

THE ZONATION MODEL FOR THE EVOLUTION OF AQUATIC FAUNAS IN ANCHIALINE CAVES

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SUMMARY

Recent biological discoveries from anchialine caves have produced great surprises and apparent contradictions, with some cavernicolous species appearing to be much older than the caves they inhabit, while others show anomalous and widely separated zoogeographic relationships or even affinities to present deep sea taxa. In addition, many fresh water cavernicoles probably have a marine origin.

Anchialine caves occur as flooded lava tube caves or as solutional, primarily limestone, caves submerged by rising sea levels or by land subsidence. Such caves have several common characteristics, e.g. their occurrence principally on islands, their tidal nature with salinities of at least the deeper waters close to that of the open sea, the isolation of their waters in some inner portions from the open sea resulting in long residence times, and their biological zonation comparable to that of terrestrial caves.

A model for the evolution of fresh water cavernicoles from marine ancestors is here proposed. This model is based upon the observed zonal patterns of submarine and anchialine caves. A suitably preadapted species would first colonize the entrance zone of a marine cave. Subsequent migration farther into the cave could result from the expansive nature of the species. Genetic isolation of the cave population could occur as a result of sea level changes, cave collapse, or temperature variations. Such dispersal and isolation would be accompanied by gradual evolutionary adaptation. In the environmentally stable but food-poor inner reaches of the cave, nutritional strategies would be a prime factor in determining a species' survival. Open inland pools formed by cave collapse would provide plentiful food resources such as photosynthetic algae or surface-derived organic detritus. Upward invasion of these pools would require further adaptation to the brackish or even fresh surface waters typically encountered in the anchialine habitat. A final step would involve dispersal from these inland pools to completely fresh water cave systems. This series of events would be a continuous process not dependent upon sea level movement or position. The great age of limestone platforms such as the Bahamas would provide long periods for these evolutionary steps to occur. The postulated mobility of cavernicoles is evidenced by their powers of dispersal to colonize comparatively young caves.

RÉSUMÉ

Les découvertes récentes dans des grottes anchialines ont apporté de grandes surprises et d'apparentes contradictions, certaines espèces cavernicoles se montrant plus anciennes que les grottes qu'elles habitent, tandis que d'autres présentent des affinités curieuses avec des éléments de la faune marine bathyale/abyssale à des distances considérables.

Les grottes anchialines sont soit des tubes de lave inondés, soit des grottes creusées surtout dans les calcaires, et submergées lors de hausses du niveau des mers, ou par subsidence des terres. Il y a plusieurs caractéristiques communes à ces grottes, à savoir: leur présence surtout sur les îles; leur nature tidale faisant que la salinité au moins des couches plus profondes de leurs eaux est proche de celle de la mer ouverte; l'isolement par rapport à la mer, de leurs eaux situées

plus à l'intérieur, ce qui se traduit par de longs temps de résidence; et leur zonation biologique comparable à celle des grottes de l'intérieur.

On propose un modèle pour l'évolution de cavernicoles dulcaquicoles à partir d'ancêtres marins; ce modèle est basé sur la zonation observée dans les grottes submarines et anchialines. Une espèce convenablement préadaptée coloniserait initialement la zone de l'entrée d'une grotte marine. La nature expansive de l'espèce pourrait donner une migration vers les parties plus profondes de la grotte. Une isolation génétique de la population cavernicole pourrait être le résultat d'oscillations du niveau de la mer, d'effondrements de la grotte, de variations thermiques. Une telle dispersion et isolation seraient accompagnées par une adaptation graduelle. Dans les parties profondes de la grotte, à milieu stable mais à ressources trophiques pauvres, ce sont les stratégies concernant la nutrition qui joueraient le rôle principal dans la survie de l'espèce. En ce qui concerne les "pools" à jour, déterminés par effondrement du toit de certaines grottes, les ressources trophiques sont ici abondantes (algues, détritiques organique en provenance de la surface). L'invasion des creux souterrains à partir de ces "pools" demanderait une adaptation subséquente aux eaux saumâtres ou même douces si typiques pour les couches supérieures dans les habitats anchialins. Une étape finale sera la colonisation, à partir de tels "pools", de systèmes de grottes à eaux parfaitement douces. Cette succession d'événements serait un processus continu, non dépendant des oscillations du niveau marin et de l'endroit où elles se produisent. L'âge considérable de plateformes calcaires telle celle des Bahamas aurait pu fournir le temps nécessaire pour la succession de ces étapes. La mobilité des cavernicoles, postulat de cette théorie, est prouvée par leur capacité coloniser des grottes comparativement jeunes.

INTRODUCTION

Recent biological investigations of marine caves have revealed the presence of an unexpected variety of endemic species including relict taxa such as Remipedia, a new class of Crustacea (Yager, 1981); Mictacea, a new order of peracarid Crustacea (Bowman et al., 1985); Atlantasellidae, a new family of Isopoda (Sket, 1979); in addition to a new family of Caridea now under study. Several puzzling inconsistencies have turned up as a result of these discoveries. Cavernicolous species from some caves appear to be much older than the caves they inhabit. For example, the phylogenetically ancient Remipedia as well as other old troglobitic species have been found in the 3,000 to 5,000 year old Jameos del Agua lava tube cave in the Canary Islands (Iliffe et al., 1984b). A disjunct distribution is encountered for some cavernicolous species which inhabit isolated but widely separated caves. Remipedia, along with the anthurid isopod *Curassanthura*, the mysid *Heteromysoides*, and the amphipod *Spelaeonicippe*, have species on both sides of the Atlantic and are probably Tethyan relicts (Iliffe et al., 1984b). Other species such as the galatheid *Munidopsis polymorpha* and the polychaete *Giesiella jameensis*, both from the Jameos del Agua, show affinities to now deep water species (Iliffe et al., 1984b). Furthermore, various fresh water cavernicoles including many nematodes, polychaetes, copepods, mysids, thermosbaenaceans, isopods, and amphipods are marine relicts (Vandel, 1965:470).

TYPES AND ORIGINS OF MARINE CAVES

To understand and explain these problems, it is necessary to first examine the nature and origin of marine caves as well as factors affecting the coloniza-

tion of these caves and evolutionary pressures influencing marine cavernicoles. The definitions of terms used in this paper correspond with those proposed at the Bermuda International Symposium on the Biology of Marine Caves (Stock et al., this issue).

Submarine and anchialine caves are typically of either volcanic or solutional origin. Flooded lava tube caves can be of impressive dimensions. The Jameos del Agua lava tube in the Canary Islands has been explored by cave divers for over 1300 m to a depth of 53 m without an end being reached (Exley, 1983; Power, 1984). As this cave was reportedly formed by an eruption 3,000 to 5,000 years BP when sea level was only slightly below its present position, a major portion of the speleogenetic process would have been submarine. Other evidence of underwater lava tube formation comes from Hawaii where small tubes have been observed to originate as lava flowed into the sea. If completely submarine lava tubes can form, then such caves could exist at any depth within the ocean as a result of eruptions along mid-ocean ridges or at other hot spots on the sea floor.

Much more common are limestone caves formed by acidic fresh or brackish water solution and later submerged by rising sea levels or land subsidence. The longest such cave is Lucayan Caverns on Grand Bahama Island which has been explored by cave divers for over 10 km. Other large sea water-flooded limestone caves are known from elsewhere in the Bahamas as well as Bermuda and Belize, although many other large underwater cave systems in both the Atlantic and Pacific await discovery. Prolonged subsidence of shallow water limestones as has occurred in the Bahamas for the past 200 million years (Meyerhoff & Hatten, 1974) has resulted in the formation of a huge platform honey-combed with caves at all depths.

Crevicular micro-caves occurring in both limestone and volcanic rocks may extend to great depths. Submersible dives to depths below 1,000 m along the sides of the Bermuda sea mount have revealed a highly fissured volcanic relief (John M. Peckenham, personal communication). Similar features have been observed along the sea bottom on the area of the mid-ocean ridges (Heezen & Hollister, 1971). The colonization of anchialine pools in recent lava flows by shrimp and other invertebrates (Maciolek, 1983) demonstrates the degree of interconnections of voids within the rock.

Anchialine caves have several characteristics in common. First, they occur primarily on islands. The explanation for this is probably hydrologic. The high ratio of coastline to land area for smaller islands in comparison with larger islands or continents means that fresh water runoff per unit length of coastline is decreased such that salt water can penetrate farther inland. Also, the tidal lag between the waters of a shallow bank or a partially enclosed lagoon on one side of an island and a more open, deep water coast on the other produces a hydrostatic head generating tidal currents through caves connecting one side to the other. Second, waters of marine caves are tidal, with salinities of at least

their deeper waters nearly equivalent to those of the open sea. Third, the isolation of inland cave waters from the sea results in long residence times and corresponding temperature and salinity stratification of the water column, subsurface dissolved oxygen sags (Iliffe et al., 1984a), and near absence of suspended particulates. Fourth, distinct zonal patterns comparable with those observed in terrestrial caves (Poulson & White, 1969) are found. The coastal or open sea entrance zone contains a rich biota with especially large numbers of sponges, hydroids, bryozoans and other encrusting organisms. Most of these species can also be found in shaded sites outside the cave. Owing to the proximity to the open sea and to strong tidal currents passing through this part of the cave, residence times are on the order of hours. The middle zone shows a marked decrease in species abundance, but begins to include animals not normally found outside the caves. As the strength of tidal currents decreases, residence time increases to periods of several days to a week. The far interior of anchialine caves has a lower species diversity but organisms inhabiting this part of the cave are almost exclusively troglobionts. No noticeable tidal currents are observed and residence times may range from months to years. Local alteration of this zonation can result from cave collapse producing surface openings and anchialine pools.

BIOGEOGRAPHICAL MODELS

Three biogeographical models discussed by Stock (1977) have been proposed to explain the observed distribution patterns of the flora and fauna of islands in the Caribbean region. The Dispersal Model states that chance dispersal over or through the sea produced the present day flora and fauna. The Vicariance Model utilizes plate tectonics as a mechanism for transporting taxa (Rosen, 1976). According to the Regression Model, originally marine species were stranded by sea level regressions and subsequently adapted to mixohaline or fresh water conditions.

Each of these models has certain drawbacks in explaining the origins of marine-derived cave faunas. Since troglobitic species are by definition not normally found outside of caves and since most lack pelagic larvae, their dispersal across large distances of open ocean seems highly unlikely. The occurrence of marine cave faunas on oceanic islands such as Bermuda and Ascension which have never been part of continental land masses rules out the Vicariance Model. Although the distribution patterns of many cave species do coincide with the shorelines of past seas, the Regression Model is not applicable to islands such as Bermuda where sea levels at most have only been several meters above present levels. Additionally, the ability of marine species to adapt rapidly to fresh waters as sea level recedes is questionable.

THE ZONATION MODEL

Considering the distinct zonation patterns observed in marine caves, it is possible to envision an evolutionary model for the development of freshwater cavernicolous species from marine ancestors. The first step would consist of the colonization of the cave entrance zone by a suitably preadapted species. The presence of a significant food resource including externally-derived plankton and suspended particulates as well as the lack of competition from organisms which require light such as algae or most hermatypic corals makes this habitat attractive to many species. Next, migration farther into the cave could result from the expansive nature of the species and be aided by the stable environmental conditions of the cave even during periods of climatic flux. A third step would involve genetic isolation of the cave population from individuals still living outside the cave. This could result from sea level changes, cave collapse, or changes in the external water temperature. Once isolated, gradual evolutionary adaptation to the cave environment would produce troglomorphic characters. Animals in the early stages of this adaptive process (i.e., troglophiles) may still leave one cave to colonize others, but once an evolutionary "point of no return" is reached, species become committed to a troglobitic existence in one cave system. Fourth, food-finding adaptations could lead to the colonization of food-rich anchialine cave pools. As the interior regions of marine caves are environmentally stable but food-poor, the ability to obtain food is a primary factor determining the survival of cavernicolous species. Partially or totally open anchialine pools formed by cave collapse can provide new and important food resources. Upward invasion of these pools would however require adaptation to their brackish or fresh surface waters. Lastly, those species successfully colonizing anchialine pools could later disperse to totally freshwater cave systems.

Species of the caridean shrimp genus *Typhlatya* appear to provide evidence for such a Zonation Model of evolutionary development. All nine species within the genus are troglobitic but individual species inhabit waters with a wide range of salinities (table I). Two species, *T. rogersi* from anchialine pools on Ascension Island and *T. iliffei* from anchialine caves on Bermuda, live in fully marine salinities. Another two species, *T. galapagensis* and *T. garciai*, can inhabit brackish waters, although the latter has also been found in completely fresh waters far inland. The remaining 5 species are limited to fresh water caves. Except for *T. monae* from Mona (W of Puerto Rico), Barbuda and the Dominican Republic, all the fresh water species lack eye pigmentation, while, with the exception of *T. galapagensis*, all marine or brackish forms possess eye pigmentation. Since decreased eye pigmentation generally indicates greater phylogenetic age (Wilkens, 1979), the fresh water forms appear to be earlier cave colonists than their marine relatives. Interestingly, all 5 species lacking eye pigment and thus showing a greater degree of troglomorphic adaptation

TABLE I:

The caridean shrimp genus *Typhlatya*: Distribution, salinity range, presence or absence of eye pigmentation and local abundance.

Species	Distribution	Salinity Range			Eye Pigment	Local Abundance
		Marine	Brackish	Fresh		
1. <i>T. iliffei</i>	Bermuda	X			+	
2. <i>T. rogersi</i>	Ascension Is.	X			+	+
3. <i>T. garciai</i>	Cuba, Caicos Is.		X	X	+	+
4. <i>T. monae</i>	Puerto Rico (Mona Is.), Barbuda, Dominican Republic			X	+	+
5. <i>T. galapagensis</i>	Galapagos Is.		X		—	
6. <i>T. consobrina</i>	Cuba			X	—	
7. <i>T. campecheae</i>	Mexico (Campeche)			X	—	+
8. <i>T. mitchelli</i>	Mexico (Yucatan)			X	—	
9. <i>T. pearsei</i>	Mexico (Yucatan)			X	—	

are each known only from a single locality. At least 4 species within this genus show tendencies to aggregate in large numbers particularly in the surface waters of anchialine pools where food is most abundant. Such behavior together with their obvious ability to invade fresh waters would be likely to lead to the establishment of fresh water populations. *T. garciai* is apparently an example of a species in transit from marine to fresh waters as evidenced by its presence in both brackish anchialine pools in the Caicos Islands and fresh water caves in the interior of Cuba. Species within the genus appear to have evolved from an open water marine ancestor in the Atlantic which spread westward through the Caribbean and into the Pacific with prevailing currents before the closure of the Panama land bridge. Indeed, the closely related *T. iliffei* on Bermuda and *T. rogersi* on Ascension have been proposed to have existed in a stable state since the early Cenozoic, surviving on submerged and emergent sea mounts along the Mid-Atlantic Ridge (Iliffe et al., 1983).

This proposed evolutionary model appears attractive for several reasons. It would have occurred as a continuous process not dependent upon sea level position or movement. The Regression Model involving the stranding of formerly marine species by receding sea levels can be incorporated into this sequence, although, in the Zonation Model, adaptation of species to fresh water would have occurred before stranding and not after. However, sea level regression is not necessary for the Zonation Model to operate. The great age of shallow water carbonate platforms such as the Bahamas which have maintained their position with respect to sea level for about 200 million years provides a long, stable existence for the described cave environment. Considering the large number of marine relict species among fresh water cavernicoles, a continuous evolutionary process occurring in a stable environment is more plausible than one relying wholly on the ability of species to rapidly adapt to episodic environmental changes. The mobility and expansiveness required of

species by this model is demonstrated by the presence of old species in geologically recent caves and related habitats. Dispersal from older to recently-formed habitats probably occurs via the crevicular medium. The prime habitat of many cave species indeed may be these systems of micro-caves. Additionally, cavernicolous species might not be limited to surface waters, but could also occur in suitable cave-like habitats at bathyal or even abyssal depths. Such a continuum of habitats extending to all depths within the sea could provide a possible means for deep water species to migrate internally within sea mounts or similar steep relief features to invade shallow water caves. The natural geothermal gradient which has been measured as shallow as 30 m below present sea level in Bermuda (Hyndeman et al., 1974) could warm crevicular deep water habitats thus facilitating the adaptation of the deep water species to higher temperatures. Application of the Zonation Model can thus help to explain some of the problematic observations concerning the age and origins of the fauna of marine caves.

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