Cavernicoles in Lava Tubes on the Island of Hawaii

Abstract. *Cave-adapted arthropods have evolved in lava tubes in Hawaii. This is the first report of cavernicoles from the Hawaiian islands. The specialization of the cavernicolous insects and the recent origin of the lava tubes suggest that subterranean connections between lava tubes regularly occur and provide dispersal routes. The discovery that lava tubes were colonized by representatives of the adaptively radiating native fauna offers significant potential for evolutionary studies.*

Troglobites (obligatory cavernicoles) have been reported almost exclusively from limestone caverns. In fact, Vandel (*1*) omits lava tubes entirely from his comprehensive monograph on biospeleology, and Poulson and White (*2*), in their article on the cave environment, limit their discussion to limestone caves, although a few troglobites have been reported from lava tubes in the United States (*3*) and Japan (*4*). Also, the few troglobites from tropical areas or from oceanic islands (*1*, p. 26) are, according to Barr (*3*), almost entirely aquatic. Consequently, it was surprising to discover a rich, specialized arthropod fauna in the relatively young lava tubes on the island of Hawaii (*5*).

The Hawaiian islands provide an extreme example of a disharmonic fauna on an isolated oceanic island chain and some of the most remarkable examples of adaptive radiation among those groups with early successful colonists (*6*). The biota are uniquely suited for evolutionary studies (*7*). Therefore, the discovery of lava tubes as a specific biotope for native fauna in the Hawaiian islands offers a significant potential for further insights into evolutionary processes and adaptive radiation.

During July 1971, I collected representatives of five groups of insects, in four orders, that have independently become specialized for life in lava tubes on Hawaii. All of these cave forms have been collected only in the dark zone of lava tubes. At least one of these, a cixiid plant hopper (Homoptera, Cixiidae) (Fig. 1), is a true troglobite (*8*). It has vestigial compound eyes, the antennal bases are remarkably enlarged, it is almost completely depigmented, and it is brachypterous. All its epigean relatives, a large endemic complex of species, are fully winged, eyed, and colored. All instars of the cave cixiid were taken on tree roots that hang in caves, and the last nymphal instars and adults were collected as they moved on the walls and floor far from tree roots.

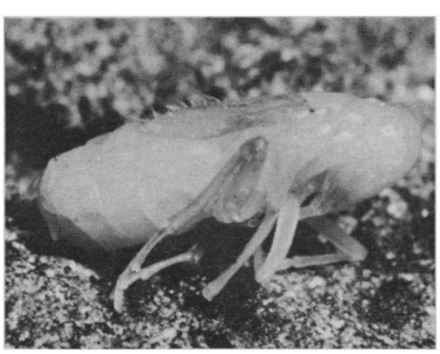

Fig. 1. A specialized cave cixiid from Hawaii. Ventrad of the highlight on the head is the enlarged antenna. The lateral ocellus is visible as a diamond-shaped spot anterior and dorsad of the antenna. The compound eye consists of three vestigial ommatidia near the lateral ocellus and is visible only in slide mounts. The length of the body is 4.5 mm. [G. A. Samuelson, Bishop Museum]

Two groups of endemic crickets (Orthoptera, Gryllidae) have independently evolved cavernicolous species. One species can be placed in *Thaumatogryllus*, previously known only from an epigean form on the island of Kauai. It has markedly reduced eyes, elongation of legs and antennae, vestigal tegmina, and marked depigmentation of the integument compared to the surface species. The other is not related to anything in the known Hawaiian fauna and is possibly an apterous nemobiine cricket.

A terrestrial, apterous, and nearly eyeless water treader (Fig. 2) (Hemiptera, Mesoveliidae) was collected on the cave walls. It is the first representative of this family in the native Hawaiian fauna and may be related to *Speovelia maritima* Esaki, known only from a sea cave in Japan (*9*). I have also collected a species of ground beetle belonging to the widespread genus *Tachys* (Coleoptera, Carabidae). The latter is most closely related to *T. arcanicola* Blackburn, a native epigean species known only from Oahu. All of the above species from lava tubes may be troglobites, but further studies are necessary to confirm this. Other arthropods, including other insects, with reduced or absent eyes and depigmented integument that were collected in lava tubes are thysanurans, collembolans, spiders, isopods, and diplopods. Their status in the cave ecosystem is not yet clarified.

Many taxa common in caves in the continental tropics, for example, bats, cockroaches, and ants, are absent in the disharmonic native fauna of the Hawaiian islands. The resulting empty biotope in lava tubes has been colonized by representatives of the native groups in the process of adaptive radiation. The main source of energy input in the lava tubes appears to be the tree roots that penetrate the lava through cracks and dangle into the caverns. The roots, both living and decaying, serve as a direct food source, and they also form a path for percolating water carrying organic matter.

Two of the lava tubes visited in this study are on the Mauna Loa massif at 300 m and 1140 m, and the other is on the Kilauea massif at 480 m. The ages range from 90 years (Kaumana Cave) to less than 20,000 years (*10*). Lava caves, unlike limestone caves, tend to degrade and collapse in a brief geological time. It is not plausible that the specialized morphology of the species in the lava tubes could have evolved since these tubes were formed. In contrast to the opinions of Torii (*4*), I suggest that dispersal from one lava tube to another is a regular, though perhaps infrequent, occurrence in Hawaii. It may involve dispersal through aa clinker, extensive lava tubes, great earth cracks, fault lines, fissures, and perhaps the large gas bubbles in pahoehoe basalt. In that case, the fauna of a given volcanic massif may be similar in similar climatic regions, and there may be continuous evolution from the earliest occupation of lava tubes to the mature and eroded volcanic massif. Dispersal across sea gaps is much less easily envisioned than for the

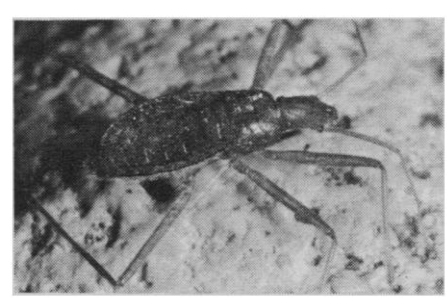

Fig. 2. A specialized cave mesoveliid. The remnant of the compound eye is visible near the posterior lateral corner on the right side of the head. It is not visible on the left side. The length of the body is 3.5 mm. [G. A. Samuelson, Bishop Museum]

surface fauna, and studies have shown that the rate of such dispersal for epigean forms is low (*7*, pp. 534–535).

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7. For example, see H. L. Carson, D. E. Hardy, H. T. Spieth, W. S. Stone, in *Essays in Evolution and Genetics in Honor of Theodosius Dobzhansky*, M. K. Hecht and W. C. Steere, Eds. (Appleton-Century-Crofts, New York, 1970), pp. 437–543.
8. Only one other cixiid is reported to be cavernicolous, *Typhlobrixia namorokensis* Synave from Madagascar. Vandel considered it a soil form accidental in caves (*1*, p. 183), but morphologically it is intermediate between epigean species and the Hawaiian cave cixiid. In Cixiidae, the adult is the dispersal stage, and most root-feeding cixiids molt to epigean adults. Field observation has shown that the nymphs of the Hawaiian cave cixiid feed on exposed tree roots in the caves and not on those roots within the soil and that the adults disperse entirely within lava tubes and associated cavities.
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11. This study was supported by NSF grant GB 23075 and is part of an integrated program of studies on island ecosystems, the International Biological Programme, Hawaii Subprogram. I thank F. J. Radovsky for his review and encouragement; G. A. Samuelson for identifying the carabid; and both of them and W. A. Steffan, W. C. Gagné, F. D. Stone, and N. C. Howarth for technical assistance. Contribution No. 1, Island Ecosystems IRP/IBP Hawaii.

31 August 1971; revised 15 October 1971

Sexual Stage of Histoplasma capsulatum

Abstract. *Twelve primary subcultures of* Histoplasma capsulatum, *paired in all possible combinations on agar containing yeast extract and Alphacel, produced fertile cleistothecia, resembling those of* Ajellomyces dermatitidis (Blastomyces dermatitidis).

In 1967, Ajello and Cheng (*1*) reported the sexual stage of *Histoplasma capsulatum*, a pathogenic fungus. The claim was refuted by Kwon-Chung in 1968 (*2*) on the basis that the cultures were mixed, and that the cleistothecia they observed were not produced by *H. capsulatum* but by a nonpathogenic Gymnoascaceous fungus. The refutation was subsequently supported by various mycologists (*3*).

Recently, I isolated 12 strains of *H. capsulatum* from soil samples collected under bird roosts in Miller County, Arkansas (*4*), and cultured them in pairs of 144 possible combinations on agar medium containing Alphacel (*5*) and yeast extract. Cleistothecia were found in 70 combinations after 3 weeks at 25°C. The cleistothecia resemble those of *Ajellomyces dermatitidis* (*6*), the etiologic agent of North American blastomycosis, by the formation of tightly coiled hyphae radiating from a common source at the base of the young ascocarp (Fig. 1, A and B). The main difference in the fruiting body of the two fungi can be found, however, in the shape and size of the branches originating from the coils.

In contrast to *A. dermatitidis*, the highly branched short hyphae arising from the coil in *H. capsulatum* are irregularly curved and never constricted at the cross walls (Fig. 1D).

The mature cleistothecia are globose (Fig. 1C) with buffy pigment, ranging in size from 80 to 250 μm in diameter. When a cleistothecium is mounted in a solution of lactophenol and cotton-blue for microscopic examination, intensely stained clusters of asci (Fig. 1E) are visible at the central part of the ascocarp. The pear-shaped asci contain eight smooth, hyaline spherical ascospores that are 1.5 μm in diameter (Fig. 1F). The single ascospore isolates obtained by micromanipulation were found to be heterothallic and produce conidia typical of *H. capsulatum*. The cultures also transform into the yeast phase typical of *H. capsulatum* at 37°C on blood-cysteine glucose agar.

A detailed account of the heterothallism, development of the cleistothecia, and a Latin description is in preparation.

Fig. 1. (A) Cleistothecium mounted in lactophenol showing (arrows) tightly coiled hyphae (×300). (B) Young ascocarp with three coils and ascogenous hyphal mass at the central part (×485). (C) Mature cleistothecium (×300). (D) Irregularly curved hyphae originated from the coils (×1250). (E) Cluster of young asci stained with cotton-blue (×750). (F) Mature asci with ascospores (×1250).

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26 November 1971