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Hawaiian Lava Tube Cave Associated Lepidoptera from the Collections of Francis G. Howarth and Fred D. Stone[1]

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Abstract. The lepidopteran fauna of caves remains poorly known largely because of the difficulty in collecting specimens suitable for identification in the physically demanding environment. Here we provide the results of biological surveys spanning more than 40 years in Hawai'i. Lava tube caves are an important landform throughout the islands and especially on the younger islands of Maui and Hawai'i. These caves support communities of a diverse array of organisms including Lepidoptera. We list 25 morphospecies of moths now known occur in Hawaiian caves. Of these, six are nonnative and mostly are found only in the entrance and twilight zones. Three native species are typical surface species, that probably entered caves accidentally. Three species of endemic *Mestolobes* seek shelter in caves and other dark habitats, and some may be associated with caves. *Schrankia altivolans* are occasionally found living in caves. The remaining species display behavioral or morphological adaptations to utilize cave habitats. The speciose endemic genus *Hyposmocoma* is represented in caves by at least six species. Four species of large native moths were known historically to use caves for communal daytime roosts including *Hypocala velans* and three species of *Peridroma*; these emerge at dusk and fly long distances to forage and reproduce, and then return to the same caves at dawn. Most interesting are three species (*Schrankia howarthi, Pseudoschrankia nohoana*, and *Orthomecyna* species) that live and reproduce deep in caves and show some morphological features characteristic of obligate cave animals. These results indicate that Lepidoptera are an important component of cave ecosystems and should be included in faunal surveys of caves. We also provide a brief biography of our co-author and dear friend, Dr. Fred D. Stone 1938–2018.

INTRODUCTION

Lepidoptera are rarely included in faunal surveys of caves, especially in the permanently dark deeper passages. Most historical accounts have recorded the few moth and butterfly species that habitually enter caves for estivation or shelter during seasonal climate shifts

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(Capuse & Georgescu 1962–1963; Vandel 1965; McKillop1993; Warrant *et al*. 2016). A few moth species inhabit the entrance and twilight zones; i.e., the parietal biotope (Vandel 1965), where they scavenge on nest debris of cave roosting vertebrates and organic material falling into entrances. A predisposition for hypogean living has been documented in *Schrankia* Hübner including Japanese populations of *S. costaestrigalis* (Stephens), which readily colonize railroad tunnels and other underground spaces at all life stages (Yoshimatsu 1995) and an unidentified species of *Schrankia* from lava tubes in Queensland, Australia (Howarth & Stone 1990). In addition, individuals of many surface-inhabiting species occasionally enter caves accidentally. Moths in the family Tineidae are frequent scavengers on guano in caves, especially in tropical Southeast Asia (Robinson 1980). Thirty-six species have been collected in caves, of which 20 maintain permanent cave populations. Eleven species are known only from caves, of which one, *Tinea microphthalma* Robinson, from the Philippines, has reduced eyes and is considered an obligate cave dweller (= troglobite).

The first accounts of moths in caves in Hawai‘i were made by R.C.L. Perkins, who conducted a monumental insect survey of the islands from 1892 to the early 1900s (Perkins 1913). Perkins observed that native *Hypocala velans* Walker utilized caves and crevices in lava as daytime roosts. These moths sometimes emerged in the evening in great numbers (Perkins 1913; Zimmerman 1958a). The surprising discovery of obligately cave-adapted arthropods in young lava tubes on Hawai‘i Island (Howarth 1972) led to a multi-year project to survey the fauna of Hawaiian caves by Howarth and a team of collaborators, including the late Dr. Fred D. Stone. Among the insects collected in total darkness were specimens of a species of *Schrankia*, which had reduced wings and eyes, and unmarked pale grey coloration. Their larvae feed on plant roots that penetrate the lava and enter caves (Howarth 1973).

Schrankia howarthi Davis & Medeiros is the second known lepidopteran that lives permanently underground and displays the typical adaptations found in other obligate cave species. Its discovery intrigued Don R. Davis, of the Smithsonian Institution, who visited the islands in 1974 and 1977 and collected additional specimens for species description. However, the kaleidoscopic variation in morphology displayed by specimens from different caves defied sorting by conventional taxonomic methods. Species determination was further complicated by the existence of populations of related moths with normally developed eyes, wings and bodily color that inhabited twilight areas in the same caves. Subsequently, one of us (MJM) joined the project and used DNA analysis to assist with classifying the various populations. Remarkably, all specimens belonged to a single polymorphic species with an obligate cave form occurring in darkness; a volant, sighted population occurring in the twilight zone; and occasional hybrids between them (Medeiros *et al.* 2009). Additional surveys have revealed the existence of a diverse moth fauna in Hawaiian caves, which is the subject of the current review.

The cave environment is zonal with three main zones recognized based on the presence of light: these are the “entrance zone” a lighted zone where the surface and cave environments mix; a “twilight zone” where light is progressively diminished from the limit of conspicuous green plants to complete darkness; and a “dark zone” where light is absent. The dark zone can often be subdivided into subzones based on the physical environment: a “transition zone” where the atmosphere within the passage is subjected to frequent disturbances resulting from weather and diurnal events occurring on the surface; a "deep zone" where the air remains permanently saturated or supersaturated with water vapor; and a "bad air zone" where air exchange with the surface is restricted and decomposition gases can accumulate. The presence and extent of each of these zones is delineated by the size and shape of the entrance(s) and passages (Howarth 1980, 1987).

Animals found in caves can be classified into four main categories based on their theorized relationship to cave life. These are "troglobites" (species obligately adapted to live only in deep and stagnant air zones); "troglophiles" (species able to live and reproduce in caves as well as in similar damp, dark habitats on the surface); "trogloxenes" (species that habitually use caves for roosting or shelter and return to the surface for food and dispersal); and "accidentals" (species accidentally entering caves but that cannot survive there) (Howarth 1983; Howarth & Moldovan 2019).

METHODS

Biological inventory of caves is often logistically and physically challenging (Wynne *et al*. 2018). This is especially true for Lepidoptera, which require special handling to ensure suitable specimens are collected and preserved for taxonomic study (Robinson 1980). In the current project, as many caves as possible on each island were sampled. Caves were explored using accepted precautions for safety and protection of speleological resources; e.g. biologic, geologic, archaeologic, and paleontological deposits. Cave passages were surveyed visually for animals. Surveys were often concentrated in passages that contained promising habitats, especially those with potential food resources (e.g., root curtains, flood detritus, etc.). Baits (sprouted grain, tubers, meat, and cheese) were placed in various locations throughout caves. Adult moths rarely came to baits, but larvae responded to sprouted grain and rotting plant material. Adult moths were coaxed into individual vials and kept alive until they could be curated outside the cave. Larvae and pupae were also collected into individual vials but kept alive to rear adults. Larvae not reared were stored in 90–95% ethanol. Because many of the caves are considered "culturally and/or biologically significant," precise locations are treated as confidential; therefore, locality information is rounded to general area only. Precise locality data are archived with the agency responsible for managing each cave.

Genitalia were prepared and mounted on slides using the following protocol: Abdomens were soaked in simmering 10% potassium hydroxide solution for one hour, genitalia were removed, stained with lignin pink and/or Chlorazol black, then soaked in a sequence of 30% ethyl alcohol, 90% ethyl alcohol, 100% isopropyl alcohol and Euparal essence, and then spread on microscope slides and mounted in Euparal. Unless otherwise noted, digital photographs of genitalia and adults were taken with a digital imaging system mounted on a Nikon SMZ25 stereo microscope. All of the following specimens and associated genitalia slides are deposited in the Entomological Collection, Bernice Pauahi Bishop Museum, Honolulu, Hawai‘i.

RESULTS

Twenty-five morphospecies of Lepidoptera are herein recorded from Hawaiian caves. Nineteen are endemic to the islands and six are nonnative. As expected, most native species and all of the non-native species occur in caves opportunistically as troglophiles, trogloxenes, or accidental waifs and display no morphological or behavioral adaptations to underground life. Several endemic species in five genera are obligately associated with caves. Two remarkable endemic species, *Schrankia howarthi* and an undescribed *Orthomecyna* sp., are obligate cave dwellers. Surprisingly, *S. howarthi* is polymorphic with populations obligately adapted to living permanently in caves on Hawaiʻi and Maui islands. Additional populations less specialized for cave life, which occur in the twilight zones of caves, are able to disperse outside caves. Larvae of the *Orthomecyna* species are blind, pale, and feed on flushing root tips in the deep zone of caves. Adults of *Pseudoschrankia nohoana* Medeiros & Howarth occur throughout caves, but most frequently in the twilight zone. They are volant and presumably can disperse on the surface when climatic conditions allow. The presumed larvae are blind and adapted to cave habitats. In addition, *Hypocala velans* and several species of *Peridroma* Hübner are obligately associated with caves as daytime roosts. They leave their caves in huge numbers at dusk and, and then return to the same caves at dawn. Finally, several endemic species in *Hyposmocoma* Butler and *Mestolobes* Butler appear to be closely associated with cave habitats, but their biology and status in caves remain poorly known.

ANNOTATED CHECKLIST

The following is a list of the 25 moth morphospecies found in Hawaiian caves with notes on their biology, association with the cave habitat, and localities. Taxa are arranged as in Nishida (2002); i.e., each species listed alphabetically within its genus, which is listed alphabetically within its family.

Autostichidae

1- *Oecia oecophila* (Staudinger, 1876). Nonnative: **Troglophile?**

HAWAIʻI I, N. Kona, Kīholo Bay, 0–3 m from entrance of Ana Lima Kipo Lava Tube, entrance zone. 19.8°N; 155.9°W. 10 Jan 1982. F. Howarth. The larvae feed on dried feces and probably other decaying organic matter (Nasu *et al*. 2016). Dry rat feces from *Rattus rattus* Linnaeus are often common in the twilight and transition zones of caves and provide food for this and other scavenging species. Slide LB78, male. See Zimmerman (1978) for illustrations and more information.

Cosmopterigidae

Differences in wing pattern suggest each of the following entries represent different species of *Hyposmocoma*.

2 - *Hyposmocoma (Euperissus)* sp. A. Endemic: **Troglophile?**
(Fig. 1A, B)

HAWAIʻI I, Hawaiʻi Volcanoes National Park, "HAVO, Chain of Craters Rd, 19.3°N; 155.2°W. 750 m elev. ~800 m from entrance of Keahou Trail Cave # 3, deep zone. 5 May 2006, F.G. Howarth & F.D. Stone. Slide LB66, male. Genitalia are similar to those of *Hyposmocoma (Euperissus) chilonella* Walsingham.

3 - *Hyposmocoma* sp. B. Endemic: **Troglophile?**

MAUI: Haleakalā, Ulupalakua, Thaumatogryllus Cave #2, 20.6°N; 156.4°W. 700 m elev. deep zone. 16 Jul 2002, F.G. Howarth & W. McDowell. Female, not illustrated.

4 - *Hyposmocoma* (*Hyposmocoma*) sp. C. Endemic: **Troglophile?** (Fig. 1C, D)

HAWAI'I I, Hawai'i Volcanoes National Park: Mauna Loa Strip Road. 5000-Foot Cave. 19.5°N;155.3°W. 1,500 m elev. transition zone. 12 May 2005, F.G. Howarth & F.D. Stone. Slide LB75, male. Genitalia are very simple, and similar to *Hyposmocoma (H.) nohomeha* Medeiros, Haines, & Rubinoff.

5 - *Hyposmocoma (Hyposmocoma)* sp. D. Endemic: **Troglophile?** (Fig. 1E, F)

HAWAI'I I, Pōhakuloa Training Area, Bobcat Trail, 19.7°N; 155.7°W. 1,600 m elev. Dead Cat Cave Entrance, T28, transition zone. 9 Mar 2017, M.J. Medeiros. Slide 17A18, male. This specimen is not *Hyposmocoma (H.) malornata* Walsingham, though the genitalia are similar.

6 - *Hyposmocoma* sp. E. Endemic: **Troglophile**

HAWAI'I I, Pōhakuloa Training Area, Bobcat Trail Cave #10265-T-40DE. 19.7°N; 155.7°W. 1,600 m elev. Deep zone. 30 Dec 1994. F.G. Howarth. Two pupae were collected that were suspended horizontally in loose silk hammocks strung between walls in a narrow crack (approx. 3–5 cm wide) in the deep zone. They were kept alive, and one female with brown wings with two dark spots emerged on 24 Jan 1995. This may be the same species as *Hyposmocoma* species D, as the two caves are in the same lava flow and separated by ~200 m. Not illustrated.

Crambidae

7 - *Eudonia* species: Endemic: **Accidental** (Fig. 1G, H)

HAWAI'I I, Hawai'i Volcanoes National Park, Kalanaokuaiki Pali, 19.4°N; 155.2°W, 1,000 m elev. Cave #1, twilight zone. 4 Jul 1976, F.G. Howarth. Slide LB72, male. Genitalia in this genus are extremely similar (Zimmerman 1958b). This specimen's scales are badly rubbed, so it is difficult to ascertain which species this may be, or whether it is a new species. Nearby, flying along the surface of an area close to many lava tubes, was found the following specimen: Hawai'i Volcanoes National Park, Mauna Ulu Lava flows, 950 m, 31 Dec 1981. "Flying over 'barren' lava." FG Howarth, BPBM Acc #1982.6. Slide LB68, male. Based on wing pattern alone, this specimen appears closest to *Eudonia isophaea* (Meyrick), or perhaps *E. peronetis* (Meyrick), though this specimen is also somewhat rubbed. These two moths may or may not be the same species.

8 - *Mestolobes olali* Medeiros & Howarth 2017. Endemic: **Trogloxene**

HAWAI'I I, Locality data are provided in Medeiros & Howarth (2017). This species is known from several caves on the Big Island and has metallic bands running from the costal to anal margin of the forewing. It is possibly resident in the entrance and twilight zones. See Medeiros & Howarth (2017) for description and photographs.

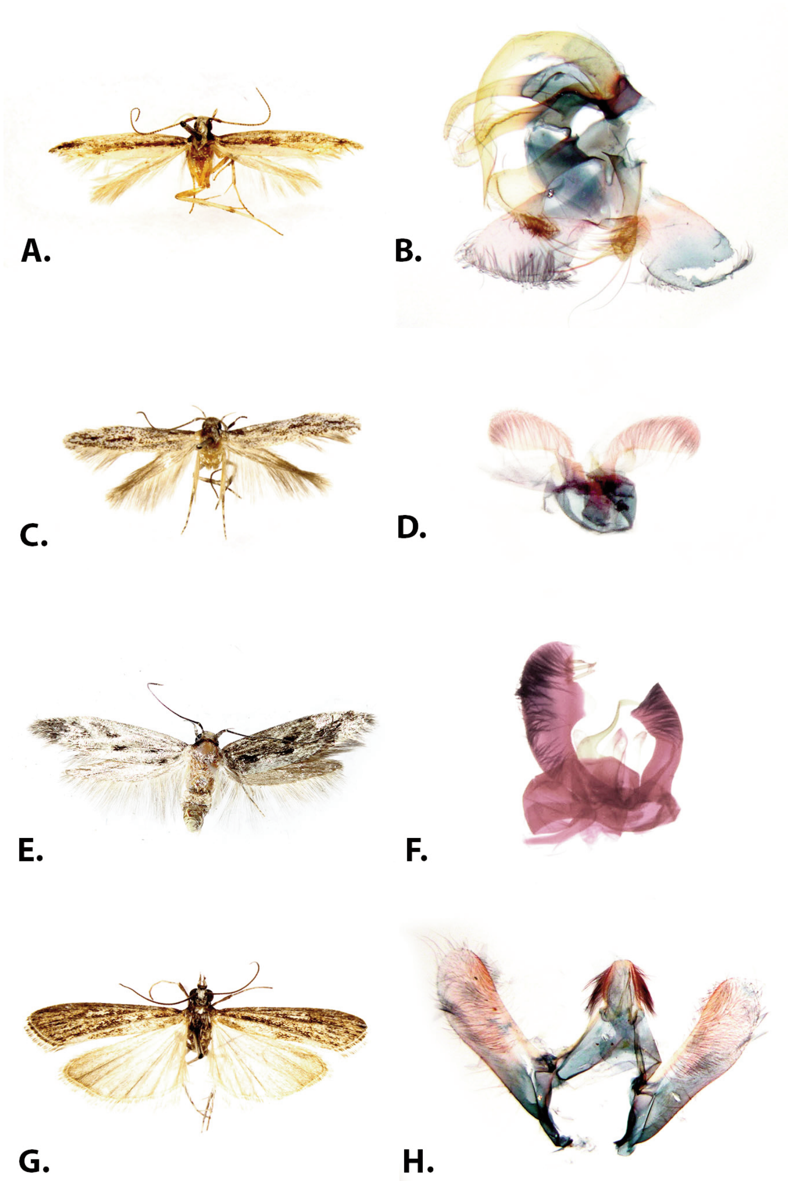

Figure 1. **A.** adult *Hyposmocoma (Euperissus)* sp., specimen LB66, wingspan 11 mm. **B**. male genitalia of specimen LB66. **C**. *Hyposmocoma* (*Hyposmocoma*) sp., specimen LB75, wingspan 10 mm. **D**. male genitalia of specimen LB75. **E**. *Hyposmocoma* (*Hyposmocoma*) sp., specimen 17A18, wingspan 15 mm. **F**. male genitalia of 17A18. **G**. *Eudonia* sp., specimen LB68, wingspan 15 mm. **H**. male genitalia of LB68.

9 - *Mestolobes* undescribed species: Endemic: **Trogloxene**
(Fig. 2 A, B)

MOLOKA‘I, Kalaupapa National Historical Park, 21.2°N; 157°W. 5 m elev. Fisherman's Shack Cave #1 (Kaupikiawa Cave), entrance and twilight zones. 2 Jun 2010, F.G. Howarth & F.D. Stone. Slide LB67, male. Compared to other known *Mestolobes*, the valvae are shorter and wider, and the gnathos is more blunt. This specimen appears closest to *M. pessias* Meyrick, or *M. minuscula* (Butler). This and other species of *Mestolobes* typically fly at dusk and apparently hide in darkness at other times (FGH, unpubl. observ.).

10 - *Mestolobes* sp.: Endemic: **Trogloxene**
(Fig. 2 C, D)

HAWAI‘I I, Hawai‘i Volcanoes National Park: Mauna Loa Strip Road. 5000-Foot Cave. 19.5° N;155.3° W. 1,500 m elev. Twilight zone. 10 May 2006, F.G. Howarth & F.D. Stone. Slide LB69, male. This specimen is either closely related to, or is actually, *Mestolobes minuscula* (Butler). However, this species is poorly delineated (Zimmerman 1958b).

11 - *Omiodes localis* (Butler, 1879): Endemic: **Accidental?**

HAWAI‘I I, Hawai‘i Volcanoes National Park Cave Survey, Mauna Loa Strip Road. "Fred's Cave" (= segment of 5000-Foot Cave). 19.5°N; 155.3°W. 1,500 m elev. Twilight zone. 22 Mar 2005, F.G. Howarth & F.D. Stone. 1 female. Larvae feed on grasses and probably are residents of the entrance zone. See Zimmerman 1958b for illustrations and additional information.

12 - *Orthomecyna* species. Endemic, **possible Troglobite?**
(Fig. 2E)

HAWAI‘I I, south slope of Mauna Loa, Keahou Ranch, 19.5°N; 155.34°W. 1,700 m elev. Keamoku Cave, deep zone. 8–11 July 1976, F.G. Howarth. Seven blind larvae on tree roots. Hawai‘i Volcanoes NP. Mauna Loa, Frank's Cave in Spur Road Cave System, deep zone. 5–7 May 2005, F.G. Howarth & F.D. Stone. Several dead adults and live larvae. Hawai‘i Volcanoes NP. Mauna Loa, 5000-Foot Cave System, 1,525 m, deep zone. 10 May 2006, F.G. Howarth & F.D. Stone. One dead moth. The larva is unusual and displays some troglomorphies (Fig. 2E). It lacks pigmentation and any trace of eyes. Antennae are relatively robust, porrect. Head is nearly prognathous. All larvae so far known were found feeding on swollen flushing etiolated root tips in the deep zone of caves.

13 - *Udea* species. Endemic: **Accidental?**
(Fig. 2 G and H)

HAWAI‘I I, Hawai‘i Volcanoes National Park Cave Survey, Mauna Loa Strip Road. Keana Kīpuka Pua‘ulu # 1 (a.k.a. Bird Park Cave #1), 19.4°N, 155.3°W, 1,220 m, entrance zone. 9 Dec 1976, D & M Davis. LB70, male. Based on genitalic and wing pattern similarities visible in Zimmerman (1958b), this specimen is quite similar to

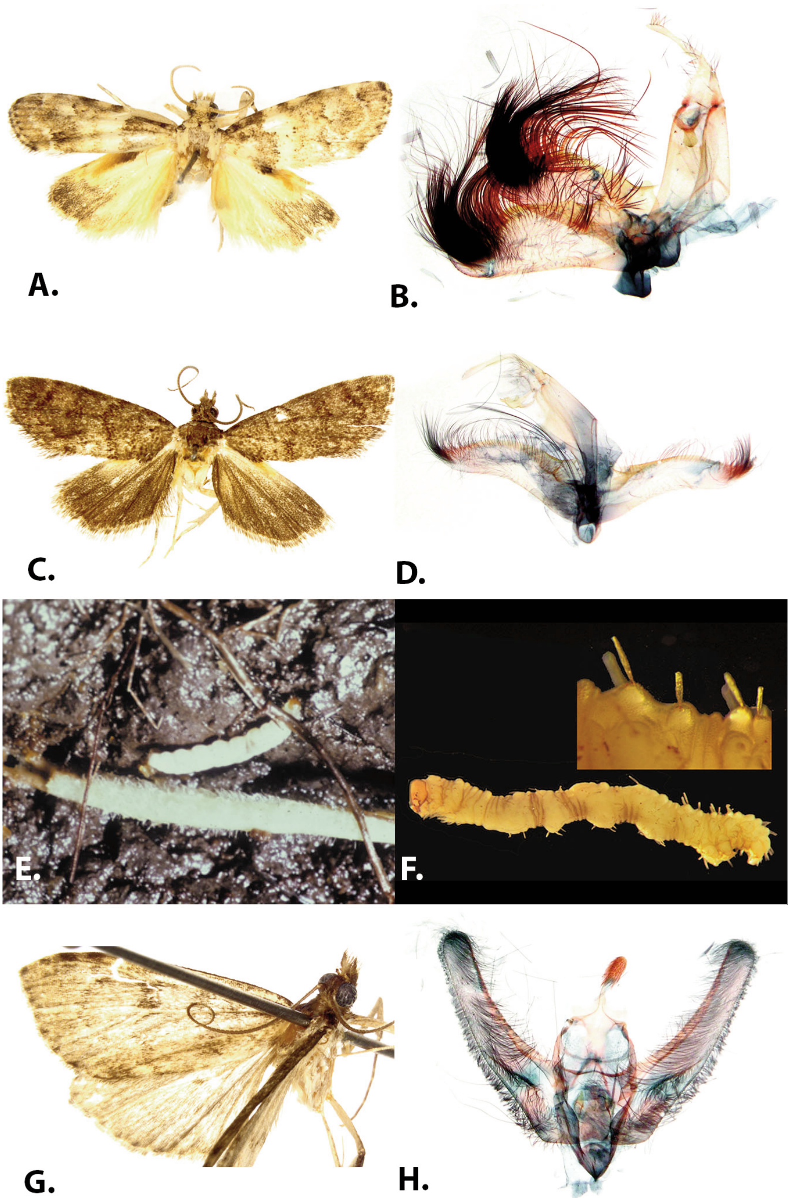

Figure 2. **A**., *Mestolobes* undescribed species, specimen LB67, wingspan 13 mm. **B**. male genitalia of LB67. **C**. *Mestolobes* sp., specimen LB69, wingspan 13 mm. **D**. male genitalia of LB69. **E**. larva of *Orthomecyna* sp. next to etiolated root tip on floor in Keamoku Cave, at 1,700 m on Hawai'i I. Note feeding damage at left of image. Photo by D.R. Davis. **F**. Likely *Pseudoschrankia nohoana*, larva. **G**. *Udea* sp., specimen LB70, left wing length 8 mm. **H**. male genitalia of specimen LB70.

Udea despecta (Butler) but may be *U. liopis liopis* (Meyrick) or *U. pyranthes* (Meyrick) as these species are difficult to differentiate.

Erebidae

14 - *Hypocala velans* Walker, 1857: Endemic: **Trogloxene**

HAWAIʻI I, Pōhakuloa Training Area, Kona Highway Cave, 19.76°N; 155.69°W. 1,400 m elev. transition / deep zone, Aug 1994. Single adult collected while roosting. This is the only cave specimen found during our surveys, but Perkins (1913) reported the native *Hypocala velans* commonly frequented caves and rock crevices during the day and emerged in great numbers at sunset. Although Perkins (1913) recounted that the species was more abundant in the lowlands, he noted that this moth used an unnamed cave at 9,000 feet [~2,750 m] on Haleakalā, Maui. Zimmerman (1958a) and Ziegler *et al*. (2016) summarized observations of cave moth roosts in Hawaiʻi. However, this species is now either rare or possibly extinct.

15 - *Pseudoschrankia nohoana* Medeiros & Howarth, 2017: Endemic: **Troglophile** (Fig. 2F)

HAWAIʻI I. Hawaiʻi Volcanoes National Park, 19.4°N; 155.2°W. 750 m elev. Ainahou Cave, below entrance #22, deep zone. 13 Jun 2005, F Howarth & F Stone, 1 male, slide LB65. *Pseudoschrankia nohoana* has been recorded from several caves on the Big Island and is most abundant in the twilight zone. See Medeiros & Howarth (2017) for more information. The species has not been reared, and the larval habitat is unknown. However, an undetermined hypenodine larva occurs in many of the same caves as *P. nohoana* and most likely is this species. The larva is similar to larvae of *Schrankia howarthi*, but differs significantly in the form of its setae and integument. *S. howarthi* has elongate, simple acuminate setae, whereas the unknown larva has enlarged flattened rod-like setae that are slightly wider near the middle (Fig. 2F). Also, the integument is strongly shagreened rather than smooth like *Schrankia* larvae. No *P. nohoana* larvae have been collected on plant roots, and all reared adults from roots were *Schrankia*. However, it is possible that *P. nohoana* also feeds on roots, but were missed during our surveys since the larvae of the two species are similar in life. *Pseudoschrankia nohoana* does respond to baits, including sprouting grain and rotting vegetable matter, suggesting that it has a different behavior than *Schrankia*; it may also pupate in crevices rather than on plant roots.

16 - *Schrankia altivolans* (Butler, 1880): Endemic: **Troglophile**

MAIN HAWAIIAN ISLANDS FROM KAUAʻI TO HAWAIʻI. This moth is found widely on all the main Hawaiian Islands as a surface dweller, but has been recorded in four caves on Maui and six caves on the Big Island (Medeiros *et al.* 2009). This species has been found in caves near sea level to over 1,200 m elevation and in all cave zones from the entrance to deep zones. *Schrankia* species that feed on plant roots are able to colonize caves and other underground spaces where roots occur. Other cave inhabiting *Schrankia* populations have been reported from Japan (Yoshimatsu 1995) and Australia (Howarth & Stone 1990). Medeiros *et al.* (2009) illustrated both sexes of adults and discussed its phylogeny and great morphological variation.

17 - *Schrankia howarthi* Davis & Medeiros, 2009: Endemic: **Troglobite & Troglophile**

HAWAIʻI & MAUI islands. *Schrankia howarthi* is widely distributed in caves on Hualālai, Mauna Loa, and Kīlauea volcanoes on the Big Island from sea level to over 1,500 m elevation and from all cave zones. It is expected to occur in any lava tube that contains suitable plant roots and environment. It is also known from two caves on the south slope of Haleakalā on Maui (Medeiros *et al.* (2009). This species is polymorphic, with very pale individuals found in the deep zone of caves on Maui and the Big Island, and slightly more pigmented individuals found closer to cave entrances and on the surface. Some individuals of both morphs are flightless, though flightlessness is most common in deep zone females. Pale adults in the deep zone often lack eye-shine, whereas more pigmented adults display a distinct pink glow in a bright beam of light. Larvae feed on tree roots that dangle into caves. The conspicuous pupal cocoons are composed of silk and short root fragments and are attached to the host root. Larvae, pupae, and adults are commonly found in caves with suitable living roots. *Schrankia howarthi* is the most commonly encountered Lepidoptera found in Hawaiian caves. See Medeiros *et al.* (2009) for description, illustrations and distribution.

Noctuidae

18 - *Peridroma albiorbis* (Warren, 1912): Endemic: **Trogloxene**

HAWAIʻI: northern slope Mauna Loa, ~3,000 m elev, in the dark zone of Big Red Cave. Jan 2000, D. Bunnell and J. Giffin. Dead *Peridroma albiorbis* adult. The cave also contained large numbers of *Lasiurus cinereus semotus* (Allen) (Hawaiian Hoary Bat) remains (Bunnell & Giffin 2000). See Zimmerman 1958a for illustrations and additional information.

19 - *Peridroma* sp. A. Endemic: **Trogloxene**

HAWAIʻI: Hawaiʻi Volcanoes National Park, ~4,000 m elev, Mauna Loa Lava Tube, transition zone. 1980s, F.G. Howarth. A huge colony of moths numbering tens of thousands were roosting in the cave. This colony persisted for several years then disappeared. On 28 Sep 2005, a second colony was discovered in a nearby cave at 3,800 m elevation by F.D. Stone & F.G. Howarth. The second colony was smaller numbering a few hundred individuals. An accurate count was not possible since the moths were packed together in crevices on the walls and ceiling (Howarth & Stone 2020). The floors of both caves were paved with a thick layer of permanent ice. Illustrated in Howarth & Stone (2020).

20 - *Peridroma* sp. B. Endemic: **Trogloxene**

MAUI, Haleakalā National Park, Haleakalā Crater, Crystal Cave, 20.7°N; 156.2°W, 2,300 m elev. Twilight zone. 23 Jun 1976, F.G. Howarth. Fragments of moths found on the cave floor. The wide low cave entrance leads to a single room 10 to 15 m in diameter, which is all in twilight. At the time of the survey, the dry floor was entirely covered with a several centimeter-deep layer of moth fragments. The wing shape and color pattern matched *Peridroma*. No living moths were found. The volume of fragments indicate that the cave once housed a huge colony of moths. Rat feces were also abundant, which suggest the reason for the collapse of the colony of moths.

Oecophoridae

21 - *Hofmannophila pseudospretella* (Stainton, 1849) nonnative: **Troglophile**

HAWAI'I I. Pōhakuloa Training Area, Dan's Cave, Multi-Purpose Range Complex, 19.66°N; 155.70°W, ~2,000 m, twilight zone 23 Sep 1994. FG Howarth. Known as the "brown house moth," this stored product pest is native to Asia but has been widely distributed by commerce. In Hawaiʻi, it is known from high-elevation buildings. The twilight zone of caves provides a similar habitat. Not illustrated.

Pterophoridae

22 - *Stenoptilodes,* probably ***taprobanes*** (R. Felder & Rogenhofer, 1875). Nonnative: **Accidental**

HAWAI'I I, Big I, Pōhakuloa Training Area, 19.64°N; 155.54°W, Puʻukoli Trench Cave 11D, 2 070 m, twilight zone. 1 Aug 1994, FG Howarth, FD Stone, ED Toole. Specimen at BPBM. This or related species has been observed in Long Cave (20.7°N; 156.2°W) in Haleakalā Crater on Maui. See Zimmerman 1958b for illustrations and additional information about *Stenoptilodes taprobanes*.

Pyralidae

23 - *Pyralis manihotalis* Guenée, 1854: Nonnative: **Troglophile**

HAWAI'I I. Pigeon Cave off the Saddle Road near Pu'u Waʻawaʻa 19.8°N; 155.8°W. 29 Apr 1974. Entrance and twilight zone, DR Davis and FG Howarth. This species is a scavenger on dry pigeon feces in the entrance and twilight zones of caves. It is not common in Hawaiian caves as there are no guano deposits, but it may be found wherever dry dung accumulates, such as beneath chicken coups. See Zimmerman 1958b for illustrations and additional information.

Tineidae

24 - *Monopis crocicapitella* (Clemens, 1859). Nonnative; **Troglophile**

HAWAI'I I, Hawaiʻi Volcanoes National Park: Mauna Loa Strip Road, 19.5°N;155.3°W. 1,500 m elev. 5000-Foot Cave, transition zone. 12 May 2005, FG Howarth & FD Stone. Slide LB74, female. **MAUI**, Ahihi-Kinau Natural Area Reserve, 20.6°N; 156.4°W, 120 m elev, Kalua O Lapa Cave; transition zone, 22 May 1988, FG Howarth. Slide LB73, female. It may be the same or a closely related species. See Zimmerman 1978 for illustrations and more information.

25 - *Phereoeca allutella* (Rebel, 1892): Nonnative; **Troglophile**

HAWAI'I I. N. Kona; Pigeon Cave off the Saddle Road near Puʻu Waʻawaʻa. 19.8°N; 155.8°W. Entrance and twilight zone. 29 Apr 1974, DR Davis. Specimens were reared from pigeon feces collected from within the entrance and twilight zones. The larvae of this moth are scavengers feeding on fungi and organic matter in the entrance and twilight zones of caves. The characteristic purse-shaped larval cases are commonly seen attached to walls in the twilight zone in dry lowland caves on all the main Hawaiian Islands. See Zimmerman 1978 for illustrations and more information.

DISCUSSION

Of the 25 morphospecies of Lepidoptera recorded herein from Hawaiian caves; nineteen are native and six are nonnative. Five nonnative species are synanthropic and were introduced through commerce. The drier twilight and transition zones within caves often provide similar habitats for these household pests. The sixth nonnative species, a pterophorid, was inadvertently introduced to Hawai‘i by humans and is probably an accidental visitor within caves. Three of the native species are typical surface species, that probably also enter caves accidentally. The three species of endemic *Mestolobes* listed may habitually enter caves. Additional *Mestolobes* species will certainly be found in caves during further surveys. Their larval habits are poorly known, and some species (e.g., *M. olali)* may be residents (i.e., troglophilic) in caves.

The remaining species display behavioral or morphological adaptations to utilize cave and other subterranean habitats. The endemic genus *Hyposmocoma* is incredibly speciose with more than 350 species known from the Hawaiian Islands (Zimmerman 1978). Their ecology is equally diverse; they feed on lichens on the driest lava flows, submerged algae in streams, and all parts of living plants in the wettest rainforests (Rubinoff & Schmitz 2010). A few are even predatory (Rubinoff & Haines 2005). Many more species than the five listed here probably occur in Hawaiian caves. Their function within cave ecological communities is unknown but likely unique.

At least four species of large native moths historically were known to use caves for communal daytime roosts: an underwing, *Hypocala velans*, and three species of *Peridroma* cutworms (Perkins 1913; Zimmerman 1958a, Ziegler *et al.* 2016). They emerge at dusk and fly long distances to forage and reproduce, and then return to the same caves at dawn. Their remarkable ability to navigate between roosting and feeding sites is analogous to behavior of the Bogong Moth (*Agrotis infusa*) in Australia (Warrant *et al.* 2016). Lowland colonies of these moths appear to have been extirpated, but a few colonies may still occur in high elevation caves on Mauna Loa on Hawai‘i (Ziegler *et al.* 2016, Howarth & Stone 2020). Additional colonies of these moths were documented in the literature from moth wing fragments in caves. These cave deposits suggest that a diverse assemblage of cave-roosting moths once existed in Hawai‘i. This assemblage probably included many additional species of *Peridroma* and possibly some *Agrotis* species. These roosts were exploited by the native bird, the ‘apapane (*Himatione sanguinea*), which nested in the entrance and twilight zones of occupied caves (Van Riper 1973, Howarth & Stone 2020). The remarkable phenomenon of large communal colonies of moths is disappearing along with the food resource and unusual nesting behavior of the ‘apapane. The cause of this demise is unknown, but a main culprit may be the black rat (*Rattus rattus*), which readily enters caves and would find roosting moths easy prey (Howarth & Stone 2020). *Peridroma* and *Agrotis* were also targets of parasites and predators purposefully introduced for biological control of related pest species (Gagne & Howarth 1985).

Three native species are strongly associated with caves and live and reproduce underground. *Pseudoschrankia nohoana* displays few morphological adaptations to the cave environment. Its biology remains poorly known. It is widespread in caves on Hawai‘i Island with adults found most often in the twilight zone. Its presumed larva is attracted to and feeds on decomposing plant material in deep zone environments. *Orthomecyna* sp. is so far known from a few caves between 1,500 and 2,000 m elevation on the southern slope of Mauna Loa. Its larvae feed on fleshy etiolated root flushes, and represent only the second report of larval biology for any of the 15 endemic species of *Orthomecyna*. The only previous record is Swezey's rearing of a single larva of *O. mesochasma* found among roots of sugarcane on the island of Kauaʻi (Swezey 1924, Zimmerman 1958b, p 295).

The most interesting Hawaiian species is *Schrankia howarthi*. It is one of only two known lepidopterans morphologically and behaviorally adapted to live in the deep cave environment. The other cave-adapted species is *Tinea microphthalma* Robinson, 1980 from the Philippines. Surprisingly, *Schrankia howarthi* is polymorphic with eyeless, depigmented weakly volant forms largely restricted to the deep zone, but also has an eyed, flighted form occurring in the entrance and twilight zones. The two forms hybridize where their habitats overlap, creating a kaleidoscope of intermediate forms. Also, unexpectedly, the cave-adapted morph occurs on both Hawaiʻi and Maui. DNA analysis revealed that the cave-adapted population on Maui originated from flighted individuals from adjacent areas on Hawaiʻi Island (Medeiros *et al.* 2009).

On the active volcanoes, new lava flows create new cave habitats while simultaneously destroying older habitats. Thus, cave ecosystems are dynamic with the fauna playing leapfrog from older to younger flows. New caves are colonized sequentially as the physical and biotic environment develops. The order in which species arrive is both random and non-random; that is, some generalists and predators can colonize rapidly soon after the habitat cools; while others can only establish after the habitat matures. In this way, lava tubes and their ecosystems of different ages provide model systems for the study of community development and evolutionary ecology (e.g., Medeiros *et al*. 2009, Wessel *et al.* 2013). Within *Schrankia*, the troglophilic morph can colonize caves by overland dispersal as soon as roots become available, often within a few decades after the lava flow cools. However, the cave-adapted morph arrives later. In 1971, when surveys began in Kaumana Cave, which is within the 1881 lava flow from Mauna Loa at 300 m elevation, the troglophilic morph of *S. howarthi* and *S. altivolans* were common in the cave, even in the deep zone. Sometime in the late 1980s to early 1990s (i.e., circa 110 years after the cave formed), the troglomorphic morph appeared, and subsequently *S. altivolans* became rare and the troglophilic morph became more restricted to the twilight and entrance zones. It is unknown whether the Kaumana Cave morph evolved *in situ* from the polymorphic troglophilic form, or arrived via subterranean dispersal, but both scenarios are possible and not mutually exclusive (Medeiros *et al*. 2009). The majority of root biomass in young pahoehoe occurs in the intermediate-size voids that permeate the flows. This hidden resource would be largely unavailable to the troglophilic form but represents the principle habitat for the cave-adapted morph (Howarth *et al*. 2019).

Hawaiian cave moths and their associated plants and animals are vulnerable to a variety of anthropogenic threats (Stone and Howarth 2007). Disturbance of the surface of inhabited flows destroys the life-giving roots as well as blocks food and water from entering voids and caves. Areas near agriculture or urban development can be affected by pollutants in runoff and from pesticide use. Fortunately, major government agencies and conservation organizations have established protective management policies for caves and their biotic and cultural resources. These entities include the U.S. National Park Service, U.S. Fish and Wildlife Service, Hawaiʻi Natural Area Reserves System, and The Nature Conservancy.

A more pervasive and insidious threat is posed by invasive alien species, which can invade across property boundaries. Several non-native species have invaded caves. The impact of the black rat was discussed above and in Howarth & Stone (2020). Fortunately, many invasive animals (e.g., *Rattus rattus* and the American cockroach, *Periplaneta americana* L.) appear to be limited to larger, more accessible cave passages, a circumstance that affects some cave species as well as research programs, but these invaders may have less effect in the more isolated smaller voids (Howarth 1981). A few species appear to be able to colonize large sections of the underground habitat and may be reducing populations of cave moths. The latter include the predatory nemertine worm, *Argonemertes dendyi* (Dakin, 1915) (Howarth & Moore 1984) and several small web-building spiders. Some alien biological control agents purposefully introduced to control pest species have expanded their host range to attack native species (Howarth 1993). Their role in the reduction of cave-roosting moths was described above. The impacts of purposefully introduced microorganisms for biocontrol is not well researched, but theoretically, their effect on the cave fauna could be severe. These biological pesticides, which include strains of bacteria, fungi, and nematodes, are soil organisms reared to attack pest species. They survive well in damp, dark habitats such as caves. However, their potential impacts have not been studied in part due to the difficulty in correctly identifying the pathogen in novel hosts. For example, *Schrankia howarthi* pupae are often attacked by an unknown fungus. Cave populations occasionally experience severe epizootics that greatly reduce moth populations. The "ghosts" from these epizootics are represented by numerous moth cocoons and some dead moths covered with fungal fruiting bodies. Whether these outbreaks are the result of natural population cycles or are caused by a novel alien pathogen is unknown. Future research in this area would be worthwhile to identify the pathogen(s) and determine the cause of resultant moth declines.

The lepidopteran fauna of caves is often ignored in biological surveys and remains poorly known, largely because of the difficulties of collecting and preparing specimens suitable for study and identification. The advent of molecular techniques for identification will ameliorate this problem. Additional species of Lepidoptera will be discovered in caves both in Hawai'i and elsewhere. The 16 species of native moths that are recorded herein and that are associated with cave habitats demonstrate that the lepidopteran fauna of caves can be exceptionally diverse and should be recognized as a significant component of cave ecosystems. Some species may be keystone species in cave ecosystems as consumers and as prey for other species. For example, moths that roost in caves import abundant food resources into the caves; scavenging moths such as tineid moths on guano (Robinson 1980) can be important in recycling organic material. Lepidoptera should be included in future biological surveys of caves.

BIOGRAPHY OF FRED STONE

Frederick Doren Stone, 79, of Kurtistown, Hawai'i, passed away May 29, 2018 from complications of a serious caving accident that left him partially paralyzed. Fred (Fig. 3) was born 24 July 1938 on the family dairy farm in Freetown, New York. He earned a B.S. in agricultural engineering, an M.S. degree in entomology from Cornell University, and a doctorate in biogeography from the University of Hawai'i. He kept his love for farming throughout his life and career. From 1964 to 1970, he served as an agricultural adviser in Vietnam with the International Voluntary Service and subsequently with the Thai Border Police in Thailand. After returning to the U.S.A., he taught agricultural science, organic farming and permaculture at SUNY Oswego, NY, Evergreen State College in Olympia,

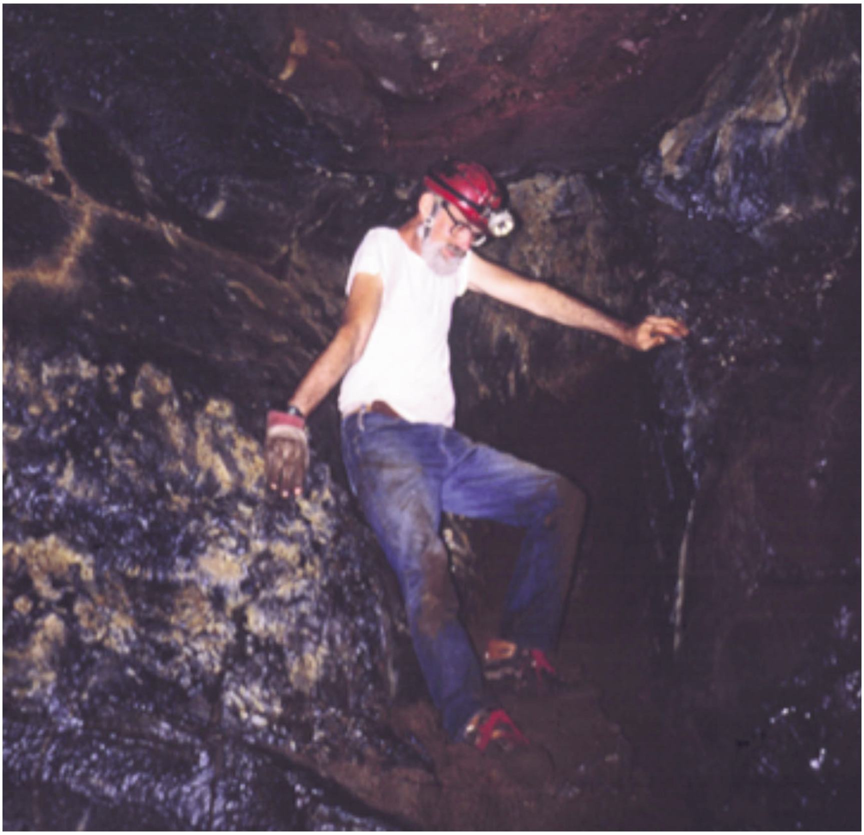

Figure 3. Fred Stone in a piping cave (Ziegler *et al.,* 2016) in the montane rainforest of East Moloka'i. Photograph taken in January 1983 by FGH.

Washington, and environmental science at the University of Hawai'i, Hilo. Fred developed a new educational unit at Hawai'i Community College in Hilo, the Tropical Forest Ecosystem and Agroforestry Management (TEAM) and was its director for many years. The TEAM program inspired and trained students to competently manage native Hawaiian forest ecosystems, grow native plants, establish sustainable agroforestry operations, as well as create and use environmental and geospatial databases.

But Fred's passion was cave exploration and cave science, and he went caving at every opportunity beginning as a student at Cornell and continuing until his accident in 2012. Stone and Howarth began caving together in New York in 1961 and formed a lifelong partnership exploring caves in the eastern U.S.A., Hawai'i, Southeast Asia, and Australia. During their time at Cornell, Fred discovered previously unknown passages in McFails Cave in Schoharie County, New York, which made the cave the longest and most significant cave in the northeast. He then led a successful effort to raise funds to purchase and donate the cave to the National Speleological Society (NSS). The donation initiated an interactive cave management model now used by the NSS and numerous land management agencies (Stone 2007).

Fred enjoyed teaching and frequently took his students on field trips into caves to inspire them in natural history and resource protection. He also assisted visiting scientists on their research in caves especially on Hawai‘i Island where he lived from 1985 onwards. He published more than 25 articles on cave biology, many co-authored with collaborators (e.g., Northrup *et al.* 2011, Wessel *et al.* 2013). He had two long-term projects: the diversity and evolution of nocticolid cockroaches of SE Asia and Australia (Stone 1988) and *Caconemobius* crickets in Hawai‘i.

Fred also worked diligently on biodiversity conservation and led many biological surveys of caves and threatened habitats in Hawai‘i, Thailand, and Australia (Howarth & Stone 1993, Stone & Howarth 2007). The protocol for these surveys evolved into a more efficient and comprehensive strategy wherein all would enter and explore a cave together until the party reached a suitable sampling site. Howarth would lead the survey at the site while Stone and others explored further into the cave looking for potentially rich biological sites. When found, Stone would report back, and the survey group would move to sample the new site while the exploration group searched for the next new site.

Stone willingly provided expert witness testimony on projects affecting biodiversity including the contested case regarding industrial development of Mauna Kea’s vulnerable biologic ecosystems. A life-long farmer, Stone applied his childhood farm experience to his farm in Hawai‘i where he developed a Cordyline (ti leaf) nursery and where he bred novel purple cultivars.

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