

## THE ORIGIN OF TROGLOBITES

by  
PHILIP CHAPMAN

### ABSTRACT

Explanations concerning the origin of obligate cavernicoles, or troglobites, have long been a source of controversy among biospelaeologists. It is suggested here that troglaphiles become troglobites as the result of an adaptive shift to an ecological niche which cannot occur in epigeal communities. This adaptive shift is facilitated by preadaptation of the incipient troglobite through the development of genoclines in its troglaphilic ancestral population. The shift to troglobitism is forced by competitive exclusion of the incipient troglobite from its original troglaphilic niche by an invading species or community. The major changes of fauna produced in temperate latitudes by the climatic fluctuations of the Pleistocene have resulted in a particularly rich troglobitic fauna composed mainly of cryophilic relicts inhabiting temperate caves.

### INTRODUCTION

Darwin's great contribution to biology was his realization (1859) that species are moulded by environmental pressures. In the struggle for survival only the best adapted individuals of each species manage to reproduce and so pass on their adaptive characteristics to the next generation. Whichever environment we care to examine is found to contain a huge variety of plants and animals of different size, shape and habits. Far from being in competition with each other, many of these species are essential to each other's continued survival. Their great variety of lifestyles and their inter-dependence show that they have been moulded by different but inter-related evolutionary pressures which stem from the community in which they live as much as from their physical environment. The effect of these pressures is to adapt each species to its own individual niche.

The concept of the species-niche is central to the modern study of synecology and will form the focus of this paper. By the term 'niche' ecologists mean the way of life peculiar to individuals of each species within an interacting community. The community is a mosaic of lifestyles. Competition between two species for the same resource is an unstable situation which is eventually resolved by the extinction of one competitor, or specialization of each to a different aspect of the disputed resource. This latter process is called niche partitioning or niche specialization. Increased specialization of individual niches allows a greater number of species to co-exist in the community. The more complex community allows more food choices to its individual members, decreasing the effect of any one species' extinction on the community as a whole, and therefore increasing community stability.

The complexity of a community is to a large extent controlled by species occupying the 'producer' niches. The producers generate the

community's 'wealth' in energy terms, by producing the energy-rich molecules on which organisms occupying 'consumer' niches depend. In most ecosystems the producers are green plants which trap incident solar energy in the end products of photosynthesis. Hypogean communities (i.e. inhabiting caves and related sub-soil habitats—from now on referred to simply as 'caves') are exceptional in that producer niches are occupied by only a very few chemo-autotrophic bacteria which contribute little to the energetics of the community. The main energy source of the cave community is the detritus of epigeal communities which falls into the cave, or is carried there by water, and the faeces of visiting bats. Such foods are readily available in epigeal habitats, so it is not surprising to find that many primarily epigeal detritus feeders and their predators are able to live and reproduce underground. These facultative cave dwellers are termed TROGLOPHILES. Yet there are other cave dwellers which are able to complete their entire life cycle only in hypogean habitats. These TROGLOBITES are often, but not always, white and eyeless, and are sometimes the sole surviving local representatives of ancient groups. Their existence in caves has long interested and puzzled biologists. What niche characteristics originally confined and continue to confine troglobites to caves? How do they survive the constant invasion of their habitat by more 'successful' modern species? Is the cave habitat a protective 'terminal ward' for senescent species nearing the end of their evolutionary span? Or is it a fiercely contested evolutionary battleground where, as in other habitats, only the well-adapted survive? Are there any recognizable characteristics of troglobite-held niches which differ from those of troglophile-held niches? This paper discusses such questions, and proposes a speculative model of cave colonization and the evolution of troglobites which it is hoped will stimulate and direct research along productive lines.

#### CAVES AS TRAPS FOR THE BLIND

Lankester (1893) suggested that troglobites are the descendants of eyeless mutants which become trapped in caves because, unlike their sighted fellows, they were unable to escape towards the daylight at the cave entrance. However, the chance of eyeless mutants of the same species simultaneously becoming lost in the same part of a cave in sufficient numbers to form a viable breeding population is so remote that Lankester's idea is not nowadays given any credence.

#### CAVES AS 'TERMINAL WARDS' FOR DYING SPECIES

Vandel (1965) and fellow organicists, have stated that troglobites are derived from species at the end of their phyletic line (i.e. undergoing evolutionary senescence) which have become unable to autoregulate and are therefore confined to stable, humid conditions such as are found in the 'conservative environment' of caves. Jeannel (1965) states that these ancient faunas have persisted until the present in the deep soil and humus of montane tropical rainforests. The Pleistocene glaciations, by destroying the great humid forests which covered much of Europe and North America, have supposedly driven their 'preadapted fauna' under-

ground. Organicists ascribe 'troglobitic' characters such as extreme attenuation of appendages to orthogenesis—the metaphysical idea that a particular evolutionary direction may be maintained in the absence of selection pressure. The only evidence which might give credence to the organicists' belief would be if troglobites could be shown to belong exclusively to ancient, now increasingly unsuccessful epigeal groups. However Barr (1968) and Howarth (1981) have clearly shown that troglobites include many species within successful, actively speciating groups, and Howarth (1980) has argued convincingly that, far from being unable to autoregulate, terrestrial troglobites possess specialized water balance mechanisms evolved to cope with the physiological problems caused by the hydrating atmosphere of cave habitats.

### CAVES AS HAVENS FOR PLEISTOCENE REFUGEES

Biospelaologists have long appreciated the importance of the major climatic fluctuations during the Pleistocene in initiating troglobite speciation. Caves of the temperate zones have served as refugia for ancestors of troglobites against the climatic vicissitudes of the Pleistocene (Barr, 1968). The ancestral species were in many cases cryophilic, becoming widespread in taiga-like forests which bordered advancing continental glaciers (Jeannel, 1923), but becoming extinct or surviving in caves as the glaciers retreated and the climate of the cave regions became warmer and drier (Barr, 1968). Holdhaus (1933) and Vandel (1958, 1965) have documented much of the evidence that the present distribution of European cave faunas reflects the influence of Pleistocene glaciations. Barr (1968) points out that elements of the North American cave fauna are thermophilic relicts dating from warm interglacial or pre-Pleistocene periods. Almost all biospelaologists now accept that climatic fluctuations during the Pleistocene led to elements of warm- or cold-adapted communities becoming stranded in the protective environment of caves as their community retreated from an increasingly adverse surface climate.

One or two biospelaologists have gone so far as to imply that all terrestrial troglobites have been isolated in caves by climatic change. Mitchell (1969) pronounced that, in the absence of glaciations in the lowland tropics during the Pleistocene, "there are very simply few ways in which to isolate *any* terrestrial animals in tropical caves". However, Peck (1975, 1977), Chapman (1976, 1982) and Howarth (1973, 1981) have shown that terrestrial troglobites do occur in significant numbers in tropical caves. It seems that drastic climatic fluctuations are not essential in initiating troglobitic speciation. I shall argue that it is invasions by foreign animals which leads to the appearance of new troglobitic species. Climatic fluctuations during the Pleistocene brought about a number of such invasions, but they may equally result from the removal of geographical barriers between formerly separate biota, or the spread of animals by man.

### THE DISTINCTION BETWEEN A TROGLOPHILE NICHE AND A TROGLOBITE NICHE

As stated earlier, animal communities in caves, as in other habitats, comprise a closely-fitting mosaic of individual species niches. A number of dimensions (size, fecundity, dietary specialization, humidity requirement, vagility, etc.) defines each niche. Let us consider just one such dimension, that of food-energy requirement. Some species need a large input of food-energy in order to sustain a rapid rate of metabolism, a high fecundity and an active lifestyle. Other species are less exacting in their food-energy requirements. The range of energy requirements exhibited by animals with otherwise similar niche characteristics within a single community is limited at its upper end by the rate at which food-energy becomes available to the community. This is usually a function of the rate of food production by photo-autotrophs. It is limited at its lower end by availability of space and by predation. In a food-rich environment, much of the space is occupied by high-energy consumers which can exclude the less active and slower-breeding low-energy consumers where space is limiting. Low consumers are also selected against by predation, as they are slower in making up population losses. Each habitat, or group of habitats, therefore has a characteristic food-energy availability spectrum containing individual bands which represent the range of exploitation (or niche breadth in that dimension) of individual species.

Caves represent an unusual environment in that the rate of food production is negligible and the density of introduced detritus, and consequently the cave biomass, is small in relation to epigeal habitats (the exceptions are those caves which are frequented by large numbers of troglonemes). In cave communities, the upper end of the niche spectrum along its energy-requirement dimension is therefore much lower than for comparable (i.e. detritus-based) epigeal communities. This situation is more easily visualized in terms of a simple model (Fig. 32).

As can be seen from the model, some epigeal species (niches A-D) have such a high food-energy requirement that they will simply die of starvation in caves. Such species do not become troglonemes (though they may become TROGLOXENES—animals which frequent caves but which depend to some extent on resources outside the cave). Other species (niches E-J) are 'preadapted' to cave life in this particular niche-dimension and so may become troglonemes. Of course, any such species may have other niche characteristics (e.g. successful reproduction dependent on visual courtship display, or whatever) which precludes them from cave life. Then again, there may be several species with different dietary specialisms but the same range of food-energy requirement. The model has limitations in that it cannot have a 1:1 correspondence with complex reality, but with this in mind, let us develop it further.

The constraints previously discussed set a lower limit on the range of energy-requirements within epigeal niches. However, the large area

A MODEL OF NICHE STRUCTURE IN RELATED EPIGEAN AND HYPOGEAN COMMUNITIES FROM THE PERSPECTIVE OF THE FOOD-ENERGY REQUIREMENT NICHE DIMENSION (FERN)

(see text for explanation)

Fig. 32. FERN structure in adjacent detritus-based epigeal (upper) and hypogeal (lower) communities. FERN units A-M represent ranges of exploitation by individual species in decreasing order of available energy.

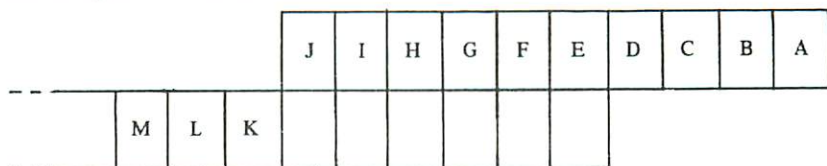


Fig. 33. Clinal niche-shifts along the FERN in hypogeal populations of trogliphiles e-j in response to interspecific competition for space.

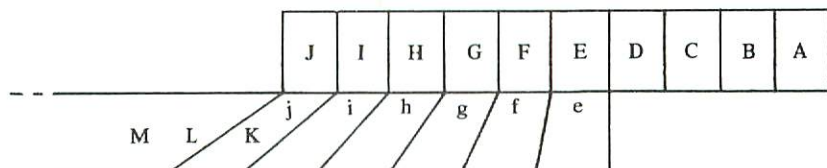


Fig. 34. Former trogliphilic species i and j (see Fig. 2) are forced to make an adaptive shift into troglomite niches K and L under competition from invading species o-x.

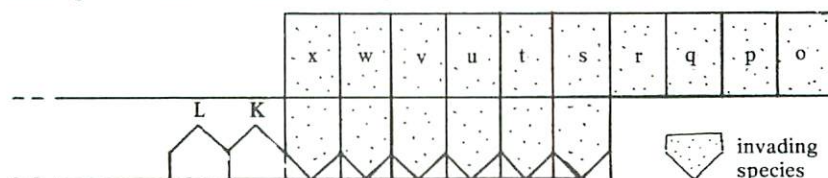
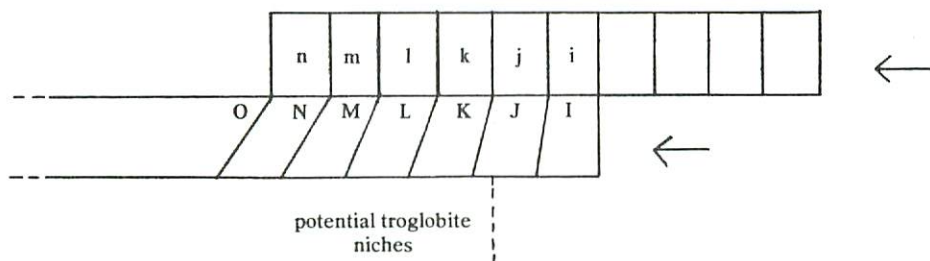


Fig. 35. Periglacial climate reduces primary production on the land surface, producing a downward shift in FERNs of both epigeal and hypogeal communities (arrows). Cryophilic trogliphiles i-n occupy niches (I-O), of which K-O will become troglomite niches with the return to a warmer climate.



of low-energy cave habitat extends this lower limit in the hypogean realm so that potential niches with energy-requirement characteristics KLM, etc., are open to exploitation. These niches cannot be occupied in epigean habitats. They are available only in caves and similar low-energy hypogean habitats. They are TROGLOBITE NICHES.

#### COMPETITION BETWEEN TROGLOPHILES AND THE SHIFT TO TROGLOBITISM

As the cave environment becomes available for colonization, so epigean species move in to occupy troglophile niches. Those which do so are already specialized to a particular niche within their epigean community, and are thus preadapted to the corresponding hypogean niche. No epigean species is preadapted to a troglobitic niche. However, once the hypogean community is established, competition between species with similar niches provides the selection pressure for low-energy troglophiles to make an adaptive shift into troglobite niches. This tendency is counteracted by the selection pressures acting on the epigean component of the troglophilic population. Gene flow between epigean and hypogean populations prevents a complete shift to troglobitism. However if such gene flow is limited by the spatial discontinuity of habitable patches within the hypogean environment, clines may develop in the relative frequencies of certain genes in the epigean and hypogean populations of the troglophile. These 'genoclines' have an irregular, or bumpy profile, due to localized restrictions in gene flow, intensified by patchiness of the species' distribution within the range of its population. The situation may be represented on our model as in Fig. 33.

The stage is now set for the shift to troglobitism. All that is required is for the potential troglobites to be forced into troglobite niches by competition from an invading fauna. The invaders may be introduced to the area by man, or may arrive as part of a wave of colonization which results from a major climatic change. The cockroach *Periplaneta americana*, the centipede *Orphnaeus brevilabiatus*, and the psocopteran *Psyllipsocus ramburii* are examples of animals widely introduced by man which quickly appropriate troglophile niches when they arrive in cavernous regions. Whole thermophilic faunas (i.e. adapted to a warmer climate than the faunas they supplanted) which followed the northward retreat of the glaciers at the end of the last ice age contributed the majority of troglophiles to the cave faunas of Europe and central North America. Let us consider the likely effect upon our model of the introduction of newly arrived troglophiles into the cave ecosystem. Such species will initially occupy those hypogean niches which most closely correspond to the epigean niche which they occupy within their community. The impact of the invading species (o-x for convenience) may be simply to capture all of the available epigean niches (Fig. 34). The new arrivals are better adapted to epigean niches with our featured dimensional characteristics A-J (Fig. 32) simply because the whole invading community is structured as a different, co-evolved niche mosaic which is better adapted to the changed climate. A few 'outsider'

species, such as the widespread cosmopolites to which reference has already been made, may successfully break into the community niche-mosaic, paradoxically because they are not narrowly specialized to one niche, but possess a competitive ability which tokens some profound physiological advance over other related species. Such species may be termed 'ecoplastic' in their niche characteristics.

Returning to the model under consideration—what is to be the effect of the invading species o-x on the hypogean fauna? We may assume that the conquering s-x species will rapidly appropriate their corresponding hypogean niches, causing the extinction of the old troglaphiles occupying niches E-J. However, the old troglaphiles i and j (occupying niches I and J) include within their hypogean populations individuals whose genotypes preadapt them to niches K and L. Their epigeal populations are destroyed, and a portion of their hypogean niches are under siege. They are under tremendous selection pressure to make an adaptive shift into the available (and so far unclaimed) troglobite niches to which part of their populations are preadapted. Their response is to become troglobitic!

The model so far proposed has assumed that genetic isolation is required for the preadapted troglaphile to be able to make the necessary adaptive shift to troglobitism. This is in keeping with the currently fashionable views of evolutionary geneticists such as Mayr (e.g. 1970) who argue that speciation is invariably allopatric. However, some very plausible non-allopatric models of speciation have recently been proposed by a number of authors and are reviewed by White (1978). One model, proposed by Endler (1977) may be applied to caves thus: The genocline which exists within a long-established troglaphilic species (Fig. 33: J in our model) would be intensified at the boundary of hypogean and epigeal habitats (which represents an abrupt habitat transition), forming a 'step', or localized change in the gradient of the cline. Any genes which have a negative effect on some genotypes in either the hypogean or epigeal habitat might increase the size and abruptness of the 'step' in the major genocline, resulting in differential co-adaptation on either side of this 'step'. This might lead to assortative mating, resulting in the formation of hybrid zones or even in parapatric speciation, producing a separate troglobitic and troglaphilic species. Such models are presently unfashionable, but may one day be accepted as plausible explanations for the close occurrence of sibling epigeal and troglobitic species or subspecies.

#### THE ROLE OF GLACIATIONS IN THE ORIGIN OF TROGLOBITES

When two biotas with a long-separate evolutionary history are brought together by continental drift (e.g. North and South America, India and Eurasia, Australia-New Guinea and Laurasia) or the formation of land bridges during a fall in sea level (e.g. Europe and Great Britain, Islands of the Sunda Shelf) there is a competitive scramble for niches which results in the formation of a 'hybrid' biota containing elements from both parent biotas. This is because both parent biotas are well adapted to the climatic conditions of the contact zone. Our model would

predict that in caves subject to such a situation, a few troglaphiles may be driven by competitive pressure to make the adaptive shift to troglobitism, but the major effect will be the establishment of a hybrid troglaphile fauna containing elements of both parent faunas.

In the case of the major invasion by a climatically-adapted fauna into an area which is undergoing profound climatic change, the result will be quite different as the native fauna is poorly adapted to the new climatic conditions. In this case our model predicts the appropriation of most troglaphile niches by members of the invading fauna. Whether or not any native troglaphiles become troglobites depends on the effect of the climatic change on the hypogean niche-structure.

A land surface exposed to periglacial conditions supports a far lower rate of primary production than it would under a warmer climatic regime. Our model predicts that the range of epigeal niches along the food-energy availability dimension will undergo a shift to the left as primary production is lessened (Fig. 35). There will be a corresponding leftward shift in the range of available hypogean niches (Fig. 35). Thus, the invading cryophilic fauna during a Pleistocene cold spell may be expected to occupy most niches previously held by an older, more thermophilic, fauna, and some more besides (MNO).

With inter- or post-glacial warming of the climate, a thermophilic fauna may be expected to re-occupy the niches to which it is adapted (Fig. 32: A-J), destroying the cryophilic epigeal fauna and isolating the low-energy cryophilic species occupying niches KLMNO as troglobites. Thus our model predicts that glacially affected caves will contain a preponderance of cryophilic troglobites. This is indeed the case (Barr, 1968)!

It may be that highly cave-adapted thermophilic troglobites are able to hold their own against the cryophilic invaders of a Pleistocene cold spell. In this case, the modern (post-glacial) cave fauna will contain a mixture of ancient thermophilic troglobites and of more recent cryophilic troglobites—as indeed we find in the European and North American cave faunas.

I have used the niche-dimension of food-energy availability in the model proposed here as this may be of particular significance in the origin of troglobites. I do not wish to suggest that it is the only important niche-dimension. Howarth (1980) has argued strongly for the importance in the evolution of terrestrial troglobites of the refinement of water-balance systems in order to cope with the hydrating atmosphere of hypogean habitats. I have argued elsewhere (Chapman, 1981) that adaptation to an unusual niche characterized by very high food consumption coupled with dependence on a hydrating atmosphere confines the Bornean leiodid beetle *Ptomaphagus chapmani* and millipede *Plusioglyphiulus* sp. to caves in the Gunung Mulu National Park, Sarawak. Perhaps other niche dimensions will prove to be important in differentiating troglaphiles from troglobites.



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