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THE CAVERNICOLOUS FAUNA OF HAWAIIAN LAVA TUBES, 1. INTRODUCTION[1]

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Abstract: The Hawaiian Islands offer great potential for evolutionary research. The discovery of specialized cavernicoles among the adaptively radiating fauna adds to that potential. About 50 lava tubes and a few other types of caves on 4 islands have been investigated. Tree roots, both living and dead, are the main energy source in the caves. Some organic material percolates into the cave through cracks associated with the roots. Cave slimes and accidentals also supply some nutrients. Lava tubes form almost exclusively in pahoehoe basalt, usually by the crusting over of lava rivers. However, the formation can be quite complex. Young basalt has numerous avenues such as vesicles, fissures, layers, and smaller tubes which allow some intercave and interlava flow dispersal of cavernicoles. In older flows these avenues are plugged by siltation or blocked or cut by erosion.

The Hawaiian Islands are a string of oceanic volcanic islands stretching more than 2500 km across the mid-Pacific. The western islands are old eroded mountains which are now raised coral reefs and shoals. The eight main eastern islands total 16,667 km^2 and are relatively young in geologic age. Ages range from 5+ million years for the island of Kauai to 1 million years for the largest island, Hawaii (Macdonald & Abbott, 1970). The native fauna and flora are composed of those groups which dispersed across upwards of 4000 km of open ocean or island hopped and became successfully established. Thus the fauna is remarkably disharmonic. The disharmony on oceanic islands has been discussed by Zimmerman (1948) and Gressitt (1971). Zimmerman (1948) estimated that only 250 successful introductions to the Hawaiian Islands have given rise to the entire native insect fauna of more than 5000 species. The aquatic, soil, and cave arthropods of the continents are conspicuously poorly represented because of their inherent lack of dispersal ability.

Although the existence of lava tubes in Hawaii has been known for many years, they remained virtually unexplored biologically until my chance discovery of a blind brachypterous cixiid and a new endemic cricket in a lava tube on the island of Hawaii in July, 1971 (Howarth 1972). Since that time about 50 different cave systems (Table I) have been at least partially surveyed faunistically, and additional cave-adapted arthropods have been found in lava tubes on the islands of Hawaii, Kauai, Maui, and possibly Oahu. These are among the first troglobites known from oceanic islands, and open the door to a vast new area of the world biospeleologically.

Although the survey is far from complete, the interest in the fauna of this newly discovered biotope and the uniqueness of some of the organisms justify publication

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Table I: Caves Investigated in this Survey.

No.	Name of Cave	Locality	Elevation	Length (approx.)	Dark Zone[1]
	Lava Tubes on Hawaii (Mauna Loa Massif)				
1.	Kaumana Cave	Kaumana	290 m	1500 m	+
2.	Bird Park Cave #1	Hawaii Volcanoes National Park	1250 m	100 m	+
3.	Bird Park Cave #2	Hawaii Volcanoes National Park	1250 m	20 m	0
4.	Bird Park Cave #3+4	Hawaii Volcanoes National Park	1250 m	400 m	+
5.	Bird Park Cave #5	Hawaii Volcanoes National Park	1250 m	20 m	0
6.	Mauna Loa Strip Road #1	Hawaii Volcanoes National Park	2440 m	30 m	0
7.	Mauna Loa Strip Road #2	Hawaii Volcanoes National Park	2040 m	17 m	0
8.	Mauna Loa Strip Road #3	Hawaii Volcanoes National Park	1525 m	70 m	0
9.	Mauna Loa Strip Road #4	Hawaii Volcanoes National Park	2130 m	60 m	?
10.	Transect 1 Cave	Kilauea Forest Reserve	1650 m	30 m	+
11.	Kilauea Forest Reserve #2	Kilauea Forest Reserve	1650 m	20 m	0
12.	Powerline Trail Cave	Keahou Ranch	2000 m	100+ m	+
13.	Pigeon Cave	Puu Waawaa Ranch	670 m	300 m	+
14.	Kau Cave #2	Naalehu	600 m	50 m	?
	Lava Tubes on Hawaii (Kilauea Massif)				
15.	Kazumura Cave	Mountain View	408 m	6000 m	+
16.	Thurston Lava Tube	Hawaii Volcanoes National Park	1200 m	400 m	+
17.	Hongo Store Cave	Volcano	1130 m	400 m	+
18.	Blair Cave	Volcano	910 m	1000 m	+
	Lava Tubes on Hawaii (Hualalai Massif)				
19.	Puu Waawaa Ranch Cave #1	Puu Waawaa Ranch	1250 m	100 m	0
20.	Puu Waawaa Ranch Cave #2	Puu Waawaa Ranch	1250 m	30 m	0
21.	Huehue Ranch Cave	North Kona	610 m	50 m	0
	Lava Tubes on Hawaii (Mauna Kea Massif)				
22.	Hamakua Forest Reserve Cave #1	Honokaa	600 m	20 m	0
23.	Hamakua Forest Reserve Cave #2	Honokaa	600 m	250 m	+
	Lava Tubes on Maui (Haleakala Massif)				
24.	Kalua O Lapa Cave	La Perouse Bay, Keoneoio	120 m	60 m	+
25.	Puu Mahoe Cave	Ulupalakua	700 m	100 m	+
26.	Offal Cave	Hana	90 m	3400 m	+
27.	Holoinawawai Stream Cave	Hana	290 m	700 m	+
28.	Lower Waihoi Valley Cave	Hana	300 m	100 m	+
29.	Waihoi Valley Trench Cave	Hana	450 m	30 m	0
30.	Upper Wananalua Cave	Hana	180 m	100 m	+
31.	Lower Wananalua Cave	Hana	180 m	75 m	+
32.	Long Cave	Haleakala Crater	2000 m	250 m	+

1. += Dark zone present: 0= dark zone absent; ?= dark zone questionable.

	Lava Tubes on Oahu			
33. Burial Cave #1	Niu	33 m	115 m	+
34. Judd Street Cave	Honolulu	30 m	70 m	0
	Lava Tubes on Kauai			
35. Koloa Cave #1	Koloa	37 m	200 m	+
36. Koloa Cave #2	Koloa	37 m	100 m	+
37. Koloa Cave #3	Koloa	25 m	50 m	0
38. Koloa Cave #4	Koloa	20 m	20 m	0
39. Knudsen Cave #1	Koloa	45 m	100 m	0
40. Knudsen Cave #2	Koloa	45 m	50 m	0
41. Koloa Mill Cave	Koloa	60 m	—	—
42. Koloa Mill Twilight Cave #1	Koloa	70 m	30 m	0
	Other Caves and Caverns			
43. Waianapanapa Sea Cave	Hana, Maui	10 m	50 m	+
44. Makua Sea Cave	Makaha, Oahu	5 m	50 m	0
45. Kaena Point Sea Cave	Makaha, Oahu	5 m	15 m	0
46. Dry Sea Cave	Makapuu Point, Oahu	5 m	20 m	0
47. Limestone Quarry Cave	Koloa, Kauai	5 m	100 m	+
48. Maniniholo Dry Sea Cave	Haena, Kauai	5 m	70 m	0
49. Waikanaloa Wet Sea Cave	Haena, Kauai	5 m	50 m	0
50. Kauaikinana Stream Water Tunnel (man-made)	Kokee State Park, Kauai	1040 m	300 m	+
51. Kokee Ditch Water Tunnel (man-made)	Waimea Canyon State Park, Kauai	1000 m	100 m	0

now. Two of the favorite biotopes of evolutionary biologists are oceanic islands and caves. The discovery of troglobites among representatives of the adaptively radiating fauna on oceanic islands will surely lead to a better understanding of evolution on islands, in caves, and in general. We plan to publish descriptions of the cavernicoles as a series of papers authored by collaborating specialists.

Not much is known of the cave fauna of Oceania. Buxton (1935) reported a rhaphidophorine cricket and a pseudoscorpion from a lava tube in Samoa. A shrimp, Atyidae, with reduced eyes is known from caves in Fiji (Vandel 1964). Torii (1960) reported on a survey of the fauna of limestone and sea caves in the Marianas but found nothing of significance and felt that recent uplifts of the low islands precluded the existence of any obligatory cavernicoles. The first obligatory cave organisms on oceanic islands were reported by Leleup (1967 and 1968) from a collection of cave and soil organisms from the Galápagos Islands. The systematic papers on these collections are being published in a series entitled *Mission zoologique aux îles Galápagos et en Ecuador* (*N. et J. Leleup, 1964–1965*). The Galápagos cave fauna does show some parallels with the Hawaiian cave fauna in that some of the specialized organisms are closely related to the adaptively radiating epigean forms. Other cave species may be relicts. The Galápagos fauna is not so disharmonic as that of Hawaii and shows clear affinities with the fauna of South America.

A comprehensive review of biospeleology was given by Vandel (1964) and the history of biospeleology in the United States was discussed by Barr (1966). Very few cavernicoles are known from lava tubes in the United States (Peck, in press). The fauna of Japanese lava tubes has been reviewed by Ueno (1971). Barr (1968), Poulson & White (1969) and Vandel (1964) have stated that the distribution of obligatory troglobites is almost entirely restricted to the temperate regions just outside of the limits of Pleistocene glaciation but inside the line of normal frost. Rich faunas are known in Europe, North America, Japan, New Zealand, and the limestone highlands in Mexico, and most of the troglobites known from the tropics are aquatic and relicts of past rises in sea level. Mitchell (1969) considered some of the Mexican caves to be tropical but he still felt the tropical terrestrial troglobite fauna to be depauperate. However, Vandel (1968) recognized that all the tropical cave regions do have a significant specialized terrestrial cave fauna, but that it is not as rich as that in temperate regions. Most biospeleological work has involved limestone caves in temperate regions.

Classification of Cave Animals

The ecological terms used to define organisms living in caves have become generally accepted and are used in this paper according to the definition of Barr (1968). Cavernicoles can be divided into 3 groups: 1. Troglobites, those species which are obligatory and unable to survive outside of the hypogean environment; 2. Troglophiles, those species which live and reproduce in caves but which are also found in similar dark humid microhabitats; 3. Trogloxenes, those species which regularly inhabit caves for refuge but normally return to the epigean (surface) environment to search for food. A fourth group, which is not cavernicolous, consists of accidentals which wander into caves but cannot survive there. They may be important in bringing in nutrients.

These are ecological categories and as such it is not always possible to assign a species to its correct category without detailed knowledge of its ecology and distribution. Most recent authors (see Vandel 1964, and Barr 1968) have used a morphological interpretation whereby troglobites are those species displaying anophthalmy, depigmentation, attenuated appendages and other characters which would appear to restrict the animals to an underground existence. The few possible obligatory species not displaying such morphological features are classified as troglophiles.

Lava Tube Formation

Limestone caves can be considered an integration of the erosion and degradation processes coupled with the dissolution of limestone to form new passages in a dynamic continuing process over a long geologic period. Lava tubes, on the other hand, have an initial period of formation and then the processes of erosion and siltation degrade the caves in a brief geologic time. There is no chance for enlargement of the passage in a lava tube.

The phenomenon of lava tube formation is little understood. However, the recent independent discoveries that lava tubes are one of the major mechanisms for building shield volcanoes by insulating the flowing lava and distributing it great distances from the vent (Swanson et al. 1971), and the indirect evidence that large lava tubes exist on the moon (Greeley 1971a) have given great importance to understanding the mechanism of lava tube formation. The traditional theory was described by Macdonald & Abbott (1970). However, detailed study of lava tubes elsewhere in the world have produced other theories and some controversy exists. Ollier & Brown (1965) described lava tubes in Australia and proposed a theory requiring laminar flow of the lava. Harter & Harter (1970) present theories for the formation of 5 different types of lava tubes. Harter (1971) has prepared a bibliography of lava tubes.

Lava tubes form solely in basaltic lava flows. The andesite flows of the continents contain no lava tubes. The two types of basaltic lava deposition differ in viscosity and heat and gas content. Aa flows are cooler, contain less gas, slower moving, and more viscous than pahoehoe flows. In aa flows the crust cracks into large chunks of clinker which are pushed along and buried by the flow. This type of flow rarely forms caves, but the buried clinker and, if thick enough, the surface clinker may offer dispersal routes for cavernicoles. Pahoehoe lava flows in rivers and nearly always crusts over and forms lava tubes. However, not all tubes drain to form caves and not all caves open to the surface. The caves range in size from tiny, finger-size tunnels to caverns more than 6000 m long and 17 m in diameter.

Near the vent a highly fluid flow may travel as a river. As it flows it loses heat and gas and tends to crust over. Away from the vent the front of a pahoehoe flow advances much like an amoeba. A toe of molten lava breaks its surface crust and the draining lava spreads as a thin sheet. This new surface solidifies and then breaks again to drain the interior and form a new toe. Toes also form on older toes, layer on layer, as the front advances. This builds a levee in which the main river flows. These toes are fed by small distributary tubes from the main river. Escaping gas often swells the plastic crust of pahoehoe toes forming lava blisters, some of which may be several cubic meters in volume. The pahoehoe flow becomes deeper as the thin layers of lava, 5 to 40 cm in thickness, flow out as toes. Many of these layers are separated by spaces of 0.5 to 10 cm for part of their area. The total thickness of the flow may be 15 m or more.

The surface of the main river usually solidifies for part or all of its length. With the cessation of flow the lava drains from the main tube by gravity and leaves a void or cave. Most distributary tubes do not or only partially drain.

During the eruption the level of the flowing lava in the tube can vary considerably from small sluggish flows to completely filling the tube and even overflowing the levee through skylights. Such oscillations can leave linings 1 to 20 cm thick on the walls and ceiling of the tube.

Major lava tubes can also form by roofing over of the vents and then the lava draining away under the roof (Harter & Harter 1970).

The structure of the cave is a function of the method of formation, percent of draining of molten lava, and deformation by spalling (breakdown) and slumping of the walls, both while the lava is flowing and during cooling. Whether the flowing lava river can erode the substrate and alter its channel is unknown.

The escaping gas bubbles in basaltic lava are often trapped by the solidifying lava, forming vesicls. Often these vesicles interconnect forming channels 1–10 mm in diameter through the rock.

When a pahoehoe river does not roof over or the roof collapses for a considerable length the resulting narrow, steep-sided valley is called a lava trench or channel. Often the flowing river divides and recombines, forming braided streams of lava.

Lava tubes and trenches are common features of the recent lava flows on Kilauea, Mauna Loa, Hualalai, Mauna Kea, and Haleakala volcanoes. Most caves on the older volcanoes have been destroyed by erosion. A few caves do exist in the secondary lava flows on Oahu and Kauai. Remnants of buried lava tubes occasionally open on the sides of river canyons on the older mountains, but these are rarely more than shelter caves.

The Cave Environment

A typical lava tube, fig. 1, can be divided into 4 environmental regions: the entrance zone, which is very often richer than either the epigean environment or the hypogean environment; the twilight zone, where light is reduced and green plants progressively drop out; the transition zone, in darkness but where the rigorous outside environmental effects are still felt; and the true dark zone, where constant darkness and usually constant climatic conditions prevail. The extent of these zones depends to a very great extent on the size and exposure of the entrance and the size of the cave. Caves with a very small entrance may even have no entrance zone and a small twilight zone. In those with a large entrance the twilight and transition zones may extend far into the cave. In lava tubes with two entrances the passage between may be entirely transition zone, since a chimney effect between the entrances allows wind and air movement which increases evaporation and introduces the effects of epigean climatic changes.

Moisture, even a ceiling drip or pools on the floor, can mitigate the environment and may extend the active area of colonization by troglobites well into the twilight zone, especially under and behind rocks. Up to this writing only one cave has been visited with a specialized fauna and no zone beyond the twilight. This is a short section of lava tube preserved in a large lava trench in Waihoi Valley on Maui. The cave was under 30 m long and had an entrance at both ends. The small population of cixiids and *Caconemobius* crickets was restricted to a small room separated from both entrances by constrictions in the passage. A large amount of ceiling drip and a small pool on the floor and tree roots allowed the organisms to survive. This small room probably was connected to a larger cave by fissures and vesicles in the lava.

In limestone caves on the continents sinking streams and debris washed in through cracks and domes, and trogloxenes, especially bats, cave crickets (rhaphidophorine Orthoptera), and certain birds, are the most important energy sources. Less is known of the energy sources in continental lava tubes, although they are probably the same as those for limestone caves.

The main energy source in Hawaiian lava tubes appears to be tree roots. Lava tubes generally have little overburden, that is they are close to the surface. Also, some of the native Hawaiian trees, notably *Metrosideros polymorpha*, can colonize relatively young lava flows. The roots dangle into the caverns and supply food, either directly as living or decaying roots, or by forming pathways for the percolation of organically rich water.

Several different types of slimes on the cave walls and floor support smaller animals including nematocerous Diptera larvae, oligochaetes, carabid beetles, and Collembola. Some of this slime may be bacterial or fungal growth on organic material from rotting roots, rotting detritus, and debris washing in through cracks. Other slimes may be, at least in part, chemiautotrophic bacteria utilizing the iron or sulfur in the lava.

Streams do not appear to be important as sources of energy in Hawaiian lava tubes, as once a stream enters a lava tube cave the siltation and erosion processes speed up

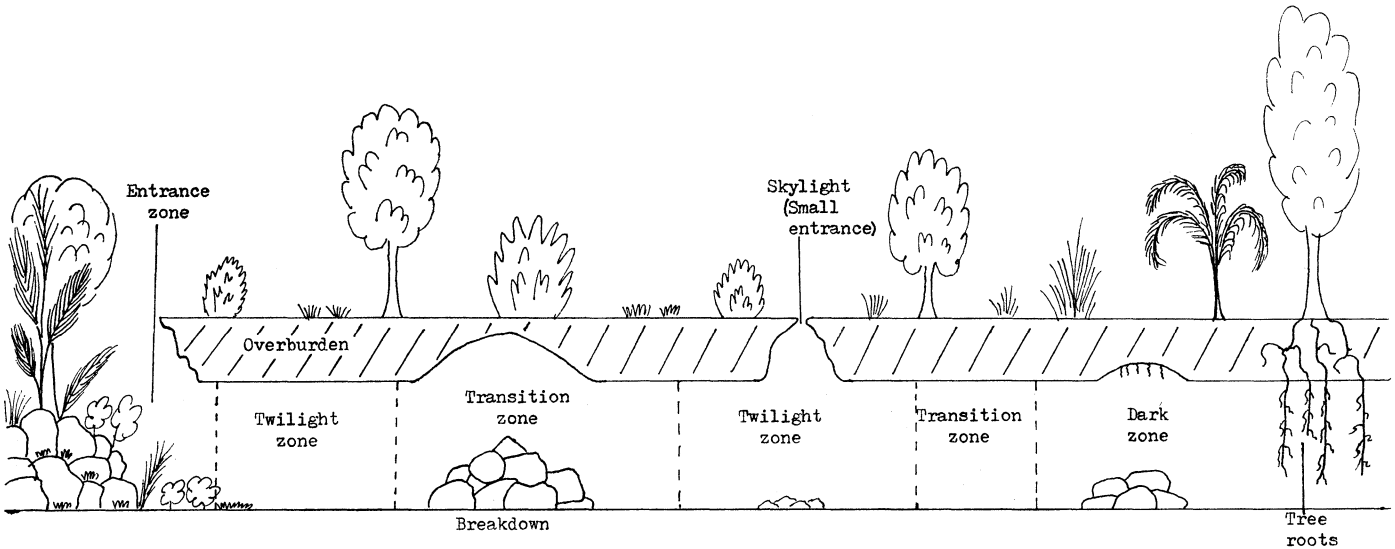

Fig. 1. A typical lava tube in Hawaii. Simplified longitudinal section showing ecological zones. Height of cave to length of zones exaggerated.

and the lava tube is short lived. It is unusual for a stream to enlarge a lava tube as it can a limestone cave. Those lava tubes visited that had a temporary stream were partially or almost entirely filled with silt, had signs of periodic flooding, and had a poor fauna.

A native trogloxenic component has not yet been delineated in Hawaiian caves. Hawaii's only bat, *Lasiurus cinereus semotus*, the only native land mammal, is a forest species and is not known to enter caves. Skeletons and dung of *Rattus rattus* and the mongoose (*Herpestes auropunctatus*) are occasionally met with on the floor far from any known entrance. *Rattus rattus* has been seen in the twilight zone and in the passages near the entrance of a few caves, and is probably a regular inhabitant of the entrance and twilight zones. Whether it regularly enters or lives in the dark zone or is an accidental there is not known. These mammals only indirectly add nutrients to the native cave community, since their dung and carcasses support only introduced coprophagous and sarcophagous troglophiles which in turn may become prey to the cave predators.

Accidentals, mostly soil and leaf litter arthropods, which wander or fall into caves may supply some nutrients into the cave ecosystem. Once into the dark zone these organisms would have difficulty returning to the surface and would fall prey to predators. The proportion of nutrients brought in by accidentals is unknown but may account in part for the high proportion of cave-adapted predators,

In caves in the younger lava flows on the island of Hawaii and even a few on Maui, the paucity of organic detritus on the floor is surprising. Even in caves in prehistoric flows with many tree roots and obviously of some antiquity, the amount of detritus is small and this is difficult to explain, but must be related to the slow process of soil formation on lava and to the high porosity of the lava into which the organic material is washed.

A preliminary interpretation of the food chain in Kazumura Cave is presented in fig. 2. Kazumura Cave, Mountain View, Island of Hawaii, one of the largest known lava tubes in the world. The main entrance is at 400 m on Kilauea Volcano. Its estimated length is 6000 m and it has 7 small entrances. The temperature in the cave is 20°C. The forest over the tube has recently been altered by fire and cutting for a subdivision and is now swampy savanna with scattered *Metrosideros* trees. Many of the tree roots are dead but still hang from the ceiling. The cave appears young with little detritus, and is probably under 20,000 years old. Much of the cave is stable and nearly without cracks and without roots. Such sections of the passage are nearly sterile, except for occasional patches of "slime". Other sections with tree roots support a varied fauna. But passages in and around breakdown piles support the highest populations of many arthropods, especially *Caconemobius* crickets and lycosid spiders. Such breakdown piles are usually associated with roots and organic debris since they are under areas with more cracks. The pile may afford more hiding places, higher humidity, and more food than the adjoining cave passage.

Interlava Tube Dispersal and Isolation of Biota

Data on distribution of cavernicoles in Hawaii to date and observations on geology of Hawaiian lava tubes indicate that degradation of caves and colonization follows a pattern. Young volcanic regions are characterized by little soil formation and the young lava is fractured and contains numerous vesicles, much like a sponge. There are no

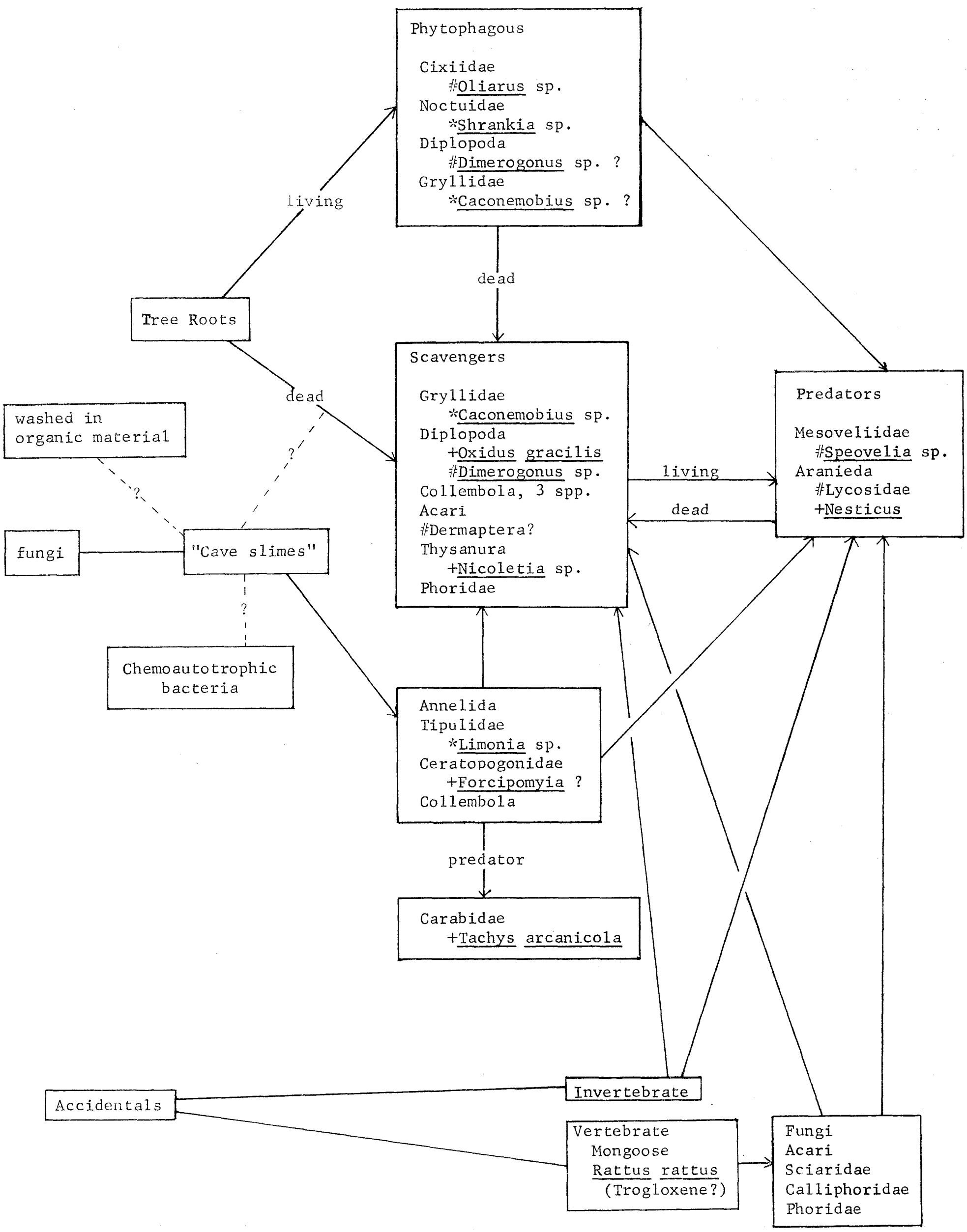

Fig. 2. Preliminary interpretation of the food chain in Kazumura Cave. Arrows indicate direction of energy flow. Dotted lines = unconfirmed relationship, # troglobite, * endemic troglophile, + introduced troglophile, ? suspected feeding habits.

surface streams. Rain water percolates into the lava almost as it falls. The lava is porous enough to allow dispersal between lava tubes, either through the gas vesicles in the lava, smaller tubes, or fissures created on cooling or enlarged by roots or fault lines. The younger flows cross and cover older lava flows, and it is not difficult to envision a constant invasion of new flows by the fauna as the buildup in organic material allows colonization. Colonization and evolution may be continuous if the lava flows are frequent enough to allow dispersal. The Mauna Loa and Kilauea massifs on Hawaii are at this stage, and lava fields on the lower slopes of Haleakala, Maui, probably also still allow intercave dispersal even though the caves are much older.

Large lava flows may form several parallel tubes which usually do not interconnect for human passage but probably create much more area for colonization than one can deduce from surface or speleological investigations.

As soil formation progresses and erosion and siltation occur the smaller cracks are filled and these dispersal routes are closed to cavernicoles. The larger passages start to fill with silt and break down. At this stage these lava tubes tend to approach limestone caves in their environmental conditions. Finally, breakdown continues, cave passages shrink in size, fill with silt, and breakdown. Erosion fills the passage until the cave is no longer able to support its specialized fauna and these become extinct. Such is the case with the majority of caves visited on Kauai and Oahu. Man has modified the siltation processes by agriculture and development so that some of the history is now speeded up and obscured.

Cavernicoles do show different patterns of distribution on young lava flows. Some may be able to colonize larger cracks and the smaller avenues in the lava. Other cavernicoles in young lava fields are only known from single caves or single cave systems, and it is not known at this time whether environmental factors or lack of dispersal mechanisms affect their distribution. The ***Thaumatogryllus*** cricket is known from two systems, one on the saddle between Kilauea and Manua Loa, and the other less than 10 km away near Kilauea Volcano, both at approximately 1200 m elevation. ***Speovelia*** sp., Mesoveliidae, is known only from Kazumura Cave. In contrast, the Hawaii cave cixiid, which has the widest distribution, is known from caves on the windward Mauna Kea massif at 610 m to the 90 year old Kaumana Cave on Mauna Loa at 290 m, and to many other caves on the Mauna Loa and Kilauea massifs. The Hawaii ***Caconemobius*** cricket is known from various caves surveyed on the Mauna Loa and Kilauea massifs from 290 to 1200 m.

The apparent ease of dispersal and specializations of some of these organisms in younger tubes suggest that they might be appropriately called "lavacoles" as well as cavernicoles. This intercave dispersal may be analogous to the dispersal of aquatic troglobites in temperate limestone caves (see Culver 1970).

Disturbance

Many of the arthropods recently introduced by man, especially household pests and soil forms coming in with plant materials, have successfully colonized Hawaiian lava tubes, sometimes making it difficult to assess whether the species is an introduced soil species or a native cave organism. Where the cave organisms are closely related to native surface forms or where a closely related species is known from caves on another island, I believe we are safe in assuming endemicity. On the other hand, if a species appears on 2 islands it probably has been moved by man and is probably introduced. Other species must await detailed study of the soil and cave organisms in the tropics before their status in Hawaii can be established. Such studies may modify the status of some of the species we treat. These introductions have surely vastly altered the ecology of the caves and probably have replaced certain species in the cave ecosystem, and are now part of the food web of the caves. These arthropods include representatives of Isopoda, spiders, cockroaches, Dermaptera, Collembola, Thysanura, and other groups.

Many of the caves visited have been directly disturbed by man, or more importantly the overlying forest has been cut or removed, thus drastically altering the ecology of the cave beneath. Kauai has few extant lava tubes but is old enough to have a highly specialized fauna. Only one cave surveyed there had troglobites and these are among the most bizarre discoveries to date. One is the world's first eyeless lycosid spider and the other the first troglobitic terrestrial amphipod. Regrettably, the fields with the largest caves known on Kauai were covered by 5 m of sugar cane bagasse shortly before I visited the area. The caves are now gone, the fauna extinct, and no one will ever guess what that fauna might have been!

Cave ecosystems in continental regions are simple, fragile, and share many attributes with the fragile native ecosystems of islands. It seems axiomatic then that cave ecosystems on islands must be tenuous. We must guard against the loss of this special and extremely interesting biotope. The problem is so acute in North America that the National Speleological Society recommends not publishing cave locations until adequate protection is assured for significant caves (Anon. 1972).

Evolution

Since Darwin and Wallace's time islands have been favorite biotopes for evolutionary research. The exceptional and spectacular examples of adaptive radiation among the early colonists on oceanic islands can be viewed as experimental controls for understanding the complex evolutionary processes occurring on the continents. Cave organisms also have been favorite objects of study by evolutionary biologists. The apparent regressive evolution displayed by cave adaptation played a prominent role in the rise of neo-Lamarkianism in the late 19th and early 20th centuries However, the rise of population genetics replaced the disuse theory.

The theories on evolution of cave organisms have been excellently reviewed by Barr (1968) and he presents his own hypothesis in that paper. However all of the theories assume that the distribution of troglobites is limited to (1) relicts of Pleistocene glaciation in the temperate regions and (2) aquatic relicts of changes in sea level in the tropical regions. The relictual nature of the distribution weighs heavily in most modern theories of cave adaptation. These theories also imply separation of the regressive evolution of cave organisms from the wealth of other examples of reductive evolution, such as adaptions in soil organisms and parasites, and the flightlessness among birds and insects on oceanic islands.

Briefly stated, Barr's (1968) theory relies on the extinction of the surface populations and a consequent reconstruction of the epigenotype. Barr's theoretical model employed a widespread troglophilic species which inhabited many caves and surface situations. Changing environmental conditions, for example glacial epochs, extinguished the surface populations and isolated the cave populations in separate caves. Without damping by invasion of surface forms the cave populations then changed under the influence of relaxed natural selection and became cave-adapted.

Vandel (1968) was the first to recognize that the tropical caves have a significant specialized fauna. However, he believed that troglobites are phylogenetic relicts. He restates the orthogenetic theory of evolution, that phyletic lines evolve along a pathway of rejuvenation, adaptive radiation, specialization, and senescence similar to the birth, growth, and old age of individuals. Therefore, cave-adapted organisms are ancient groups which have lost the genetic power to adapt to epigean environments and either live in caves or similar protected habitats or become extinct.

The discovery of troglobites among representatives of the adaptively radiating fauna in Hawaii will modify the currently accepted paradigm that troglobites are relicts. Caves in Hawaii have empty niches and I suggest that these niches are invaded by the speciating native fauna through a process of adaptive shifts. Their evolution is similar to that exemplified by other organisms that have exploited specialized habitats. This suggests that they are relicts only if the surface forms become extinct, not that they became cave-adapted after extinction of the surface population.

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