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## **ECOSYSTEMS OF THE WORLD 30**

# **SUBTERRANEAN ECOSYSTEMS**

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A ... rich area of enquiry is the study of refugia, 'ecological museums' that in both the geological record and selected modern habitats appear to house archaic biotas. ... useful insights may well be obtained from habitats as diverse as deep-water marine faunas and terrestrial swamp floras. (Conway Morris, 1995, p. 293)

## RELICT FAUNAS AND THEIR DERIVATION

W.F. HUMPHREYS

### INTRODUCTION

Underground ecosystems may be buffered from the vicissitudes of climate through geological time (e.g., Stock, 1986a) and hence, perhaps more than any others, have retained a broad diversity of living relicts, both phyletic and distributional. The pioneering studies of cave life were made, predominantly, in the karst areas of Europe and North America, areas directly or closely associated with regions repeatedly covered by ice during the Pleistocene. It is not surprising, then, that the effects of glaciation came to dominate the debate about both the distribution and the origin of troglobitic animals. These were viewed as the remnants of surface populations that took refuge underground from the adverse climatic conditions, which eliminated surface populations (Barr Jr, 1968; Banarescu, 1975; Sbordoni, 1982; Barr Jr and Holsinger, 1985), and where, in addition, effete lineages could survive under conditions that protected them from both the changeable climate and competition from more vigorous animals (Jeannel, 1943; Vandel, 1965). Hence, the early history of biospeleology is replete with studies of remnant distributions and taxa, respectively relicts and relics.

So dominant was this theme – that glacial cycles were the driving force for the evolution of troglobites – that it was widely held that the tropics, where such effects would be minimal, would contain few troglobites (Vandel, 1965; Barr Jr, 1968, 1973; Mitchell, 1969; see especially Sbordoni et al., Chapter 24, this volume), a view now thoroughly dispelled (Howarth, 1980, 1987, 1988; Humphreys, 1993a,b,d).

Recent work on the processes driving the evolution and distribution of troglobites has increased considerably the scope, as well as the temporal and

global scale, of biospeleology. Examples of para- and peri-patric speciation are known from both aquatic and terrestrial systems (Stock, 1980; Wilkens and Hüppop, 1986; Howarth, 1987) and hence, the ablation of surface populations may not be a prerequisite for troglogenesis. Compelling evidence for sympatric speciation of cavernicolous species has been provided for the Mexican cave fish *Astyanax fasciatus* (Pisces: Characidae) (Wilkens and Hüppop, 1986) – sympatric speciation occurs on the basis that individuals with more than average cave preadaptation have a selective advantage in the cave over the epigeal relatives, most cave species developing within the distribution range of their ancestral form. Many cave-living species are characterized by the fact that they start cavernicolous evolution within the distributional area of their epigeal ancestral species (Wilkens and Hüppop, 1986). Furthermore, convergent adaptation to the cave environment in a number of locations has been demonstrated in the amphipod *Gammarus minus* (Culver et al., 1995).

The discovery of troglobite faunas in the finer voids within fractured substrates (Uéno, 1977; Juberthie, 1984; Oromi et al., 1991), in the superficial underground compartment (Juberthie and Delay, 1981) – the submarine equivalent is Iliffe's (1986) crevicular habitat – and in lava tubes (Howarth, 1972, 1973; Oromi et al., 1991), has both extended the type and area of study, and the range of plausible hypotheses for their dispersal and evolution. Similarly, the distributional debate has now been set in a global context. Rich tropical troglobite faunas have been discovered; and it has been hypothesised that plate tectonics have been involved in the distribution of troglobites, both in islands (Manning et al., 1986) and in continental systems (Stock, 1994). These changes in perception

have provoked some of the most vigorous debates in biospeleology (Iliffe et al., 1984; Stock, 1986b; Rouch and Danielopol, 1987; Danielopol, 1990; Botosaneanu and Holsinger, 1991), in which the firm positions taken are likely to be resolved by diverse theories (Peck, 1990; Botosaneanu and Holsinger, 1991: p. 34), some even of hybrid character (see Humphreys, Chapter 30, this volume).

In many debates on relicts, confusion arises because the distinction is not clearly drawn between the process of regional vicariance and those resulting in the movement of species into the hypogean realm (e.g., Botosaneanu and Holsinger, 1991: p. 16). This is irrespective of whether the ancestors were driven underground [refugial – under constraint (cf. Botosaneanu and Holsinger, 1991)] or drawn underground [active colonization (Juberthie, 1984, 1989; Rouch and Danielopol, 1987)], or even whether the process depended on stochastic events (Wilkens and Hüppop, 1986; Fong and Culver, 1994). In this chapter I concentrate on the means by which the distributions of relict species arise; in doing so I necessarily draw selectively from an extensive literature, often citing only synoptic papers.

Darwin (1859: chapter 4) recognized the importance of vicariance and, in a brief discourse into cave life (chapter 5), he expected that conservative habitats, such as caves, which exert a low selective pressure, would be richer in “living fossils” than was known at that time. He also recognized many of the concepts important to biospeleology, namely (using descriptive terms) refugia, preadaptation, troglomorphies, parapatric speciation, regressive evolution, relics and relicts. From the inception of modern biospeleology it was recognized that Recent subterranean troglobites are relicts of pre-Quaternary faunas (Racovitza, 1907).

#### DEFINITIONS, SCALE, AND DISPERSAL ABILITY

In evolutionary terms a refuge is a region in which certain types or suites of organisms are able to persist during a period in which most of the original geographic range becomes uninhabitable because of climatic change (Morton et al., 1995). Continuing climatic change may result in the development of **refugia** – characterized by an accentuated long-term stability of various environmental parameters – which allow the survival of a species, through fragmentation of the refuge. This fragmentation may itself be the

vicariant event, namely the division of the biota or taxon through the development of a natural barrier. Such relictual faunas are especially widespread in the subterranean world, and are represented by eco-geographic **relicts** (separated from a parent population by some vicariant event – French *relictés*) and phyletic **relicts** (the last survivors of an ancient radiation: Newman, 1991 – French *reliques*). It should be noted that, while a lineage may be old, many species are likely to have evolved after the lineage invaded the hypogean environment (Wägele, 1990; Holsinger, 1994), especially in aquatic systems.

It is necessary to distinguish between the processes causing the separation of the fauna, which leads to their recognition as relicts, from those that result in the taxa entering the hypogean realm in the first place. While the same processes may be involved, their contributions must in most cases remain unproven; once a relict pattern has been established and the surface populations are, by definition, lost, one can only speculate about the processes causing the populations to move underground. I draw examples from terrestrial and aquatic faunas.

In northwestern Australia a rich terrestrial troglobite fauna occurs in humid caves in arid Cape Range, the affinities of which lie with the litter fauna of temperate and tropical rainforest now several thousand kilometres distant (Humphreys, 1993a,c). While the vicariant event was probably the loss of rainforest resulting from the onset of aridity (see Humphreys, Chapter 30, this volume), the fauna was not necessarily driven (drawn?) underground by the onset of aridity but may already have actively colonized the underground – that is, the colonization of the subterranean realm was not necessarily ‘under constraint’ (Botosaneanu and Holsinger, 1991).

Recent analyses of tropical cave biota have provided evidence for widespread parapatric, even sympatric, speciation (e.g. Wilkens and Hüppop, 1986; Howarth, 1987; Hoch and Howarth, 1989a, 1993); this has been argued also for glaciated regions (Rouch and Danielopol, 1987). For example, in the Hawaiian archipelago, the islands of which vary in age from 1 to 6 Ma (million years), colonization of emergent land led to explosive adaptive radiations. These resulted in swarms of closely related species exploiting different habitats, including the hypogean habitat (e.g., *Oliarus* planthoppers: Hoch and Howarth, 1993), in which troglobites independently evolved on each island, in at least ten different radiating groups (Howarth, 1987).

Howarth categorized 27 of the 43 species of troglobites present, and considered that speciation in 22% was sympatric (related species occur in the same cave), 48% parapatric (related species occur in neighbouring habitats), and 30% allopatric (related species are geographically isolated). Similarly in Australia a great diversity of *Solonaima* and *Undarana* planthoppers occurs, with closely related epigeal and cavernicolous species (Hoch and Howarth, 1989a,b).

A widely disjunct, but recognizable and predictable, community inhabits anchialine waters (inland ground-water affected by marine tides and with limnic and marine influence, and usually with limited aerial connection) of northwestern Australia, the Canary Islands and the Caribbean region (Holsinger, 1989, 1992; Yager, 1987a,b, 1994; Humphreys and Adams, 1991; Poore and Humphreys, 1992; Bruce and Humphreys, 1993; Humphreys, 1993b; Knott, 1993; Yager and Humphreys, 1996). This specialized, relic and relictual fauna comprises mainly obligate stygobiont taxa containing several species congeneric between the three regions. While this distribution is consistent with the hypothesis that movement of tectonic plates was the vicariant event, and thus that the genera were already present in cave habitats, possibly as early as the Jurassic, certainly by the Middle Cretaceous (Yager and Humphreys, 1996; see also Humphreys, Chapter 30, this volume), this adds nothing to the understanding of the events that resulted in their entering, and becoming restricted to, the underground realm.

### Scale

The vicariance event necessary for relictualization can occur at any scale, from the level of adjacent unconnected caves, to the global scale. Of the vicariant agents, some are physical (e.g. geological, stratigraphic, geomorphological, fluvial, stream capture, spring failure, perched water tables, plate tectonics, and the relative changes in level between land and sea that result from many processes), some are environmental (e.g., temperature, humidity, anoxia) and some temporal or merely stochastic. Clearly the effectiveness of these factors as barriers, or even their existence, depends on the biological attributes of the species (e.g., rivers may be barriers to terrestrial but not to aquatic troglobites: Barr Jr and Holsinger, 1985), and the temporal scale (e.g., plate-tectonic events are irrelevant to Quaternary relictualization).

### Dispersal ability

Despite the occurrence of troglobites in the superficial underground compartment (Juberthie and Delay, 1981), such animals have very poor dispersal abilities, as is evident, *inter alia*, by the polytypic genera with high endemism (Strayer, 1994), the low frequency of sympatry of congeners (Notenboom, 1991), the lack of easily dispersed stages (e.g., larvae: Stock, 1980), low reproductive potential, the production of relatively large offspring and the long period of brood care (K-strategists: Stock, 1986a). Because of poor dispersal abilities, troglobites are excellent palaeogeographical monitors (Sbordoni, 1982; Danielopol, 1980).

## MECHANISMS OF RELICTUALIZATION

### Historical

The classic view of the evolution of troglobites is, in essence, that climatic instability in the epigeal environment, especially the temperature and humidity changes associated with the onset and retreat of Pleistocene glaciations, led to the extinction of surface populations of species inhabiting soil and litter, mostly in the boreal forests. This disrupted gene flow between the various troglomorphic populations, and permitted adaptation to cave conditions in the now relictual cave populations (Barr Jr, 1968; Sbordoni, 1982; Barr Jr and Holsinger, 1985).

The relatively dry climates of the interglacials caused epigeal cryptozoic terrestrial lineages to retreat to the wetter conditions to be found at higher altitudes and latitudes. Hence, the extinction of the epigeal populations permitted cave adaptation to proceed at lower latitudes and altitudes. This thesis, with aridity as the driving mechanism, has been extended globally to any area where the Pleistocene glaciations would have had climatic implications. For example, changes in the altitude range of vegetation zones associated with the onset of aridity that accompanied the glacial periods are evident in the Grand Canyon (Peck, 1980) and the Galapagos Islands (Peck, 1990).

In aquatic lineages, the onset of colder conditions during the glacial periods resulted in thermophilic lineages seeking refuge in groundwater (winter-warm conditions), while psychrophilic lineages colonized groundwater as the climate warmed and dried during interglacials (Gibert et al., 1994). Repeated cycles of

glaciation eliminated surface populations and allowed cave populations to speciate.

The presence of cave-adapted species on tropical oceanic islands, and widely within the lowland tropics, has suggested that the extinction of surface populations is not necessary for the evolution of troglobites. In both northeast Australia and Hawaii closely related surface relatives of troglobites still exist, hence, rather than being relicts isolated in caves by changing climate, such troglobites seem to have become highly specialized in order to exploit resources within the system of interconnected medium-sized voids (Howarth, 1987; Hoch and Howarth, 1989b).

### Terrestrial

On a global scale, the dipluran genus *Litocampa* contains 32 species in the Americas, Europe and Africa, of which 20 species are confined to caves in the United States where no epigeal forms are known. The distribution and perceived retention of plesiomorphic characters suggests that the genus predates the fragmentation of Pangaea in the Mesozoic (Ferguson, 1981).

The eastern United States of America has been the focus of intense biospeleological study, and provides well-worked examples of terrestrial relictualization. There, for example, the trechine beetles (Carabidae) are the most widely represented and abundant group of terrestrial troglobites, the genus *Pseudanopthalmus* alone containing 240 species, and another seven genera containing from one to five species each. There are no obvious ancestors for the cave genera in North America, but there are oculate relatives in Eurasia. This distribution pattern suggests that the trechines of North America are relicts of formerly widespread epigeal faunas (Barr Jr and Holsinger, 1985).

The evolution of cave beetles of the subfamily Bathysciinae is a good European example of relictualization of a terrestrial lineage (Juberthie, 1988). Just two examples from the extant taxa may be considered – the separation of *Batinoscelis*, known from southern Sardinia, from the species complex of *Speonomus delarouzei* found in the eastern Pyrenees. The ancestors of the Bathysciinae inhabited tropical forest at low altitude (Jeannel, 1952) – they are currently found under relict tropical forest at an elevation of 1000 m in Tenerife (Oroni et al., 1986) in the mesovoid shallow substratum (Juberthie, 1988). During the Oligocene (35 million years ago) the Corsico-Sardinian plate abutted

the Pyrénées (which then had a tropical climate), and the range of bathysciine cave beetles included southern Sardinia and the Pyrenees (Fig. 22.1a). Palaeomagnetic evidence shows that, with the opening of the western Mediterranean, the Corsico-Sardinian plate broke free in the Miocene (25–20 million years ago), rotating anti-clockwise as it moved to its present position near Italy, and isolating the Sardinian beetle population in the south of the island (Fig. 22.1b). Other populations were isolated by marine transgressions into the Rhône and Saône Valleys during the Pliocene (Juberthie, 1988). Estimates of genetic distance suggest that the genera separated about 25 million years ago (Sbordoni, 1982), in broad agreement with the palaeogeographic evidence [one may note that Sbordoni (1982) used a conversion factor between genetic distance and age that is about twice that of Juberthie (1988)]. Hence, the current distribution is explained by the close proximity of southern Sardinia and the Pyrenees during the Oligocene.

There are good-quality palaeoclimate data for the Pyrenees, and they have been used to interpret the speciation there of the *Speonomus delarouzei* complex. Juberthie (1988) assembled a wealth of palaeoclimatic, behavioural, ecological and electrophoretic evidence to support his thesis that the three species arose owing to the effects of successive Pleistocene glaciations. During glacial periods the forests retreated to lower altitudes to be replaced by steppe, while during interglacials the forest zone migrated to higher altitudes. These repeated events served both to permit movement of the beetles through altitude, and to isolate the populations, permitting their adaptation to different thermal conditions (Juberthie, 1988).

### Aridity

Analysis of pollen and pack-rat middens, for example, has allowed determination of the altitudinal migration of forest associated with climatic cycles over wide areas of the earth, not simply on the margins of glaciated regions. The association of these migrations with the altitudinal occurrence of troglobitic animals has been used to support the climatic-refuge hypothesis for the origin of troglobites (Peck, 1980, 1981b, 1990; Juberthie, 1988). Peck (1984) developed a coherent hypothesis associating speciation events (branching in the cladogram) in the *Ptomaphagus hirtus* species complex of leiodid beetles inhabiting North American caves with particular dry periods, using a combination of studies on speleothems, allozymes and hybridization (Fig. 22.2).

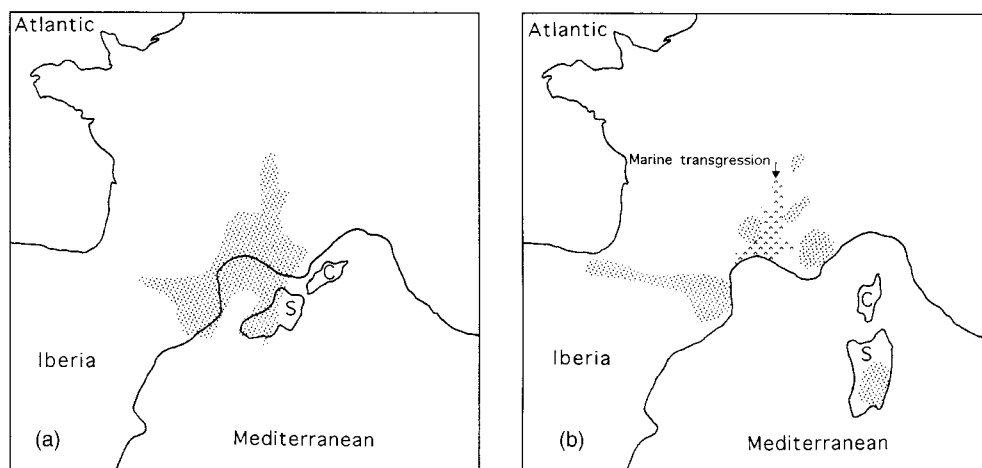


Fig. 22.1. Reconstruction of the western Mediterranean in the (a) Oligocene (35 million years ago) and (b) Late Miocene (5 million years ago), showing the fragmentation of the range of bathysciine cave beetles (dots). Marine transgression is depicted only in (b) and only for the Rhône and Saône valleys. The maps are greatly simplified from sequential plots in Juberthie (1988). C, Corsica; S, Sardinia.

In Puerto Rico the community of terrestrial troglomorphs found in the arid tropical zone of the south coast is similar to that found in the moist forest zone of the north coast. The 43% similarity is primarily due to species requiring a moist environment which, on the north coast, are also to be found outside caves in leaf litter of the moist forest; this suggests that the northern habitat once extended over the southern part of the island (Peck, 1981a). An analogous argument has been applied to the community resemblance between arid-zone caves on the western seaboard of Australia and lowland rainforest on the east coast of the continent, thousands of kilometres away (Humphreys, 1993b,c).

#### Survival beneath continental ice sheets

There are several well-founded examples involving both terrestrial species (mites: Zacharda and Pugsley, 1988) and aquatic species (amphipods and isopods: Holsinger, 1978; Holsinger et al., 1983) where caves seem to have served as deep, subglacial refugia for some preglacial fauna, during periods when continental ice sheets removed surface populations.

### Aquatic

#### Stranding

The stranding of faunas due to the marine regressions resulting from eustatic, orogenic or tectonic events, especially during the Late Tertiary, has been a major focus for theory on the origin of aquatic hypogean faunas as well as their relictualization.

Although many studies have focused on the Late Tertiary (e.g., Por, 1986; Stock, 1986a, 1990, 1994; Boutin and Coineau, 1987), others have recognized the likely ancient vicariance in many stygofaunas (e.g., Boutin and Cals, 1985a,b; Boutin and Coineau, 1987; Rouch and Danielopol, 1987). The occurrence and distribution of aquatic hypogean species is commonly explained by marine regressions having forced their ancestors underground and stranded them inland (Stock, 1977, 1980; Wagner, 1994). The distinction between the processes driving the evolutionary process (troglogenesis) and those driving the distribution of species (vicariance, relictualization) is not always clearly established. Alternative explanations, for which there is wide-ranging evidence, include suggestions that colonization is an active process (Juberthie, 1984; Rouch and Danielopol, 1987), and that speciation may not be vicariant, but rather peripatric, parapatric, even sympatric (see pp. 418–419 above). Furthermore, much of the fauna must have already been hypogean long before the occurrence of the stranding events described. For example, there are higher taxonomic categories (classes, orders, families) whose entire membership is highly troglomorphic and for which non-troglomorphic members are unknown, including the remipedes and most genera of Thermosbaenacea (Newman, 1991). Many of these taxa contain species congeneric on either side of the Atlantic – some also in northwestern Australia – and are thus likely to have been dispersed by plate tectonics and sea-floor spreading starting in the Mesozoic. Despite this, the

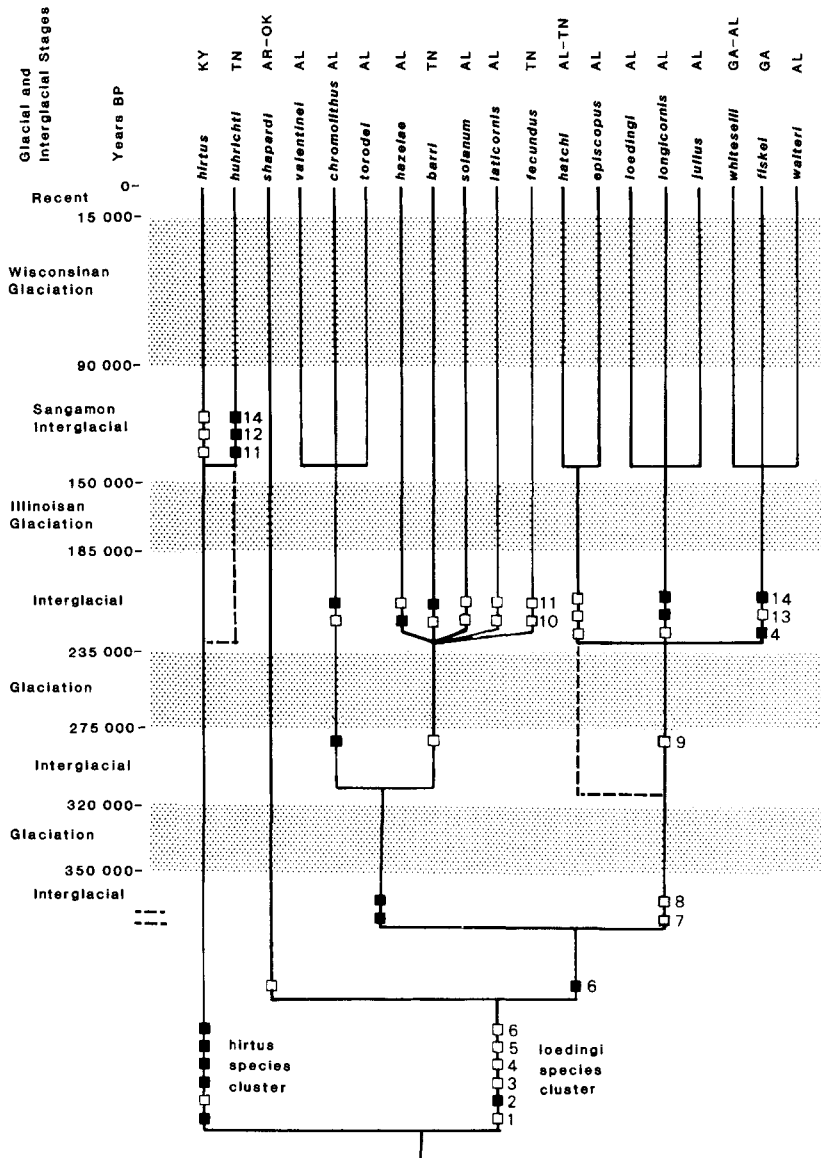


Fig. 22.2. Cladogram of the *Ptomaphagus hirtus* species group of cavernicolous leiodid beetles in the southeastern USA. The distributions are indicated by the state abbreviations (AL, Alabama; AR, Arkansas; GA, Georgia; KY, Kentucky; OK, Oklahoma; TN, Tennessee). Apomorphic character states are shown by solid squares, plesiomorphic character states by open squares. Isotope studies of cave stalagmites were used to determine the time and temperature of the glacial and interglacial periods. Branching times were determined by a combination of allozyme and hybridization studies. The lineage splits and character origin are shown at the most recent likely times for the events. From Peck (1984), with permission.

distribution of these forms is commonly explained by invoking changes in sea level during the Late Tertiary, especially during the Miocene (Stock, 1986a, 1990).

In essence the 'regression model' (Stock, 1977) is an explanation of stranding: marine transgressions allow marine stygobionts to expand their range by

invading new areas and habitats, and subsequent marine regressions isolate the lineages inland where they adapt to the decreasing salinities (Fig. 22.3). Although the distributions of hadziid amphipods in the Caribbean (Stock, 1977) and *Pseudoniphargus* (Amphipoda) in Europe (Fig. 22.3) are consistent with this model, Stock (1980) recognized that the model did not account

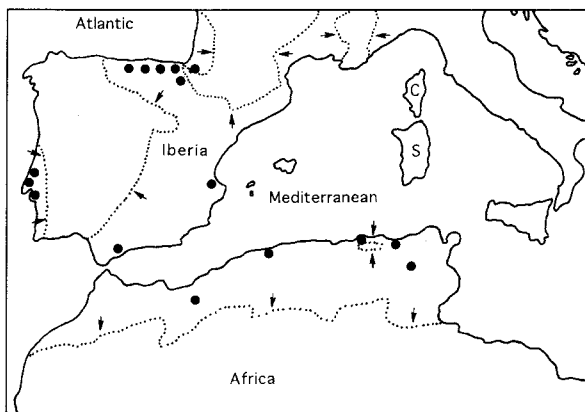


Fig. 22.3. The actual localities of *Pseudoniphargus* (points) in continental waters of Europe with the position (dotted line) of the maximum marine incursion from the Eocene to the present (arrows point inland). They are found in a wide range of habitats – island and continental, from marine/polyhaline to fresh-water at 1000 m altitude. All localities of *Pseudoniphargus* were on dry land in the Pliocene. During the Miocene most species were located on the edge of land and sea. The populations in northern Spain were submerged only during the Eocene. Much simplified from sequential plots in Stock (1980).

for the presence of congeneric species of obligate stygobionts on either side of the Atlantic.

Stock's (1977) model has been modified and extended by Boutin and Coineau (1990: *Modèle biphasé*; Fig. 22.4), Notenboom (1991: Two-step model; Fig. 22.5), and Holsinger (1994: Three-step model). The similar 'biphasé' and the 'two-step' models were independently derived from different exemplars. The first step included many factors, such as active dispersal of generalized animals, a vertical transition from surface marine waters to an interstitial or crevicular littoral habitat – presumably aided by some kind of adaptive shift (*sensu* Howarth, 1987) – and passive processes, such as the isolation of interstitial freshwater animals from their marine or littoral ancestral populations. Subsequently these models essentially follow Stock's regression model.

The three-step model of Holsinger (1994) describes three levels along a continuum of hypogean adaptation, from each of which various vicariant and invasional events can proceed. This complex of models is applicable to invasion from both freshwater and marine sources and thus, at the same time, is both a generalization of, and an extension to, the two-step model. The model invokes processes of troglogenesis (direct invasion by preadapted taxa, as well as passive processes such as stranding from marine or fresh waters) and relictualization (vicariance by stream

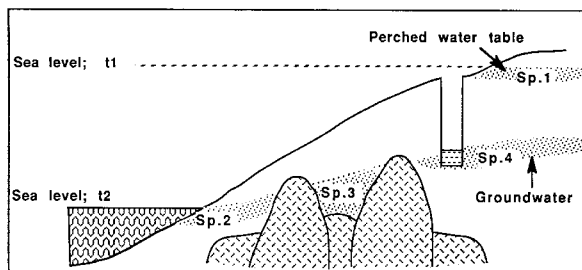


Fig. 22.4. Hypothetical origin of continental stygal species stranded inland by marine regression. Species 1 was stranded in a perched water table at the position of the beach during maximum marine transgression ( $t_1$ ); species 2 followed the regressing beach to time  $t_2$ ; species 4 followed the lowering groundwater level and is accessible in a well; and species 3 became isolated by impermeable strata. After Boutin and Coineau (1990).

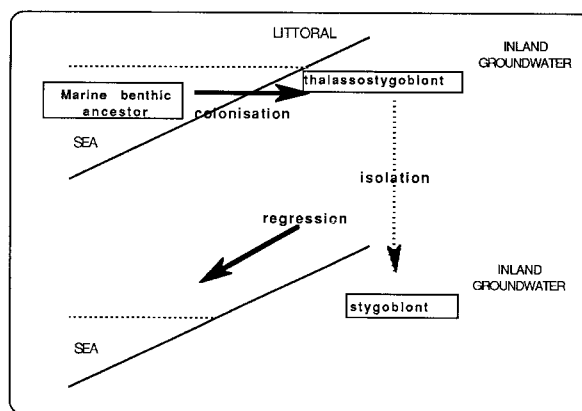


Fig. 22.5. Schematic representation of the two-step evolutionary model; of marine lineages of inland stygobionts. After Notenboom (1991).

capture, spring failure, changes in water table and marine regression).

#### Plate tectonics and Tethyan relicts

While Poulson and White (1969) proposed that some species had been relictual in caves for 100 million years, Barr Jr and Holsinger (1971) argued strongly that isolation in caves was not earlier than the Late Pliocene (1.5–2.0 million years ago). The age of relictualization of hypogean fauna has always been contentious, and will remain so until adequate distributional and phyletic data, from molecular, morphological and fossil material, are analysed appropriately.

The distributions of many higher taxa of obligatory hypogean animals, because their powers of dispersal are otherwise very limited (see above, p. 419), provide evidence that the distribution of some relict faunas occurs through rafting on tectonic plates by means of seafloor



spreading. As no order of terrestrial troglobites is restricted to the hypogean habitat, the most compelling evidence comes from aquatic groups, among which some Crustacea need to be considered: obligatory freshwater groups (e.g., Syncarida), or anchialine taxa (e.g., Thermosbaenacea and Remipedia).

**Freshwater groups:** On account of their worldwide distribution in fresh waters and absence from marine habitats, Syncarida are considered to be Pangaeal (Schminke, 1974; Boutin and Coineau, 1987), as is the amphipod family Bogidiellidae (Karaman, 1982; Stock, 1977, 1983), although with a more restricted distribution. Their biogeography is explicable if they entered fresh water before the Triassic and were subsequently dispersed by tectonic-plate rafting.

It needs to be borne in mind that the apparent affinities of rare taxa can change substantially with the addition of small amounts of information; an example of this follows. For three decades the peracarid crustacean order Spelaeogriphacea was known from a single location and species – *Spelaeogriphus lepidops*, described from a freshwater stream in a cave located at an altitude of about 900 m on Table Mountain in South Africa (Gordon, 1957), and a fossil of Carboniferous age from a shallow-water marine deposit in the Atlantic Provinces of Canada. The discovery of *Potiiocoara brasiliensis* from the Mato Grosso, Brazil, and *Mangkurtu mityula* from northwestern Australia, fulfilled Schram's (1974) prediction of the Gondwanan biogeographic affinities of the order. However, in 1997 two new fossil sites changed the complexion of the biogeography of the order. Modern looking species, close to *Spelaeogriphus*, were recognized from freshwater lacustrine deposits from the Lower Cretaceous of Spain and the Jurassic of China. Hence, it would appear that the order Spelaeogriphacea has Pangaeal affinities (Poore and Humphreys, 1998), like the Syncarida discussed above.

There are numerous troglobitic amphipods which, owing to their limited powers of dispersal, are locally endemic and thus provide many examples of relicts, both phylogenetic and distributional (Holsinger, 1991). For example, the crangonyctids, which are exclusively freshwater and lack close marine relatives, probably had a Laurasian origin prior to the separation of North America and Eurasia in the Jurassic. Five of eight described genera are exclusively troglobitic (82% of the species), and two of the genera, *Crangonyx* and

*Synurella*, occur both in Europe and North America (Holsinger, 1986).

Wägele (1990) considered that at least three groups of isopods (Aselloidea, Calabozoida, Phreatoicoidea and probably the Protojaniridae) probably existed before the opening of the Atlantic. The wide distribution of Stenasellidae in subterranean freshwater habitats also suggests a broad Laurasian distribution prior to opening of the Atlantic, as well as connection between present-day Bermuda and older continental fragments (Wägele, 1990); this is an example of how the distribution of relictual taxa may have a contribution to make to the earth sciences, in that they often suggest a history at variance with current geological interpretation (Stock, 1986a,c; Notenboom, 1991).

**Tethys Sea:** Tethys came into existence only after the Mesozoic fragmentation of the Triassic Pangaea (Por, 1986), when it became a seaway separating the continents of Gondwana and Laurasia, and it persisted from the Triassic until the late Eocene (that is, from 200 million to 40 million years ago: Smith and Briden, 1977). Cosmopolitan elements of the Tethyan marine biota girdled the earth during the Mesozoic and through the Cretaceous (from 100 to 60 million years ago) via currents and oceanic islands of Panthalassa in the epicontinental seas (see Newman, 1991; Fig. 22.3).

The Mediterranean area is often considered to epitomize Tethys, but this part of it became landlocked, and almost completely dried out for several million years in the late Miocene (6 million years ago), leaving a series of hypersaline lakes (Por, 1986). This event, the Messinian Salinity Crisis, left only stygal habitat available for animals after marine regression (Botosaneanu and Holsinger, 1991). In consequence the circum-Mediterranean subterranean waters contain relicts (tropical elements) of the last pre-Messinian marine transgressions of the Miocene (~11 million years ago: Dimentman and Por, 1991).

Sphaeromidae are typically marine isopods, but species in the genera *Caecosphaeroma* and *Monolistra* (Monolistrini) are relicts in freshwater cave environments of southern Europe, from France to Bosnia-Herzegovina. Their distribution has been related to the location of deep, long-lasting, marine incursions during the Miocene, and their isolation and evolution linked with the Messinian Salinity Crisis. Estimates of the age of divergence using genetic-distance data support the coincidence of the salinity crisis and some of the

speciation events (e.g., Sbordoni et al., 1980; Sbordoni, 1982).

**Tethyan relicts:** The term “Tethyan relicts” is variously used in the literature. Por (1986) referred to “Tethyan relicts” when dealing with subterranean species which have no congeners in the open sea, and which appear in areas that were covered by the Eocene–Miocene Tethys. While accepting vicariance by plate tectonics, and the existence of congeneric species on either side of the Atlantic, he considered that the “classical case of **Miocenic** [my emphasis] amphiatlantic patterns are those of the *Thermosbaenacea*, . . . [and] the hadziid amphipods.” (p. 73). Similarly, Stock (1986b) stated “both [stygo-biont and deep-water taxa] evolved after the Oligo–Miocene anoxia crisis in the Atlantic . . .”, although he subsequently accepted the likely role of plate tectonics in distributions (Stock, 1994).

Although there is a greater diversity of Tethyan relicts in the Indo-Pacific than in the Atlantic (Newman, 1991), several higher taxonomic groupings of Crustacea, namely the Remipedia, the *Thermosbaenacea*, the *Spelaeogriffacea* and the *Mystacocarida*, were thought to have exclusively circum-Atlantic distribution patterns. These are especially convincing as relictual distributions, since all members are blind, have life histories seemingly not conducive to long-range dispersal, and are restricted to hypogean habitats – anchialine, marine interstitial brackish, and freshwater. Furthermore, many contain species congeneric across the Atlantic, for instance *Speleonectes* (Remipedia); *Halosbaena* and *Monodella* (*Thermosbaenacea*); *Curasanthura* (Isopoda); *Gevgeliella*, *Psammogammarus*, *Pseudoniphargus*, *Spelaeonicippe* and *Stygogidiella* (Amphipoda).

The argument for vicariance due to the opening of the Atlantic is convincing, as their distribution on the reconstructed Triassic land-masses would be relatively modest (Fig. 22.6). However, the Remipedia (Yager and Humphreys, 1996), *Thermosbaenacea* (Poore and Humphreys, 1992), *Spelaeogriffacea* (Poore and Humphreys, 1998), and *Mystacocarida* (Bartsch, 1993) are now known from Western Australia. This Australian fauna contains species congeneric with members of the classically Tethyan relict fauna found on either side of the North Atlantic (*Halosbaena*: Canaries and Caribbean), or with otherwise widely disjunct distributions (*Haptolana*: Cuba, Somalia; *Lasionectes*: Turks and Caicos; *Liagoceradocus*:

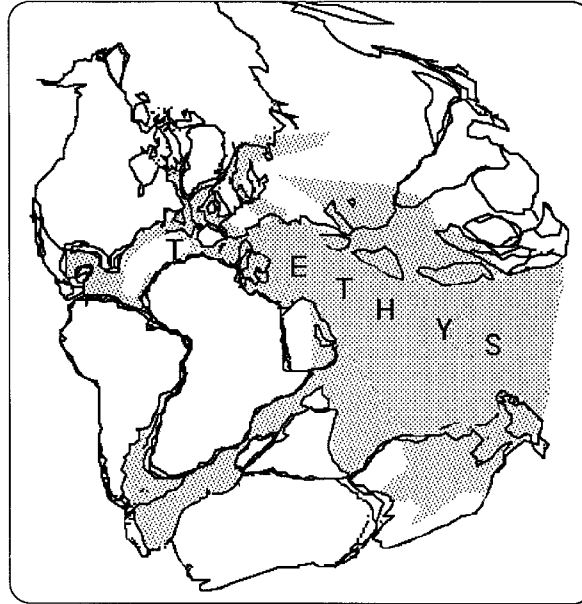


Fig. 22.6. The relative location of the continental plates and the extent of the epicontinental seas in the Jurassic (151 million years ago), when the Tethys Sea first connected the present Caribbean, Mediterranean and Indian Ocean regions. Even with this reconstruction the genera *Lasionectes* (Remipedia), *Halosbaena* (*Thermosbaenacea*) and *Haptolana* (Isopoda: Cirolanidae) (Remipedia), known from northwestern Australia, have widely disjunct distributions, variously including Somalia, the Canary and Caribbean islands. The plate map was prepared by the technique of Scotese and Denham (1988).

Canaries and Pacific (Bradbury and Williams, 1996); *Danielopolina*: North Atlantic and Pacific (Baltanas and Danielopol, 1995). In consequence, the easy acceptance of a rather constrained distribution pattern represented on a reconstructed Triassic land-mass (Fig. 22.6), gives way to a renewed broad geographic range, much broader even than the current, non-reconstructed, amphiatlantic distribution. Furthermore, many being obligate stygofauna, the genera may have been present in the stygofauna before the isolation of the Australian plate (at least 100 million years ago: Cande and Mutter, 1982).

The distribution of remipedes and their associated fauna can be explained by cave colonization along the shores of Tethys during the Triassic and Jurassic 225 to 160 million years ago (Cals and Boutin, 1985), and subsequent dispersal by the break-up of Pangaea in the Mesozoic (Wilkens et al., 1986) through sea-floor spreading and continental drift (Stock and Longley, 1981; Iliffe et al., 1984; Hart et al., 1985; Wägele and Brandt, 1985). During the early Cretaceous the edge of

the plate now lying in northwestern Australia formed the eastern shore of Greater Tethys (Howarth, 1981).

Fossil ancestors of *Danielopolina* occur in the fillings of submarine fissures, showing that they had already colonized crevicular systems by the Late Jurassic (Aubrecht and Kozur, 1995). The Australian species of *Danielopolina*, an anchialine species, constitutes a sister group to the remaining eight species, which include a deep-sea species, *D. carolynae*, from the Atlantic; this refutes (Baltanas and Danielopol, 1995) a deep-sea ancestry for the genus (Boxshall, 1989), and is inconsistent with the general model for the colonization of the anchialine habitat during the Tertiary proposed by Stock (1986a,b). Similarly, the Australian species of *Halosbaena* (Thermosbaenacea) constitutes a sister group for the other two species in the genus, known from the Canary Islands and the Caribbean (Wagner, 1994; H.P. Wagner, pers. comm.).

Together, these analyses indicate that the Australian populations underwent vicariance before those on either side of the Atlantic, which would support the proposed sequence in the break-up of Pangaea – that the Atlantic started to open up ~170 million years ago eastern and western Gondwana had almost separated by the Upper Jurassic (145 million years ago: fig. 13.9 in Howarth, 1981), were well separated by the Lower Cretaceous (~125 million years ago: fig. 13.12 in Howarth, 1981), and by the Upper Cretaceous (~80 million years ago – probably even by the Middle Cretaceous, 100 million years ago: Cande and Mutter, 1982) Australia was not even joined by epicontinental seas to land-masses other than Antarctica (fig. 13.15 in Howarth, 1981). This concordance is consistent with the hypothesis that the genera rafted on their respective tectonic plates, in which case there has been remarkable morphological conservatism following a very ancient vicariant event.

#### Oceanic islands, deep-sea ancestry and anoxia

The presence of congeneric species of obligate cavernicoles on continental land-masses, as well as on islands on mid-oceanic ridges, has always presented problems in explaining the overall distribution of the fauna (e.g., Sket and Iliffe, 1980; Iliffe et al., 1983, 1984; Hart et al., 1985; Wilkens et al., 1986). Indeed, some taxa are so widespread as seemingly to defy simple explanation. For example, some genera belonging to higher taxa of apparently monophyletic lineages of obligate subterranean freshwater inhabitants – for instance, the Bathynellacea at a continental level

(Schminke, 1974) – are present on widely separated mid-oceanic-ridge islands and on continental land-masses. The anthurid isopod *Stygocyathura* occurs widely in the Caribbean region and the western Pacific (Wägele et al., 1987); other examples have been given by Hart et al. (1985). These distributions are consistent with the hypothesis that the isolation of the lineages on oceanic islands (and hence also continental vicariance) is associated with the mid-oceanic ridges and the fragmentation of the continents.

To account for the vicariant distribution of apparently ancient relict fauna and its presence on oceanic islands it has been suggested that a connection may be made, between the deep-sea and anchialine cave fauna, through suitable habitats in submerged rock, namely the crevicular system (Maciolek, 1983; Hart et al., 1985). Recent findings have suggested that many of these groups dispersed by sea-floor spreading when the continents fragmented (Hart et al., 1985; Boxshall, 1989), and that some were isolated on islands, or in crevicular systems associated with the mid-oceanic ridges (Hart et al., 1985; Boxshall, 1989), but there is no direct evidence for such crevicular habitats except in very shallow waters. There are, for example, many common elements on Bermuda, the Bahamas and Ascension, all of which have a common origin in the mid-Atlantic ridge in the late Cretaceous (110 million years ago: Manning et al., 1986). Boxshall (1989) suggested that a continuity of the crevicular habitat through geological time along the mid-oceanic ridges may have permitted the dispersal of misophrioid copepods – e.g., *Expansophria* and *Speleophria* both having species in anchialine habitats on Atlantic and Pacific islands.

Boxshall (1989) has provided the most compelling evidence for a deep-sea ancestry for misophrioid copepods from inland marine caves (Fig. 22.7), suggesting vicariance events in three dimensions – temporal, horizontal (movement from hot spots by sea-floor spreading) and vertical (rising of islands). In this context, it is worth noting that sulphide-oxidizing mixotrophic bacteria of the genera *Beggiatoa* and *Thiothrix*, which may be primary producers using sulphide-based chemosynthesis (Brigmon et al., 1994; cf. Kane et al., 1994), occur widely in anchialine and other groundwaters (Yager, 1991; Brigmon et al., 1994), as well as in deep-sea hydrothermal vents (Belkin and Jannasch, 1989). However, as occurred with *Danielopolina* (Baltanas and Danielopol, 1995), a single new observation could reverse the argument.

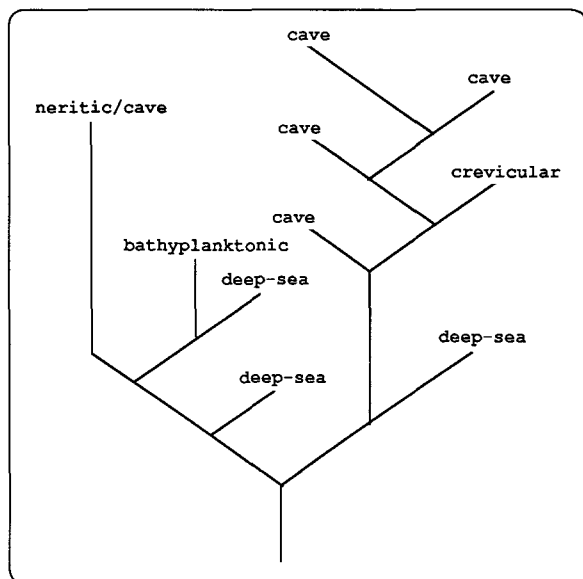


Fig. 22.7. Habitat cladogram which supports the deep-sea ancestry of the genera of misophrioid copepods. After Boxshall (1989).

Data from a number of taxa are also consistent with this hypothesis (Iliffe et al., 1983, 1984; Hart et al., 1985; Wilkens et al., 1986; Boxshall, 1989; Iliffe, 1990). However, it is not consistent with the distribution of *Bahadzia* (Hadziidae) (Holsinger, 1992), or thamatocyprid ostracods generally (Danielopol, 1990), and for the genus *Danielopolina* has been both proposed (Wilkens et al., 1986; Boxshall, 1989) and refuted (Baltanas and Danielopol, 1995).

Stock (1986a,b) strongly criticized the concept of deep-sea ancestry for the anchialine fauna and sought the origin of many stygobionts in the Oligocene and Miocene. He argued that the cooling of the oceans and the associated periods of anoxia in mid-ocean waters led to the extinction of the deep-sea Tethyan fauna after the Eocene, so that the abyssal animals must have been derived subsequently from shallow-water lineages. Hence, the presence of similar taxa on either side of the Atlantic, for example, points to a common origin, but not a derivation from deep biotas.

Stock (1986a,b) offered no explanation for amphiatlantic (or more widespread) congeners, the distribution of which cannot be explained by dispersal along deep shelf waters. However, under the constraints of his hypothesis for a Tertiary origin of much of the anchialine fauna, it would need to have dispersed through the deep oceans, and could, perhaps, have followed the surface of the anoxic zone, as do many extant anchialine forms. Stock himself suggested that

animals that prefer, or are capable of withstanding, oligoxic conditions would have found optimal habitats in the deep shelf waters just above the anoxic layer. Many taxa in anchialine habitats, including remipedes, therosbaenaceans, amphipods and isopods, are found in the highest densities in, or are even restricted to, waters very deficient in oxygen ( $<1 \text{ mg } \ell^{-1}$ ; Holsinger and Yager, 1985; Stock, 1986a, 1994; Yager and Humphreys, 1996). "There are ... intervals of geological time where a non-uniformitarian approach that goes beyond familiar appeals to climatic change and sea-level fluctuations may yield rich rewards" (Conway Morris, 1995, p. 293).

It should be noted, however, that periods of mid-oceanic anoxia ( $<0.2 \text{ mg } \ell^{-1}$  oxygen) were not especially associated with the Eocene, but occurred regularly throughout the Mesozoic, with a major anoxic episode in the Albian (~100 million years ago; Fischer and Arthur, 1977). Furthermore, while the oceans were anoxic at intermediate depths, the deep seas were oxic at the same time (Fischer and Arthur, 1977; Kaiho, 1991), and for at least 90 million years (Childress, 1995), and these processes then, as now (Kennett and Ingram, 1995), occurred synchronously in all tropical oceans (Kaiho, 1991). Stock (1994) subsequently accepted the likely role of plate tectonics in the broad disjunctions seen, for example, in *Namanereis hummelincki* (Polychaeta), *Curassanthura* and *Ingolfiella* (Isopoda), *Metaniphargus* and *Pseudoniphargus* (Amphipoda) and *Procaris* (Macrura). However, *Procaris* occurs on Christmas Island (Indian Ocean), which is not associated with a mid-oceanic ridge (Humphreys and Eberhard, 1998).

#### TRACK ANALYSIS

One of the tenets of vicariance biogeography is that the present biotic distribution resulted from the fragmentation of earlier continuous ranges of putative ancestors. As the same eco-geographic isolating events should affect disparate taxa in similar ways, these taxa should exhibit similar (covariant) distribution patterns – the generalized tracks of Croizat et al. (1974). As relictualization seems to be such a dominant theme in the story of hypogean faunas, one would expect generalized tracks to be a common theme. Holsinger (1989) used them in his analysis of the group of genera which occur almost exclusively in anchialine caves in the Caribbean area, where they occur beneath a halocline in water with a very low

oxygen content – *Danielopolina* (Thaumatocyprididae: Ostracoda), *Speleonectes* (Remipedia), *Tulumella* (Thermosbaenacea), *Bahalana* (Cirolanidae: Isopoda), *Bahadzia* (Hadziidae: Amphipoda) and *Agostocaris* (Agostocarididae: Decapoda). The broadly overlapping ranges of these genera, and their shared areas of endemism, suggests that the same fragmentation of an earlier continuous range of putative ancestors was caused by the same isolating events. At a higher taxonomic level (ostracods, remipedes, thermosbaenaceans, cirolanid isopods, gammarid amphipods and atyid shrimps), this community structure is characteristic (Holsinger, 1989, 1992; Yager, 1994) and has led to successful prediction of other members in northwestern Australia (Poore and Humphreys, 1992; Wagner, 1994) involving the genera *Danielopolina*, *Halosbaena*, *Hapitolana*, *Lasionectes* and *Liagoceradocus*.

### PROSPECT

It is generally assumed that the colonization of the hypogean realm is one-way, consistent with a traditionalist view that it houses “archaic biotas that have been displaced by competitive pressures” (Conway Morris, 1995, p. 293).

If many lineages were already present in the hypogean realm at the time that Pangaea fragmented, then some lineages could have become hypogean in association with the major global climate change at the end of the Palaeozoic; from 270 million to 200 million years ago, the atmospheric oxygen concentration fell from ~36% to 15%, with a concomitant four fold increase in atmospheric carbon dioxide (Conway Morris, 1995). In any case the hypogean fauna would subsequently have survived a number of anoxic episodes in the mid-ocean levels throughout the Mesozoic and Cainozoic (Fischer and Arthur, 1977), as well as the mass extinctions at the end of the Cretaceous which are associated with meteorite impacts. A major impact – Chicxulub on the Yucatán Peninsula – deposited a thick layer of ejecta throughout the Caribbean (fig. 9 in Hilderbrand, 1993), a stronghold of troglobitic fauna. The thick sequence of carbonate and sulphate rocks at the impact site increased the potential for disruptive climatic effects, and the resulting acid rain may have caused the extinction of both terrestrial and aquatic fauna (Hilderbrand, 1993). However, the massive carbonate deposits, in which most subterranean fauna are found, would neutralize the effects of acid rain, and would

have increased further, over and above the protection provided by their inhabiting subterranean systems, the chance that some lineages may have survived such a catastrophic event; one wonders whether they could have re-emerged to populate the non-hypogean world and re-acquire epigeal traits, in violation of Dollo’s and Arber’s laws (Lincoln et al., 1982) of the irreversibility of evolution.

Such a counterintuitive proposition finds support elsewhere; for example:

- (1) A number of epigeal species of Australian melitid and crangonyctoid amphipods are thought to have an hypogean ancestry in view of their lack of eyes (J.H. Bradbury, personal communication, 1996);
- (2) *Niphargus pectencoronatae* is a limnic immigrant into anchialine habitats (Sket, 1996);
- (3) The fact that the freshwater isopod genus *Microcrocerberus* is found on either side of the Atlantic Ocean supports the early divergence of the stygofauna (>100 million years ago). Moreover, importantly, Wägele et al. (1995) have concluded that the coastal mesopsammal taxa are derived from freshwater taxa and not, as is postulated in most models, *vice versa*.
- (4) Culver et al. (1995, fig. 8.4) have provided strong evidence that some karst-window populations of *Gammarus minus* in West Virginia have evolved from cave populations, and, in the process, have re-acquired compound eyes, in apparent violation of Dollo’s law. However, it is now recognized that eyes can evolve quickly (Osorio et al., 1996), and that the evolution of morphological complexity may commonly be reversed (see Gould, 1996).

The view expressed by Gibert et al. (1994) – that groundwater systems are not sparsely populated by rare relict forms, but are dynamic ecosystems responding to a plethora of ecological processes similar to those occurring on the surface – may have more widespread relevance in the hypogean realm.

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