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# BIOTA OF VOLCANIC CAVES: AN INTRODUCTION

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In recent years, cave biologists have been more and more of the opinion that troglobites, or so-called "obligate cave fauna," are primarily inhabitants of the network of fissures, interstices, and small cavities that is more-or-less continuous throughout large areas, rather than existing in isolated cave populations (for discussion see Husmann, 1967; Culver, et al, 1974; Henry, 1979; Crawford, 1981; and below). In view of this, one might expect that the most diverse and abundant troglobitic faunas will be found in regions where this widespread subterranean habitat has certain favorable qualities. Among these might be availability of moisture and food, and the size and interconnectivity of the "living spaces."

Clearly, a crevice system with no connection to surrounding cavities, or a material like clay, with many available spaces but all of them microscopic, is not likely to support animal life. Both these factors — size and connectivity of spaces — are reflected in the permeability of a medium to groundwater, which can be measured. Permeability is an intrinsic quality of a medium analogous to electric resistivity, and is proportional to the rate at which groundwater, under a given set of conditions, can pass through it. Its dimensions are length squared. Brown, et al, (1975) gives the permeability ranges of most common bedrock and sediment types. Three materials show maximum permeabilities near the top of the scale, or about 0.152. They are gravel, limestone, and basalt. Since both limestone and basalt contain caves, their subterranean faunas can be investigated. Both kinds of cave should be expected to have diverse and abundant troglobitic faunas, and that expectation is proving to be justified. Oddly, though, the large subterranean faunas of basaltic terrain remained almost unsuspected until very recently.

Although a few troglobites were described from volcanic caves as early as the 1930s, only a handful had been reported before the late 1960s. Beginning in 1966, lava troglobites were described individually in increasing numbers from Japan, Korea, Idaho, Washington, and elsewhere. Then Leleup (1967) reported the presence of an entire fauna in the Galapagos Islands. In quick succession, Ueno, et al, (1970, 1971) reported large subterranean faunas from volcanic caves in Japan, Howarth (1972) from Hawaii, and Peck (1973) from western North America. Thus, volcanic cave biology blossomed from nothing to a substantial subject in an extraordinarily short time.

Currently, the Galapagos fauna is being published in the Resultats Scientifiques, Mission Zoologique Belge aux Iles Galapagos et en Ecuador (1968-date); the Japanese fauna in the Bulletin of the National Science Museum, Tokyo (Volume 13, 1970, to date), and the Hawaiian Fauna in Pacific Insects (Volume 15, 1973, to date). The North American results are scattered in many journals. About 40 lava troglobites have been described from Japan; 13 from the Galapagos; 24 from Hawaii; and 16 from Washington, Oregon and Idaho, with many more awaiting description. Species described include the fish *Luciogobius albus*, Regan (Japan), and *Caecoqilbia galapagosenis*, Poll and Leleup, as well as such diverse invertebrate groups as earwigs, flatworms, harvestmen, true bugs, actinaria (Japan), and pseudoscorpions, beetles, and crickets, collembola, spiders, mites, and numerous millipede and crustacean species.

Even in these four studied areas, probably the majority of the fauna awaits discovery. Almost nothing has been done on

the cave biology of most of the world's volcanic areas. In many cases, the caves themselves have not been explored. The subject is ripe for anyone interested in primary discovery.

## VOLCANIC CAVE ECOLOGY — DIFFERENCES FROM SOLUTION CAVES

Many of the ecological differences between volcanic and solution caves arise from differences in physical structure. One of the chief distinctions of lava tube caves in this respect is their comparative shallowness. Limestone caves often have a considerable overburden; by comparison, the thickest overburden known for a lava tube is 45 m (Nieland, J. and E., 1975) and most have considerably less, in the neighborhood of 1-10 m. Seepage water penetrates readily to these depths by means of joints and fissures, carrying dissolved and fine-particulate organic matter from the soil which supports heterotrophic bacteria on the cave walls and ceiling. In many cases, this bacteria (in Washington chiefly Actinomycete) forms thick deposits known as *lava tube slime* (Staley and Crawford 1975; Stanley and Staley 1975; Howarth 1973). Lava tube caves in forested areas commonly have tree roots penetrating their shallower passages through ceiling fissures. In Hawaii, this phenomenon is so pronounced that Hawaiian caves have thick and extensive "hanging curtains" of roots, sometimes even obstructing passages. Several Hawaiian troglobites, including a millipede and a Cixiid bug, are known to feed directly on living tree roots and many scavenge dead roots. In Washington, the troglobitic millipede *Lophomus skamania* feeds on living roots at least occasionally, and some other species are suspected to do likewise. The chief trees penetrating lava tubes with their roots in southern Washington are Douglas Fir and Ponderosa Pine; in Hawaii, several tree species have been cited. Of course, caves in treeless areas such as southeastern Oregon and the Galapagos are denied this energy sources.

Another consequence of the shallow overburden, along with the comparative shortness of the caves, is increased variability in microclimate. It has been reported many times that deep solution caves maintain a nearly constant temperature and other climatic conditions. Not so lave tubes. Benedict's studies (1974, 1977 and others) of Malheur Cave showed definite penetration of surface temperature through the 2-7 m thick overburden, but even more effect from temperature exchange via the entrance of the descending cave, warmer air moving outward along the ceiling and cooler air inward along the floor. In this case, the effect is ameliorated by the presence of a large thermal lake; temperature variations in other lava tube caves may be expected to be even greater. This is borne out by more random observations by myself and others. Just what effect this variation has on cave biota has not been elucidated in detail. Kamp (1973) suggests that ice cave populations of *Grylloblatta* spp. move out of the cave proper when onset of sub-freezing temperatures lowers the relative humidity. In most volcanic caves, the variation appear to be such that the cave is always habitable, yet significant variations do occur and might well influence the behavior and ecology of the affected fauna.

A very important difference in the ecology of volcanic and solution caves is a direct consequence of their mode of formation. Solution caves form as conduits for phreatic and vadose underground waters, and a large proportion at some time receive water from surface streams which carries large quantities of organic matter and surface-water fauna. This is the major organic input for these caves and it is definitely pulsed, coming in cycles dictated by seasonal stream flow variation, storms and floods, etc. By contrast, the major organic inputs of most volcanic caves are continuous and vary relatively little. The mode of formation of volcanic caves is unrelated to hydrology, and relatively few contain streams at all; even fewer receive large quantities of stream-washed organic matter.

The entrance floras of solution caves are undoubtedly of interest, though they seem to have been little studied. Yet, the plant communities in volcanic cave entrances, particularly of collapse sinks, have unique features which relate to the physical nature of basaltic lava. As related above, basalt flows are sufficiently young that mature water-retaining soil profiles have not developed on the surface. As a consequence, the surface in most volcanic cave areas. is rather xeric or desert-like, regardless of the actual climate, because rainwater sinks rapidly into the bedrock without leaving a reserve to be tapped by plant roots.

As an example, consider Cheju Do, the volcanic cave area of South Korea. The annual rainfall on the north side of the island is 130-200 cm, comparable to that of the west slope of the Cascade Mountains in Washington, which feeds innumerable surface streams and supports a dense, lush and moist coniferous forest. In comparison, the interior of the Cheju Do has little surface water during most of the year and the surface is bleak, treeless, and desert-like, though much groundwater exists at depth. The collapse sinks associated with lava tubes present an astonishing contrast. For instance, the two collapse entrances of the cave So Cheon Gul are each only about 10-15 m in long diameter. Recorded from them are 27 species of fern and eight species of tree, as well as climbing vines and undershrubs — indeed miniature jungles. Photographs of the area show the barren lava surface with clumps of dense forest in the collapse sinks as in flower pots (Crawford, 1982).

The same phenomenon occurs in the Undara area of Australia, where lava tube systems are plainly evident from the air by the vivid contrast between the tropical rain forest in the collapse trench and the desert scrub of the surrounding plain (Stevens and Atkinson, 1976). The explanation of this phenomenon is two-fold. First, the lower level of the collapse brings the flora physically closer to groundwater, and perhaps almost in contact with perched groundwater on the "country rock" underlying the lava tube floor. Second, the enclosing walls of the collapse help retain humidity by limiting the penetration of rain and sunlight. This latter effect can be prominent even in a true desert climate (e.g., Fern Dome at Jordan Craters, Oregon [Larson, 1977]). In forested lava tube areas, such as the Mt. Adams area in Washington, the effect is less noticeable but still evident, since the surface vegetation is distinctly xerophytic (roots above groundwater), whereas that on the floors of collapse sinks and trenches includes phreatophytic species (roots in groundwater).

## VOLCANIC CAVE ECOLOGY — SIMILARITIES WITH SOLUTION CAVES

Despite the differences in energy sources and environmental conditions between volcanic and solution caves, their community structure and bioenergetics are broadly similar, although of course numerous individual differences exist. The food chains of volcanic caves, as typified by Howarth's (1973) for Kazumura Cave, Hawaii, and mine (figure 1) for Deadhorse

Cave, Washington, show no consistent difference from those published for solution caves, except in such details as the nature of energy sources and taxonomy of the biota. This is perhaps to be expected, as both are examples of ecosystems supported by organic input from outside and colonized in similar ways by biota with similar characteristics.

Another point of similarity is that volcanic and solution caves in the same region usually have very similar troglophilic and trogloxenic faunas. I can state this from my own experience with regard to the caves of the Cascade Mountains of Washington; species lists published by Ueno, et al, (see above) for Japan and Korea also support this conclusion. Even a few of the same troglobitic species occur in both volcanic and solution caves; I know of three examples. In Hawaii (island of Kauai), the terrestrial amphipod *Spelaeorchestia koloana* has been collected in three lava tube caves and one of the Hawaiian Islands' rare limestone solution caves, formed in an ancient calcareous sand dune formation (Bousfield and Howarth, 1976). The Leiodid beetle *Glacicavicola bathysciodes* occurs in many lava tube caves of southern Idaho and also in limestone caves of adjacent Wyoming (Peck, 1981). The isopod *Salmasellus steganothrix*, originally known from karst groundwater and one limestone cave in southern Alberta, has been identified in the lava tube Deadhorse Cave in southern Washington, some 750 km away (J.J. Lewis, personal communication, 1981).

## BIOGEOGRAPHY AND EVOLUTION OF TROGLOBITES IN BASALT

One reason why cave biologists formerly gave no consideration to caves in basalt is that it was assumed that such caves were too short-lived to permit the evolution of troglobites. This assumption may not be entirely valid; some cave-bearing basalts in Oregon may be one million years old or older (E.M. Benedict, personal communication, 1982). However, it is true that most of the best known lava tubes are only a few thousand years old. It is widely assumed that most lava tubes collapse fairly rapidly on a geologic time scale, although there seems to be little published data in support of this assumption. In any case, many lava tube caves containing troglobites are far too young for the species to have evolved in those caves. Kaumana Cave, Hawaii, contained several troglodyte species when it was only 90 years old (Howarth, 1972). To explain this, Howarth (1972, 1973) postulates "dispersal from one lava tube to another" via joints, aa clinker, vesicles, etc. Unfortunately, Howarth's wording implies something he clearly did not intend — the passage of individual animals from one cave to another via the small cavities between caves. Such dispersal would undoubtedly be so slow as to take several generations at least, and this in turn implies that migrants to a new cave would come directly from populations in the surrounding lava, not those in other caves.

Pahoehoe basalt formations, particularly those containing caves, generally consist of a succession of relatively thin flows rather than a single thick flow. The central massive phase of each flow is relatively impermeable; most of the permeability of basalt is concentrated near the flow contacts, and arises, in order of importance, from: scoria and other loose material; large loose blocks (like those observable on most recent lava flow surfaces); partings between flows; horizontal and vertical contraction joints; gas vesicles; cave passages; mechanical fractures; and tree casts (Brown, et al, 1975). For a diagram of these factors viewed as habitat, see Figure 2. Thus, a basalt formation contains a series of permeable layers, each presumably penetrable to troglobitic fauna. In these layers, particularly the upper ones, are the same major energy sources as present in caves: roots and organic solutes in seepage. The extent of cave passage habitat is minor in comparison to the total extent of the interflow permeable layers, particularly as most of a cave is empty space which does not constitute habitat for crawling invertebrates. A given area of the permeable layer occupied by scoria, joints, etc., must have much greater surface area than the same area occupied by a cave passage; this additional surface area is available for growth of slime, and colonization by troglobitic fauna. Howarth's implication that some of the Hawaiian troglobites have their main populations in penetrable caves is unproven and seems unlikely, at least for species known from two or more caves. The presence of a troglobitic species in more than one cave is in itself evidence that this species is able to enter, and therefore to colonize, the interflow layers. In my study area in Washington, there is much evidence that cave "populations" are minor adjuncts to the much larger populations in the surrounding lava.

I suggest, moreover, that the surface ancestors of some troglobitic species in basalt may have colonized the interflow layers directly, via joints and openings from the flow surface or erosional scarps, particularly those that have been enlarged by roots. This invasion mechanism seems especially likely for those species whose primary food source is roots. Such species would have colonized caves secondarily from the interflow layers. It should be mentioned here that most lava tubes intersect the interflow layer (as shown in Figure 2) due to erosion of the pre-flow surface by flowing lava in the active tube; thus, there is easy communication between the two habitats. Other species may have colonized caves first and the interflow layers secondarily, as Howarth suggests.

The rapidity with which subterranean fauna can colonize new lava flows is best demonstrated by the Hawaiian results, but is also evident in other regions. The Mt. St. Helens "Cave Basalt" in Washington, for example, is less than 2,000 years old and has been colonized by a few troglobites even though no other cave-bearing lava flow is closer than about 26 km. Thus, the subterranean fauna of a given volcanic region is supplied with new habitat at intervals as long as that region continues to produce basaltic lava. Even after volcanism has ceased, basalt can retain its permeability for long periods. The Miocene Columbia River Basalts of eastern Washington are 6-16 million years old and are still so permeable as to contain the dominant groundwater resource of the state. Admittedly, the climate of eastern Washington is relatively dry and soil formation correspondingly slow. Howarth (1973) and Bousfield and Howarth (1976) feel that in most maritime climate of the Hawaiian Islands, lava flows that are a few million years old have decomposed and silted up to the extent that the habitat of subterranean fauna is destroyed. This may be true, but I would like to see such conclusions supported by geologic evidence such as groundwater permeability, usually easy to obtain. I suspect that even in very old basalts some areas may retain enough permeability to support troglobites. Ultimately, geologic processes will render these accessible subterranean habitats fragmentary and isolated, whereupon additional geographic speciation of troglobites may be expected.

I conclude with a speculation based on the known layered

Figure 2. SUBTERRANEAN HABITATS OF BASALT



Figure 1. HYPOTHETICAL FOOD WEB FOR DEADHORSE CAVE, WASHINGTON

field for future investigation — assuming, that is, that human ingenuity proves equal to the problem of developing suitable techniques.

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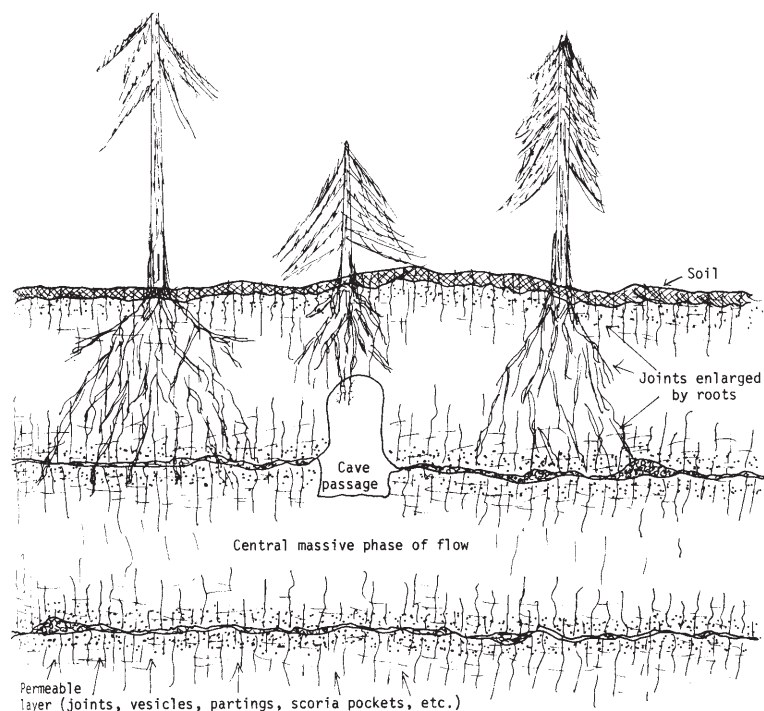
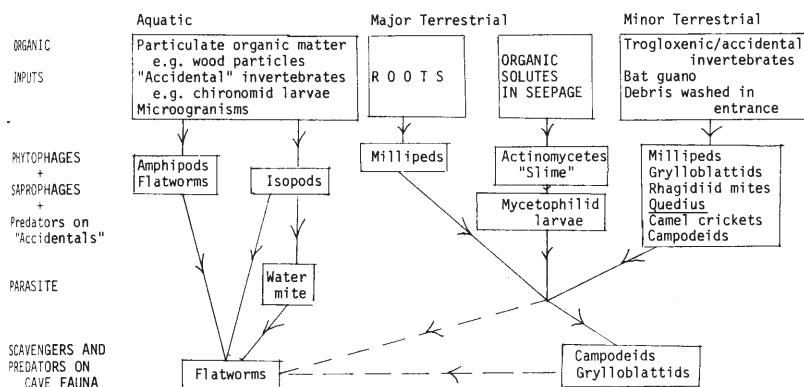structure of subterranean habitats in basalt. The different layers in a given basalt formation will obviously have differing environments; the lower layers will have successively less organic input, and also less variable climate. The lowest layers will likely be saturated by groundwater, but there may be one or more unsaturated layers below the highest one in some areas. The central massive phase of each flow makes horizontal migration far more likely than vertical. Therefore, it seems possible that the interflow layers of a basalt formation will have different, and successively more depauperate, faunas, only the uppermost of which is generally accessible to cave explorers.

In addition to the still barely-touched study of subterranean fauna in volcanic caves, then, is the completely untouched study of the fauna of deeper basalt layers and of basalts containing no caves, such as the vast Columbia River Basalts (see above) and the Deccan Basalts of India. It is an extraordinarily promising