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SURVIVAL, OPPORTUNISM AND CONVENIENCE IN THE PROCESSES OF CAVE COLONIZATION BY TERRESTRIAL FAUNAS

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SUMMARY

Modern discoveries of cave-restricted animals in many tropical limestone areas, in lava tubes and other non-calcareous caves, and in subterranean non-cave habitats, have led us to reconsider classic interpretations of cave colonization processes, which were mainly based on the direct influence of Pleistocene climatic changes. The relict concept (for cave species) and the refuge concept (for caves) have lost their value as paradigms, and cave colonization directly determined by Pleistocene glaciations should rather be considered as a localized model. Organisms can colonize caves for a variety of reasons, including survival (caves as immediate refuges), opportunism (caves as virgin spaces to be colonized) or convenience (caves as escape valves when new competitive pressures appear in surface habitats). All these styles of colonization can be well exemplified in temperate areas which suffered the direct impact of Pleistocene glaciations. However, all of them can also be postulated in other situations which have nothing to do with climatic revolutions.

KEY WORDS: Biospeleology, troglobites, cave colonization.

INTRODUCTION

The first cave-restricted animal to be studied scientifically was the amphibian *Proteus anguinus*, from Yugoslavian caves, which was described by Laurenti in 1768. However, the beginnings of a systematic research on cave biology date from the early twentieth century, when Racovitza and Jeannel sparked off the spectacular rise of modern biospeleology in Europe.

One of the first proposals made by this European school was a general division of cave animals into three categories: troglobites (cave-restricted or cave-obligated that are unable to survive in epigean habitats), troglophiles (cave facultative that can reproduce in caves but are also found in cryptic and humid epigean habitats), and trogloxenes (cave dwellers that cannot reproduce in caves, most of which usually return to epigean environment to feed). The most peculiar cave-adapted group is, of course, that of troglobites, which have been typified by a series of morphological features, including loss or reduction of eyes, wings and cuticular pigments, and an increase of sensorial devices, often accompanied by the development of longer appendages and a more slender body form: the so-called "troglobiomorphic" characters. From a physiological point of view, many troglobites tend to lose their circadian rhythms, show a lower metabolism, and display specialist reproductive and life cycle strategies: the so-called K-strategies.

In the 60's, data available on cave biology were summarized in two key monographs: VANDEL's *Biospéologie* (1964), with an encyclopaedic character although emphasizing European findings, and BARR's *Cave ecology and the evolution of troglobites* (1968), primarily focused on ecological and evolutionary studies, and emphasizing North American examples. Besides the intrinsic value of both monographs as landmarks in biospeleological literature, they had the additional value of generating a renewed interest in cave animals. Progressively, new data were added and old concepts became surpassed by new findings, especially in the last fifteen years, when there has been a virtual revolution in our understanding of cave biology. Therefore, fast progress and original research have been achieved in different domains, from organismic to evolutionary level, as shown by modern reviews (CULVER, 1982; HOWARTH, 1983; JUBERTHIE, 1984, 1989). The present essay will deal with recent discoveries related to cave colonization processes by terrestrial faunas, and how these findings have modified the classic concepts which dominated in the 60's.

CAVE FAUNAS FROM LIMESTONE TEMPERATE AREAS. THE CLASSICAL DATA

VANDEL (1964) provided a thorough overview of the whole discipline of biospeleology from a worldwide perspective. According to the information compiled in this monograph, the richest troglobitic faunas were those of calcareous regions in Southern Europe, Northern Africa and Southeastern United States. Outside these main regions, selected discoveries in lava tubes and in limestone caves in Japan, New Zealand and Mexico, suggested the occurrence of well developed troglobitic faunas in these areas as well.

Early work by Leleup in Afrotropical caves was also reviewed in VANDEL (1964), but the scarcity of terrestrial "troglobiomorphic" animals found in this region prompted the idea that the vast majority of troglobites were to be found in temperate limestone caves. This view was followed by other biospeleologists primarily working in North America, like BARR (1968), who also stressed the importance of limestone caves stating that "the presence of troglobites in lava tubes, gypsum caves, and sea caves has been established, but is exceptional" (BARR, 1968: 47).

These findings led to the proposal of *ad hoc* theories accounting for cave colonization processes, which were largely based on the direct influence of palaeoclimatic changes. Therefore, the general consensus was that the ancestors of terrestrial troglobites were stenotherm and hygrophilic species which lived in subepigean habitats, such as moss, leaf litter of deep soil, and in some way were "preadapted" to cave life.

Accordingly, it was argued that most cave animals presumably derive from subepigean thermohygrophilic ancestors which had colonized the caves before the Pleistocene to survive *in situ* during the transition from tropical to temperate climate which occurred between the Tertiary and the Quaternary (VANDEL, 1964; JEANNEL, 1965). In turn, Pleistocene glaciations should have prompted new processes of cave colonization protagonised by cryohygrophilic faunas as the glaciers retreated and the climate became progressively warmer and drier (VANDEL, 1964; BARR, 1968).

Many chorological data of selected cave species living in temperate areas fit well with these assumptions, since their distributions show a high coincidence with the limits of those areas which were ice-covered during the Pleistocene. Examples of such distributions have been shown both in Europe (VANDEL, 1964) and in North

America (BARR, 1968), and this correspondence associated the caves with the idea of refuge, which was largely exploited by the proponents of the orthogenetical theories, who postulated that troglobites were a sort of "live fossils" (JEANNEL, 1943) in a senescent stage of their phyletic evolution (VANDEL, 1964).

TROGLOBITES IN TROPICAL CAVES AND IN NON-LIMESTONE SUBTERRANEAN HABITATS

In the last fifteen years there has been an extraordinary increase in information about cave faunas in the tropics. HOWARTH's (1983) review of the ecology of cave arthropods provides a checklist of tropical areas where terrestrial troglobites from limestone caves have been discovered. These areas include Hawaii, New Guinea, Sarawak, Malaysia, Thailand, Malgasy, Jamaica, Puerto Rico, Cuba, Mexico and Central America, Venezuela and Brazil. New prospections allow us to extend this list to other tropical areas, especially in South America (Ecuador: BESSON *et al.*, 1982; Peru: MARTÍNEZ *et al.*, 1983) and the West Pacific (Australia, New Caledonia, Philippines, Fiji: STRINATI & AELLEN, 1983; PECK, 1983)

Concerning non-limestone caves, the pioneering work on lava tube faunas done in Japan (UENO, 1971) and in Hawaii (HOWARTH, 1972) was followed by new discoveries in volcanic caves in other areas, like the Galápagos Islands (see PECK &

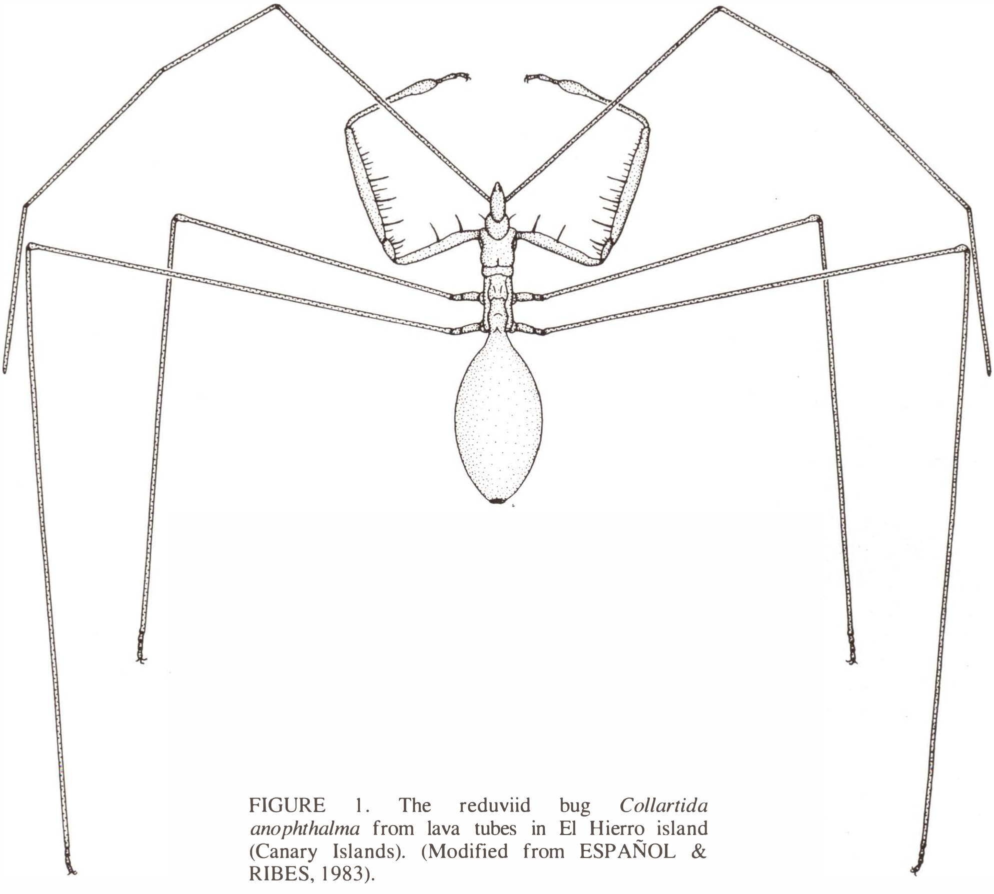

FIGURE 1. The reduviid bug *Collartida anophthalma* from lava tubes in El Hierro island (Canary Islands). (Modified from ESPAÑOL & RIBES, 1983).

KUKALOVA-PECK, 1986) or the Canary Islands (see HERNÁNDEZ *et al.*, 1986). Cave species have also been found in caves or mines excavated in different materials like sandstone, tuff, shale, chert, breccia, rhyolite, diorite and pegmatite (see HOWARTH, 1983).

In addition, the cave environment is now considered to be much larger than previously assumed, especially after the discovery of troglobites in the voids in fractured rock and talus slopes, both in calcareous and in non calcareous (volcanic and other) materials (UENO, 1977; HOWARTH, 1973; OROMÍ *et al.*, 1986), even at short distances from the surface (MSS: *milieu souterrain superficiel;* JUBERTHIE *et al.*, 1981).

It is worth noting that, although poorly modified species still dominate among tropical cave faunas, many of them show highly "troglobiomorphic" features. To give just a few examples, we can mention the reduviid bug *Collartida anophthalma* (Fig. 1) from lava tubes in the Canary Islands (ESPAÑOL & RIBES, 1983), or the paradoxosomatid millipede *Selminosoma chapmani* and the sundathelphusid crabs *Rouxana phreatica* and *Holthuisiana alba* from limestone caves in Papua-New Guinea (CHAPMAN, 1986).

From a physiological point of view, only a few studies have been made on tropical cave species. BOUSFIELD & HOWARD (1976) described some details of the reproductive biology of terrestrial talitrid amphipods from lava tubes in Hawaii, which show a tendency towards K-type strategies, just as in many troglobite species in temperate regions. Conversely, metabolic rates of cave-adapted crickets from the same islands did not show significant differences when compared with those of surface related species (AHEARN & HOWARTH, 1982).

In connexion with all these new discoveries, the realization emerged that morphophysiological features classically considered as characteristic of troglobites are neither exclusive nor extensive to all of them. Thus, morphophysiological criteria are not sufficient to assess the degree of dependence on cave environment, and even less to infer the time of cave colonization by a given species. In short, some poorly modified cave species, for example from tropical areas, could be more genuine troglobites, with a longer history in caves, than other "ultraevolved" (VANDEL, 1964) cavernicolous species living in temperate regions.

Another important piece of evidence afforded by biospeleological studies in tropical regions is that many of the troglobites discovered are not relicts, as closely related species can also be found in the surface habitats in the same area (UENO, 1977; HOWARTH, 1983; JUBERTHIE, 1984; CHAPMAN, 1986).

The discovery of cave species in the voids in fractured rock is especially significant, not only because it has an obvious ecological and chorological interest, but also because it casts new light on the reconstruction of cave invasion phenomena. Indeed, colonization of the more superficial fissures could, in most cases, be a previous stage towards cave invasion.

The fact that troglobites can be sampled in mines dug in limestone and other rock materials, as recognized by HUSSON (1936) (see also UENO, 1977), indicates that cave faunas may effectively migrate through the voids within fissured rock, and suggests that this mesocavernous system may be suitable for troglobites. In fact, quantitative studies on cave populations based on mark-recapture methods often indicate that most of these populations stay in inaccessible fissures (DELAY, 1978). These studies have also demonstrated effective migration between the cave and the voids of superficial rock (MSS) just beneath the soil level (Bellés & Gracia, unpublished).

CAVE COLONIZATION. THE PARADIGM OF CLIMATIC REVOLUTIONS REVISITED

These recent discoveries summarized above have led us to reconsider the role of climatic revolutions in the processes of cave colonization, and also the concept of "live fossils", which has been, and still is, generally applied to troglobites. It is now clear that not all the cave obligated species are relicts, but it is equally apparent that many of them can fit this definition. To give some selected examples from the Iberian Peninsula (see BELLÉS, 1987), the spider *Telema tenella,* the pseudoscorpion *Troglobisium racovitzai*, the isopod *Cantabroniscus primitivus,* the millipede *Cantabrodesmus lorioli*, the diplurans *Oncinocampa falcifer, Paratachycampa hispanica* and *P. peynoensis,* and the beetle *Ildobates neboti,* which show primitive features and are geographically very distant and isolated from their nearest relatives, can be considered as troglobite relict species.

Furthermore, recent studies combining biotaxonomical data with a good knowledge of Pleistocene glaciation timing in selected areas, and stressing the importance of the glacial-interglacial cycles, have cast new light on the paradigm of climatic revolutions. Studies by PECK (1981) based on the catopid beetles of the *Ptomaphagus hirtus* group from Grand Canyon caves in North America, and those of JUBERTHIE (1988) and coworkers carried out on the *Speonomus delarouzeei* group from Eastern Pyrenean caves, in the Iberian Peninsula, are especially representative.

According to these studies, it has been proposed that ancestors of these species invaded the cave habitat during glacial periods (when the forest extended down to the altitude of caves), and interglacial warming caused the extinction of surface populations of the species that have invaded the caves. Accordingly, species isolated in one interglacial period and supposed to be capable of overland dispersal in the next glacial, could have protagonised new processes of cave colonization, isolation and speciation, thus accounting for the taxonomic-chorological complexity which is usually found in these species groups (CULVER, 1982).

Although this scenario appears to be reasonable, it is worth underlining the fact that it serves for concrete and local cases which can be explained when conveniently contextualized, and not as a general rule. Let us examine some other situations which do not fit these explanations.

Firstly, cave species have been discovered in areas which were ice covered in Pleistocene times. In some cases, it can reasonably be argued that they might have survived extended periods of glaciation in deep subterranean habitats beneath the ice. The relict distribution of several freshwater amphipod species of *Stygobromus*, presently living in subterranean waters in Canada, could be explained by the above hypothesis (HOLSINGER & SHAW, 1986).

Secondly, and as already stated, the occurrence of cave species in tropical regions far from those which were glaciated

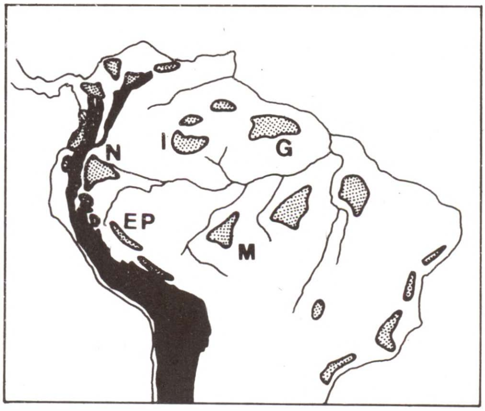

FIGURE 2. Map of tropical America showing the forest refugia during Pleistocene glacial maxima. The Andes (above 1000 m) are indicated as solid black. EP, East Perú; G, Guyana; I, Imeri; M, Madeira; N, Napo. (From LYNCH, 1988, slightly modified).

in Pleistocene times is largely demonstrated. This led us to examine the controversy between authors who claim that glaciations only influenced the glaciated areas and their boundaries (HOWARTH, 1982; JUBERTHIE, 1984), and those who maintain that glaciations influenced the whole planet (REDDELL, 1981).

Since Pleistocene refuge areas in tropical regions are well documented (LYNCH, 1988; Fig. 2), it thus seems reasonable to consider that glaciations influenced to a greater or lesser extent the entire globe. Therefore, it might be possible that, although indirectly, glaciations influenced cave colonization processes also in tropical areas.

In summary, the adventure of cave invasion could have been prompted by a variety of factors, including survival (caves as immediate refuges), opportunism (caves as virgin spaces to be colonized) or convenience (caves as escape valves when new competitive pressures appear in surface habitats). Indeed, all these styles of colonization can be well exemplified in temperate areas which suffered the impact of glaciations. However, and as we will see, all of them can also be reasonably postulated in other situations which have nothing to do with climatic revolutions.

SURVIVAL. THE CAVE AS A REFUGE

Certainly, caves could have served in some cases as immediate refuges to avoid surface abiotic stress. Many of the examples used to illustrate cave colonization by cryohygrophilous faunas prompted by the post-Pleistocene glaciers retreat seem to fit this hypothesis. Carabid beetles of the genus *Aphaenops* in the Pyrenees and of the genus *Pseudanophthalmus* in North America, are classic examples reviewed in detail by VANDEL (1963) and BARR (1968), respectively. An additional piece of evidence which tends to support the survival hypothesis for these carabid beetles is the occurrence of species living in the surface in high altitude forests (*Aphaenops ludovici* in the Northern Pyrenees and *Pseudanophthalmus sylvaticus* in West Virginia, for example) which are closely related to the cave obligated ones (CULVER, 1982; JUBERTHIE, 1984).

Habitat preferences as a function of temperature in several non-troglobite

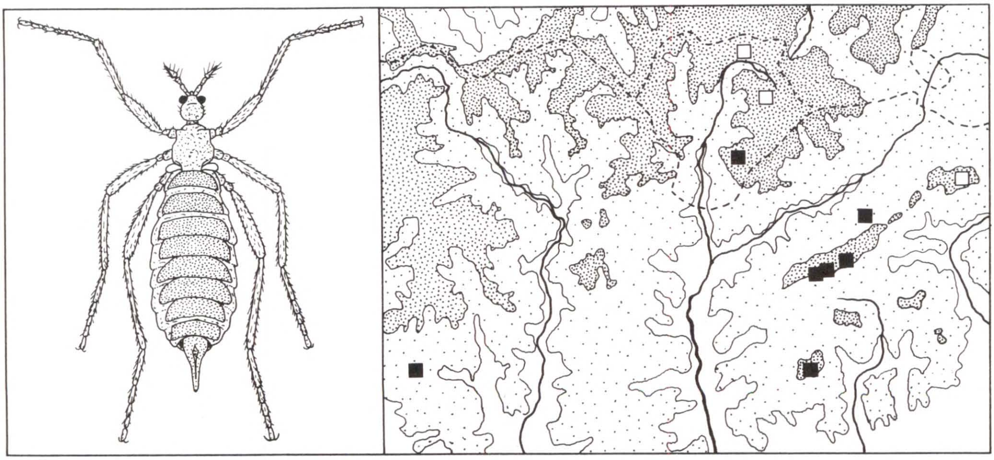

FIGURE 3. The tipulid dipteran *Niphadobata catalonica* and its distribution in the Eastern Pyrenees. The white squares indicate epigean localities and the black ones indicate caves. Areas above 2000 m are shown as densely dotted, and those between 1000 and 2000 m as sparsely dotted.

species also suggest the likelihood of such a mode of colonization being induced by abiotic stress in surface habitats. The Palaearctic carabid beetle *Porotachys bisulcatus* is an example. This species has clear preferences for forest habitats in northern localities, whereas in southern ones it shows a clear tendency to occupy caves. It finally becomes a typical troglophile in the Balearic Islands, Southern Iberian Peninsula and Northern Africa (BELLÉS, 1987). Also illustrative is the Eastern Pyrenean distribution of the dipteran *Niphadobata catalonica*, an apterous tipulid which, at altitudes higher than 2000 m, lives either in caves or in surface habitats, under stones or on the snow (for example in the Coll de la Devesa, at some 2500 m a.s.l.). However, between 1000 and 2000 m (for example in Sant Gervàs mountains), it is exclusively found in caves (Fig. 3) (ESCOLÀ & BELLÉS, 1977).

Further. In the National Park of Cutervo, established in 1961 near Cajamarca, in Peru, large areas of rain forest used to be destroyed in past decades to exploit the land for pasture or agricultural purposes. Both in the entrance and in the deeper zones of the caves located in the ancient forest areas live different species of carabid beetles (*Andinorites, Trechisibus, Incatrechus;* MATEU & BELLÉS, 1981) which are absent in epigean habitats of the same area (now occupied by pastures and agricultural land) and which show close relationships with forest species. Therefore, examples of cave colonization as a solution to survival under surface stress can also be found in present circumstances which have no relation to climatic revolutions.

OPPORTUNISM. THE CAVE AS AN EMPTY SPACE

A cave can also be envisaged as an empty space able to be colonized, also in absence of biotic or abiotic surface stress. Concepts from the island biogeography theory (SCHOENER, 1988) could be applied *a priori* to caves, at least to illustrate how the colonization of an "empty" cave could have occurred. The equilibrium theory in its strict sense (MAC ARTHUR & WILSON, 1967), which explains the number of species of an island as a balance between immigration and extinction rates, emphasizing the importance of the area effect, seems less aplicable to caves. On the one hand, because studies made on cave faunas in this respect (VILLEUMIER, 1973) failed to demonstrate any area effect; on the other, because species turnover in troglobite communities should presumably be very low, at least in terrestrial faunas. As Culver pointed out "If the time scale is evolutionary, the immigrations are the isolation of species in caves. By contrast, under a historical hypothesis, the number of species is not an equilibrium but is rather the unique result of the history of the area" (CULVER, 1982:155). However, the analogy between caves and islands applied to both evolutionary time and ecological time, is still controversial, which suggests that more data are badly needed (MAY, 1977; CULVER, 1982; JUBERTHIE, 1989).

Of course, the most favoured candidates to succeed in the adventure of colonization of a virgin cave should be those species which arrive first and which are already adapted to live in stenothermal habitats, with high humidity, and more or less cryptic as, for example, humicolous species.

Rapid colonization of mines, with the establishment of gradients and a spatial distribution of the newly arrived fauna which is similar to those found in natural caves is a clear example of a process of colonization of an empty subterranean space, although in this case most of the colonists are troglobites from the adjacent mesocavernous system.

Lava tubes offer another example of a subterranean space with a recent history of colonization. Lava tubes and their surroundings formed in each volcanic episode represent an empty space to be rapidly colonized. The existence of a mesocavernous volcanic system which harbours troglobites (OROMÍ *et al.*, 1986) suggests that dispersal between this system and lava tubes effectively occurs, just as in limestone areas. However, lava tubes usually flow near the surface and are relatively ephemeral due to erosion effects. Thus, the cycle of formation, colonization and destruction of a lava tube occurs in a relatively short time. This, and the fact that lava materials can be accurately dated, means that reconstructions of lava tube colonizations might be easier than limestone cave systems. Another difference with respect to cave faunas in limestone temperate regions is that lava tube troglobites usually have near relatives in the epigean habitats of the same area. It thus becomes clear that the concepts of refugia and relict do not have any sense in these circumstances.

In this context of invasion of virgin subterranean spaces, the influence of glaciations can also be argued, not only as promoter of cave colonization due to abiotic stress in the surface, but also as promoter of new subterranean habitats. As pointed out by JUBERTHIE (1984), mechanical erosion and gelifraction as consequences of glaciarism, generates new spaces suitable for colonization (new talus slopes and voids in fractured rock). The retreat of glaciers should be, indeed, accompanied by the availability of these new spaces susceptible to first colonizations.

CONVENIENCE. THE CAVE AS AN ESCAPE VALVE

Another way to analyze the biogeography of cavernicoles is to superimpose their distribution ranges on those areas which were forest refugia during Pleistocene. Often a remarkable concentration of troglobite species appears in these ancient refugia, whereas in zones which were tundra-like in the Pleistocene, cave obligated species are almost lacking. General distributions of terrestrial troglobites in the Iberian Peninsula offer good examples of such a correlation (BELLÉS, 1987).

Glacial-interglacial intermittencies during Pleistocene times provoked, among other things, deep modifications in the distribution of vegetation. With each glacial advance, the forest shrank into fragments and with the retreat of glaciers, these fragments expanded to cover the grassland areas again and extended considerably. Therefore, contraction (to form a sort of forest island in a sea of grassland) provoked geographical isolation and promoted allopatric speciation, whereas forest expansion led to new enlargement of species ranges and to eventual contacts with their newly differentiated relatives.

This contraction-expansion scheme paralleling the glacial-interglacial intermittencies has been exploited mainly to explain the occurrence of highly speciose species-groups in zones which were on the boundaries of Pleistocene glaciers, and to reconstruct the speciation processes. Representative of these concepts are the studies of PECK (1981) on *Ptomaphagus hirtus* complex from Grand Canyon caves, and those of JUBERTHIE (1989) and coworkers on *Speonomus delarouzeei* complex from Pyrenean caves.

In addition, it is worth noting that these ideas can also be applied in areas which were far from direct glacial influence. The speciation processes undergone by cockroaches belonging to the genus *Loboptera* in volcanic subterranean environments in the Canary Islands, also seem largely influenced by contraction-expansion cycles in the Laurel forest, which occurred from the Pleistocene to the Holocene (MARTÍN *et al.*, 1986).

However, formation of refuge areas

might also be of interest when searching for reasons to explain the cave colonization processes. As pointed out by JUBERTHIE (1984) and BELLÉS (1987), another consequence of the formation of refuges, apart from speciation phenomena, would have been the concentration of forest organisms in these privileged areas, which became crowded while new competitive pressures appeared. These circumstances could have prompted cave invasions to avoid these pressures and, again, those species already linked to cryptic and stenotherm habitats would have been the candidates most likely to succeed in such an adventure (Fig. 4). It therefore becomes apparent that abiotic stress on the surface has had a rather indirect influence on these cases of cave colonization.

Finally, over the last years the Pleistocene tropical lowland forest refugia hypothesis has gained extensive support, and different tropical areas corresponding to forest refuges during glacial maxima have been well documented (for example Napo, Imeri, Guyana, East Peru and Madeira refuge areas in the Neotropical region: LYNCH, 1988; Fig. 2). Unfortunately, though promising *a priori*, biospeleological research studies have not been focused on these special areas, and nothing is known about the relative diversity and richness of their cave animals.

SOME CONCLUSIONS

Recent discoveries which resulted in a major breakthrough in our former understanding of cave colonization processes can be summarized in the following points:

1. Not all troglobites are relicts.
2. Not all troglobites are "troglobiomorphic" or K-strategists.
3. There are troglobites with a recent history of cave colonization.
4. Troglobites inhabit areas which, during Pleistocene times, were either ice-covered or far from the glaciers.
6. Troglobites also live in non-calcareous caves (lava tubes, sandstone caves) and

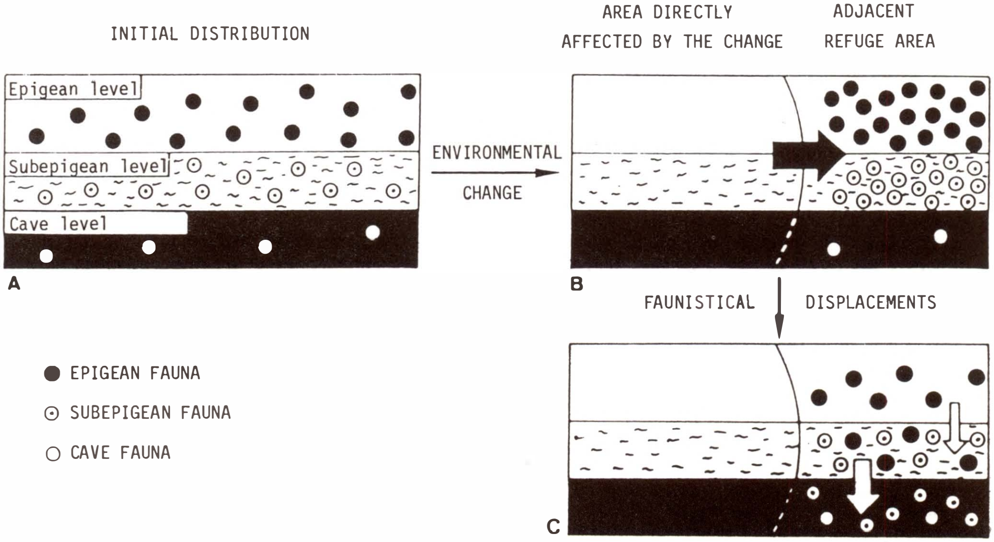

FIGURE 4. Hypothesis of competitive pressures in refuge areas. An environmental change (A) could lead to a faunal concentration in refuge areas (B), thus determining new competitive pressures and, in turn, faunistical displacements including cave colonizations (C). (From BELLÉS, 1987).

subterranean non-cave habitats, both in calcareous and in non-calcareous materials (voids in fractured rocks, talus slopes and so on).

The relict concept, for cave species, or the refuge concept, for caves, have lost their value as paradigms in cave biology; and cave colonization processes directly determined by the Pleistocene climatic revolution should rather be considered as a localized model.

It is clear that organisms colonize caves for a variety of reasons. Survival, opportunism and convenience have been pointed out here to show this variety of reasons, rather than to systematize and analyze them. Indeed, it seems probable that a cave colonization process should be more properly explained as a mixture of superimposed patterns rather than by a single pattern. Pleistocene glaciations prompted cave colonization for different reasons, including survival, opportunism and convenience. However, similar reasons can be found in other situations which have nothing to do with major climatic changes.

These new findings would, hopefully, provide a new point for more holistic reconstructions of cave colonization processes. We may have the impression that in the 60's biospeleologists were perhaps trying to run before they were able to walk. Now, although there is still much to be cleared up, we might be able to begin to walk without stumbling so often.

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