

## THE ECOLOGICAL AND HISTORICAL DETERMINANTS OF CRUSTACEAN DIVERSITY IN GROUNDWATERS, OR: WHY ARE THERE SO MANY SPECIES?

by

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### I - INTRODUCTION

"Why did some taxa colonize the subterranean waters?" This has been the main question of groundwater biology since 1851, when AGASSIZ brought up it for the first time (DANIELOPOL and ROUCH, 1991). Groundwaters have long been considered a special, unfavourable milieu, where few, highly specialized species (the stygobionts) took refuge, prisoners of their habitat (DANIELOPOL, 1992). The answers given to AGASSIZ's question gave rise to many recent debates (STOCK, 1980; ILIFFE, 1986; ROUCH and DANIELOPOL, 1987; BOTOSANEANU and HOLSINGER, 1991; DANIELOPOL and ROUCH, 1991; COINEAU and BOUTIN, 1992). Nevertheless, some of the paradigms listed above are far from being true (DANIELOPOL, 1992). One of them will be considered here: the paradigm of a low species number in groundwaters.

The volume edited by BOTOSANEANU (1986) demonstrated that the diversity of the whole subterranean aquatic fauna is high, and regional faunas may be rich as well (MARGALEF, 1993; ROUCH, 1982). In my recent research on karstic areas and alluvials in Venezia Giulia (north-eastern Italy), I discovered that the subterranean fauna of this area (450 km<sup>2</sup>) includes 80 species of crustaceans (excluding stygoxenes). Nearly 80% of them are stygobionts, the others being stygophiles. Why are there so many species? 32 of them are stygobiont copepods, while there is 1 only stygobiont cladoceran. Why are there so many copepods? Why aren't there more cladocerans? In my opinion these are the correct questions which must be addressed by groundwater ecologists. These questions are not new; they are part of the more general problem of the origin and maintenance of species diversity, a central topic in modern community ecology (GILLER, 1984). Every contribution to the solution of this puzzle is called a "Homage to Santa Rosalia" (HUTCHINSON, 1959).

In 1958, HUTCHINSON, during a visit to Sicily, was driven up Monte Pellegrino, the hill that rises to the west of Palermo. A little below the summit there was a cave, where in the 16th century a stalactite encrusted skeleton associated with a cross and twelve beads was discovered. This was the skeleton of Santa Rosalia (12th century), patroness of Palermo; following HUTCHINSON (1959), "we may take Santa Rosalia as the patroness of evolutionary studies". Just below the sanctuary there was a pond, where two species of the genus *Corixa* (Heteroptera) were living in the water. Watching the corixids, HUTCHINSON asked himself why there should be "two and not 20 or 200 species of the genus in the pond". The more general question of the title of his paper "Homage to Santa Rosalia, or why are there so many kinds of animals?" is the most famous in ecology. TILMAN (1982) wrote that this is "the most fundamental question that an ecologist can ask". Even if PETERS (1991) believed that the problem is intractable, because it will have no precise solutions, HUTCHINSON's (1959) question has been cited in several titles (see BROWN, 1981, and MASSA, 1990 for a review), and inspired the last 35 years of ecological research on species diversity.

Dealing with the origin of species diversity, the present essay aims to be a further homage to Santa Rosalia. Crustaceans are used as a reference group, because they are the most widespread (BOTOSANEANU, 1986) and numerically dominant (PENNAK and WARD, 1986) taxonomic group in groundwaters. Species diversity will be treated as species richness, its more simple formulation (MAGURRAN, 1988). The origin of gamma diversity (regional species richness) will be the main topic of discussion, but the reader is cautioned not to expect a single fully formed answer here. I will only attempt to offer some new approaches to the solution of the problem, hoping to stimulate further research directions in groundwater ecology.

### II - PATTERNS OF SPECIES RICHNESS

#### II. 1 - General overview of stygobiont crustaceans

Table 1 shows the distribution of stygobiont species within all the crustacean orders, following the classification of SCHRAM (1986) modified by FRYER (1987). One of the paradigms of groundwater biology

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<b>CRUSTACEA</b>	<b>N° stygobiont species</b>	<b>N° freshwater species</b>	
			* = scarce
<b>BRANCHIOPODA</b>			** = common
<i>Anomopoda</i>	*	***	*** = exclusive
<i>Ctenopoda</i>		***	
<i>Onychopoda</i>		*	
<i>Haplopoda</i>		***	
<i>Anostraca</i>		***	
<i>Spinicaudata</i>		***	
<i>Laevicaudata</i>		***	
<i>Notostraca</i>		***	
<b>MAXILLOPODA</b>			
<i>Tantulocarida</i>			
<i>Branchiura</i>		***	
<i>Mystacocarida</i>	***		
<i>Ostracoda</i>			
<i>Palaeocopida</i>			
<i>Myodocopida</i>			
<i>Podocopida</i>	**	**	
<i>Copepoda</i>			
<i>Calanoida</i>	*	**	
<i>Cyclopoida</i>	**	**	
<i>Harpacticoida</i>	**	**	
<i>Gelyelloida</i>	***	***	
<i>Misophrioida</i>			
<i>Mormonilloida</i>			
<i>Siphonostomatoida</i>			
<i>Monstrilloida</i>			
<i>Poecilostomatoida</i>			
<i>Thecostraca</i>			
<i>Facetotecta</i>			
<i>Rhizocephala</i>			
<i>Ascothoracida</i>			
<i>Cirripedia</i>			
<b>MALACOSTRACA</b>			
<i>Stomatopoda</i>			
<i>Syncarida</i>	**	**	
<i>Euphausiacea</i>			
<i>Amphionidacea</i>			
<i>Decapoda</i>	*	*	
<i>Mysidacea</i>	*	*	
<i>Lophogastrida</i>			
<i>Mictacea</i>	*		
<i>Isopoda</i>	**	**	
<i>Amphipoda</i>	**	**	
<i>Thermosbaenacea</i>	***	***	
<i>Hemicaridea</i>	*	*	
<b>REMIPEDIA</b>			
<i>Nectiopoda</i>	***		
<b>Total:</b>	<b>16/39</b>	<b>21/39</b>	
	<b>41.03%</b>	<b>53.85%</b>	

Tabl. 1 - List of crustacean orders (following Schram, 1986, and Fryer, 1987); the presence of stygobiont taxa is indicated by a gray shaded label. Totals are reported as number of orders with stygobiont representatives versus total number.

was that the colonization of hypogean habitats is a rare phenomenon (DELAMARE DEBOUTTEVILLE, 1960), and stygobiont species were perceived as few, unusual creatures (DANIELOPOL, 1992). Table 1 shows that this idea is wrong: nearly 41% of crustacean orders have stygobiont representatives in groundwaters. Moreover, six of the orders are exclusively or essentially stygobiont (Mystacocarida, Gelyelloida, Syncarida, Mictacea, Thermosbaenacea, Nectiopoda). This percentage is high, for example in comparison with the orders which have freshwater representatives (54%): groundwater habitats did not constitute a strong evolutionary barrier to crustaceans. Once this barrier was breached (and this happened several times in independent evolutionary lineages), sometimes radiation was extensive. This happened in Syncarida (SCHMINKE, 1981), to a lesser extent in Thermosbaenacea (WAGNER, 1994), and in several families of Podocopida, Cyclopoida (especially *Cyclopidae*), Harpacticoida (especially *Parastenocarididae*), Isopoda and Amphipoda. Some examples are reported in figure 1; it may be observed that several genera of freshwater isopods and copepods colonized independently the groundwater habitats. Furthermore, the more species-rich genera comprise mainly stygobiont species, suggesting that extensive radiation did occur. This is not a general rule; other groups (e.g. cladocerans) contain only few groundwater representatives.

It is rather evident that the success in the colonization of subterranean waters depends mainly on the structure and physiology of the organisms (e.g. exaptation: ROUCH and DANIELOPOL, 1987). Only exclusively planktonic, parasitic and sessile groups have few or no species in groundwaters.

## II. 2 - Species richness

Several generations of biospeleologists considered the subterranean domain poor in resources and hence in species number. BOTOSANEANU and HOLSINGER (1991) wrote that the richer hypogean aquatic systems of the world have "a few tens of hypogean-adapted species - and yet the contrast with the surface fauna is amazing!". This is true for certain taxa; for example insects are exceptionally rare in groundwaters, while in epigean freshwaters they constitute rich species assemblages (an interesting discussion on this subject is reported in BOWMAN, 1981). Crustaceans do not conform to this paradigm; they were extremely successful in the colonization of groundwaters, and in certain areas the number of hypogean species may be equal to or exceed that of epigean ones.

Good data for epigean and hypogean assemblages in the same territory are lacking. This is due to the specialization of researchers, who are often concentrated either on surface or groundwater environments. For this reason a research program was started more than ten years ago in Venezia Giulia (north-eastern Italy and neighbour Slovenia, approximate area 450 km<sup>2</sup>) to obtain good faunistic lists of crustaceans from both epigean and hypogean environments and to study the distributional ecology of crustacean assemblages. The study area comprises several kinds of habitats (pools, ponds, small lakes, streams, sources, interstitial habitats, karstic waters in the vadose, amphibian and phreatic zones) and includes karstic areas (45% of the territory), alluvial plains (30%) and marmous-arenaceous hills (25%). The details of this study will be referred elsewhere (STOCH, in prep.; STOCH and DOLCE, 1994). I have summarized some preliminary results in table 2. The species richness in epigean water bodies is high when compared with those found in other areas in the temperate zone, but the number of species in groundwaters (stygophiles + stygobionts) is still higher. Similar numbers of stygobiont crustaceans were found in other well known karstic areas (Postojna-Planina cave systems: SKET, 1979; BRANCELJ, 1986, 1987), and in few other regions (BOTOSANEANU and HOLSINGER, 1991).

The species richness of a territory is closely related to sampling effort. Previous detailed surveys in Venezia Giulia (STAMMER, 1932) highly underestimated species numbers. REID (1992) recently reported that increased sampling in North American groundwaters "is revealing the extent of present taxonomic ignorance of the faunas of such habitats". A comparison of benthic copepod faunas shows that fewer than half as many species are known from North America as from Europe (REID, 1992). In the stygobiont family *Parastenocarididae* the equivalent proportion is less than 10%! The conclusion that North America has a very poor copepod fauna is erroneous. The increase in the rate of description of new taxa in North American groundwaters is very high (REID, 1992), indicating that the discrepancy is due to a lack of taxonomic studies. Even in the well known European fauna several species are likely to be described in a near future, but the rate of increase is much lower than in North America. In Venezia Giulia, a fairly well investigated area (STAMMER, 1932), at least twelve species of stygobiont crustaceans new to sciences have been discovered during my research.

The rate of increase in species number of stygobionts can be visualized using Steyskal's curves (STEYSKAL, 1965), and may be high (fig. 2). As figure 3 clearly shows, the total rate of increase in species description is due to stygobionts. Species description rates differ within taxa; for example, amphipod species in the stygobiont genus *Niphargus* s.l. have slower rates of increase, and most of the existing species seem to be known (fig. 2). Nevertheless, as the historical data clearly show, increases in the rates of discovery are to be expected when new specialists begin to work, or new sampling and taxonomic techniques are performed. An attempt to estimate the total number of troglobites in the world was made by CULVER and HOLSINGER (1992), but their numbers could be underestimated due to the increasing rate of discovery of sibling species in crustaceans (COBOLLI SBORDONI *et al.*, 1990).

Habitats	Number of species
Pools and Ponds	29
Lakes	31
Sources	31
Brooks	31
Alluvials	19
Hypothelminorheic zone	15
Caves (vadose zone)	14
Caves (amphibian zone)	14
Caves (phreatic zone)	47

TAXA	Epigean	Stygobiont	% stygobiont
<i>Cladocera s.l.</i>	18	1	5.26
<i>Copepoda</i>	37	33	47.14
<i>Ostracoda</i>	15	4	21.05
<i>Isopoda</i>	3	7	70.00
<i>Amphipoda</i>	5	16	76.19
<i>Bathynellacea</i>	0	2	100
<i>Thermosbaenacea</i>	0	1	100
<i>Decapoda</i>	1	3	75.00
Totals (141 species)	79	67	47.52

Species numbers	Cladocera excluded	Cladocera included
Species number in epigean environments	65	83
Species number (stygophilic+stygobiont) in groundwaters	82	83
% stygobitic/(stygophilic+stygobiont)	80.25%	79.52%
% stygophilic/epigean	26.15%	20.50%
% stygobiont/total	52.85%	46.48%

Percent similarity of stygobiont species within habitats	Alluvials	Hypoth. z.	Vadose z.	Amphibian z.	Phreatic z.
Alluvials	***	2	2	1	6
Hypothelminorheic zone	16.7	***	1	2	1
Caves - vadose zone	9.5	6.3	***	1	1
Caves - amphibian zone	3.7	13.3	4.8	***	5
Caves - phreatic zone	12.5	2.1	2.2	12.5	***
Total number of stygobiont species	16	6	10	12	37

Tabl. 2 - Epigean and hypogean species richness in various environments in Venezia Giulia (northeastern Italy and southeastern Slovenia).

These facts demonstrate that our faunistic and taxonomic knowledge of groundwater organisms is rather scarce, and some considerations follow:

- 1) species richness of stygobiont crustaceans is highly underestimated in several areas;
- 2) complete species lists are scarce, and, when available, obtained using different sampling efforts and techniques: comparisons may be difficult or impossible;
- 3) the species reported in the treatise edited by BOTOSANEANU (1986) are mainly stygobiont; we have few data on stygophiles and stygoxenes: these data often are omitted from species lists, but are needed to formulate a correct theory of hypogean species diversity.

For these reasons, patterns of  $\beta$  - diversity in groundwater communities are poorly understood. Obvious biogeographical statements are that stygobiont species are scarcer in glaciated areas (HUSMANN, 1956; CULVER, 1982; JUBERTHIE, 1989; STRAYER, 1988; HOLSINGER and LONGLEY, 1980; RUFFO, 1982; WÄGELE, 1990; HOLSINGER, 1994) and tropical caves (MITCHELL, 1969; SBORDONI, 1994), where hypogean communities seem to be poor. This is likely to be true (even if more data are needed from tropical caves: ROUCH and DANIELOPOL, 1987, did not agree with this opinion), but our knowledge on the non-stygobiont component of the subterranean fauna is too scarce to support these views.

### II. 3 - Dispersal abilities

Another paradigm in groundwater biology regards the low dispersal abilities of stygobionts, and subterranean animals were considered like "prisoners in an inhospitable habitat" (DANIELOPOL, 1991). This concept is wrong. DANIELOPOL (1992) demonstrated that meiobenthic crustaceans disperse and colonize new habitats depending on their ecological tolerances and preferences, and many cases of rapid colonization of newly formed alluvial sediments (BOTOSANEANU and HOLSINGER, 1991, give several good examples) or lava tubes (ILIFFE, 1976; PECK and FINSTON, 1993) by stygobiont species are reported. If it is true that many stygobionts have small ranges (WÄGELE, 1990; HOLSINGER, 1994), several others have a broad distribution: examples are reported in ROUCH and DANIELOPOL (1987), STOCH (1987), PESCE (1985), HENRY (1976), MAGNIEZ (1976). Some species of *Parastenocaris* are surely present in the whole Palearctic region (REID, in litt.), as well as some ostracods (ROGULJ *et al.*, 1993).

The large distribution of these species may be due to a lack of taxonomic studies; furthermore, sibling species may exist. I encountered several such cases in my revision of the *Diacyclops languidoides* - complex (cyclopoid copepods); nevertheless, the wide distribution of some species was established. This fact confirms that aquatic species have larger distributions than terrestrial ones (CULVER, 1982), and may have high dispersal abilities, at least in some groups.

## III - ECOLOGICAL DETERMINANTS OF SPECIES RICHNESS

Species richness is determined by several environmental and biotic factors (BROWN, 1988; RICKLEFS and SCHLUTER, 1993), which can interact in a complex way. I will deal here briefly with four main topics which may be relevant in groundwaters.

### III. 1 - Habitat heterogeneity

Heterogeneous physical environments should contain more complex communities and hence maintain a higher species diversity than simply structured habitats. Several studies confirm this topic (see a review in BELL *et al.*, 1991). Recent researches on groundwater systems indicate that the structure of these environments is more complex than was earlier presumed (DANIELOPOL and ROUCH, 1991).

The interstitial habitats of alluvial sediments have a complex spatial structure. DANIELOPOL (1991), MARMONIER (1985, 1988), ROUCH (1988, 1991) and ROUCH and LESCHER MOUTOUÉ (1992) clearly demonstrated the patchiness of these kinds of habitats. More recently YACOUBI-KHEBIZA *et al.* (1994) discovered a high correlation between coarse grain-size content and the richness of stygobiont taxa. A high degree of heterogeneity can be found in karstic environments as well (ROUCH and BONNET, 1977; HOLSINGER and LONGLEY, 1980; GIBERT, 1986; STOCH, 1992). A recent research on karstic and interstitial waters in north-eastern Italy and Slovenia (STOCH, unpubl.) clearly show that different habitats have different species richness (Tabl. 2).

Nevertheless, these differences as well as those reported by previous authors, may be explained by other determinants of species diversity (environmental stability and resources supply), which interact with habitat heterogeneity in a complex way.

### III. 2 - Area

The well known species - area relationship (MACARTHUR and WILSON, 1967; HART and HORWITZ, 1991) suggests that area per se may be important in determining species richness in groundwater communities.

WILLIAMSON (1988) stated that the causes of species - area effect are rather simple. Following

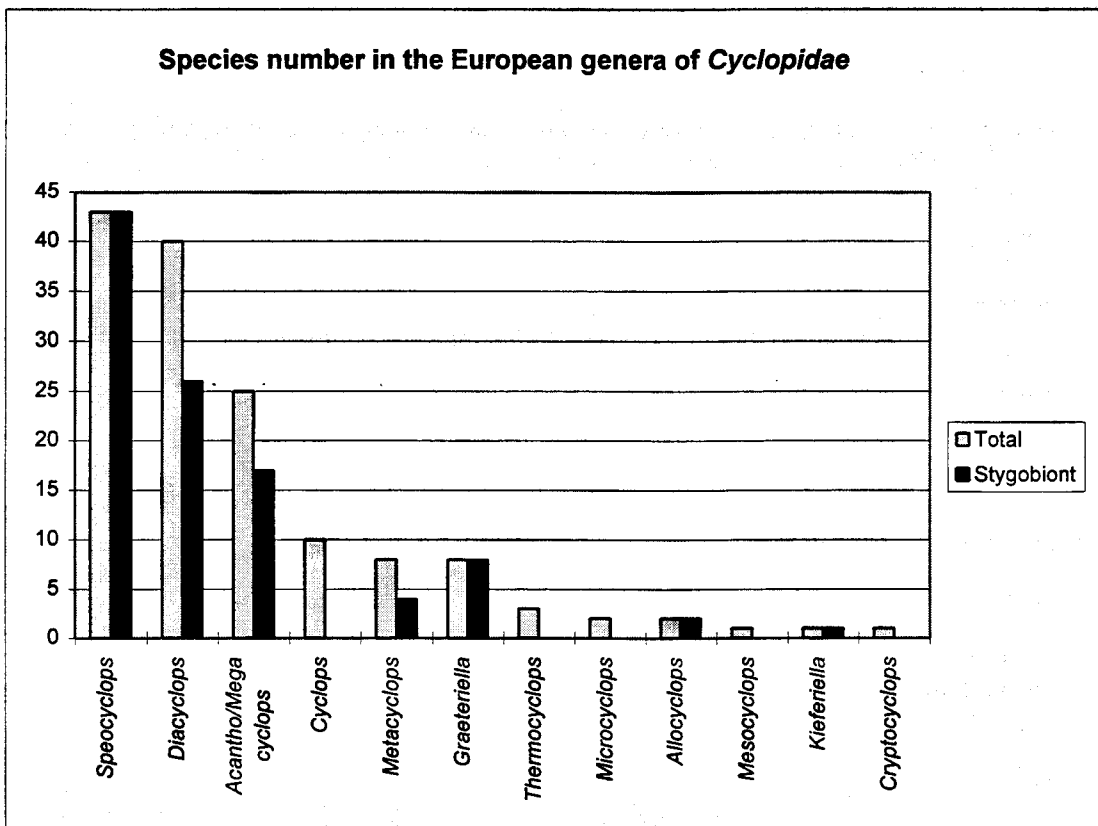
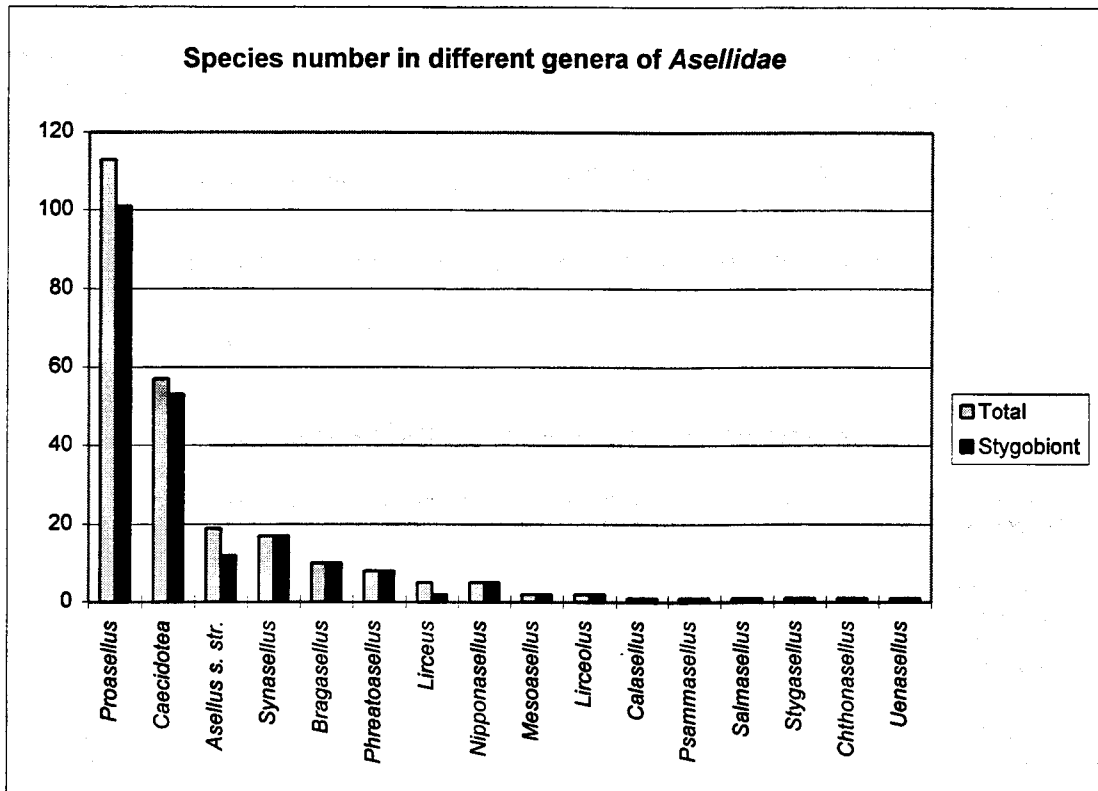


Fig. 1 - Species number distribution in the genera of asellid isopods and European cyclopid copepods.

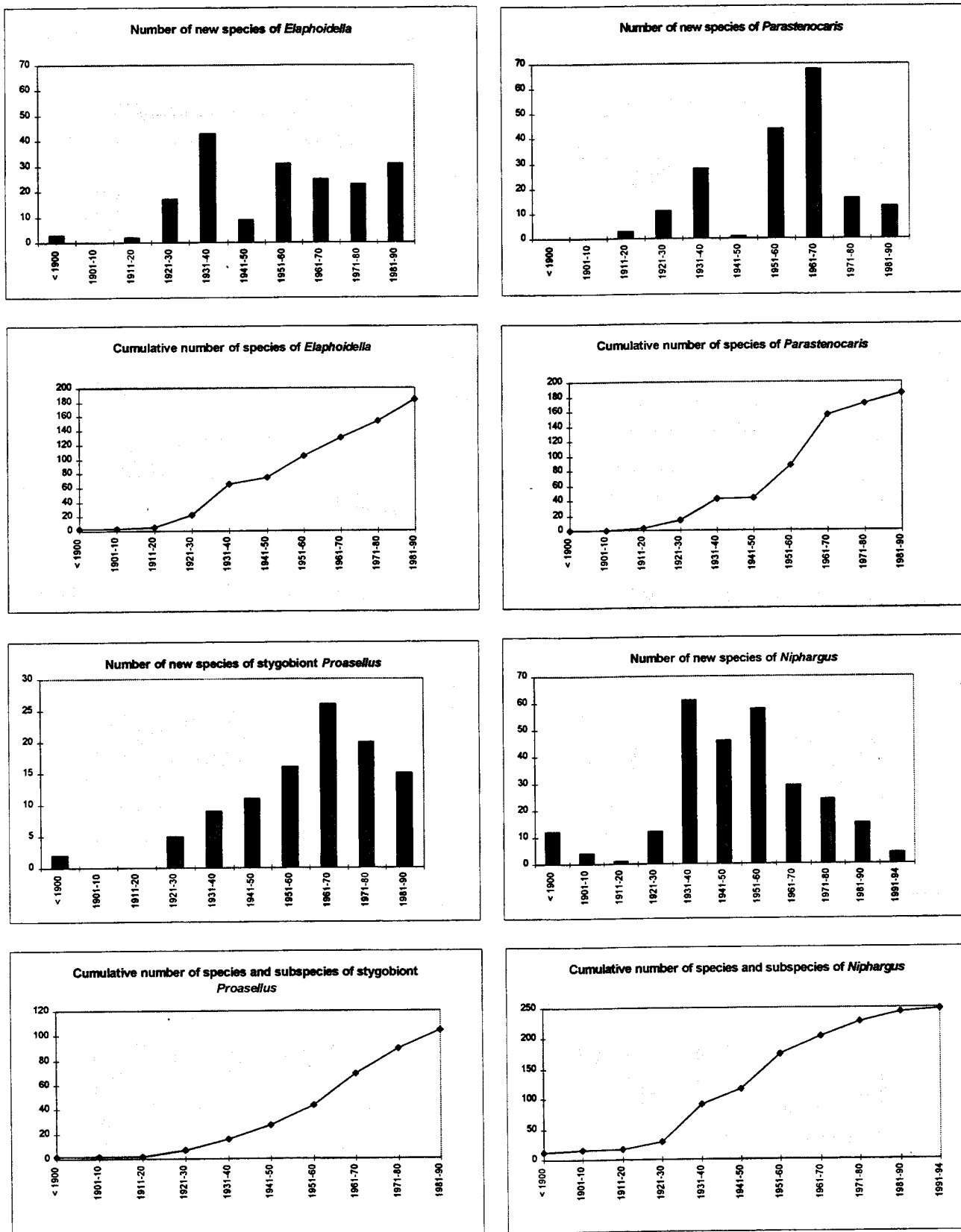


Fig. 2 - Description of new species of harpacticoid copepods (*Elaphoidella* and *Parastenocaris*), isopods (*Proasellus*) and amphipods (*Niphargus* s.l.); linear graphs are Steyskal's (1965) curves.

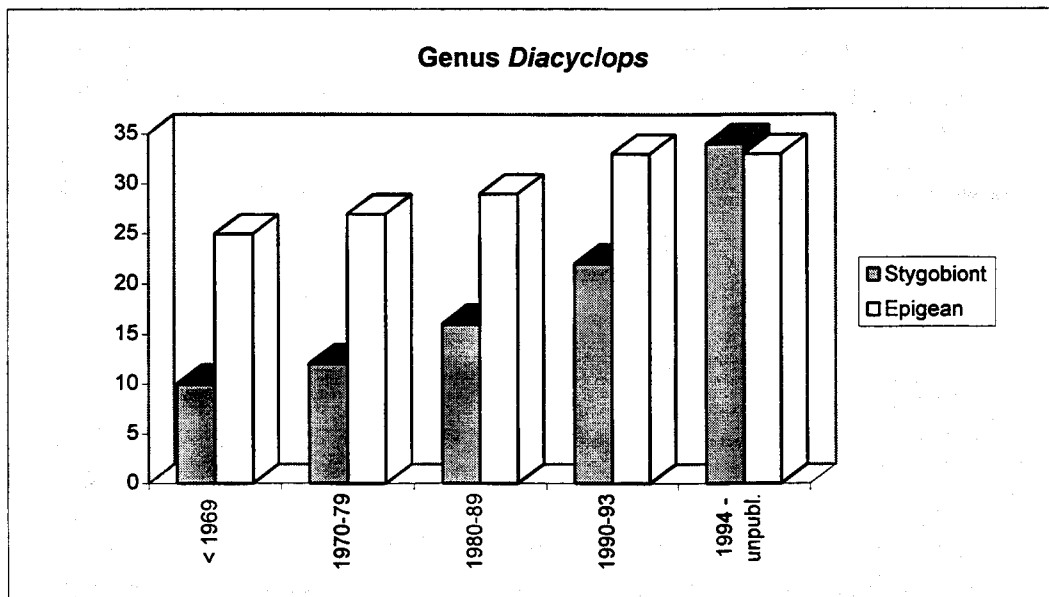
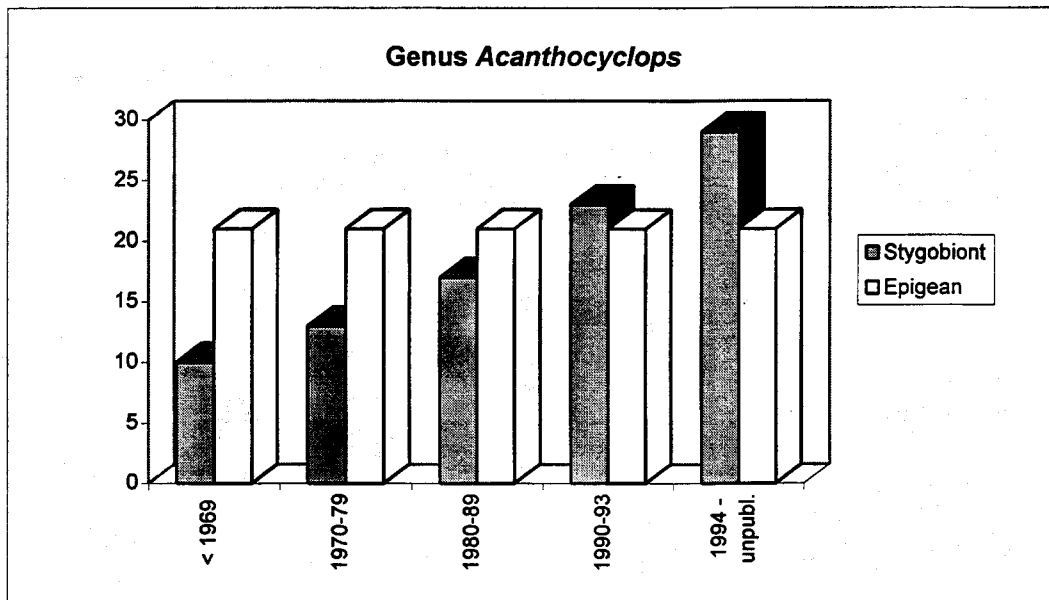
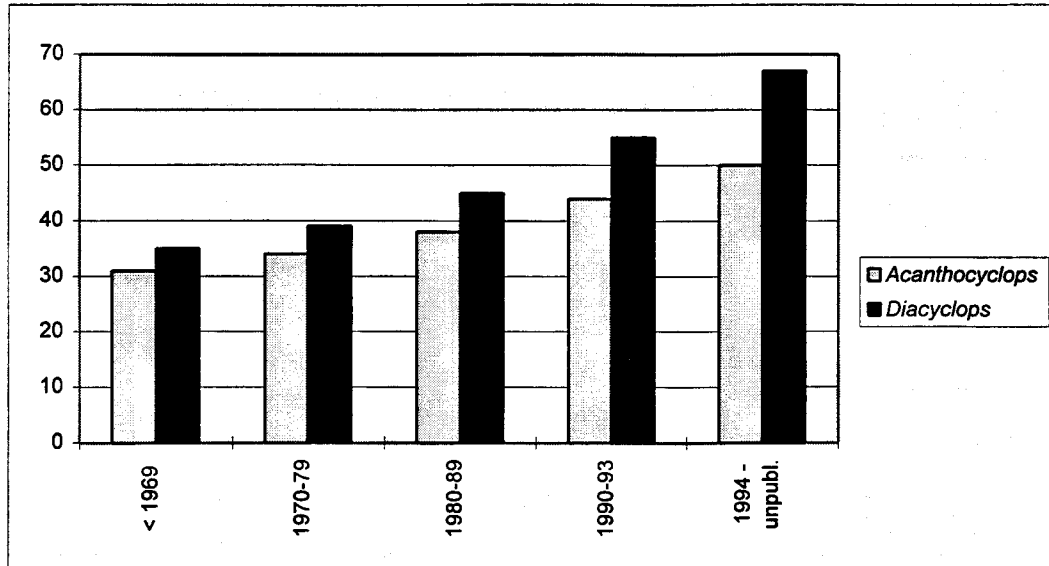


Fig. 3 - Cumulative number of species of cyclopoid copepod genera *Acanthocyclops* and *Diacyclops*.



WILLIAMSON, in small areas passive sampling effects are important, while in large areas the effect of habitat heterogeneity will take over: larger areas are likely to be more heterogeneous than smaller ones and hence have more species. For this reason area per se could have little or no effect on species diversity, and the theory of island biogeography (MACARTHUR and WILSON, 1967) is probably not helpful in explaining the species-area effect. Furthermore, it is probable that cave communities do not conform to the equilibrium model of MACARTHUR and WILSON (1967), for at least two reasons.

First of all, caves are not true islands, but "windows" on a large karstic hydrographic system, even if an archipelago-like structure of cave systems has been envisaged by some authors (JUBERTHIE, 1989; MINELLI and MANNUCCI MINELLI, 1978). The application of the island biogeography model to caves failed (VILLEUMIER, 1973; CULVER, 1982). MINELLI and MANNUCCI MINELLI (1978) applied the principles and methods of island biogeography to the study of three cave systems, and concluded that the importance of area is subordinated to that of resource availability; their data relating terrestrial species richness and cave size might be strongly influenced by passive sampling. This explanation applies to the correlation species - area reported in CULVER (1982) for aquatic species. The second reason is the lack of species turnover. CULVER (1982) stated that "the number of species is not an equilibrium, but is rather the unique result of the history of the area".

The data cited above refer to cave communities. As regards interstitial habitats, we simply have no reliable data to accept or refuse the area effect. However, a limited species turnover seems to be a general rule in nature, and the importance of the theory of island biogeography in explaining the observed patterns of species diversity may be scarce. As WILLIAMSON (1989) wrote, the theory is probably "true but trivial".

### III. 3 - Environmental stability

Species diversity should increase with environmental stability. Stable conditions allow evolution of finer specializations, whereas fluctuating environmental variables demand broad tolerance limits favouring generalists and *r* strategists (MACARTHUR, 1972; PIANKA, 1978; GILLER, 1984 among many others). The paradigm of environmental stability in subterranean waters (GINET and DECOU, 1977) has lost part of its importance. DANIELOPOL (1991), studying the spatial distribution of interstitial crustaceans in alluvial sediments, concluded that hypogean fauna normally lives in the superficial sediment layer, which is a fluctuating environment. Karstic waters may have fluctuating environmental parameters as well, at least in the vadose zone, where the degree of water saturation of microfissures varies greatly throughout the year (DELAY, 1968; PLESA, 1972; ROUCH, 1968).

The relationship between environmental stability and species diversity may not be a linear one; the intermediate disturbance hypothesis (CONNELL, 1978) predicts that a greater biotic diversity will be maintained in communities subjected to intermediate levels of disturbance than in those undergoing either greater or less perturbation. In this case, more stable communities will not have the greatest diversity. This hypothesis was successfully applied to lotic ecosystems (WARD and STANFORD, 1983), and is consistent with diversity patterns observed in streams and rivers. The possibility of application to groundwater ecosystems is still unexplored.

More important than stability seems to be environmental predictability. If some parameters fluctuate in a regular and predictable way, organisms may evolve some degree of dependence and specialization on temporal patterns of resource availability, enhancing diversity. A high correlation has been discovered among resource availability and reproduction and/or population fluctuations in stygobiont crustaceans (GIBERT, 1986), considering that an increase in resource availability in groundwaters depends on the external patterns of precipitations. ROUCH (1988) and ROUCH and LESCHER MOUTOUÉ (1992) did not find clear examples of seasonal species successions in their research on interstitial crustaceans. The role of environmental predictability as a determinant of species diversity in these studies remains undetected.

### III. 4 - Productivity and amount of resources

Species richness should increase with the amount of resources. In oligotrophic habitats, foraging animals should have wider diets, but in more productive habitats, greater resources availability can lead to increased specialization, and hence support more species. Thus increased productivity should lead to a higher species diversity. A relationship between species richness and productivity in caves has been found (SBORDONI, 1994; MINELLI and MANNUCCI MINELLI, 1978; POULSON, 1992). POULSON and CULVER (1969) and POULSON (1992) stated that abiotic factors are primary, productivity is secondary, and biotic interactions are tertiary determinants of species diversity in Mammoth Caves terrestrial ecosystems. The differences of species found in stream habitats of the same cave are partially attributed by POULSON (1992) to how competition is modulated by food supply. There are some problems with this model; first of all, it predicts that the values of species diversity in hypogean environments should be lower than those found in epigean, more productive communities; this is not always the case (ROUCH, 1982).

The subject has been extensively reviewed by TILMAN (1982). Many studies in several kinds of ecosystems demonstrate that the resource richness - species richness curve have a hump, with highest diversity occurring in relative poor resource habitats (ROSENZWEIG and ABRAMSKY, 1993). Spatial heterogeneity and

resource richness are correlated; for this reason the relationship productivity - species richness was not correctly understood by several students. Another important contribution of this theory comes from studies of microcrustacean assemblages in lakes and ponds: species richness decreases with increasing food resources, and a negative correlation with productivity has been found (WETZEL, 1983). Data from groundwater communities are to be re-evaluated in the light of these important patterns.

#### IV - HISTORICAL DETERMINANTS OF SPECIES RICHNESS: THE ADAPTIVE ZONE MODEL

In the following part of the present paper I will attempt to develop a general model to explain the origin of groundwater species diversity. This is a multi-step model, and every part will be discussed in some detail. The model will be referred as the "adaptive zone model" (A.Z.M.), because adaptive zones are a central topic in the following discussion, even if the whole model is more ample and articulated.

The term "adaptive zone" has been used by evolutionists (see for example SIMPSON, 1944; MAYR, 1963), but its interest in general ecological theory is more recent (GILLER, 1984; PIMM, 1991). The term is not new to biospeleology, and extensively used for example by MATILE (1970), HOWARTH (1987), DESUTTER-GRANDCOLAS (1993) and implicit in the "active colonization model" of ROUCH and DANIELOPOL (1987). The "adaptive zone hypothesis" (that diversification is accelerated in new adaptive zones) has been developed in ecological literature by HUTCHINSON (1959), and recently by MITTER *et al.* (1988) and CORNELL (1993).

A related, important term is that of "empty" or "vacant" niches. This is an old one, considering that CUENOT (1892) more than one century ago published a paper entitled "Le peuplement des places vides dans la nature et l'origine des adaptations"; the paper referred to the empty spaces of mines or hypogean water pipes. DELAMARE DEBOUTTEVILLE (1960) used the same term ("place vide"); this concept has been "rediscovered", as many others, by today's theoretical ecologists, and is now being rediscovered another time by biospeleologists and groundwater ecologists. The main problem in the usage of the term "niche" lies in its definition (HERBOLD and MOYLE, 1986). In this paper the niche is not defined on the basis of an organism's characteristics, but in fact in this case a colonist should bring its own niche with it into the new community (PIMM, 1991). The definition I shall use here is that of "habitat" and "trophic" niche (GILLER, 1984).

##### IV. 1 - The model

I shall define the following steps in the model:

1) **Colonization.** Epigeal freshwater species colonize the subterranean domain where they can exploit previous unutilized resources and occupy empty niches. The modalities of colonization, extensively discussed by several authors (ILIFFE, 1986; ROUCH and DANIELOPOL, 1987; BOUTIN and COINEAU, 1990; NOTENBOOM, 1991; COINEAU and BOUTIN, 1992; HOLSINGER, 1994), may be either active or passive. External factors (climatic changes and other stressing situations, as well as subterranean stream captures in karst areas and similar events) may interrupt the genetic flux with epigeal populations. Nevertheless, stressing situations are not considered a primary driving force for colonization, even if under certain circumstances they may enhance colonization rates. New, empty spatial resources are likely to be exploited due to less competition and predation. If the niches to be colonized are not empty, competition may occur. In this case the colonizer is likely to be outcompeted by hypogean species, more successful in hypogean habitats (DANIELOPOL, 1991), even if this may not be the general rule.

At this stage, after a successful colonization, there are two possibilities:

2.1) **First speciation event.** The colonizer has to become genetically isolated from the epigeal populations in order to become a stygobiont. Speciation will be discussed in a paragraph below: it may be a consequence of a founder effect (BARR, 1968), a phenomenon following a genetical bottleneck (WILKENS, 1988) or a gradual one sensu ILIFFE (1986), COINEAU and BOUTIN (1992) or KANE and CULVER (1992). The kind of speciation mechanism is not important for the adaptive zone model to operate. Speciation rates are not correlated with colonization rates, as will be discussed in the next paragraph.

2.2) Speciation does not occur, and the colonizer has to be considered a stygophylic species. In any case, it contributes to the make-up of the groundwater species assemblage.

If speciation took place, two further possibilities open:

3.1) **Radiation.** Rapid phylogenetic diversification is encouraged by the new adaptive zone and this is likely to occur during the karstification process or the deposition of alluvial sediments, or whenever empty niches are available. This concept has analogies with the "adaptive radiation" of evolutionists (SIMPSON, 1944; LARSON, 1989; see also the critiques in MASTERS and RAYNER, 1993). In this context two rather distinct formulations are incorporated under the name "adaptive zone hypothesis" and are as follow:

3.1.1) there may be an adaptive zone diversification via niche differentiation;

3.1.2) diversification of subterranean animals may be promoted by increased opportunities for geographic speciation arising from expanded species ranges (i.e. dispersal) in a new adaptive zone, without requiring niche differentiation.

3.2) Radiation does not occur; in this case an explanation of diversification requires multiple colonization events, and we have to repeat step 1 and 2. Multiple colonizations (already hypothesized by MAYR, 1963, for caves) may be simultaneous or spaced out in time and give rise by vicariance to several species with more or less contiguous ranges (BARR and HOLSINGER, 1985; BOTOSANEANU and HOLSINGER, 1991; COINEAU and BOUTIN, 1992).

Radiation and multiple colonization are not mutually exclusive hypotheses; a combination of the two events is likely to explain many of the observed patterns, as will be discussed in paragraph V.

#### IV. 2 - Sequence of the phases

In the adaptive zone model one of the steps does not imply that the next one must operate. Speciation is not a consequence of colonization and an increase in the rate of colonization is not necessarily followed by increased speciation rates (CARSON, 1987). Generalist colonizers (often *r* strategists) accomplish the expansion of their range due to efficient adaptations to dispersal and, after arrival, to the establishment at the new site. Repeated colonizations into the same site are likely to occur and colonization rates may be high. But generalist colonizers, even if preadapted to the new environment, do not appear to speciate (CARSON, 1987): the efficiency of colonization effectively prevents the accumulation of genetic differences from the source, and a speciation event in this case is unlikely. Following CARSON (1987), stochastic colonization by a founder with only minor preadaptation to the new site is an event conducive to speciation. I think that this topic of genetical ecology deserves further investigations, and must be taken into account by groundwater ecologists, considering the importance of stygophile generalists in groundwater communities (ROUCH, 1986; ROUCH and DANIELOPOL, 1987; DANIELOPOL and ROUCH, 1991; DANIELOPOL, 1992).

As speciation is not an obligatory consequence of colonization, diversification may or may not follow the first speciation event (genetic separation from the epigeal ancestor). CARSON (1987) clearly stated that colonization followed by speciation produces two kinds of endemic species: those that are represented by a single species only (non-speciose lineages), and those that have produced two or more or sometimes many species (speciose lineages). The difference has both ecological and genetic explanations (CARSON, 1987): 1) availability of further open niches (this is not a general rule, following MASTERS and RAYNER, 1993); 2) sufficient spatial isolation so that the evolving subpopulation is not inundated by gene flow from the external population. In my opinion age (period of time since colonization long enough to allow for diversification), dispersal abilities (and hence possibility to expand species range and undergo geographical speciation) and intrinsic properties of taxa must be taken into account as well.

#### IV. 3 - Colonization

Various approaches to different colonization models are reported so extensively by several authors with so many good examples that there is no reason to repeat them here. The reader is referred to ILIFFE (1986), ROUCH and DANIELOPOL (1987), BOUTIN and COINEAU (1990), BOTOSANEANU and HOLSINGER (1991), NOTENBOOM (1991), COINEAU and BOUTIN (1992) and HOLSINGER (1994) for aquatic species, and to JUBERTHIE (1989), HOWARTH (1987, 1991), BELLÉS (1991), ASHMOLE (1993) and PECK and FINSTON (1993) for terrestrial ones.

The term "colonization" in the adaptive zone model means "active colonization" sensu ROUCH and DANIELOPOL (1987). The term "active" is not referred by these authors to the mechanical way used to reach the groundwater environment, and in this context may generate confusion. In this I agree with BOTOSANEANU and HOLSINGER (1991), and I will attempt to avoid this kind of terminology. In the present paper both active colonization and passive transport are allowed. Passive transport may be very common, if this is the preferred way of dispersal of the organism. Colonization has no finalistic implications, and in this sense "active colonization" is not synonymous of "voluntary".

One of the most common questions on colonization addressed by biospeleologists is not "how" epigeal species colonize the hypogean domain, but "why" they did so (BELLÉS, 1991). This is an old question (AGASSIZ, 1851), and is due to the interpretation of the subterranean milieu as a special one (the paradigm of caves as "refugia"). ROUCH and DANIELOPOL (1987) correctly challenged this ingenuous idea, and no one of the ecologists studying other environments addresses this question (see GRAY *et al.*, 1987). If a species invades new habitats as a tentative to exploit a new set of resources, there are no compelling forces to do so. It may be true that, owing to "difficult" climatic conditions, depletion of resources, high competition rates or a strong predation pressure colonization rates may increase, but colonization processes do exist without such stresses. This was clearly demonstrated for terrestrial fauna too by JUBERTHIE (1984), HOWARD (1987, 1991), BELLÉS (1991). Colonization is not performed only by epigeal species; groundwater organisms are active and apparently cognitive subjects (DANIELOPOL, 1991), and the process of dispersal (and hence colonization) of new habitats is a permanent one. This continuous process has been taken in account by several workers (BARR and HOLSINGER, 1985; HOWARTH, 1987; ILIFFE, 1986; COINEAU and BOUTIN, 1992; PECK and FINSTON, 1993, and many others).

## IV. 4 - Speciation

Speciation in subterranean animals has been reviewed by SBORDONI (1982), BARR and HOLSINGER (1985), CHRISTIANSEN (1992), and PECK and FINSTON (1993). Several references are listed in BOTOSANEANU and HOLSINGER (1991).

ROUCH and DANIELOPOL (1987) wrote that the main difficulty with their "active colonization model" was "son inaptitude apparente à expliquer les phénomènes de spéciation"; for this reason, they abandoned the allopatric model in favour of mechanisms of sympatric or parapatric speciation. This opinion was highly criticized by BOTOSANEANU and HOLSINGER (1991) on the basis of the lack of evidence for such kinds of speciation events in subterranean animals. In fact SBORDONI (1982) affirmed drastically that "speciation processes in caves are strictly allopatric". Similarly HOWARTH's (1987) paper, favouring parapatric speciation, was criticized by SBORDONI (1994), and BOTOSANEANU and HOLSINGER (1991) stated that HOWARTH's examples may be better explained using MAYR's (1963, 1988) peripatric speciation model. Several of the debates raised around this subject may be based on wrong assumptions. MAYR (1963) more than thirty years ago discussed allopatric speciation, adaptive radiation and niche shift into adaptive zones without arising any conflict among them. Furthermore, geographical isolates fail to produce new species if they do not find open niches (WRIGHT, 1982; GILLER, 1984; CARSON, 1987; WILKENS, 1992).

While the hypothesis of multiple colonizations (step 3.2 of the adaptive zone model) and that of diversification via dispersal and geographical speciation (point 3.1.2) are congruent with an allopatric model, the diversification via niche differentiation (point 3.1.1) may be open to the same kind of criticism. The allopatric model of speciation has been considered another paradigm of biospeleology (PECK and FINSTON, 1993). BOTOSANEANU and HOLSINGER (1991) wrote that "we know almost nothing about barriers inside the subterranean realm that have often determined spectacular speciation in aquatic groups". They refer probably to the remarkable species flocks of stygobionts (BOTOSANEANU, 1986), already described by DELAMARE DEBOUTTEVILLE (1960: "pulvérisation des espèces"). Species flocks are common in freshwater epigean crustaceans as well (for example in Lake Baikal: BROOKS, 1950; BOXSHALL and EVSTIGNEVA, in press), but their origin is not yet clear, despite a rich literature. MAYR (1963) proposed an allopatric model, while PECK and FINSTON (1993), dealing with tropical troglobites, wrote that "parapatric speciation may be relevant as partial explanations for the origins of some "species swarms" of terrestrial invertebrates on islands". PECK and FINSTON (1993) distinguished two different modalities of origin of troglobites: a "climatic relict hypothesis", related to temperate areas, and a "local habitat shift" supported by evidence in tropical latitudes, which is synonymous with HOWARTH's (1987) "adaptive shift model". This distinction is not clear-cut, at least for three reasons: 1) the two models are not mutually exclusive; 2) there is no reason to consider most of temperate caves stygobionts as climatic relicts (ROUCH and DANIELOPOL, 1987); 3) the different modes of speciation in tropical and temperate caves (parapatric versus allopatric model) are not supported by recent genetic analyses (SBORDONI, 1994).

Most of the models developed to explain speciation in caves invoke founder effect events (BARR, 1968), or periodical bottlenecks in population size (WILKENS, 1988; CULVER, 1982; SBORDONI, 1982; BOTOSANEANU and HOLSINGER, 1991; PECK and FINSTON, 1993). But this is not a general rule because KANE and CULVER (1992) have demonstrated clearly that the colonization may be active, as in the case of *Gammarus minus*, without the necessity of a genetic bottleneck. The hypothesis of the graduality of the interruption of genetic flux proposed by BOTOSANEANU and HOLSINGER (1991) and COINEAU and BOUTIN (1992) perform well in these situations. Furthermore, the clinal patterns observed in adaptive characters in some cave animals (SKET, 1985: *Asellus aquaticus cavernicolus*, *Asellus aquaticus cyclobranchialis*, *Synurella ambulans f. subterranea*) require an explanation of this kind. Niche differentiation and isolation may follow this mechanism.

The conclusions of PECK and FINSTON (1993), as well as those of other authors, can be falsified. MYERS and GILLER (1988) stated that it is impossible to distinguish between sympatric, parapatric and allopatric speciation models observing the pattern alone. Even if sympatric and parapatric speciation models cannot be ruled out completely (OTTE and ENDLER, 1989), SBORDONI (1994) pointed out that genetic analyses demonstrated that their importance in cave habitats might be negligible, both in the tropics than in temperate regions (but we have no data for interstitial habitats). A logical conclusion to these debates was given by BARTON (1988): "...it may not matter much whether divergence is sympatric or allopatric ... The net pattern would then be independent of the original processes".

## IV. 5 - Speciation rates, extinction rates and species diversity

A historical explanation of hypogean species richness in certain areas could be related only to a favourable balance between rates of speciation and extinction.

The high species/genus ratio in some subterranean taxa in temperate regions (*Niphargus*, with more than 200 species, *Stygobromus*, *Proasellus*, *Caecidotia*, *Elaphoidella*, *Speocyclops*, *Diacyclops*), certainly higher than those found in epigean ones, is the single most important factor that contributes to the impression of a high speciation rate in these groups. However, this explanation needs not to be true. The epigean-hypogean interface

is a barrier, which causes few colonists to contribute to the make-up of a hypogean community. In epigeal environments, a larger number of colonists contribute to the final biota, and results in a lower species/genus ratio: consequently it is premature to conclude that speciation in hypogean environments is faster than in epigeal ones.

On the other hand, it is reasonable to suppose that extinction rates are very slow, at least in certain kinds of hypogean habitats, where environmental conditions are more stable. Phylogenetic diversification into new adaptive zones might also occur through decreased rates of competitive extinctions of new reproductive isolates (CORNELL, 1993). As concerns direct measurements of extinction rates in hypogean populations, we simply have no data (CULVER, 1982, CULVER *et al.*, 1991, and ROUCH, 1986, examined competitive interactions among stygobiont crustaceans)

Another interesting topic is the relationship between speciation rates and species diversity (GILLER, 1984). If it is true that open niches are required for speciation (but this point is criticized by MASTERS and RAYNER, 1993), speciation rates should decrease with increasing diversity; on the other hand, the more species there are, the greater the number of isolates formed by geographical barriers, and the more quickly new species are formed. In this case speciation rate is an increasing function of diversity. However, the relationship is not a simple one. High speciation rates lead to high species diversity, which controls speciation rates in one of the two ways. Either way, diversity is predicted to reach a steady state when the community is saturated (GILLER, 1984; RICKLEFS and SCHLUTER, 1993). We do not know if groundwater communities are saturated; certainly they are not in some areas. ROUCH (1982) wrote: "le milieu souterrain aquatique des zones tempérées doit être considéré comme non saturé en espèces". Studies on this topic require further investigations.

#### IV. 6 - Habitat specialization

Specialization is requested by adaptive zone radiation via niche differentiation (hypothesis 3.1.1) to allow coexistence with each species occupying a small subset of the total niche space. In this case diversity would be a function of the total range of resources and the degree of specialization of species to part of that range.

A high degree of specialization is to be expected in communities inhabiting stable environments. K selection should be strong, and, if competition occurs, specialists should be at competitive advantage. On the contrary, populations in epigeal, variable environments (such as streams, lakes and ponds) are often less stable and in this case selection for rapid reproduction (*r* selection) is strong. Epigeal species often have larger niches, and hence are more generalist, while hypogean species might be more closely packed. Even if some hypogean habitats are not stable (DANIELOPOL, 1992), and competition may be low in unsaturated communities (ROUCH, 1982), subtle specializations to the subterranean lifestyle are known (SBORDONI, 1980; BOTOSANEANU and HOLSINGER, 1991; MARGALEF, 1993; YACOUBI-KHEBIZA *et al.*, 1994).

These subtle specializations require natural selection. ROUCH and DANIELOPOL (1987), DANIELOPOL and ROUCH (1991) and ROGULJ *et al.* (1993) pointed out that the troglomorphic traits can develop independently of the environmental conditions (neutral theory). Nevertheless KANE and CULVER (1992) recently demonstrated that both the enhanced and regressed specialized troglomorphic features of cave populations of the amphipod *Gammarus minus* have been strongly influenced by natural selection, and the role of neutral mutations is negligible. Further discussions on the topics of specialization and of adaptation are found in SKET (1985), DANIELOPOL and ROUCH (1991), WILKENS (1992), MARGALEF (1993).

Habitat diversity (DANIELOPOL and ROUCH, 1991) and habitat specialization must lead to strong differences in species composition of assemblages inhabiting different habitats and this has been discussed in the first part of the present paper. Even if some stygobionts can live in several kinds of habitats (for example the isopod *Proasellus cavaticus*: HENRY, 1976; the ostracods *Cryptocandona kieferi* and *Fabaeformiscandona wegelini*: ROGULJ *et al.*, 1993; the amphipod *Niphargus wolffi*: KARAMAN and STOCH, in prep.; the copepod *Diacyclops antrincola*: STOCH, 1987a) and can be considered generalists (see DANIELOPOL and ROUCH, 1991, for further examples), most of the stygobionts have well defined patterns of distribution. As already stated in the first part of the present paper, different kinds of hypogean habitats may be inhabited by completely different, well adapted stygobiont species (see Tabl. 2).

Following ELDREDGE (1976) and CORNELL (1993), diversification can be promoted by habitat specialization alone, which encourages isolation and divergent selection imposed by each habitat, without requiring open niche space as a prerequisite to diversification. This is an alternative to the adaptive zone hypothesis, but it remains untested. The speciation models required to explain this process are strictly sympatric (DIEHL and BUSH, 1989), and the term "microallopatric" must be avoided, considering that true extrinsic barriers between habitats do not exist.

Another interesting topic is specialization for resource exploitation within a single habitat. This kind of specialization was considered unlikely to occur in groundwaters. DELAMARE DEBOUTTEVILLE (1960) first of all wrote about the "conservation of lifestyle" in interstitial waters, and this concept implies no trophic niche differentiation. Regarding food specialization, ROUCH and DANIELOPOL (1987) stated that "il est évident qu'en raison même des caractéristiques de l'environnement, les animaux souterrains sont des généralistes polyphages plutôt que des spécialistes". YACOUBI-KHEBIZA *et al.* (1994) suggested nevertheless a high degree of specialization of stygobiont crustaceans to different grain-sizes within the same habitat, and hence in the

allocation of spatial resources and food exploitation. High specialization in the allocation of trophic resources was observed in terrestrial cave populations by SBORDONI (1980).

My observations on several closely related, coexisting cyclopoid copepods of the genera *Acanthocyclops* and *Diacyclops* (STOCH, unpubl.) show little variation in the mouth appendages, indicating a low food specialization. However, coexisting species may differ in size, indicating efficient food resources partitioning. This is not a general rule, because other stygobiont cyclopoids can display a certain degree of variability in mouthpart structure (REID and STRAYER, 1994). In epigeal species flocks the variation of mouthpart structure may be strong, as in the *Acanthocyclops-Diacyclops* complex in Lake Bajkal (BOXSHALL and EVSTIGNEEVA, in press, called it "hypervariation"), or simply non-existent, as in the *Moraria (Bajkalomoraria)* species flock in the same lake (BOXSHALL and EVSTIGNEEVA, in press). This fact suggests that size and structure of mouthparts are not the only features which indicates food specialization. In marine benthic harpacticoids, the differences among coexisting sibling species of the genus *Tisbe* are not based on morphology, but on feeding behaviour, swimming behaviour (and hence in the use of spatial resources) and reaction to predators (MARCOTTE, 1983). This seems to be a general rule for congeneric benthic copepods, but its importance in stygobiont species is unknown.

#### IV. 7 - Age of colonization

Communities of more recent origin should not have evolved as much interspecies adjustment or speciation as older ones and, as a result, they are predicted to be less rich (OTTE, 1989; GILLER, 1984; PUTMAN, 1994). In other words, older karstic areas and hydrographic basins are more likely to have more species than younger ones, other things being equal. But in groundwater environments other things are not equal. Habitat heterogeneity changes with age, and geomorphic processes modify the hypogean environments (lowering of water tables, erosion, siltation, glaciations, evolution of stream morphology and many others). As a consequence, the groundwater communities inhabiting dissimilar areas may have different evolutionary rates.

Despite these facts, older karstic areas might have a higher number of stygobionts as compared to younger ones (JUBERTHIE and DECU, 1994). Groundwaters in previously glaciated areas are poor in stygobionts as already discussed, but may have a high species richness of stygophiles (HUSMANN, 1956; STRAYER, 1988; and others).

#### V - A TEST OF DIVERSIFICATION IN ADAPTIVE ZONES

Diversification may or may not follow the first speciation event after colonization. A test can be performed to verify if the subterranean domain increases diversification as compared to the epigeal habitats (e.g. step 3.1 of the adaptive zone model), following MITTER *et al.* (1988). This test is performed by comparing the species richness of two sister groups, one of which occupies the epigeal environments and the other the hypogean ones of a study area. The two groups must constitute a monophyletic unit; in this case they are of equal age. The hypogean group must have developed key innovations that have allowed it to exploit the new adaptive zone, and hence it must contain stygobiont species. If the adaptive zone model via radiation is correct, the hypogean group should be more species-rich than the epigeal one, subject to the constraints that the sister groups of a given lineage are dominant clades in both zones (CORNELL, 1993). The method may be improved by examining multiple lineages with independent evolutionary history. This test implies that simple counts of relative diversities in epigeal and hypogean environments do not suffice for this purpose because they do not control for the possibility that there has been more time for diversification in one of the two environments. For this reason the test must be performed using cladistic methodologies. A failure of the test in spite of a high hypogean species diversity would be a strong support for the multiple colonization model (step 3.2).

Unfortunately, we have no good data in hand to perform an unequivocal test. Some examples of phylogenetic reconstructions are reported in figure 4, and others are listed below. Evidence is given for both radiation (hypothesis 3.1) and multiple colonization patterns (hypothesis 3.2), even if the results must be handled with circumspection.

In several phylogenetic reconstructions (NOTENBOOM, 1988; HOLSINGER, 1992; WAGNER, 1994; BOUTIN, 1994) no epigeal species are taken in account because the colonization of groundwaters was too ancient. These patterns are open to speculation, but do not constitute a good test: adaptive radiation and multiple colonizations cannot be ruled out nor accepted (the dendrogram of NOTENBOOM, 1988, at a generic level suggests that radiation did occur in the genus *Pseudoniphargus*).

An important phylogenetic tree (fig. 4) for some species of the genus *Niphargus* and related, epigeal genera, was reported by BULLINI and SBORDONI (1980) and gives us several useful informations:

- 1) the genus *Niphargus* s. str. is probably distinct from the genus "*Orniphargus*" (even if SKET, 1990, raised some doubts on this fact), suggesting a double colonization of the subterranean domain;
- 2) the genus *Niphargus* s. str., which has to be considered monophyletic, is known to be dramatically more species rich than the epigeal Gammaridae, suggesting extensive radiation;
- 3) the closely related species of the genus *Niphargus* in peninsular Italy are linked in such a way that a dispersal followed by vicariance events of speciation (hypothesis 3.1.2) might explain the observed pattern.

This hypothesis is congruent with the ideas expressed in the papers of SBORDONI *et al.* (1979) and SKET and NOTENBOOM (1993). These latter authors performed a phylogenetic analysis of the *Niphargus transitivus* - group: dispersal through interstitial waters followed by vicariance events is a simple explanation of the phylogenetic and distributional patterns.

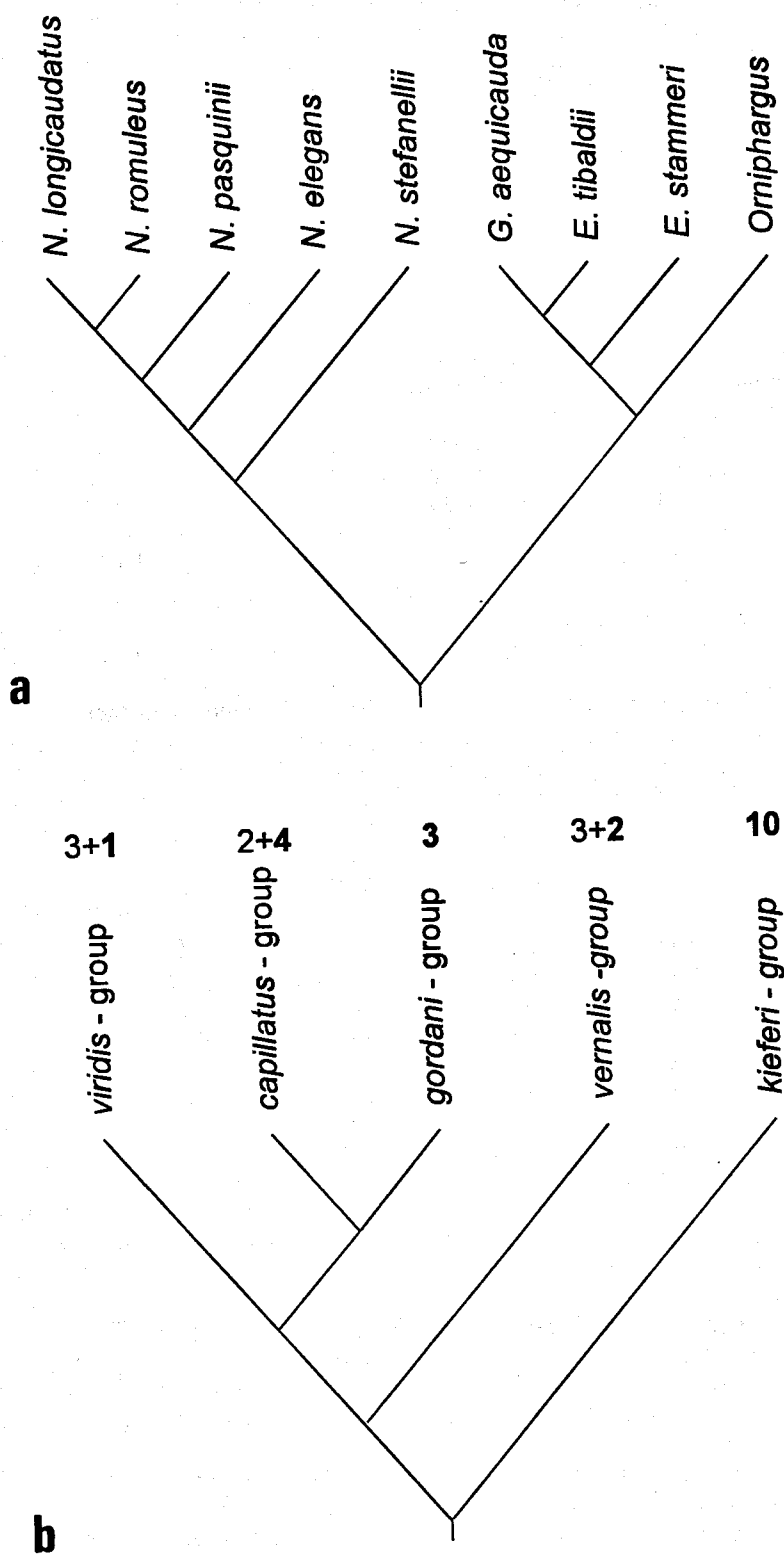


Fig. 4 - Phylogenetic relationships of (a) some gammarid and niphargid species from peninsular Italy (from Bullini and Sbordoni, 1980) using biochemical data, and (b) cyclopoid species from Europe (Stoch, unpubl.) using morphologic data. Phylogenetic relationships of the species-groups in the genus *Acanthocyclops* (Stoch, unpubl.) represented by a consensus cladogram of nine trees (Camin-Sokal method, Phylip package). The numbers represent epigean plus stygobiont (bold) species within the group in Europe. Note: cladograms do not take in account tree-length.



Another pattern is revealed by the copepod genera *Speocyclops*, *Acanthocyclops* (fig. 4) and *Diacyclops*, closely related each other, in which a better explanation requires a sequence of multiple colonization events and extensive radiation. Radiation is evident in the monophyletic genus *Speocyclops*, which is the most species-rich genus in Europe, where it is represented by more than forty stygobiont species. Within the *Diacyclops languidoides* group, there seems to be a mixture of speciation events due to geographical isolation (where probably a differentiation in mating behaviour did occur) and niche differentiation (STOCH, unpubl.).

The pattern of phylogenetic evolution of the genus *Monolistra* given by CACCONE *et al.* (1982) was supposed to agree with a refugium model, or a regression model evolution (sensu STOCK, 1980; STOCH, 1987), where epigeal, marine ancestors of the genus *Sphaeroma* invaded subterranean groundwaters during the Miocene salinity crisis. This is probably wrong. SKET (1961, 1986) invoked a speciation in epigeal environments, and this hypothesis is supported by several facts. First of all, a direct marine origin is incongruent with the distributional patterns of species groups. Multiple colonizations of groundwaters from epigeal freshwaters and extensive radiation may explain the distributional (SKET, 1986) and phylogenetic (STOCH, unpubl.) patterns in this genus. The salinity crisis probably interrupted the genic flux between a freshwater species and the marine ancestor, but is in no way the compelling force of the colonization of groundwaters. In this case the intermediate stage (freshwater ancestor) disappeared, and we cannot know how many freshwater species were present.

Unfortunately, the studies cited above as well as the test proposed by MITTER *et al.* (1988) give no unequivocal results in most cases, because multiple, simultaneous colonizations of contiguous areas by a single epigeal species are difficult to be distinguished from a radiation event, especially if several epigeal species disappeared following unfavourable climatic changes in the epigeal environment. This can bias the results toward an acceptance of radiation. A second problem regards the scale used for the analysis. The area has to be the evolutionary theatre of the whole group under consideration, because the exclusion of some species may create problems to the phylogenetic reconstruction: this was not the case for some of the examples discussed above. Furthermore, it is difficult to find out epigeal and hypogean species groups forming monophyletic units at a regional scale. Another problem is due to the difficulties to obtain good cladograms using stygobiont species (NOTENBOOM, 1988; SKET and NOTENBOOM, 1993). It is probable that more sophisticated biochemical or morphological studies may give a more precise answer to which mechanisms are underlying the observed diversity pattern in local situations.

As CHRISTIANSEN and CULVER (1987) clearly showed for collembola, there is no reason to suppose a unique scenario even for a restricted taxonomic group. The phylogenetic reconstructions examined above does not allow to make a choice between different hypotheses, but suggest that a combination of multiple colonization (hypothesis 3.2) and radiation (hypothesis 3.1) events is likely to give a better explanation of the observed patterns.

## VI - CONCLUSIONS

This paper begins with a further "Homage to Santa Rosalia" (HUTCHINSON, 1959). Can we answer the question: "Why are there so many species of groundwater animals?" In my opinion, to a certain extent, we can. The number of species in groundwater environments is determined by both ecological and historical factors. Following GILLER (1984): "A complete explanation of species diversity would need to link biotic processes and environmental variables to explain how patterns of immigration, speciation, competitive exclusion and extinction produce the observed patterns". We are clearly far away from there. However some facts seem to be well established, and we know that: 1) species diversity in groundwater communities is built up by generalists and specialists; 2) the number of potential niches in the habitat determines how many species can possibly coexist; 3) local species richness is influenced by habitat heterogeneity, productivity, environmental stability and biotic interactions; 4) colonization and speciation, following the modalities discussed above, determine the supply of potential members of the groundwater communities; 5) regional species pools were assembled through multiple colonizations, dispersal in the subterranean environment followed by isolation, diversification via niche differentiation.

These explanations are not simple and, following BOTOSANEANU and HOLSINGER (1991), a "unique scenario" does not exist. There is no better phrase to explain this complexity than that used by BROWN (1981): "Ecological communities are perhaps the most complex of biological structures. Who ever thought it would be easy to find out why there are so many species?" And groundwater communities do not seem to be too less complex than epigeal ones.

The "adaptive zone model" attempts to integrate groundwater ecology with broad ecological theory and it seems attractive for at least two reasons. First of all, it includes in one context both colonization and diversification without requiring several "ad hoc" explanations. These explanations are not ruled out, but the model states that colonization and diversification in the subterranean domain are common phenomena and local environmental conditions are not important for the model to operate. Second, it allows several modalities of colonization and speciation, and two modalities of diversification. If none of these two performs well, a multiple colonization explanation has to be taken into account. Another point is that the model could be tested to a certain extent using phylogenetic analysis.



The concepts expressed in this paper are not new to groundwater ecology, and the foundations of the adaptive zone model are to be found in several other papers, first of all by JUBERTHIE (1984), ILIFFE (1986), ROUCH and DANIELOPOL (1987), HOWARD (1987), BOUTIN and COINEAU (1990), BOTOSANEANU and HOLSINGER (1991), and COINEAU and BOUTIN (1992). However it is remarkable that most of previous students of this subject concentrated on two topics (colonization and first speciation event), and did not build up a model dealing with the origin of hypogean species diversity. This is probably due to the old idea that the origin of stygobionts must differ in a certain instance from that of other animals. These ideas are wrong: groundwaters are no more than one of the several types of environments the ecologists are dealing with, and one of the most widespread on the earth surface (DANIELOPOL and ROUCH, 1991). DANIELOPOL (1991) correctly concluded his paper writing that "we shall not anymore consider groundwater ecology a special science, Stygology, but just one of the many ecological research directions with which we are now confronted".

Unfortunately, the history of biospeleology and groundwater ecology is full with "paradigms": structural simplicity, low number of species, low resources availability, stability of climatic conditions, low dispersal ability and high specialization of stygobionts. These "facts" may be true or not, as in any other ecosystem. Several times models based on wrong assumptions were proposed, dismissed, and rediscovered or reinvented, without giving a satisfactory answer to the question "Why are there so many kinds of subterranean animals?". I will attempt to explain why this happened quoting WHITE (1896). He wrote about Santa Rosalia, the patroness of evolutionary studies: "When Prof. Buckland, the eminent osteologist and teologist, discovered that the relics of St. Rosalia at Palermo, which had for ages cured diseases and warded off epidemics, were the bones of a goat, this fact caused not the slightest diminution in their miraculous power". A serious warning for ecologists!

**Acknowledgements.** I am deeply grateful to professors Dan Danielopol, Claude Boutin and John R. Holsinger. They kindly read and commented on an early draft of the manuscript, improved the text and provided helpful suggestions and encouragement. Thanks are due to prof. Sandro Ruffo, for the critical discussion of the phylogenetic tree of the genus *Niphargus*. The paper benefited from discussions and exchanges of information with several friends and colleagues at the International Meeting in Florence.

## SUMMARY

Species diversity in groundwater crustacean assemblages have received little attention by biospeleologists, and the subterranean domain has been considered a special milieu inhabited by few specialized species. This paper summarizes our present knowledge on ecological and historical determinants of regional species richness in groundwaters and attempts to offer some new approaches to build up a theory of hypogean species diversity. The main conclusions are:

- 1) Regional species richness in groundwaters depends on sampling effort and number of taxonomists. Steyskal's curves clearly show that for many taxa the rate of new species description in stygobionts is high, and hence species richness in hypogean habitats is largely underestimated.
- 2) Regional faunas may be very rich. The number of species in hypogean crustacean assemblages may be equal to or exceed that of epigeal ones in the same area.
- 3) Dispersal abilities of subterranean crustaceans may be high or not, depending on the taxon under examination.
- 4) The ecological determinants of species richness are habitat heterogeneity, area, environmental stability, productivity and amount of resources; every topic is discussed in detail.
- 5) A new model on the origin and diversification of groundwater animals is presented; the model consists of three steps: colonization, speciation, radiation. One step does not imply that the next one must operate. Every step is discussed in detail, and special emphasis is given to the topics of speciation, habitat specialization and age of colonization. If radiation is unlikely to occur, a multiple colonization model is proposed as a better explanation of the origin of hypogean species diversity.
- 6) A test of diversification in adaptive zones using cladistic analysis is proposed, and several examples are discussed. It is suggested that a combination of multiple colonization and radiation events gives a better explanation of the observed patterns.

Groundwater ecology is not a special science and must be integrated with broad ecological theory. We have to give up the paradigms of biospeleology and attempt to answer the question: "Why are there so many kinds of groundwater species?" The adaptive zone model is a first step towards this direction.

## RESUME

Le travail présenté traite de la diversité spécifique des Crustacés dans les eaux souterraines. Il résume nos connaissances sur les facteurs écologiques et historiques déterminant la richesse spécifique régionale des eaux souterraines, et vise à dégager quelques nouvelles voies pour construire une théorie de la diversité spécifique hypogée. Les principales conclusions sont :

- 1) La richesse spécifique régionale des eaux souterraines dépend de l'effort d'échantillonnage et du nombre de taxonomistes. La courbe de Steyskal montre clairement que, pour de nombreux taxons, le rythme de description de nouvelles espèces stygobies est élevé, et que la richesse spécifique dans les habitats hypogés aquatiques est grandement sous-estimée.
- 2) Les faunes souterraines régionales peuvent être très riches. Le nombre des espèces souterraines de Crustacés peut être égal ou dépasser celui des habitats épigés de la même région.
- 3) Les capacités de dispersion des Crustacés souterrains sont élevées, ou non, selon le taxon examiné.
- 4) Les facteurs écologiques déterminant la richesse spécifique sont : l'hétérogénéité de l'habitat, son étendue, la stabilité de l'environnement, la productivité et la quantité de ressources ; chacun est discuté en détail.
- 5) Un modèle sur l'origine et la diversification des animaux des eaux souterraines est présenté. Le modèle consiste en

trois étapes : colonisation, spéciation, radiation. Une étape réalisée n'implique pas que la suivante le soit. Chaque étape est discutée en détail, et on insiste sur la spéciation, la spécialisation des habitats et l'âge de la colonisation. Dans les cas où la radiation est peu probable, un modèle de colonisation multiple est proposé pour expliquer l'origine de la diversité constatée.

6) Un test de diversification dans les zones d'adaptation sur la base d'analyses cladistiques est proposé, et plusieurs exemples sont discutés. Il est suggéré que la combinaison de colonisations multiples et de radiations donne une meilleure explication des aspects observés.

L'écologie des eaux souterraines n'est pas une discipline scientifique spéciale, mais elle doit être intégrée dans une large théorie écologique. Nous devons tenter de répondre à la question : "Pourquoi y a-t-il tant de sorte d'espèces aquatiques souterraines? Le "adaptive zone model" est une première étape dans cette direction.

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