



Multiple cave invasions by species of the planthopper genus *Oliarus* in Hawaii (Homoptera: Fulgoroidea: Cixiidae)

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Although geologically young, the Hawaiian Islands harbour a rich and remarkably diverse fauna of terrestrial troglobites: more than 70 cave species are known from Kauai, Oahu, Molokai, East Maui, and Hawaii Island. Among the more speciose groups that have invaded the subterranean biome are the planthoppers (Homoptera Cixiidae) of the genus *Oliarus*. Five new obligately cavernicolous (troglobitic) *Oliarus* species which differ in their degree of troglomorphy and male genital structures, are described from lava tubes on the Hawaiian Islands: *O. lorettae* sp. nov. and *O. makaiki* sp. nov. from Hawaii Island, *O. gagnei* sp. nov. and *O. waikau* sp. nov. from Maui Island, and *O. kalaupapae* sp. nov. from Molokai Island. Short diagnoses of the two trogllobitic species already known, *O. polyphemus* Fennah, 1973 from Hawaii Island and *O. priola* Fennah, 1973 from Maui are provided. Notes on the ecology and distribution of all cavernicolous species are given. Morphological evidence suggests that each of the seven cavernicolous *Oliarus* species from Hawaii represents a separate, independent adaptive shift to underground environments. Potential relationships to the extant epigeal species are discussed.

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ADDITIONAL KEY WORDS:—new species – adaptive shift – parapatric speciation – troglobites – troglomorphy – root-feeders – caves – lava tubes – Hawaiian Islands.

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INTRODUCTION

The discovery of highly specialized terrestrial troglobites on geologically young oceanic islands like Hawaii (Howarth, 1972) has prompted discussion of scenarios which support the evolution of troglobites. The bioclimatic model suggested by Howarth (1980) challenged the traditional view which assumes the extinction or extirpation of epigeal populations due to deterioration of surface conditions as prerequisite for the evolution of terrestrial troglobites. Accordingly, populations 'trapped' in subterranean habitats subsequently acquire adaptive traits (Barr, 1968, 1973). In contrast, Howarth's model of parapatric speciation assumes an active adaptive shift to exploit novel food resources such as tree roots which descend into young Hawaiian lava tubes. It explains the existence of terrestrial troglobites in tropical regions which have never undergone climatic catastrophes, the parapatric occurrence of epigeal species and closely related cave species, and it corresponds to the pattern of adaptive radiation present on oceanic island archipelagoes like Hawaii.

The insect fauna of the Hawaiian Islands provides some of the finest examples of adaptive radiation. Only 350–400 colonizing species are assumed to have given rise to an estimated total Hawaiian fauna of more than 10 000 species (Howarth & Mull, 1992). Among the more speciose lineages is the planthopper genus *Oliarus* with 78 named epigeal taxa endemic to Hawaii (Zimmerman, 1948), which are likely to have arisen from a single introduction whose descendants colonized a wide range of habitats (Giffard, 1925). Howarth (1987) pointed out that the evolution of Hawaii's non-relictual obligate cave animals (troglobites) which occur parapatrically with closely related epigeal species also fits this pattern of adaptive radiation. Roots of native Hawaiian trees, especially *Metrosideros polymorpha* Gaud. (Myrtaceae), provide a novel food resource which is unavailable to surface-living organisms. The exploitation of this food resource, which is constantly created by the colonization of new lava fields by pioneer plant species, has most likely been the driving force for the evolution of the troglotic Cixiidae on Hawaii (Howarth, 1986).

Cixiidae are generally pre-adapted for a subterranean way of life (Remane & Hoch, 1988). Even surface-dwelling Cixiidae deposit eggs not in plant tissue but in the soil (Müller, 1942). The five nymphal instars develop in dark and humid habitats, e.g. in rotting logs, leaf litter, in crevices within the soil, and even in abandoned galleries of fire ant nests where they feed on roots (O'Brien & Wilson, 1985; Remane

& Hoch, 1988). In epigeal species, the adults leave the habitat of the nymphs to feed and reproduce above ground. From here, it seems to be only a small evolutionary step to switch to a complete life cycle underground. In cavernicolous species, the adults remain underground and permanently share the nymphal habitat. This ecological shift requires behavioral and physiological adaptations to cope with the physical conditions of the subterranean environment such as permanent darkness, constant temperature, high relative humidity (Howarth, 1983, 1988), and occasionally, abnormally high carbon dioxide concentrations (Howarth & Stone, 1990). Morphologically, troglomorphic cixiids are usually characterized by reduction of compound eyes, ocelli, tegmina, wings and bodily pigmentation (Hoch, 1994). Within the Cixiidae, numerous evolutionary lineages have made this shift: more than 40 troglomorphic species are known from many other parts of the world, e.g. Australia, New Zealand, Galápagos, Canary Islands, Azores, Mexico (Hoch, 1994).

In Hawaii, two cavernicolous species of *Oliarus* have been described: *Oliarus polyphemus* Fennah (1973) from Hawaii Island and *Oliarus priola* Fennah (1973) from Maui. Both species lack compound eyes and ocelli, and display strongly reduced flight organs and bodily pigment. Recent field and laboratory studies have revealed a much higher degree of diversity among Hawaiian cave *Oliarus*. For example, *Oliarus polyphemus* populations found in the numerous lava tubes of Mauna Loa, Mauna Kea, Kilauea and Hualalai volcanoes likely represent a species complex. Analyses of their substrate-borne courtship signals revealed that seven populations differ significantly in several parameters of their calling patterns, thus suggesting that they are reproductively isolated and may in fact represent separate biological species (Hoch & Howarth, 1993).

In addition, recent faunistic surveys of Hawaiian lava tubes have revealed the existence of five cavernicolous *Oliarus* species which differ from *O. polyphemus* and *O. priola* in their degree of troglomorphy and their male genital structure. These new species of *Oliarus* include two species from Hawaii Island, *O. lorettae* sp. nov. and *O. makaiki* sp. nov.; two species from Maui, *O. gagnei* sp. nov. and *O. waikau* sp. nov.; and one species from Molokai, *O. kalaupapae* sp. nov. These 'morphospecies' are described below as new. Based on morphological information, we attempt to estimate how many separate evolutionary lineages of *Oliarus* have invaded the subterranean biome, and whether or not relationships to extant epigeal *Oliarus* species can be readily recognized. According to Asche (1997) all Hawaiian *Oliarus* taxa are likely to be monophyletic. Autapomorphies include characters of the hind tarsi and those of the male and female genitalia (Asche, 1997). A detailed revision and cladistic analysis comprising all Hawaiian *Oliarus* species is needed to elucidate the evolutionary history of this groups but would have been beyond the scope of the present work.

MATERIAL AND METHODS

All specimens of cavernicolous *Oliarus* were located by visual search, hand-picked from the roots or rock by using an aspirator, and were preserved in 80% or 95% ethanol. Genitalia were macerated in 10% potassium hydroxide (12 h at room temperature), washed in distilled water and stored in glycerol. Drawings were made using glycerine-gelatine as a fixing medium, and a Leitz compound microscope with a camera lucida.

Explanatory comments on the figures

Characters used to separate species are mainly found in the male genitalia, and in those related to cave-adaptions, such as head and thorax proportions, reduction of compound eyes, ocelli, tegmina, wings and lack of pigmentation.

In all species except *O. waikau*, body length measurements equal the distance between apex of head and distal margin of tegmen; in *O. waikau* body length was measured between apex of head and tip of abdomen. Length of tegmen refers to the distance between base of tegmen and distal margin; the width is measured at the apex of the clavus. Pronotum width equals the distance between the bases of the tegulae.

The terminology of tegmina and wings is adopted from Ossiannilsson (1978).

Depositories

The specimens studied here are deposited in the following collections: Type material in the Bernice P. Bishop Museum, Honolulu (BPBM), U.S.A.; reference material in the Museum für Naturkunde (MFN), Berlin, Germany.

TAXONOMY

*The cave-dwelling Oliarus species of Hawaii Island**Oliarus polyphemus* Fennah

Oliarus polyphemus Fennah, 1973: 181.

Material examined. Holotype male (Bishop 9796): HAWAIIAN IS.: Hawaii I., Hawaii Volcanoes National Park, Kipuka Puauulu, 1140 m, Bird Park Cave, dark zone, 3. vii. 1971, F. G. Howarth, in Bishop Museum; 1 male paratype: Bird Park Cave, final room, 90 m inside cave, 20. vii. 1971, F.G. Howarth; 1 additional (non-type) male: Hawaii I., Hawaii Volcanoes National Park, Bird Park Cave # 1, deep zone, 28.iii. 1981, F.G. Howarth, R.C.A. Rice, Bishop Museum.

Diagnosis. Strongly troglomorphic species (habitus figured in Fennah, 1973: 182, fig. 4), body white to light yellow, compound eyes absent, head rounded, carinae on head and thorax weak, tegmina and wings vestigial; pretarsal claws slender, arolia minute. Male genitalia slightly different from figures given by Fennah (1973: 182, figs 6–11): aedeagus with basal part bearing one spine near its apex; distal part (flagellum) with 3 spinose processes (versus 2 as described by Fennah); one flagellar spine arising apically on its left side, the other dorsally at about half the length of distal part, and, in addition, a minute one at tip near phallotreme on left side. This minute flagellar spine is present in all 3 specimens from the type locality.

Ecology and distribution. *O. polyphemus* is restricted to underground habitats, usually in the deep cave zone. Since the original description, morphologically similar populations have been found in similar habitats in numerous lava tubes, from sea level to over 2000 m within the range of the host tree, *Metrosideros polymorpha*, on Mauna Kea, Mauna Loa, Kilauea and Hualalai volcanoes, and were preliminarily assigned to *O. polyphemus* (Fennah, 1973, Howarth, 1973; Hoch & Howarth, 1993). A study

on the mating behaviour of populations from different caves (Hoch & Howarth, 1993), especially the analysis of substrate-borne communication signals, revealed a high degree of divergence: the signals of all 7 populations studied differ significantly. As the vibrational communication signals are the pivotal element in the specific mate recognition system of blind and flightless planthoppers (Hoch & Howarth, 1993; Hoch, 1996) the high variation observed between populations from different caves suggests that the *Oliarus polyphemus* populations studied are reproductively isolated, i.e. represent separate biological species (Hoch & Howarth, 1993). It is likely that the paratype specimens from Kaumana Cave and Kazumura Caves are not conspecific with individuals from Bird Park Cave.

It is unclear whether divergence occurred after a single colonization event or is the result of multiple invasions of caves by one or more ancestral epigeal species. Although preliminary data from a study on the molecular genetics of *Oliarus polyphemus* populations may indicate multiple colonization events within *O. polyphemus* (K.E. Williamson, pers. comm.), *Oliarus polyphemus* is treated here for the time being as a single evolutionary line, referred to as *Oliarus polyphemus sensu lato* (s.l.).

***Oliarus lorettae* sp. nov.**

(Figs 1–13)

Habitus (Fig. 1). Troglomorphic with rudimentary eyes, reduction of body pigmentation and slight reduction of tegmina.

Coloration. Head and thorax generally light brown, abdomen dark brown. Transition between vertex and frons with trapezoidal dark marking. Compound eyes dark brown. Pronotum anteriorly darkened. Frons and clypeus irregularly darkened. Tegmina and wings translucent; venation in distal third partly dark brown, otherwise yellow brown. Legs stramineous.

Head (Figs 2–4). Vertex shallowly concave, short, posteriorly about 2.5 times as wide as medially long. Anterior transverse carina shallowly convex, median carina obsolete. Vertex broadly rounded into frons. Frons slightly broadened at level of the antennae, medially about 0.7 times as long as wide at maximum; lateral carinae ridged and directed laterad; median carina of frons and clypeus obtuse. Frontoclypeal suture strongly arcuate. Median ocellus obscure. Post- and anteclypeus together about 2.7 times as long as frons. Rostrum surpassing metatrochanters. Compound eyes present, but small, with ommatidia-bearing area nearly planar. Lateral ocelli indistinct. Antennae with basal segment short, ring-like, second segment ovoid, covered by microtrichia and irregularly distributed placoidal sense organs.

Thorax (Figs 1, 5). Pronotum posteriorly deeply incised, with median and lateral carinae distinct, the latter enclosing a discoidal field behind each eye. Pronotum in middle line about 0.7 times as long as vertex, and 1.7 times as wide as maximum width of head. Tegulae present. Mesonotum quinquecarinate, about 6 times as long in the middle line as pronotum. Metatibia with 6–9 lateral and 6 apical teeth. Basitarsus of hindleg only slightly shorter than 2nd and 3d tarsal segments together. Basitarsus and 2nd tarsal segment with 6 apical teeth. Pretarsal claws strong, arolia well developed. Tegmina reduced, about 2.5 times as long as maximum width, surpassing the tip of the abdomen with about one fifth of their total length. Costal

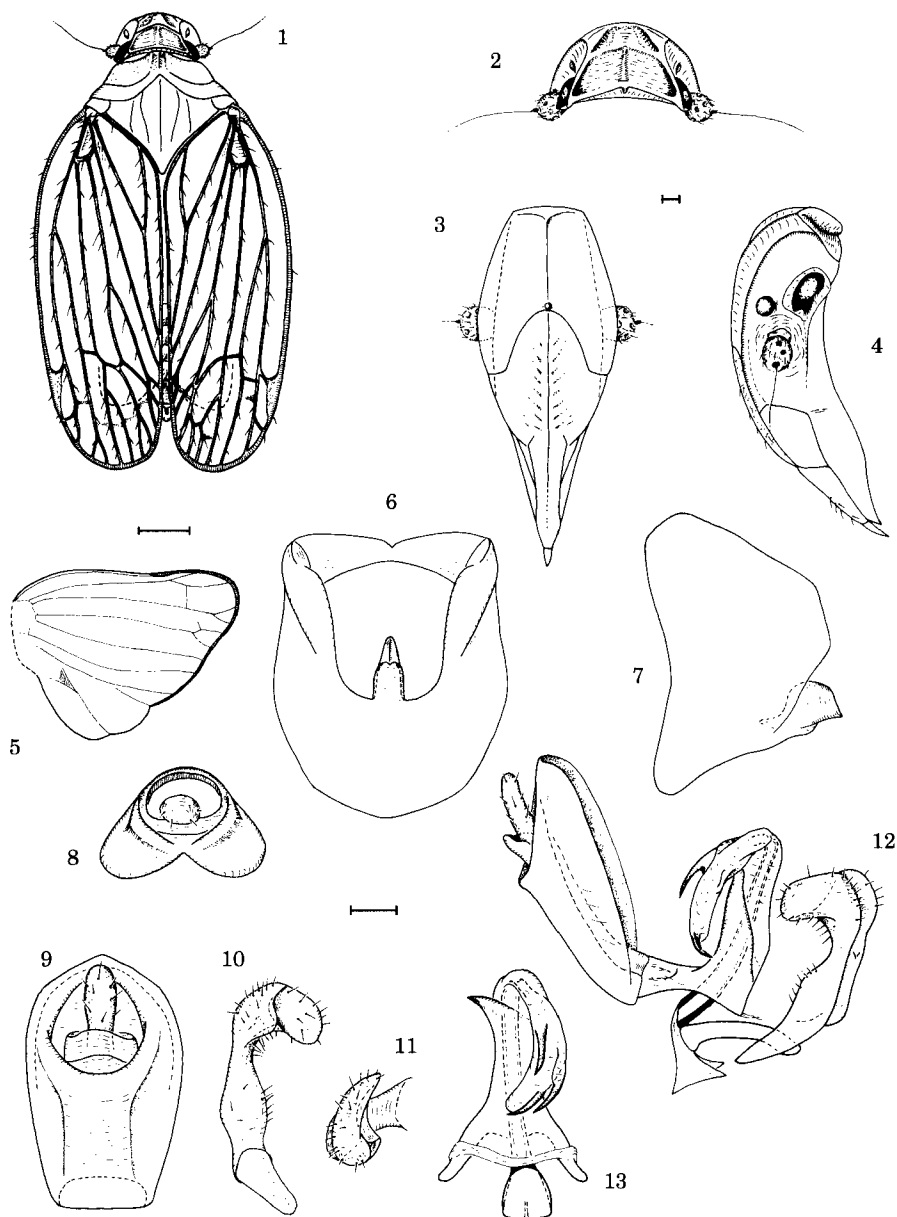


Figure 1–13. *Oliarus lorettæ* sp. nov. (male). 1, habitus; 2, head, dorsal aspect; 3, same, ventral aspect; 4, same, lateral aspect; 5, tegmen; 6, genital segment, ventrocaudal aspect; 7, same, left lateral aspect; 8, anal tube, caudal aspect; 9, same, dorsal aspect; 10, left paramere, mediolateral aspect; 11, same, caudal aspect; 12, anal tube, aedeagus, parameres *in situ*, left lateral aspect; 13, aedeagus, dorsal aspect. Scale bars = 0.5 mm (Figs 1, 5), 0.1 mm (Figs 2–4, 6–13).

margin shallowly convex, pterostigma indistinct. Sc + R furcation at about one third, Cu furcation at about one half of total length of tegmen. Venation in distal third of tegmen variable, even within individuals.

Longitudinal veins densely papillate. Wings reduced to less than two thirds of tegmen, with distal veins variable; anal field small.

Male genitalia (Figs 6–13). Genital segment in caudal aspect slightly higher than wide; in lateral aspect, ventrally 4.3 times longer than dorsally. Medioventral process slender, about two times longer than wide at base, with its dorsal surface sharply ridged medially. Anal segment ventrally concave, in caudal aspect medially incised, in dorsal aspect oval, longer than wide. Parameres with subapical median process not distinctly produced, obtuse. Aedeagus with basal part apically bearing a slender spine (directed laterad) on its right side; distal part with three spines: a long slender one arising from its upper margin slightly basad of middle, and two shorter spines, arising from near its distal tip, in repose curved to the right.

Female genitalia. Seventh abdominal sternite (pregenital sternite) subtriangular, posterior margin medially slightly produced caudad; ovipositor as in other Hawaiian *Ollarus* species (Giffard, 1925, Zimmemman, 1948) comparatively short but distinctly surpassing the anal segment; tergite 9 caudally truncate, ceriferous; anal segment subcylindrical, short, lateral margins ridged and moderately produced laterad.

Length. Males 4.1–4.9 mm (4.5 ± 0.199 ; $n = 17$). Females 5.2–5.6 mm (5.47 ± 0.138 ; $n = 7$).

Etymology. This species is dedicated to the country singer Loretta Lynn, who kindly provided access to the lava tubes on her property at Waikoloa, Hawaii Island.

Type material. *Holotype*: 1 male, Hawaiian Islands, Hawaii, N Kona, Kiholo Bay, Ana Lima Kipo Lava Tube, 12.i.1987, F. G. Howarth, F. D. Stone, L. Lynn, M. Asche, H. Hoch coll., BPBM, type # 15199. *Paratypes*: 8 males, same data as Holotype. 5 males, 1 female, same locality as holotype, 8.i.1982, F. G. Howarth, F. D. Stone, P. Duefrene coll. 3 males, same locality as holotype, 10.i.1982, F. G. Howarth, F. D. Stone coll., BPBM, MFN; 10 males, 6 females, same locality as holotype, 10.viii.1995, M. Asche, H. Hoch, K. Williamson, F. D. Stone coll., BPBM, MFN.

Additional material: 1 nymph III. instar, 1 nymph V. instar, same locality as holotype, 8.i.1982, F. G. Howarth, F. D. Stone, P. Duefrene coll.. 1 nymph III. instar, same locality as holotype, 12.i.1987, F. G. Howarth, F. D. Stone, L. Lynn, M. Asche, H. Hoch coll., BPBM; 2 males, North Kona, Kiholo Bay, Blue Lake Cave, 10.viii.1995, M. Asche, H. Hoch, K. Williamson, F. D. Stone coll., BPBM.

Ecology and distribution. Although this species displays a less advanced degree of troglomorphy than *O. polyphemus* s.l. it has been found only in deep cave zone passages. It is likely to be unable to survive outside the cave environment, and therefore is considered an obligate cave species. Its probable host is roots of the indigenous shrub, *Sida fallax* Walp. (Malvaceae); *Metrosideros polymorpha* is not represented in the surface vegetation above Ana Limo Kipo Lava Tube and Blue Lake Cave. *O. lorettae* is known from two neighbouring lava tubes, Ana Lima Kipo Lava Tube and Blue Lake Cave, Kiholo Bay, Hawaii Island, in a 3000–5000 year old lava flow from Hualalai Volcano (Moore *et al.*, 1987) at an altitude of 1–10 m. Ana Lima Kipo Lava Tube is a shallow, complex maze cave with three parallel passages leading to mixohaline pools near sea level. Small woody plant roots (presumably *Sida fallax*) penetrate the one or two meters of overburden into the cave in only a few places. The cave cixiid has been found in damp passages near the

mixohaline pools and usually in association with the roots. The temperature measured in the deep-cave zone is *c.* 23°C. Blue Lake Cave is a large, tunnel-like lava tube, with a freshwater pool over much of the explorable passage. The climate is damp (89% RH) and warm (22.5°C). Adults of *O. lorettae* were found in the vicinity of sparse roots on an upper ledge and floating on water.

Remarks. *O. lorettae* can be easily distinguished from other troglobitic cixiid species of Hawaii Island by the configuration of the male genitalia and by the different degree of troglomorphy: compound eyes, ocelli as well as pigment, tegmina and wings are less reduced than in *O. polyphemus s.l.* Moreover, it does not display modification of the pretarsal claws which has been interpreted to be an adaption to walk on wet and rocky surfaces (Howarth, 1983). As has been shown by Howarth *et al.* (1990), it also differs from *O. polyphemus s.l.* in the structure of the male calling song.

Oliarus makaiki sp. nov.

(Figs 14–23)

Habitus. Troglomorphic with rudimentary compound eyes and ocelli, reduction of body pigmentation and slight reduction of tegmina.

Coloration. Head and thorax whitish, abdomen dull brown. Vertex medially dull brown; frons, post- and anteclypeus with a longitudinal yellowish stripe on each side of middle line. Areolets brownish. Compound eyes dark brown, dark pigmentation variable. Mesonotum pale dull brown, darkened anteriorly. Tegmina and wings translucent, venation yellow, in distal third brown. Abdominal segments ventrally and dorsally dull brown; legs white.

Head (Figs 14, 15). Vertex trapezoidal, shallowly concave; posteriorly, about 2.3 times as wide as medially long. Anterior transverse carina straight, median carina absent. Vertex broadly rounded into frons. Frons widest at the level of the antennae, medially about 0.8 times as long as wide at maximum; lateral carinae ridged and directed laterad; median carina of frons and clypeus obtuse. Post- and anteclypeus together about twice as long as frons. Rostrum surpassing metatrochanters. Compound eyes vestigial, ommatidia-bearing area slightly vaulted. Lateral ocelli indistinct, median frontal ocellus obsolete. Second antennal segment 3 times as long as first, ovoid, with few and irregularly distributed placoidal sense organs.

Thorax. Pronotum posteriorly deeply incised, with median and lateral carinae distinct, the latter enclosing a discoidal area behind each eye; in middle line about 0.7 times the length of vertex, and 1.5 times as wide as maximum width of head. Tegulae present. Mesonotum indistinctly quinquecarinate, about 7 times as long in middle line as pronotum. Metatibia with 4–5 lateral spines (individually variable) and 6 apical teeth. Basitarsus of hindleg slightly longer than 2nd and 3rd tarsal segments together, distally with 6–8 teeth (individually variable), 2nd metatarsal segment with 6–7 distal teeth (individually variable). Pretarsal claws strong, arolia well developed. Tegmina reduced, *c.* 2.3 times as long as wide, slightly surpassing the tip of the abdomen. Coastal margin shallowly convex, pterostigma indistinct. Cu-furcation at about one half the total length of tegmen, Sc + R- furcation slightly proximad of Cu-furcation. Venation in distal third of tegmen variable, even within one individual.

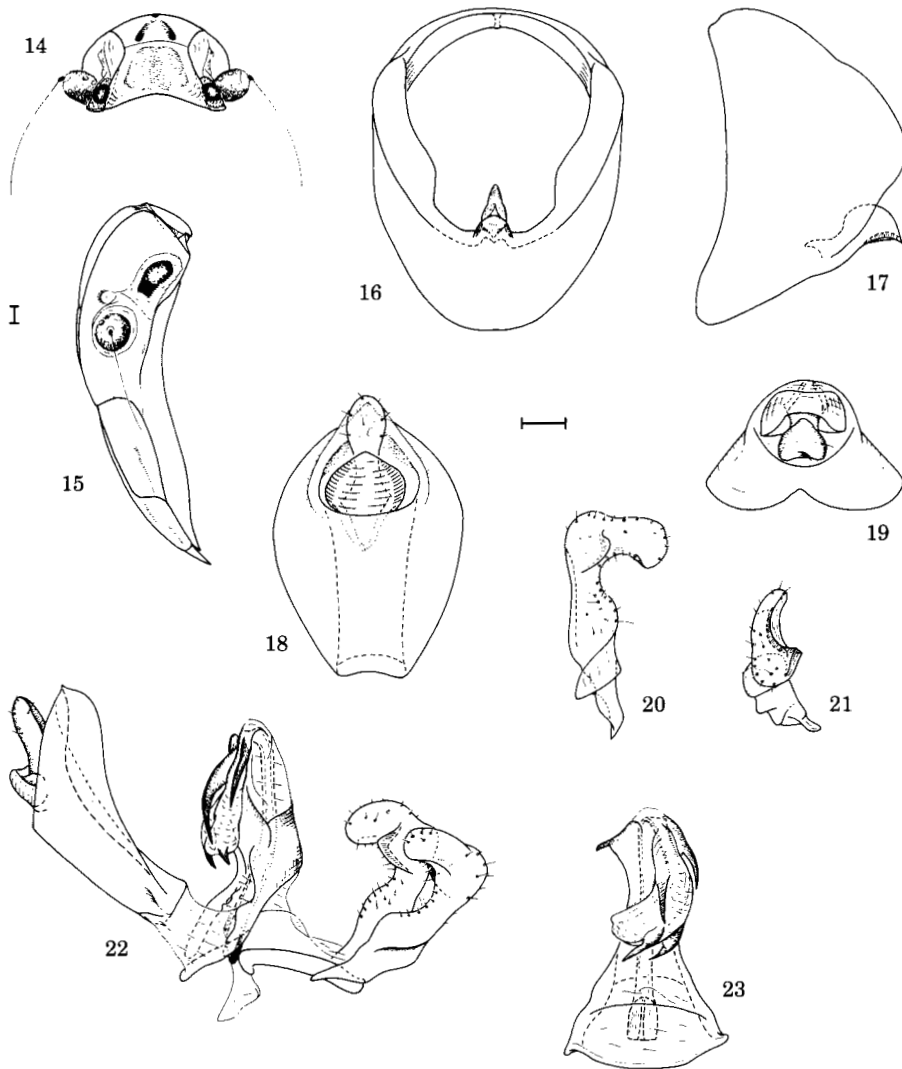


Figure 14–23. *Oliarus makaiki* sp. nov. (male). 14, head, dorsal aspect; 15, same, lateral aspect; 16, genital segment, ventrocaudal aspect; 17, same, left lateral aspect; 18, anal tube, dorsal aspect; 19, same, caudal aspect; 20, paramere, mediolateral aspect; 21, same, caudal aspect; 22, anal tube, aedeagus, parameres *in situ*, left lateral aspect; 23, aedeagus, dorsal aspect. Scale bar = 0.1 mm.

Longitudinal veins densely papillate. Wings about two thirds length of tegmen, anal field developed.

Male genitalia (Figs 16–23). Genital segment in caudal aspect slightly higher than wide, in lateral aspect about 5.6 times longer than dorsally. Medioventral process slender, about 2 times as long as wide at base, its dorsal surface in lateral aspect arcuate, distinctly ridged medially. Anal segment ventrally concave, in caudal aspect medially incised, in dorsal aspect oval, longer than wide. Parameres laterodistally projected, apically rounded, medially with an oblique, sharp-edged ridge. Aedeagus with basal part apically bearing a short, stout spine (directed laterad) on its right

side; distal part with four spinose processes: one arising proximad on its left side, one arising from distal part's dorsal margin, in repose directed straight right laterad, 2 smaller spines flanking the left margin of the distal tip in proximity of the phallotreme.

Female genitalia. As in *O. lorettae*.

Length. Male 4.5–4.8 mm ($n=4$). Female 5.0 mm ($n=1$).

Etymology. The species name is composed of the Hawaiian words *maka* (=eyes) and *iki* (= small), and refers to the reduced size of the compound eyes.

Type material. *Holotype*: male, Hawaiian Islands, Hawaii, Hualalai Volcano, Pu'u Wa'a Wa'a Ranch, Yellow Jacket Cave, 17.vii.1995, M. Asche, H. Hoch coll., BPBM # 15967. *Paratypes*: 1 female, same data as holotype, except K. Williamson coll.; 3 males, 1 female, same locality as holotype, 24.vii.1995, M. Asche, H. Hoch, K. Williamson, J. Giffin coll., BPBM, MFN.

Ecology and distribution. *Oliarus makaiki* displays a similar but slightly more pronounced degree of troglomorphy than *O. lorettae* suggesting that *O. makaiki* is also restricted to underground environments and should be considered an obligate cavernicole. Its probable host is roots of *Metrosideros polymorpha*, which is abundant in the surface vegetation above the cave. *O. makaiki* is known from a single lava tube of Hualalai volcano, Yellow Jacket Cave, at an elevation of c. 1300 m the estimated age of the lava flow is between 1500 and 3000 years (Moore *et al.*, 1987). Yellow Jacket Cave consists of a maze of medium-sized crawlways, the climate is cool (15.8°C) and moist (94–95% RH). The entrance is situated within a patch of open, wet *Metrosideros* forest. Adult specimens were found walking on moist rocky substrate, in the vicinity of roots within the transition zone, not far away from the entrance. One nymph was observed in a damp downslope passage near a big, woody root (presumably of *Metrosideros*).

In Yellow Jacket Cave, *O. makaiki* was found to occur with a species of the *O. polyphemus* complex. This is so far the only known case where two troglobitic *Oliarus* species occur syntopically. Moreover, nymphs of an epigeal *Oliarus* species, *O. koanoa* Kirkaldy, which were reared to adults (Hoch, unpublished data), were found inside Yellow Jacket Cave. *O. koanoa* is abundant on the surface around the cave entrance. Adult specimens of *O. koanoa* were also found in the dark zone of neighbouring caves.

Remarks. *O. makaiki* is similar to *O. lorettae* but differs from it by the proportions of the head and the presence of 5 aedeagal spines (rather than 4 as in *O. lorettae*).

The cave-dwelling Oliarus species of Maui

Oliarus priola Fennah

Oliarus priola Fennah, 1973: 183.

Material examined. Holotype male (Bishop 9797): HAWAIIAN IS.: Maui I., Hana, Holoinawawai Stream Cave, 290 m, 14.xii.1971, F.G. Howarth, in Bishop Museum.

Diagnosis. Highly troglomorphic species, in habitus very similar to *O. polyphemus* s.l., but differing in the presence of 3 aedeagal spines rather than 4 as in *O. polyphemus*.

Remarks. *O. priola* is known from the type material only, collected in East Maui, near Hana, in Holoinawawai Stream Cave.

Although superficial similarity in genital configuration (aedeagus without left apical spine) between *O. priola* and the epigeal species *O. tarai* Kirakaldy was noted by Fennah (1973:184), the closest living relative of *O. priola* is yet to be determined (see discussion).

***Oliarus gagnei* sp. nov.**

(Figs 24–36)

Habitus (Fig. 24). Degree of troglomorphy similar to *O. lorettae*, with rudimentary eyes, pigmentation and reduction of tegmina.

Coloration. Body more or less uniformly pale stramineous; transition between vertex and frons with slightly darker markings; rudimentary compound eyes unpigmented. Tegmina and wings translucent with venation pale yellow; distal crossveins of tegmen as well as longitudinal veins of wing distally darkened. Legs stramineous.

Head (Figs 25–27). Vertex short, posteriorly about 3.3 times as wide as medially long. Anterior transverse carina shallowly convex, obsolete. Vertex broadly rounded into frons. Frons broadened at level of the antennae, about half as long medially as wide at maximum; lateral carinae ridged and directed laterad; frons and postclypeus with median carina distinct, anteclypeus with median carina obsolete. Frontoclypeal suture strongly arcuate. Median ocellus obscure. Post- and anteclypeus together about three times as long as frons. Rostrum surpassing metatrochanters. Compound eyes rudimentary, ommatidia-bearing area weakly defined. Lateral ocelli obscure. Antennae with basal segment short, ring-like. Second segment subcylindrical, covered by microtrichia and irregularly distributed placoidal sense organs.

Thorax (Figs 24, 28). Pronotum posteriorly deeply incised with median carina distinct and lateral carinae obsolete. Pronotum in middle line about as long as vertex, and 1.9 times as wide as maximum width of head. Tegulae present. Mesonotum quinquecarinate with lateral carinae distinct, and inner carinae obsolete, in middle line about 7.4 times as long as pronotum. Metatibia with 4–5 lateral and 6 apical teeth. Basitarsus of hind leg about as long as 2nd and 3rd tarsal segments together. Basitarsus with 5–6, second tarsal segment with 3–5 apical teeth. Pretarsal claws strong, arolia well developed. Tegmina reduced, about 2.3 times as long as maximum width, surpassing the tip of the abdomen with about one eighth of their total length. Costal margin shallowly convex, pterostigma obsolete. Sc + R furcation at about one third of total length of tegmen, Cu furcation only slightly distad of Sc + R furcation. Venation in distal third of tegmen variable within the same individual. Longitudinal veins densely papillate. Wings reduced to about half the length of tegmen, with distal veins variable; anal field small.

Male genitalia (Figs 29–36). Genital segment in caudal aspect slightly higher than wide, in lateral aspect ventrally about 7 times longer than dorsally. Medioventral process slender, about 2 times as long as wide at base, with its dorsal surface sharply ridged medially. Anal segment ventrally concave, in caudal aspect medially incised, in dorsal aspect oval, longer than wide. Parameres with subapical median process distinctly produced medially. Aedeagus with basal part apically bearing a short, tooth-like spine (directed laterad) on its right side; distal part with 3 spines, one

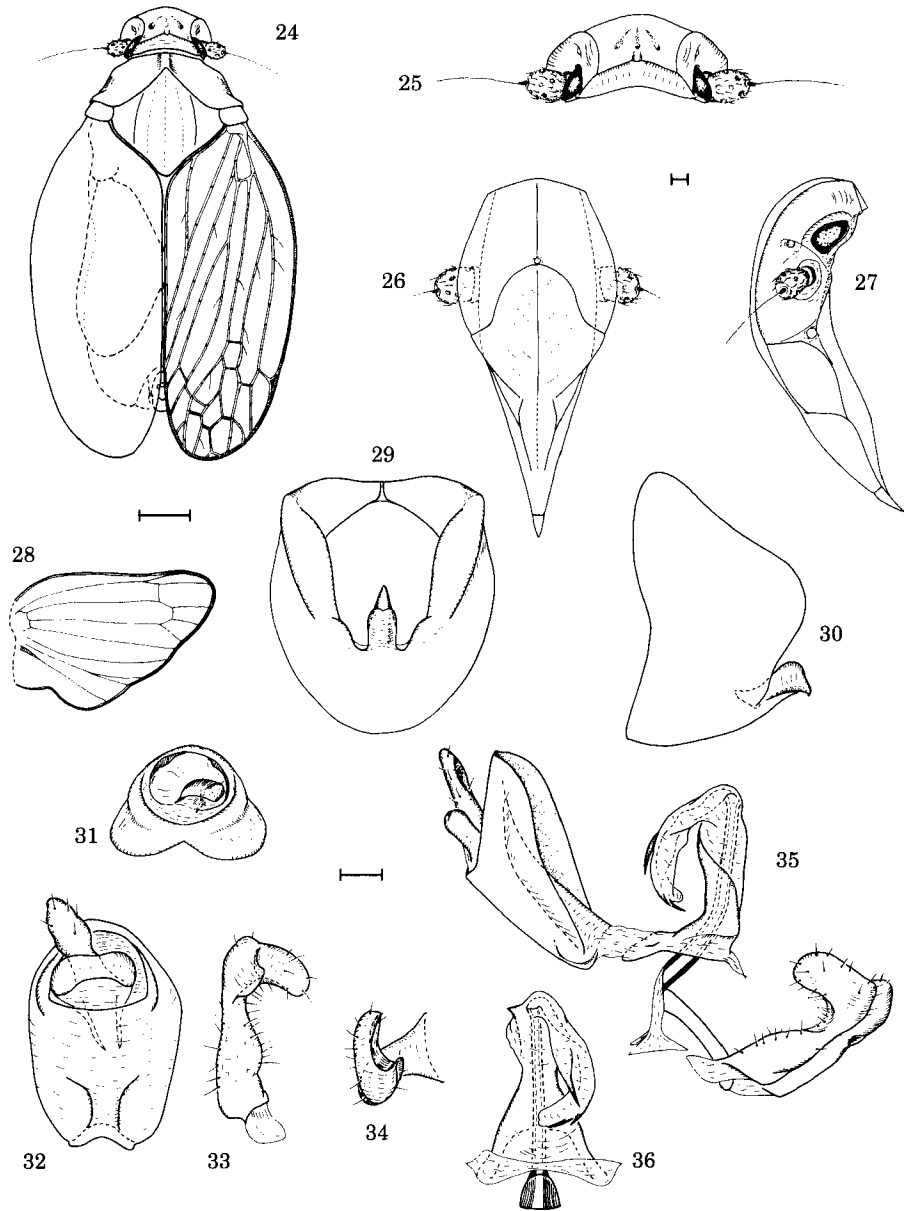


Figure 24–36. *Oliarus gagnei* sp. nov. (male). 24, habitus; 25, head, dorsal aspect; 26, same, ventral aspect; 27, same lateral aspect; 28, wing; 29, genital segment, ventrocaudal aspect; 30, same, left lateral aspect; 31, anal tube, caudal aspect; 32, same, dorsal aspect; 33, paramere, mediolateral aspect; 34, same, caudal aspect; 35, anal tube, aedeagus, parameres *in situ*, left lateral aspect; 36, aedeagus, dorsal aspect. Scale bars = 0.5 mm (Figs 24, 28), 0.1 mm (Figs 25–27, 29–36).

arising from the upper margin at about half the length of distal part, and two arising from near its distal tip, in repose curved to the right.

Female genitalia. Resembling those of *O. lorettae*; ovipositor with median gonapophyses straight; tergite IX caudally truncate, concave; wax-bearing area dorsomedially divided into two suboval portions.

Length. Male 4.3–4.4 mm ($n=2$). Female 4.2 mm ($n=1$).

Etymology. This species is dedicated to the memory of our good friend and stimulating colleague Dr Wayne C. Gagné.

Type material. *Holotype*: 1 male, Hawaiian Islands, Maui, Ulupalakua Cave # 2675 m, 23.ii.1988, F. G. Howarth coll., BPBM, type # 15200. *Paratypes*: 1 male, same data as holotype. 1 female, same locality as holotype, 12.xii.1989, F. G. Howarth coll., BPBM.

Additional material: 2 nymphs V. instar, same locality as holotype, 13.vi.1989, F. G. Howarth, M. Asche and H. Hoch coll., BPBM.

Ecology and distribution. *O. gagnei* is considered to be an obligate cave species. It is slightly more troglomorphic than *O. lorettae*, and its cave habitat is deeper and environmentally more stable than the habitat of *O. lorettae*. *O. gagnei* is known from Ulupalakua Cave #2 only, East Maui, in a prehistoric lava flow from the southwest rift zone of Haleakala at an altitude of 600–800 m. The lava flow is undated, but based on the degree of weathering its age is estimated to be about 1000 years. The cave has more than 600 m of passage. The cixiid has been found in an upper-level dead-end alcove at the lower end of the cave more than 400 m from the entrance. The air is still and humid, the substrate constantly wet. The room is relatively deep below the surface, there being approximately 4–6 m of overburden, but numerous tree roots penetrate the roof and dangle into the room. The host of *O. gagnei* is presumably the indigenous tree *Dodonaea viscosa* Jacq. (Sapindaceae).

Remarks. Although this species is very similar to *O. lorettae* in the structure of the male genitalia and degree of troglomorphy, it differs from this and the other Hawaiian cavernicolous *Oliarus* species by proportions and carination of head and thorax, posttibial spination, and degree of reduction of tegmina and wings.

Oliarus waikau sp. nov.

(Figs 37–47)

Habitus (Fig. 37). In general appearance and degree of troglomorphy similar to *O. polyphemus* s.l. and *O. priola*, but considerably larger.

Coloration. Body and legs uniformly pale yellowish, antennae whitish. Tegmina and wings translucent with venation concolorous to light yellow; granules and bristles on tegmina, spines and bristles of legs as well as pretarsal claws tawny.

Head (Figs 38–40). Vertex trapezoidal, at posterior margin about 1.75 times wider than medially long, area shallowly concave, posteriorly with a central depression; areolae very faintly defined; transverse carinae at transition to frons medially obtuse-angularly projected and then continuing basad over frons as a sharply ridged median

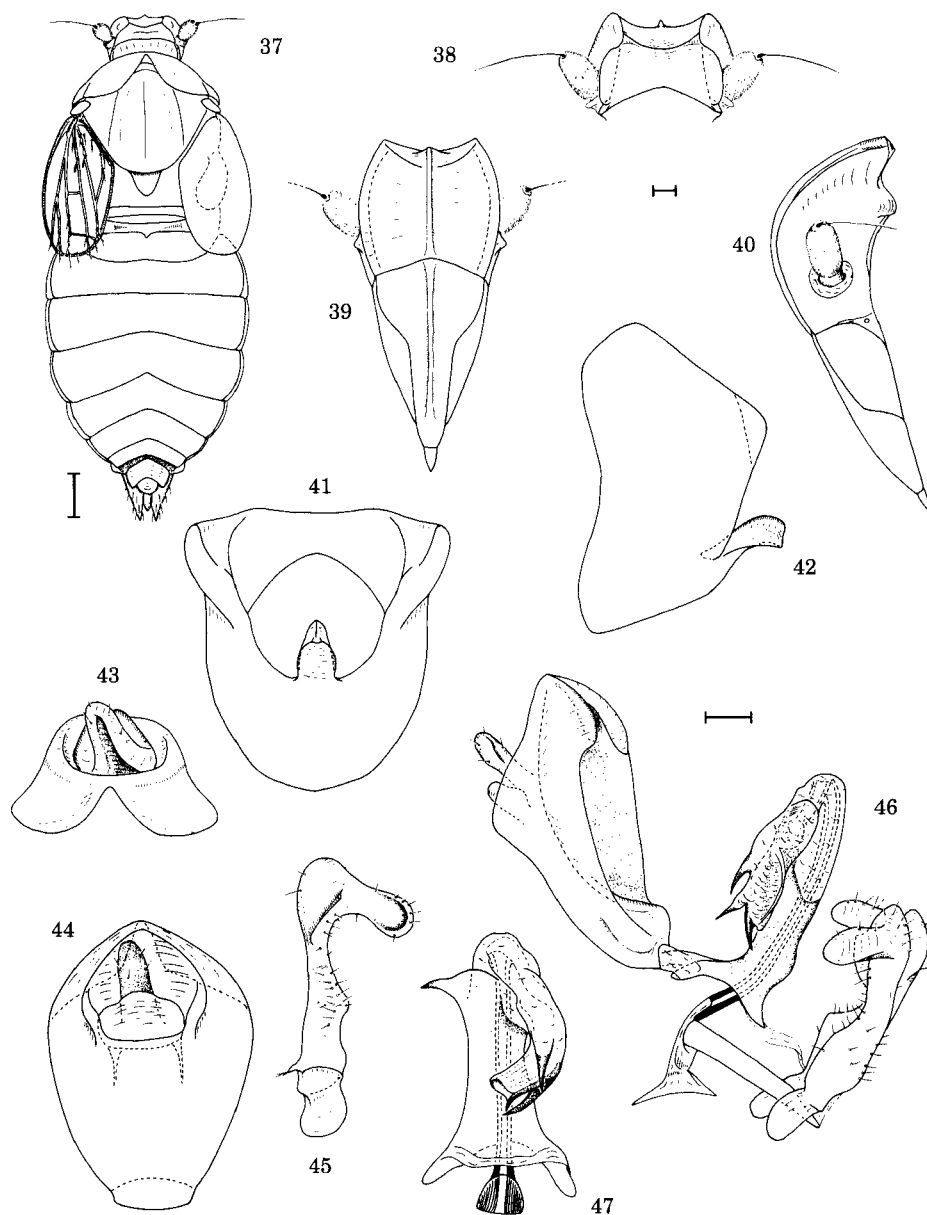


Figure 37–47. *Oliarus waikau* sp. nov. (male). 37, habitus; 38, head, dorsal aspect; 39, same, ventral aspect; 40, same, lateral aspect; 41, genital segment, ventrocaudal aspect; 42, same, left lateral aspect; 43, anal tube, caudal aspect; 44, same, dorsal aspect; 45, paramere, mediolateral aspect; 46, anal tube, aedeagus, parameres *in situ*, left lateral aspect; 47, aedeagus, dorsal aspect. Scale bars = 0.5 mm (Fig. 37), 0.1 mm (Figs 38–47).

carina. Frons about 1.2 times wider than medially long (maximum width at level of antennae); median carina distinctly projected, lateral margins convex, lateral carinae foliately produced anterolaterad and continuing onto postclypeus but interrupted by an incision at frontoclypeal suture; lateral areas of frons shallowly concave,

ascending to median carina. Frontoclypeal suture shallowly arcuate. Post- and anteclypeus together medially about 1.5 times longer than frons. Rostrum slightly surpassing metatrochanters. Compound eyes and ocelli absent, former position weakly marked by vaulted scars. Basal segment of antennae short, ring-like, second segment subglobose with placoidal sensory organs feebly defined, beset with fine hairs.

Thorax (Fig. 37). Pronotum about 6.75 times wider than medially long, medially about as long as vertex, about twice as wide as head; posteriorly acute angularly excavate, median carina broadly projected; lateral carinae ridged, attaining posterior margin. Tegulae small. Mesonotum medially about five times longer than pronotum, quinquecarinate with sublateral carinae obsolete. Tegmina strongly reduced, posteriorly attaining middle of 4th abdominal tergite; veins rudimentary, apically beset with small granules bearing bristles. Wings vestigial. Metatibiae laterally unarmed, apically with 6 teeth (longest on inner side), first metatarsal segment apically with 4 teeth, second with 2 teeth; first metatarsus slightly longer than 2nd and 3rd together (1.15 : 1). Pretarsal claws slender and elongate, aroliae vestigial. Bristles on undersides of tibiae and tarsi of all legs strongly developed.

Male genitalia (Figs 41–47). Genital segment bilaterally symmetrical, in caudal aspect ovoid, slightly higher than wide (1.16 : 1), laterodorsal margins lobe-like projected laterocaudad; ventrally about 4.6 times longer than dorsally; in lateral aspect trapezoidal, ventrocaudal margin deeply emarginate; medioventral process in lateral aspect helmet-shaped, double as long as wide, ventral side concave, mediodorsally with a sharp ridge. Anal segment as in other Hawaiian *Ollarus* species in dorsal aspect oval, longer than wide; 1.42 times as long as its maximum width; ventrally shallowly concave; laterocaudal margins distally lobe-like produced and bent mediad. Parameres distally on outer side with a finger-shaped projection directed dorsad, on inner side with an oblique, sharp-edged ridge. Aedeagus with basal part slender, stronger sclerotization on ventral and dorsal side; subapically on dorsal side with a tooth-like projection directed right laterad; distal part in repose reflected and slightly curved to left base attaining the basal third of the aedeagus' basal part; dorsally in middle of distal part arising a short, rigid spine pointing apicolaterad; distal tip forming a membranous funnel bearing the phallotreme, dorsal and left side of funnel each bearing a distinct, rigid spine.

Female genitalia. Similar to those of *O. lorettae* and *O. gagnei*; ovipositor with lateral gonapophyses IX conspicuously longer than gonapophyses VIII and median gonapophyses IX, apically sinuately bent dorsad; tergite IX with wax-bearing area weakly defined.

Length. Male 4.3–4.5 mm ($n=2$). Female 5.2–6.2 mm ($n=4$).

Etymology. The name of this species is derived from its type locality, Waikau Cave.

Type material. *Holotype*: 1 male, Hawaiian Islands, East Maui, Koolau Gap, Waikamoi Nature Reserve, Waikau Cave, 1900 m, 16.vi.1989, F. G. Howarth, M. Asche, H. Hoch coll., BPBM, type # 15201. *Paratypes*: 3 females, same data as holotype. 1 female, same locality as holotype, except 6–7.iii.1984, F. G. Howarth, F. D. Stone coll.; 1 male, same locality as holotype except 19.vi.1976, F. G. Howarth, R. C. A. Rice coll., BPBM, MFN.

Additional material: 2 nymphs V. instar, same locality as holotype, except 6–7.iii.1984, F. G. Howarth, F. D. Stone coll., and 19.vi.1976, F. G. Howarth, R. C. A. Rice coll., BPBM.

Ecology and distribution. Specimens of *O. waikau* have been found in a humid upper-level alcove offset from the main passage of Waikau Cave. Such dead-end upper levels often trap moisture and maintain the stable saturated environment characteristic of the deep cave zone (Howarth, 1983, 1991). Both the strong degree of troglomorphy and the apparent restriction to the deep-cave zone indicate that *O. waikau* is an obligately cavernicolous species. The host is possibly *Metrosideros polymorpha*, although other potential hosts also occur over the cave, including native Hawaiian species in the genera *Styphelia* (Epacridaceae), *Dodonaea* (Sapindaceae), *Coprosma* (Rubiaceae), and *Vaccinium* (Ericaceae). The temperature measured in the deep-cave zone was ca. 13°C.

O. waikau is known only from Waikau Cave at the upper fringe of the Waikamoi Rain Forest Reserve in Koolau Gap of Haleakala Canyon at c.1900 m. The prehistoric lava flow is undated but appears to be no more than 2000 years old and is perhaps younger. A photograph of a living female of this species was published as *Oliarus* species B in Howarth and Mull (1992).

Remarks. *O. waikau* displays a similar degree of troglomorphy as *O. priola*, but differs considerably in the shape of the male genital structures, especially the aedeagus (with three spines at the movable distal part instead of two in *O. priola*). From the other cavernicolous *Oliarus* species from Maui, *O. gagnei* it differs by its much higher degree of troglomorphy, proportions of head, and by details of the male genitalia (e.g. spine configuration of the aedeagus, apex of parameres).

The cave-dwelling Oliarus species of Molokai

***Oliarus kalaupapae* sp. nov.**

(Figs 48–58)

Habitus (Fig 48). Least troglomorphic of the cavernicolous Hawaiian *Oliarus* species; eyes, tegmina and wings only slightly reduced.

Coloration. Body more or less uniformly yellow; vertex and transition between vertex and frons with light brown markings; VII. sternite and X. tergite brownish. Rudimentary compound eyes pigmented, brown. Tegmina and wings translucent with venation yellow-brown, in some sections along longitudinal veins and crossveins dark brown. Legs yellow.

Head (Figs 49–51). Vertex trapezoidal, posteriorly about 2 times as wide as medially long. Anterior transverse carina obsolete, medially projected, forming a right angle. Vertex broadly rounded into frons. Frons broadened at level of the antennae, about 0.6 times as long medially as wide at maximum; lateral carinae ridged and directed laterad; frons and upper half of postclypeus with median carina distinct, lower half of postclypeus and anteclypeus with median carina obsolete. Frontoclypeal suture strongly arcuate. Median ocellus obscure. Post- and anteclypeus together about 3.4 times as long as frons. Rostrum surpassing metatrochanters, nearly reaching cephalic margin of VII. sternite. Compound eyes rudimentary, ommatidia pigmented. Ommatidia-bearing area shallowly convex. Lateral ocelli obscure. Antennae with basal

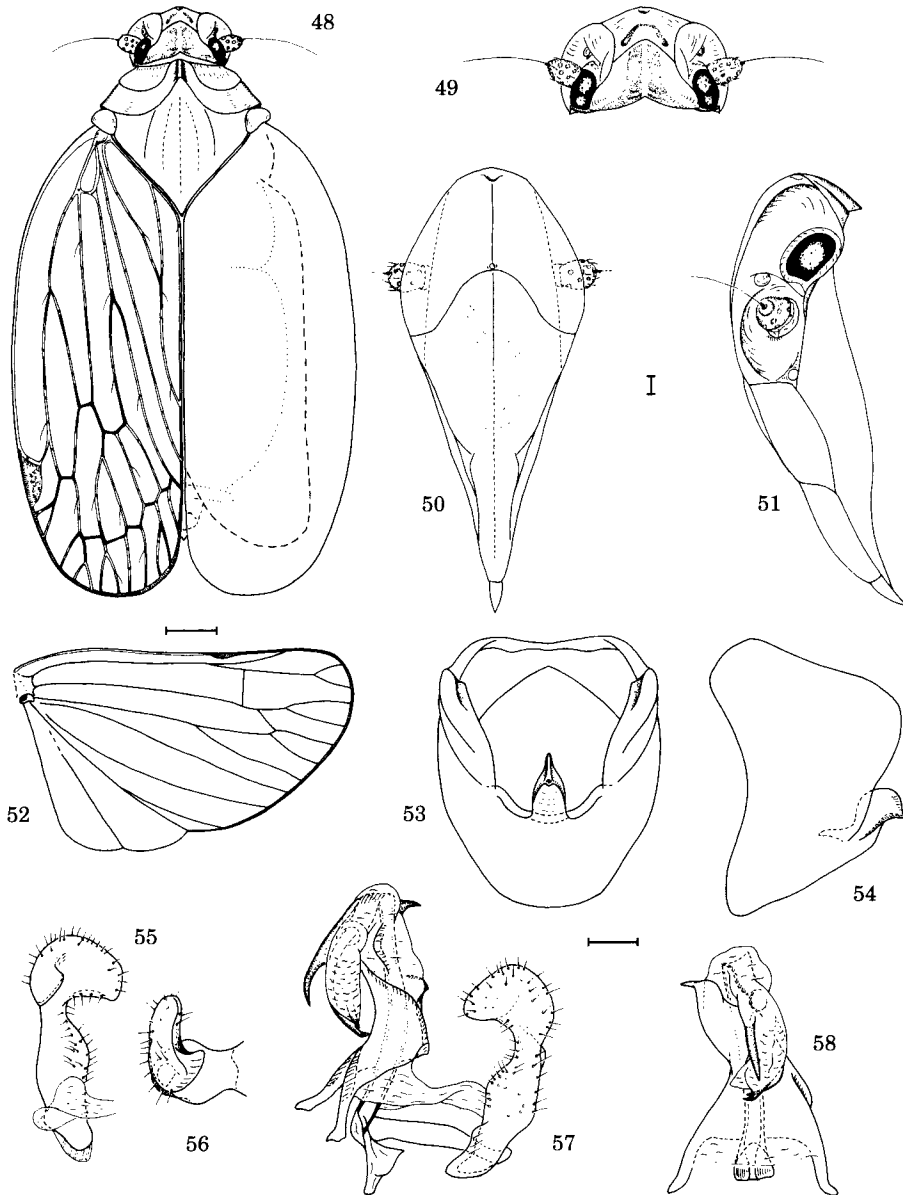


Figure 48–58. *Oliarus kalaupapae* sp.nov. 48, habitus (female); 49, head (female), dorsal aspect; 50, same, ventral aspect; 51, same, lateral aspect; 52, wing (female); figs 53–58. Male genitalia. 53, Genital segment, ventrocaudal aspect; 54, same, left lateral aspect; 55, paramere, mediolateral aspect; 56, same, caudal aspect; 57, aedeagus and paramere *in situ*, left lateral aspect; 58, aedeagus, dorsal aspect. Scale bars = 0.5 mm (Figs 48, 52), 0.1 mm (Figs 49–51; 53–58).

segment short, ring-like, second segment subcylindrical, bearing irregularly distributed placoidal sense organs and microtrichia.

Thorax (Figs 48, 52). Pronotum posteriorly deeply incised, with median carina distinct and lateral carinae obsolete. Pronotum in middle line about half as long as vertex,

and about 1.7 times as wide as maximum width of head. Tegulae present. Mesonotum quinquecarinate with carination more or less obsolete, in middle line about eight times as long as pronotum. Metatibia with 4 lateral and 6 apical teeth. Basitarsus of hind leg about as long as 2nd and 3rd tarsal segments together. Basitarsus and 2nd tarsal segment each with 7 apical teeth. Pretarsal claws strong, arolia well developed. Tegmina about 2.7 times as long as maximum width, surpassing the tip of the abdomen with about one seventh of their total length. Costal margin shallowly convex, pterostigma distinct. Sc + R furcation at about one third of total length of tegmen; Cu furcation only slightly distad of Sc + R furcation. Longitudinal veins densely papillate. Wings fully developed, no obvious reduction compared to epigeal species.

Male genitalia (Figs 53–58). Genital segment in caudal aspect about as high as wide, in lateral aspect ventrally about 10 times longer than dorsally. Medioventral process slender, about twice as long as wide at base, with its dorsal surface sharply ridged medially. Anal segment ventrally concave, damaged in holotype. Parameres apically rounded, with subapical median process sharply ridged, directed mediodorsad. Aedeagus with basal part apically bearing a strong, acute spine (directed lateroventrad); distal part with 3 spinose processes: one arising dorsally about half the length of distal part, and two arising from near its distal tip close to the phallotreme, in repose curved to the right.

Female genitalia. Ovipositor reduced in length like in other Hawaiian *Oliarus* species; IX. tergite truncate, with wax-secreting field slightly concave.

Length. Male 4.9 mm ($n=1$). Female 5.6 mm ($n=1$)

Etymology. This species is named after its type locality, Kalaupapa Cave, Molokai.

Type material. *Holotype*: male, Hawaiian Islands, Molokai, 30 m, Kalaupapa Natl. Hist. Pk., Fisherman's Shack Cave #1, 15.xi.1995, F. G. Howarth, S. Taiti coll., BPBM, type #15202. *Paratype*: 1 female, Hawaiian Islands, Molokai, Kalaupapa Cave #3; 25 m, 13.viii.1973, F. G. Howarth and W. C. Gagné coll., BPBM.

Ecology and distribution. Although the troglomorphies displayed by *O. kalaupapae* are less developed than in other cavernicolous *Oliarus* species from the Hawaiian Islands, we also regard this species as an obligate cave species. In its natural habitat it has not been observed flying. Fisherman's Shack Cave and Kalaupapa Cave #3 are different sections of the same lava tube system; the lower end of Kalaupapa Cave #3 being *c.* 100–150 m directly upslope of the upper end of Fisherman's Shack cave. Kalaupapa Cave #3 is a short shallow cave, having less than 50 m of passage. Here the cixiid was collected near a small woody plant root at the end of a short upper-level crawlway where the air was stagnant and humid and the temperature at 24°C. Its host is unknown; the surface environment over the cave supports a low elevation dryland shrub, which is subject to coastal wind shear and salt spray. The caves are among the few surviving segments of lava tubes that formed the Kalaupapa Shield, a post-erosional volcano forming an isolated peninsula on the windward north shore of Molokai. The Kalaupapa Volcanics are estimated to be 350 000 to 570 000 years old (Clague & Dalrymple, 1987).

Remarks. *O. kalaupapae* resembles *O. gagei* and *O. lorettae* in the configuration of the male genitalia, but differs from these and other Hawaiian cavernicolous species by the shape and length of the aedeagal spines.

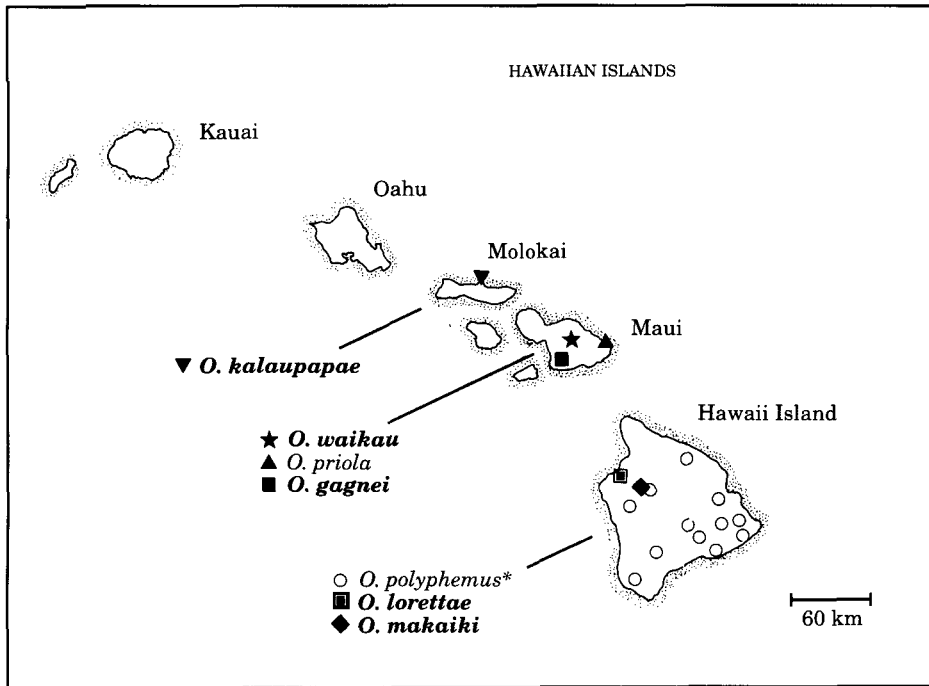


Figure 59. Distribution of cavernicolous *Oliarus* species in the Hawaiian Islands. *Localities after Hoch and Howarth (1993) and Hoch (unpublished data).

DISCUSSION

Estimated number of invasion events

The geographic distribution of Hawaiian cave Cixiidae (Fig. 59) exhibits the following pattern: one species on Molokai (*Oliarus kalaupapae*), three species on Maui (*O. priola*, *O. gagnei*, and *O. waikau*), and three species on Hawaii Island (*O. polyphemus* s.l., *O. lorettae*, *O. makaiki*). Are these seven species separate evolutionary lineages, or do we find indications that speciation may have occurred subsequent to an adaptive shift to the underground environment?

All Hawaiian cave *Oliarus* are considered troglobites, i.e. obligately cavernicolous, and presumably not able to survive outside their natural habitat. Therefore, dispersal on the surface is unlikely, and dispersal between islands is virtually impossible. The evolution of each of these species must have occurred autochthonously, i.e. on the same island where they are found today. Thus, the troglobitic species on each island clearly represent separate evolutionary lineages.

Amazingly, *O. lorettae* from Hawaii Island, *O. gagnei* from Maui, and *O. kalaupapae* from Molokai not only display a similar degree of troglomorphy, but also a similar configuration of the male genitalia (four homologous aedeagal spines). This similarity might be due to convergent evolution or to the fact that the three species—although clearly separate cave invasions—might be descendants of either the same widespread epigeic species or of three separate, but morphologically similar epigeic species.

In Hawaiian cave *Oliarus* two habitus types are found: a strongly troglomorphic habitus with compound eyes absent and vestigial tegmina and wings (*O. polyphemus*, *O. priola* and *O. waikau*), and a less troglomorphic one with small compound eyes, longer wings and fragmentary pigmentation (*O. lorettae*, *O. makaiki* and *O. kalaupapae*). On Hawaii Island and Maui both habitus types are found. From the morphological discontinuities in external characters alone, we conclude that on Hawaii Island *O. polyphemus* s.l. and *O. lorettae*/*O. makaiki*, and on Maui *O. priola*/*O. waikau* and *O. gagnei* must each represent at least one separate lineage.

O. polyphemus s.l. itself is now being regarded a complex of several separate species (Hoch & Howarth, 1993). Whether divergence among *O. polyphemus* s.l. populations occurred after a single colonization event or represents multiple invasions of caves by one or more ancestral surface species remains to be determined. Morphometric and genetic studies are under way to answer this question (Hoch, Wessel, Williamson, unpublished data). Although *O. lorettae* and *O. makaiki* are similar (yet not identical) in external morphology, they differ considerably in male genital structure and ecology. We therefore assume that they are the result of separate invasion events. The same situation is likely for *O. priola* and *O. waikau*. The profound differences between the two species, mainly in male genital characters but also in details of external morphology and ecology strongly support the assumption that the two species belong to separate evolutionary lineages.

Based on morphological information we conclude that at least seven Hawaiian *Oliarus* species have invaded caves separately, i.e. at least seven independent adaptive shifts to underground environments have occurred. All species described here (except for *O. makaiki*/*O. polyphemus* s.l. in Yellow Jacket Cave, Hualalai) occur allopatrically, and have been found to be restricted to a single or few neighbouring caves. The situation in *Oliarus polyphemus* s.l., however, may be more complicated. In our study on the behavioral divergence among *O. polyphemus* s.l. populations (Hoch & Howarth, 1993) we report two distinct call patterns by individuals from Pink Pistillaria Cave, Hualalai, and speculated that there two species of the complex may occur sympatrically.

Little is known about the phylogenetic relationships between cavernicolous Hawaiian *Oliarus* species and their epigeal relatives. No synapomorphic character supporting Fennah's (1973) assumption that *O. polyphemus* "is a member of the group of *O. inaequalis* Giffard" has been determined. Our own preliminary studies on the morphology of epigeal *Oliarus* species have revealed indications that in some cases possibly even the sister-species of the cavernicolous *Oliarus* species may occur parapatrically on the surface (Hoch, unpublished data). The most striking example is *O. makaiki*/*O. koanoa*. The two species display a nearly identical aedeagal spine configuration. In the entrance zone of the Yellow Jacket Cave, the habitats of both species were observed to even overlap to some degree. If it could be shown that *O. makaiki* and *O. koanoa* are indeed sibling species, Howarth's (1986) model of parapatric speciation would have found its most convincing confirmation. However, a cladistic analysis is needed to develop hypotheses on phylogenetic relationships between epigeal and cavernicolous species.

Possible factors determining the evolution of Hawaiian cave Cixiidae

The reasons for the varying degree of troglomorphy observed in Hawaiian *Oliarus* are unknown; however, correlations are conceivable with either geologic or evolutionary time, or with physical parameters of their environment.

Surprisingly, the youngest lava tubes (from 100 to a few thousand years old) harbour the most cave-adapted species (*O. priola*, *O. waikau* and *O. polyphemus s.l.*), while the least cave-adapted species (*O. kalaupapae*) is found in the oldest lava tube (Kalaupapa Lava Tube: 350 000 to 570 000 B. P.). In all but one case the original subterranean colonization must have taken place in a much older lava flow, now buried, and the adapting population has been dispersing to younger caves as these became available (as *O. polyphemus s.l.* is doing now on Kilauea and Mauna Loa on Hawaii Island (Howarth, 1987)). The exception is *O. kalaupapae*: when the Kaulapapa volcanics commenced 350 000 to 570 000 years ago, that region of Molokai was already more than one million years old and so eroded that subterranean habitats were probably no longer suitable for cave cixiids. Therefore, it is probable that the ancestor of *O. kalaupapae* colonized the lava tubes at Kalaupapa some time after their formation, and the population has been living *in situ* and adapting to the caves ever since. The Kalaupapa caves have been available for colonization nearly as long as the whole of Hawaii Island (Clague & Dalrymple, 1987).

The correlation is better with the physical environment. The three highly troglomorphic *Oliarus* (*O. priola*, *O. waikau* and *O. polyphemus s.l.*) live in deep, young lava tubes and feed on roots of presumably *Metrosideros polymorpha*, the dominant pioneering native tree on young lava flows. Significantly, the pioneering forms of *Metrosideros* send their roots deep into the lava in search of water and nutrients. The least cave-adapted species (*O. kalaupapae*) lives in old eroded caves in the lowlands and feeds on roots of lowland drought-adapted shrubs. The caves and associated cracks and crevices (the mesocaverns) are mostly filled with soil, and a large percentage if not all of the plant roots that would be available for a cave cixiid would be near the surface. The same situation apparently applies for *O. lorettae*. *Sida fallax* appears not to have the deeply penetrating roots as found in *Metrosideros*. In these warmer, shallower subterranean habitats, the cave cixiids would be more likely to experience higher potential evaporation rates and more frequent exposure to daylight than cixiids living in cooler deeper voids. Consequently, the lowland shrubfeeding cave *Oliarus* may be under greater selection to recognize and avoid hostile surface environments than are the *Metrosideros*-feeding cave species, and therefore retain functional even if small compound eyes. The habitat of *O. gagnei* is intermediate between the two extremes, and its degree of troglomorphy is also intermediate. *O. makaiki*, however, does not fit this pattern: although intermediate in troglomorphy, it is found in a humid cave at a higher altitude, situated in wet *Metrosideros* forest, *Metrosideros* being the apparent host. Thus the evidence suggests that *O. makaiki* is a relatively recent invasion and that the early stages of cave adaptation may be in progress.

A parallel case has been demonstrated in cavernicolous cixiid species of the genus *Solonaima* from Australia (Hoch & Howarth, 1989). In contrast to the evolutionary trends reported in *Solonaima* species (Hoch & Howarth, 1989), however, no correlation between the degree of troglomorphy and complexity of male genital structures was found in the Hawaiian cavernicolous *Oliarus* species: no obvious reductions in complexity of the genital structures are evident in the more cave-adapted species. All of the cave species show comparable degrees of complexity of their genital structures. It is remarkable, that the three most cave-adapted species (*O. polyphemus s.l.*, *O. priola* and *O. waikau*) show a very high degree of macroevolutionary convergence, not only in reductive evolutionary trends such as the complete reduction of compound eyes, tegmina, wings and bodily pigment, but also in progressive evolutionary

trends: all three species have apparently independently evolved specialized pretarsal structures which presumably serve as an adaptation to walk on wet rocky substrates (Howarth, 1991).

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