), a species widely distributed in caves in Europe and North America. The larvae weave webs on moist and sheltered areas of the walls, on which they move in pursuit of food. According to some authors, they seem to be carnivorous.

The number of subtroglaphilic dipterous species is large. We shall cite below only the most frequently found and most abundant species. *Tarnania fenestralis* (Meigen) (Fig. 18), a mycetophilid, commonly aestivates in the caves of Romania, as well as in those of central, southern, and western Europe. *Limonia nubeculosa* Meigen, a limoniid, is also common in Romania's caves, as well as in those from southern, eastern, and western Europe. More important

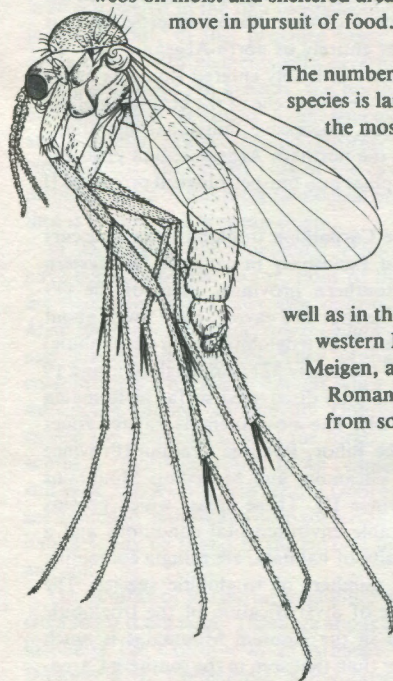
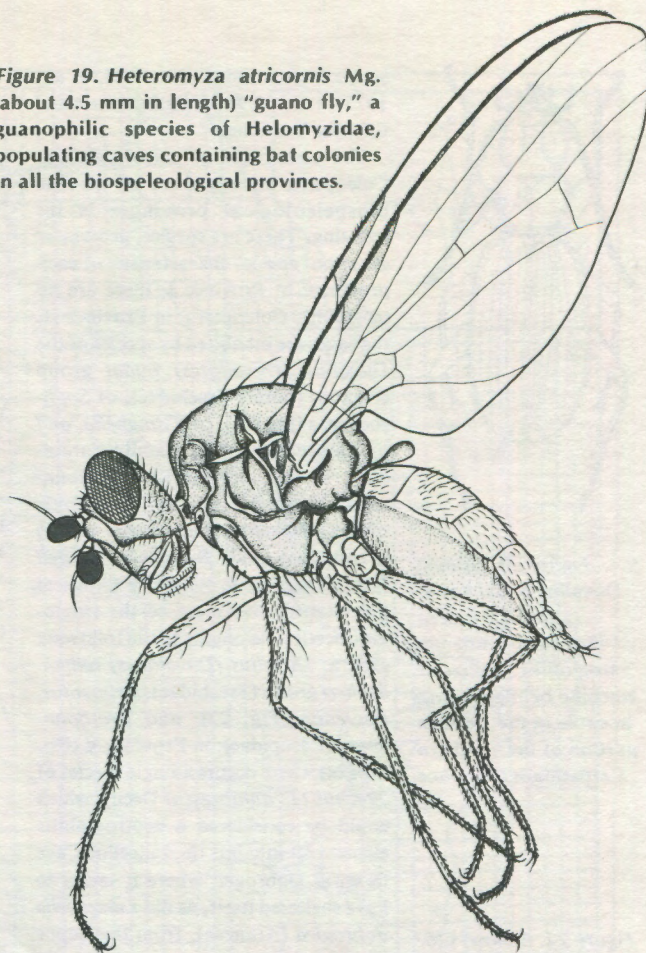


Figure 18. *Tarnania fenestralis* (Mg.) (about 6.5 mm in length), a subtroglaphilic species of mycetophilid fly, inhabiting cold and wet caves in all five biospeleological provinces.

Figure 19. *Heteromyza atricornis* Mg. (about 4.5 mm in length) "guano fly," a guanophilic species of Helomyzidae, populating caves containing bat colonies in all the biospeleological provinces.



hibernating subtroglaphilic species are: *Exechiopsis magnicauda* (Lundström) (Mycetophilidae) identified so far only from caves of Vîrghiș Schlucht and the southern Carpathians, west of the Olt River; *Culex pipiens pipiens* L. (Culicidae) widely distributed all over Romania, in Europe, and in North America; *Helomyza captiosa* Gorodkov, the most frequent species of Helomyzidae in Romania's caves (except in Dobrogea). *H. captiosa* is, likewise, common in the caves of other European countries. Unlike the other two hibernating subtroglaphilic species, it prefers colder caves.

Caves with bat guano contain *Heteromyza atricornis* Meigen (Fig. 19), the "guano fly," whose larvae feed on fresh guano. *H. atricornis* also occurs in caves in other areas of Europe and in Algeria. In caves inhabited by bats, some Diptera (Nycteribiidae) parasitic on them are also found. These show a high degree of host specificity. Among them, we cite *Nycteribia biarticulata* Hermann, a parasite especially on some species of *Rhinolophus*; *N. schmidlii* Schiner, a parasite on *Miniopterus schreibersi* Kühl; and *Penicillidia dufouri* (Westwood), parasitic on *Myotis myotis* Borkhausen.

Except for *Culex pipiens pipiens*, *Heteromyza atricornis*, and the Nycteribiidae, which are present in all five biospeleological provinces, Diptera have not been found in the caves of Dobrogea. The reason for their absence is the same as for the caddisflies, i.e., the presence of a semi-arid steppe climate in that region. (See also Decu-Burghel, 1963; Burghel-Bălăcescu, 1965 and 1966; Motaș, et al., 1967.)

COLEOPTERA: Beetles

Beetles are the order of insects possessing the largest number of troglotitic taxa in the world (more than 1500). In Romania, about 60% of the now known troglotitic species (126) are beetles of the subfamilies Bathysciinae (Catopidae) and Trechinae (Trechidae). The

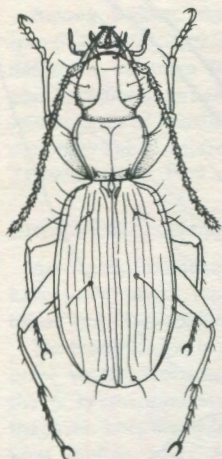
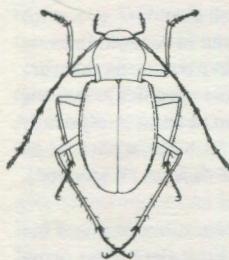


Figure 20. (above) *Duvalius budai* Kend. (about 4.7 mm in length), an endemic troglitic species of trechine beetles, found in caves in the western portion of the southern Carpathians (Province II).

Figure 22. (below) *Closania winkleri* Jeann. (about 5.2 mm in length), an endemic troglitic species of bathysciine beetles, found in several caves from the western portion in the southern Carpathians (Province II).



specialization index (Sbordoni, *et al.*, 1977) attains 0.90 for Bathysciinae and 0.74 for Trechinae.

The occurrence of paleotroglobitic Coleoptera in only three of the five biospeleological provinces is interesting. There are species, genera, or groups of species characteristic of each province. In Province I, there are no troglitic Coleoptera; in Province II, the caves are inhabited by species of the *Duvalius* (*Duvaliotes*) *budai* group (Fig. 20) (family Trechinae), of *Sophrochaeta* (Fig. 21), of *Tismanella*, and of *Closania* (Fig. 22) (family Catopidae); in Province III (Banat Mountains), there are only two troglitic species: *Duvalius* (*Duvaliotes*) *milleri* (Trechinae) and *Banatiola vandeli* (Catopidae); in Province IV (Apuseni Mountains), live most of the troglitic beetles, belonging to the following genera: *Duvalius* (*Duvaliotes*) *redtenbacheri* group (Trechinae), *Drimeotus*, *Pholeuon* (Fig. 23), and *Protophroleuon* (Catopidae); in Province V (Dobrogea), there occurs a single species of *Trechus* (*T. dumitrescui* Decu), which could be considered a neotroglobitic element. It inhabits the Liliecilor Cave in Gura Dobrogei, where it seems to have sheltered itself, as did *Lessertiella dobrogica* (Araneae), from the steppe climate.

Except *T. dumitrescui*, all the other troglitic species of beetles are old forms that entered the subterranean media a long time ago. They are blind, depigmented, and apterous. The caves are inhabited not only by troglitic species, but also by trogliphilic, sub-trogliphilic or guanophilic Coleoptera belonging to other families. The genera *Quedius*, *Atheta*, and *Aleochara* (Staphylinidae) and *Choleva* and *Catops* (Catopidae) are common in European caves. They show only physiological adaptations to the subterranean habitat. (See also Decu, 1963, 1967, 1980; Decu and Negrea, 1969.)

SIPHONAPTERA: Fleas

One family of fleas (Ischnopsyllidae) is parasitic only on bats. Species be-

longing to the genera *Ischnopsyllus*, *Rhynolophopsylla*, and *Nycteridopsylla*, like the Nycteribiidae (Diptera), are host-specific forms.

Fleas, like many other parasites, are not here considered true cavernicolous forms, as their presence in caves is more dependent upon the host than upon the subterranean environment.

CHIROPTERA: Bats

Bats are the only group of vertebrates inhabiting Romania's caves. They live in isolated colonies, and only six species (out of the 21 now known to exist in Romania) are trogliphiles; *Rhinolophus ferrumequinum* (Schreber), *Rh. hipposideros* (Bechstein), *Rh. mehelyi* Matschie, *Rh. euryale* Blasius,

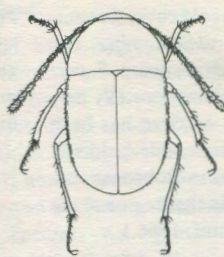
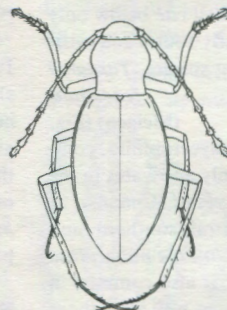


Figure 21. (above) *Sophrochaeta oltenica* Jeann. and Mall. (about 3.5 mm in length), an endemic troglitic species of bathysciine beetles, found in several caves in the western portion of the southern Carpathians (Province II).

Figure 23. (below) *Pholeuon angusticollis* Hpe. (about 4.7 mm in length), a troglitic species of bathysciine beetles, endemic to the caves of the Apuseni Mountains.



Myotis myotis, and *Miniopterus schreibersi*.

Rh. ferrumequinum has a wide palearctic distribution. It is the most characteristic species found in Romania's caves and is recorded throughout the country. It is gregarious and forms colonies when giving birth and when hibernating. In some caves (such as Liliecilor Cave from Bistrița Monastery), this species forms permanent colonies. *Rh. hipposideros* (distributed in Europe, southwestern and central Asia, and north Africa) occurs throughout Romania, but does not form colonies. *Myotis myotis* (inhabiting Europe and the southern part of palearctic Asia) and *Miniopterus schreibersi* (found in southern Europe, southern Asia, the Philippines, New Guinea, northern Australia, and northwestern Africa) are present in all the five provinces and form large colonies when hibernating or producing young.

There are some subtroglyphic species of Chiroptera which show preferred distributional patterns. *Rh. mehelyi* has been recorded only in Dobrogea, and *Rh. euryale*, which, although found in small numbers and only in a few caves (most of them in Banat), forms a large summer colony in Adam's Cave (Băile Herculane).

All species of Chiroptera from Romania are insectivorous. (See also Dumitrescu, *et al.*, 1963.)

GENERAL CHARACTERIZATION OF THE TROGLOBITIC FAUNA DISTRIBUTION

The terrestrial troglitic fauna, with the exception of that inhabiting province I, is almost entirely of north-Aegean origin. Its ancestors probably entered Romania at the end of the Oligocene or the beginning of the Miocene. Successive individual migrations from the northern Aegean region probably took place into biospeleological provinces II to V.

The Carpathian troglitic fauna occurs almost exclusively in caves of the western and southern provinces, west of the Olt River (about 170 caves). Here dwell about 195 taxa (189 troglitic and 6 edaphobitic) out of the nearly 227 (208 troglitic and 19 edaphobitic) discovered so far in Romania (Fig. 24). The most intensely karsted zones are the Bihor, Pădurea Craiului (Province IV), Vlcanului and Mehedinți Mountains (Province II). These areas, which possess favorable environmental conditions and a diversity of habitats, are refugia containing large numbers of troglitic species. The degree of diversification of the troglitic fauna in the Apuseni Mountains is much higher than that seen in the southern Carpathians and in the Banat Mountains.

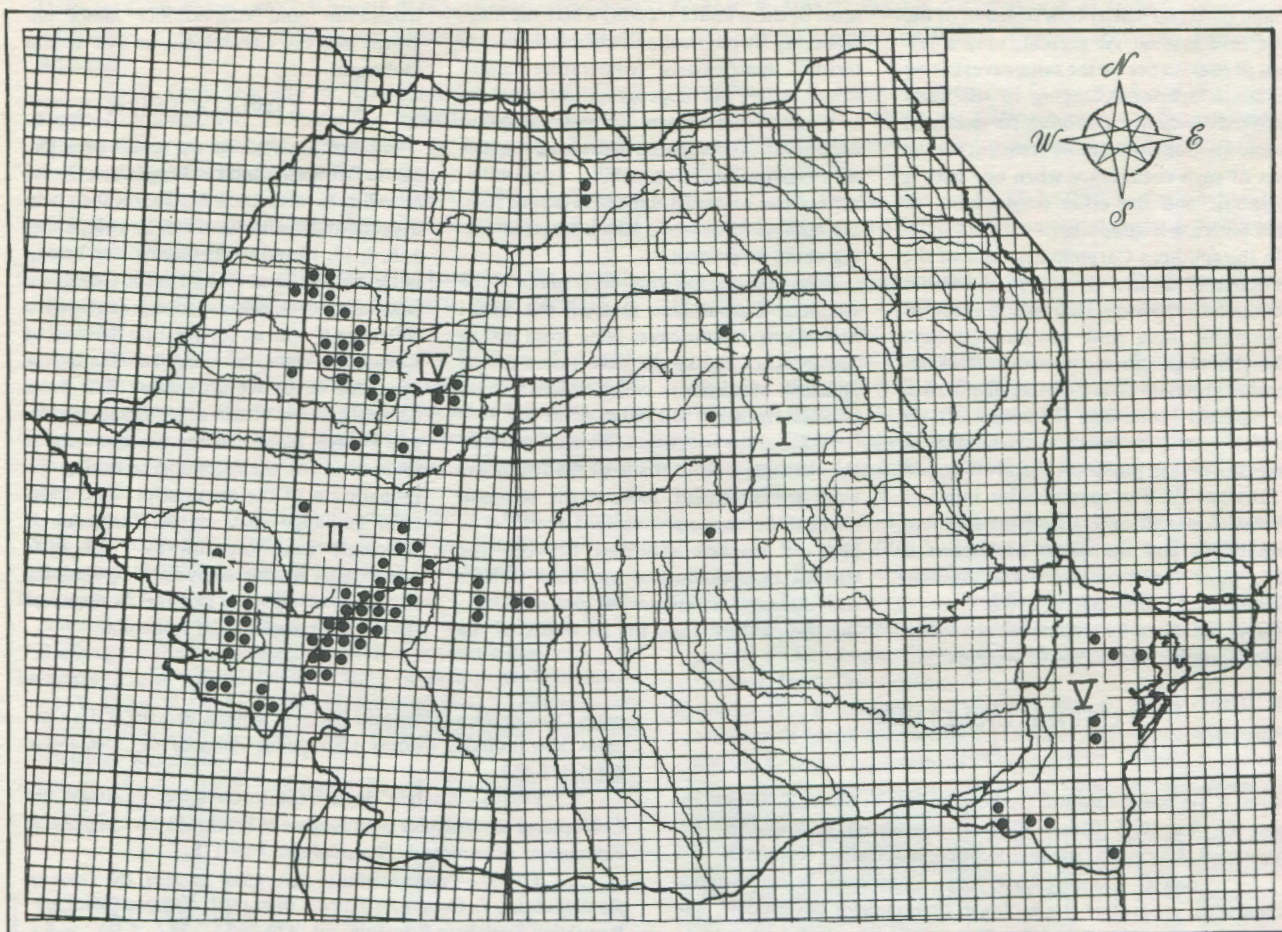


Figure 24. Distribution of terrestrial troglobitic fauna in Romania, on a map in Universal Transverse Mercator Grid. Biospeleological provinces marked I through V.

Only five troglobitic elements have so far been discovered in the first biospeleological province. But, in this province there are many edaphobitic elements with cavernicolous populations. In general, the northern elements have provided a cavernicolous subterranean fauna formed entirely of troglophiles. The largest part of the cavernicolous fauna of this biospeleological province is of central-European origin.

In Dobrogea, six troglobitic elements have been discovered so far. Four of them are neotroglobitic: *Lessertiella dobrogica*, *Meta bourneti*, *Acanthocreagris callaticola*, and *Trechus dimitrescui*. They probably entered the subterranean habitat when the developing steppe climate in Dobrogea caused the disappearance of the forests. In southern Dobrogea, where forest remnants still exist, species which in central Dobrogea are limited to shallow and deep subterranean habitats may be found in the surface litter and soil.

The number of terrestrial troglobitic taxa cited so far is not large. There are about 208, including 126 Coleoptera, 23 Araneae, 20 Diplopoda, 12 Collembola, 8 Pseudoscor-

piones, and 6 Isopoda. Most troglobitic populations are small, and cases are known where only a few specimens belonging to a species could be collected at one time. More than 97 percent of the troglobitic forms are endemic, and more than 80 percent are paleotroglobitic.

As compared to other animal species, the old troglobitic forms occupy the smallest territories and are the most isolated. Out of the total number of taxa inhabiting Romania's caves, 84 percent have been found in only 1 to 3 caves (57 percent in one cave, 10 percent in two, and 17 percent in three caves) and only 16 percent in more than three caves. This latter category generally includes the neotroglobitic taxa; a species occupying a large discontinuous area is, for instance, *Lithobius decapolitus*, a neotroglobitic element found in more than 75 caves (Decu, 1983). Many troglobitic species and races consist of single populations (such as those inhabiting only one cave).

Caves, even more than islands and mountain peaks, are the most discontinuous of terrestrial habitats. The connections be-

tween populations of terrestrial troglobites are severely restricted. The territories of the troglobitic taxa inhabiting one cave are continuous; the territories of the populations of some taxa inhabiting a group of caves also may be continuous (via less than human-sized subterranean cavities communicating through the karst), although the uninterrupted processes of mechanical and chemical deposition in the networks of fissures and cavities generally prevents that.

The number of closely related but geographically isolated troglobitic taxa (i.e., vicariants), specific and infraspecific, is large. Most of them belong to the beetle genera *Duvalius*, *Pholeuon*, *Drimeotus*, and *Sophrochaeta*. The marked vicariance is due to erosion and sedimentation within the limestone massifs as well as to the troglolitization of the troglophilic fauna in situ. Isolated in caves, the taxa that became vicariant troglobites may not be able to enlarge their territories (excepting those that inhabit interconnected cavities).

There are no instances known of two troglobitic races (or one troglobitic race and one troglophilic race) of the same species which

inhabit parts, no matter how isolated, of the same cave system. At present, only a few cases of coexistence (in the same cave) of two troglobitic species belonging to the same genus (*Neobisium* or *Duvalius*, for example) are known. Somewhat more frequent are the cases of such coexistence when one taxa is troglobitic and the other troglophilic, or when both are troglophilic.

In the southern Carpathians, west of the Olt River (Province II) and in the Banat Mountains (Province III), the number of troglophilic taxa and edaphobitic taxa belonging to genera and species with cavernicolous populations is much smaller than in the Apuseni Mountains (Province IV). In the Coleoptera, for instance, the number of these taxa is 15 in provinces II and III and 28 in Province IV. The specialization index of cavernicolous Coleoptera from the southern Carpathians and the Banat Mountains is 0.87, while for those from the Apuseni Mountains, it is 0.83 (Decu, 1980).

Caves inhabited by troglobites are found at moderate elevations (300 to 1300 m ASL,

most of them under 1000 m) where the limestone, by its physical and chemical characteristics (particularly temperature conditions), offers the biogeographical optimum of a stable environment, most favorable to endemism. As compared to the total number of cavernicolous troglophilic, troglobitic-guanobitic, and troglobitic taxa (about 500), the number of endemic taxa is large, attaining about 50 percent.

In most cases, the troglobitic fauna of the southern Carpathians and of the Banat Mountains inhabit caves lying from 300 to 750 m ASL, unlike the cave fauna of the Apuseni Mountains, which inhabit caves situated from 300 to 1300 m ASL.

As far as the zoogeographical affinities of the elements characteristic of the five provinces are concerned, most of the common elements belong to provinces II and IV. The lack of marked affinities between the various biospeleological provinces reflects past differences between the provinces during the periods when the ancestors of the

troglobitic (and edaphobitic) fauna migrated into the Carpathians as well as into Dobrogea.

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A New Species of *PROTEINUS* FROM A JAMAICAN CAVE

(Coleoptera: Staphylinidae)*

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SUMMARY

In 1972, an adult male of a hitherto unknown *Proteinus* species was collected from Jackson's Bay Cave, Jamaica. This is the first record of the genus from the West Indies. Despite at least 9 visits to the cave by entomologists, no additional specimens have yet been found. This specimen is illustrated and described as a new species, *Proteinus peckorum* Frank, and is differentiated from known New World *Proteinus*. Although no *Proteinus* is known to be a troglobite, two other species have been recorded from Old World caves, and one of these seems to be a troglophile. Occurrence of *P. atomarius* Erichson in North America is confirmed by specimens from McLean Co., Illinois.

THE PRIMARY HABITAT of *Proteinus* adults and larvae appears to be fungi, and adults of at least one species are attracted to yeast-baited pit-fall traps (Frank, 1979). Carrion provides another habitat (Puthz, 1962; Easton, 1967; Payne and King, 1970; Topp, Hansen, and Brandl, 1982) and either is a direct food source (Steel, 1963) or is a substrate for fungi. In France, *P. ovalis* Stephens is reported from rabbit (*Oryctolagus*) burrows, and *P. atomarius* Erichson from badger (*Meles*) and rabbit burrows (Falcoz, 1914). These habitats share high humidity and places of concealment from light as common characteristics and provide fungi or, at least, decaying animal or vegetable material on which fungi may grow.

Because of such habitat preferences, it is not surprising that *P. ovalis* and *P. brachypterus* (Fabricius) have been recorded from Belgian caves, where the former is common among vegetable detritus in cave entrances (Leruth, 1935). Although Leruth (1935) considered *P. ovalis* to be a troglone, it more nearly fits the definition of troglophile as restated by Barr (1967). Wolf (1935, 1937) listed *P. ovalis* only from caves, and only from Belgium and Italy.

The senior author, resident in Jamaica from December 1968 to March 1972, built a collection of epigeal and cavernicolous Staphylinidae, but found no specimens of

Proteinus. No *Proteinus* species are recorded from the West Indies (Frank, 1979). Fincham (1977) listed the Jamaican caves and described many of them, including Jackson's Bay Cave in Clarendon Parish which the senior author had visited on 4 occasions. Five other visits to this same cave (Peck, 1975) were more productive in yielding a single specimen of a distinctive new *Proteinus* species, described below.

PROTEINUS PECKORUM FRANK, NEW SPECIES

Description

General. Length 1.9 mm. Body convex. Habitus as in Fig. 1. Pronotum 1.7 times broader than long; broadest at about middle of length; hind angles obtuse. Elytral width at humeri about equal to maximum width of

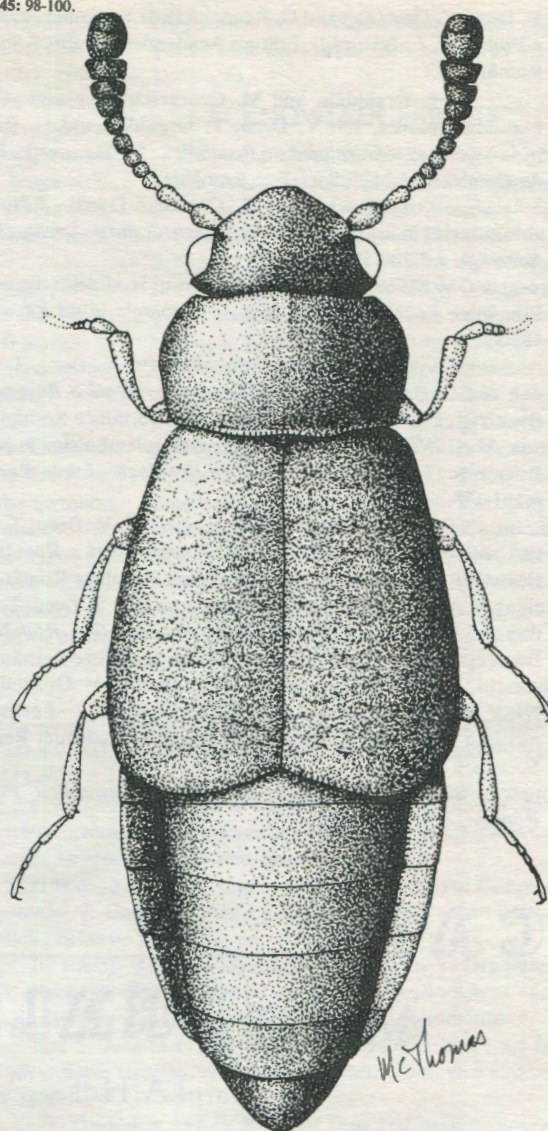


Figure 1. Habitus of *Proteinus peckorum* Frank. Length 1.9 mm.

pronotum, and elytral width increasing posteriorly to just before hind angles; elytra about 2.5 times longer than pronotum.

Head nigrous; elytra castaneous, slightly paler along suture and at hind margin; pronotum and abdomen basically castaneous but pronotum infuscate except narrowly at margins, and abdomen infuscate except for segment VIII and apical half of segment VII; legs, mouthparts, and basal antennomeres pale ferruginous, but antennomere VII infuscate and VIII-XI darkly so.

Antennomere VII feebly transverse, VIII and IX strongly transverse, 1.5 times broader than long; antennal club thus appears to be formed of at least antennomeres VIII-XI, with which VII could subjectively be included. Head and pronotum with fine shagreened microsculpture; elytra rugosely microsculptate and not shagreened; ab-

* Institute of Food and Agricultural Sciences, University of Florida, Journal Series no. 4848.

domen with feeble coriaceous microsculpture. Fine setigerous punctures present on head, pronotum, and abdomen; setae short and pale. Pronotum without evident raised basal margin. Macropterous.

Male characteristics. Protarsus with tarsomere I strongly broadened and longer than next 3 tarsomeres together; mesotrochanter with 2 darkly pigmented peg setae (Fig. 2A); mesotibia with darkly pigmented peg setae in apical quarter (Fig. 2A, B, C), with 10 of these on right mesotibia (Fig. 2B) and 9 on left (Fig. 2C); metatibia with 1 darkly pigmented seta at apex (Fig. 2D); no other darkly pigmented peg setae present. Aedeagus as in Fig. 2E (ventral view) and Fig. 2F (lateral view).

Type specimen

The holotype, in the Canadian National Collection, Ottawa, bears the following labels: JAM Clarendon Jackson Bay Cave 21-22.xii.72 S. & J. Peck/*Proteinus peckorum*, J. H. Frank HOLOTYPE. The left protarsus as well as tarsomere V of the right protarsus are missing. The aedeagus and parts of the left mesoleg and right metaleg have been mounted in Canada balsam on a celluloid rectangle on the same pin as the card-mounted specimen.

Etymology

The species is named for the collectors of the holotype: Stewart Peck and Jarmila Kukalova-Peck.

Biology

Unknown. Collection location within the cave unrecorded.

PROTEINUS ATOMARIUS ERICHSON

Frank (1979) recognized 10 *Proteinus* species from the New World and the doubtful occurrence there of an 11th, *P. atomarius*. Since then, R. W. Lundgren supplied 4 specimens of a series of *P. atomarius* he had collected on 2 September 1979 at Funks Grove, McLean County, Illinois, U.S.A. The external structures and aedeagus (Fig. 2G) of a male of this series match those of European specimens described by Tottenham (1954) and Lohse (1964).

DISCUSSION

Affinities of *P. peckorum*

The holotype of *P. peckorum* traces to *P. macropterus* (Gyllenhal) in keys to European species provided by Tottenham (1954) and Lohse (1964), but the aedeagus (Fig. 2E) is strikingly distinct from that of *P. macropterus*.

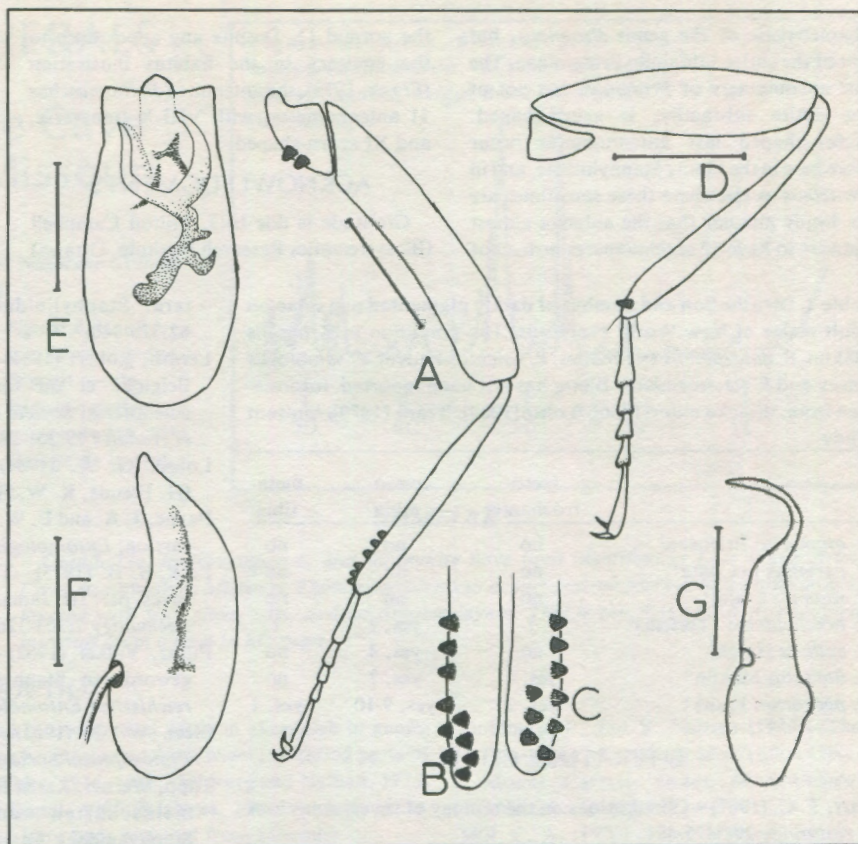


Figure 2. Diagnostic structures of *Proteinus* spp. A-F, *P. peckorum*, A. mesotrochanter showing 2 peg setae and mesotibia showing peg setae; B, apex of right mesotibia showing 10 peg setae; C, apex of left mesotibia showing 9 peg setae; D, metatibia showing 1 peg seta; E, aedeagus in ventral view; F, aedeagus in lateral view; G, *P. atomarius* aedeagus in lateral view. The scale line = 0.25 mm.

With *P. peckorum* and *P. atomarius*, 12 *Proteinus* species are now known from the New World (Table 1). The distribution of darkly pigmented peg setae among males is recorded or partially recorded for 7 of them, and can be used to distinguish *P. peckorum* males from males of 5 other species (Table 1). It differs from the other species at least as follows: *P. brachypterus* has an aedeagus of different structure (see Tottenham, 1954; Lohse, 1964); *P. basalis* is reported to have the base of the elytra pale; *P. densipennis*, *P. sulcatus* and *P. salebrosus* are reported to have the pronotum more than 2 times broader than long; *P. flavocaudatus* is reported to have the pronotum with acute hind angles (Frank, 1979).

Affinities of *P. peckorum* seem to be to *P. collaris*, judging from the form of the aedeagus, the presence of darkly pigmented peg setae, the occurrence of at least 4 antennomeres in the antennal club (not 3), and the lack of a raised basal margin of the pronotum. The slender form of the aedeagus and lack of peg setae in *P. atomarius*, *P. thomasi*, and *P. parvulus* suggest that these 3 species are more closely related to each other than to *P. peckorum* and *P. collaris*.

The structural similarity of the aedeagus of *P. peckorum* and *P. collaris* to that of some *Megarthus* species illustrated by Lohse (1964) suggests that this aedeagal form is the more plesiomorphic, so that the slender aedeagal form in *P. atomarius*, *P. thomasi* and *P. parvulus* is the more highly derived.

The antennal club

Delimitation of the club of the *Proteinus* antenna has been used as a specific characteristic by some authors (e.g., Tottenham, 1954; Lohse, 1964), who have stated that the club of some species has 3 antennomeres, whereas that of others has 4. However, unless there is an abrupt change in width of antennomeres, the delimitation of the club is subjective and would best be avoided in compilation of keys. In those species such as *P. peckorum* where the last 4 or 5 antennomeres are darkly pigmented, the pigmentation provides a contrast between the proximal and distal antennomeres and so accentuates the clubbed appearance of the antenna.

Transverse penultimate and antepenultimate antennomeres, with interspecific variation in degree of transverseness, seem

characteristic of the genus *Proteinus*, but not of the entire subfamily Proteininae. The last antennomere of *Proteinus*, but not of the entire subfamily, is acorn-shaped. Acorn-shaped last antennomeres occur elsewhere in the family Staphylinidae, and in *Proteinus* as elsewhere these sometimes are so deeply annular that the antenna almost appears to have 12 antennomeres instead of

the normal 11. Despite any appearance to the contrary in the habitus illustration (Frank, 1979), the antenna of *P. thomasi* has 11 antennomeres, with VIII-X transverse, and XI acorn-shaped.

ACKNOWLEDGMENTS

Gratitude is due to J. Milton Campbell (Biosystematics Research Institute, Ottawa)

for arranging the loan of the holotype of *P. peckorum* and of European specimens of *P. macropterus*. Stewart Peck (Carleton University) permitted the loan and encouraged this study. Randall Lundgren (Normal, Illinois) donated specimens of *P. atomarius*. R. E. Woodruff (Gainesville, Florida) and E. R. Hoebeke (Cornell University) kindly reviewed manuscript drafts.

Table 1. Distribution and number of darkly pigmented peg setae on adult males of New World *Proteinus*. The condition in *P. basalis* Mäklin, *P. densipennis* Bernhauer, *P. sulcatus* Fauvel, *P. salebrosus* Casey and *P. flavocaudatus* Bierig has not been reported. Information from: ¹Blackwelder (1936), ²Lohse (1964), ³Frank (1979), ⁴present study.

	meso- trochanter	meso- tibia	meta- tibia
<i>P. atomarius</i> Erichson ⁴	no	no	no
<i>P. parvulus</i> LeConte ³	no	no	no
<i>P. thomasi</i> Frank ³	no	no	no
<i>P. brachypterus</i> Fabricius ²	?	yes, ?	?
<i>P. collaris</i> Hatch ³	no	yes, 4	no
<i>P. limbatus</i> Mäklin ¹	yes, 4	yes, ?	no
<i>P. peckorum</i> Frank ⁴	yes, 2	yes, 9-10	yes, 1

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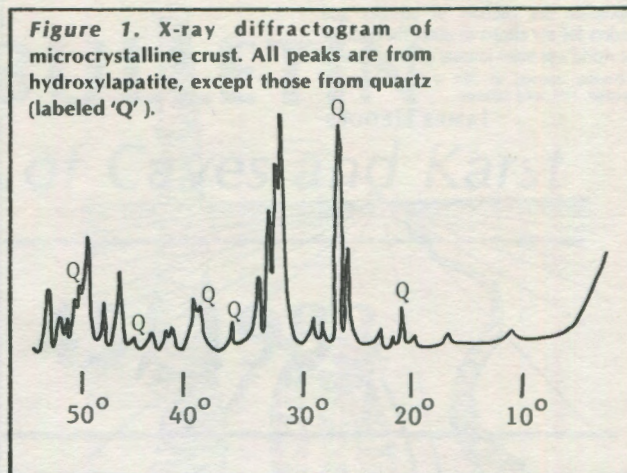
PHOSPHATE MINERALS in Low Water Bridge Cave Greene County, Missouri

MAX W. REAMS

Department of Geological Sciences, Olivet Nazarene College
Kankakee, Illinois 60901



Figure 2. Hand specimen of ledge deposit: white, microcrystalline crust over tan, silty clay (scale in cm).



SUMMARY

Crandallite, hydroxylapatite, and taranakite have been identified in Low Water Bridge Cave, southwestern Missouri. These minerals occur as surficial microcrystalline crusts or inter-layered with silty clays, silts, and/or organic layers. This is the first report of phosphate minerals from a cave in Missouri.

INTRODUCTION

PHOSPHATE MINERALS are occasionally found in caves, most often in caves rich in guano deposits. Phosphate mineralization in caves has been reported from widely scattered parts of the Earth (Sakae and Sudo, 1975; Hill, 1976; White, 1976, 1982; Goldberg and Nathan, 1975; Martini and Kavalieris, 1978; Pilkington and Segnit, 1980; Kashima, 1981; Francis, 1982). Prior to this study, no cave phosphates seem to have been reported from Missouri.

OCCURRENCE

During a study of clastic sedimentation in Missouri caves, I found unusual white and black layers in association with the clastic sediments in Low Water Bridge Cave, Greene County, Missouri (Reams, 1968). The white and black sediments are found on rock ledges and in wall cavities two to three m above the cave stream. The stratigraphy of the deposits is not uniform from place to place. White, microcrystalline crusts overlie gray silt and tan, silty clay in some localities. In other deposits, white and black layers are found by themselves or interbedded with silt and silty clays. The cave has a large population of bats and a considerable amount of guano, which pollutes the cave stream (Rimbach, 1968).

EXPERIMENTAL

Samples from two localities were studied, using a Phillips Norelco X-ray diffractometer with a graphite monochromator and copper K- α radiation. The patterns were identified as those of the phosphate minerals crandallite, hydroxylapatite, and taranakite.

A ledge deposit consisted of a white, microcrystalline crust with underlying tan, silty clay (figs. 1 and 2). The white crust was hydroxylapatite, and the tan clay below consisted of hydroxylapatite mixed with quartz and clay minerals.

The basal layer of a wall cavity deposit consisted of white sediment. This material was found to be crandallite. Above the crandallite layer was a black layer with crandallite and hydroxylapatite. Overlying the black layer was a white layer of taranakite and hydroxylapatite. Above this layer was a silty clay capped by a silt layer.

DISCUSSION

The phosphates are probably the result of reactions between the guano, cave waters, bedrock limestone, and/or clay minerals. Guano-laden cave stream waters may have flooded the passage and deposited guano on ledges and in wall cavities, or bat droppings may have accumulated in these locations directly. Clastic sediments were deposited at various times. Taranakite and crandallite are thought to form by reaction of solutions passing through guano with clay minerals, while hydroxylapatite is probably formed by leaching of other phosphates followed by redeposition (White, 1976). The extent of phosphate mineralization in other caves in Missouri is not known. Further work on the Low Water Bridge Cave phosphates is planned.

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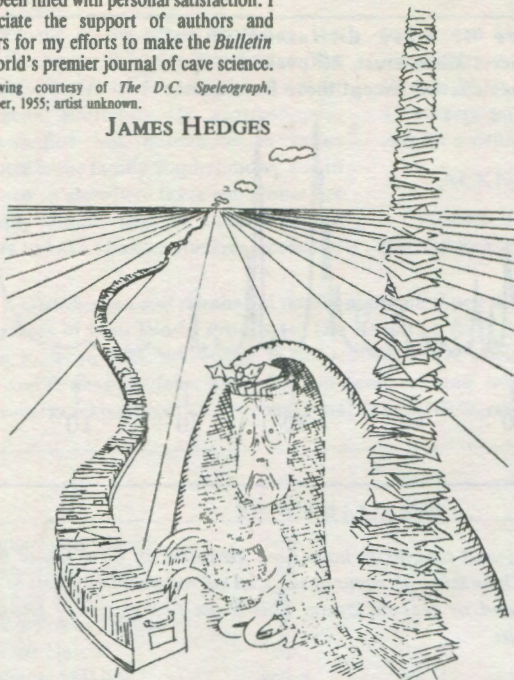
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My years as Editor of *The NSS Bulletin* have been filled with personal satisfaction. I appreciate the support of authors and readers for my efforts to make the *Bulletin* the world's premier journal of cave science.

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The next issue of *The NSS Bulletin* will be produced by Percy 'Doc' Dougherty, who may be reached at (both) Geography Department, University of Kentucky, Lexington, Kentucky 40506 and Geography Department, University of Cincinnati, Cincinnati, Ohio 45221. It has been decided that the *Bulletin* will henceforth become more like a news magazine and less like an archival journal. Dougherty wishes to receive book reviews, reports on scientific meetings, and other items of current interest, in addition to research reports. Remember that a significant proportion of the material must be written at the level of comprehension of the average caver—a liberal arts sophomore.

JH

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