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The endemic Hawaiian mealybug genus *Phyllococcus* Ehrhorn, 1916 (Hemiptera: Coccomorpha: Pseudococcidae): redescription of the type species and description of a new species on an endangered host plant, *Cryptocarya mannii* (Lauraceae)

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Abstract

The endemic Hawaiian mealybug genus *Phyllococcus* Ehrhorn (Hemiptera: Coccomorpha: Pseudococcidae) was erected in 1916 as a monotypic genus for a gall-inducing mealybug collected on the island of Oahu on *Urera sandwicensis* (now referred to genus *Touchardia*) (Urticaceae) in 1911. The species induces deep horn-shaped galls on the leaves of the host plant. Here we redescribe the adult female and adult male of *Ph. oahuensis* (Ehrhorn) and designate a lectotype; and we report a new record for *Ph. oahuensis* from the island of Maui. Additionally, we describe the adult female and second- and third-instar female nymphs of a new gall-inducing *Phyllococcus* species, *Ph. cryptocaryae* Percy, Watson & Hodgson, **sp. n.**, found in galls on the leaves of *Cryptocarya mannii* (Lauraceae) in the central Waianae Mountains on Oahu. Also found galling the same host plant, and often in close proximity on the same leaf, were immatures of the triozid psyllid, *Paurotriozana adaptata* Caldwell, 1940 (Hemiptera: Psylloidea: Triozidae). Both the new mealybug and the triozid psyllid appear to be geographically restricted to the only remaining tree of *C. mannii* on Oahu and are therefore extremely vulnerable to extinction.

Key words: Sternorrhyncha, endangered species, endemism, leaf galls, co-extinction

Introduction

The endemic Hawaiian mealybug genus *Phyllococcus* Ehrhorn, 1916 (Hemiptera: Coccomorpha: Pseudococcidae), was monotypic (Zimmerman 1948) and listed as extinct (Moir 2021). However, although the type species, *Ph. oahuensis* (Ehrhorn, 1916), has not been recorded in recent years from two of the islands from which it was originally collected, we are able to report here previously unpublished records from Maui that confirm the taxon was not extinct, at least at the time of the most recent record in 2012. Moreover, we describe a second, new species, *Ph. cryptocaryae* Percy, Watson & Hodgson, **sp. n.,** from the central Waianae Mountains on Oahu. Both species are gall-inducing: *Ph. oahuensis* induces horn-shaped galls on *Touchardia sandwicensis* (Wedd.), previously referred to the genus *Urera* (Urticaceae), and *Ph. cryptocaryae* **sp. n.** induces dome-shaped galls on *Cryptocarya mannii* Hillebr. (Lauraceae).

The host plant of the new species, *Cryptocarya mannii*, is a Hawaiian endemic that is restricted to the islands of Kauai and Oahu. This small to mid-sized tree was present on Oahu in forests in the Koolau Mountains and Waianae Mountains; but it is no longer found in the Koolau Mountains and there is only a single mature specimen remaining in the Waianae Mountains despite ongoing efforts to propagate and establish new plants at the last remaining site (Morden *et al.* 2015). The population of *Cryptocarya* R.Br. trees on Oahu was originally considered to be a distinct

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species, *C. oahuensis* (O.Deg.) Fosberg, but this taxon was subsequently synonymised with *C. mannii* Hillebr. (van der Werff 1990). However, more recent genetic analysis suggests sufficient divergence exists to recognise both species as single-island endemics (Morden *et al*. 2015). The single remaining mature tree on Oahu is now considered to be the only host for the new *Phyllococcus* species. Moreover, it is also the only host for the gall-inducing psyllid *Paurotriozana adaptata* Caldwell, 1940 (Hemiptera: Psylloidea: Triozidae). As both of these sternorrhynchan insect species appear to be currently restricted to this single tree, there is imminent danger of co-extinction of these insects and their host plant if a regenerating population of *C. mannii* cannot be re-established on Oahu.

Materials and methods

The adult female specimens of *Ph. oahuensis* (Ehrhorn) studied here had been slide mounted previously. Due to the poor condition of the syntype material, all the measurements in the redescription below are based on non-type material and are given as ranges. The two slide-mounted specimens of adult males were collected and mounted by the late Prof. Jack Beardsley from herbarium specimens. Due to restrictions on the loan of the latter material, the adult male is here described from high-powered photographs of the mounted specimens, kindly taken by Dr Andrew Polaszek (Natural History Museum, London—NHM) with a BX63 Olympus microscope using cellSens digital imaging software, to produce image stacks that were then combined using Helicon Focus software. Measurements of the males in the description below (in *italics*) are those given by Beardsley (1960).

The specimens of the new *Phyllococcus* species were cleared, stained with acid Fuchsin and slide mounted in Canada balsam, using the method described by Sirisena *et al.* (2013), apart from using Histoclear as the dewaxing reagent instead of Histoclear phenol. For *Ph. cryptocaryae* **sp. n.**, each initial measurement is for the holotype followed by the size range for the paratype specimens in parentheses. Under "Material studied", the holotype collection data are listed using "/" to indicate the line breaks on the slide label. The type material of *Ph. cryptocaryae* is deposited in the collection at the Natural History Museum, Cromwell Road, London SW7 5BD, UK (NHMUK). The lectotype and paralectotypes of *Ph. oahuensis* and a paratype of *Ph. cryptocaryae* are deposited at the Bernice P. Bishop Museum, Honolulu, Hawai'i, USA (BPBM).

Taxonomy

Family Pseudococcidae Cockerell, 1905

Genus *Phyllococcus* Ehrhorn, 1916

Type species: *Cissococcus*? *oahuensis* Ehrhorn 1912: 149.

Generic diagnosis, based on adult female morphology (modified from Ferris *in* Zimmerman 1948: 159–160). *Phyllococcus* is a genus of gall-inducing mealybugs that form deep pit galls in the leaves of their hosts. More than half of body composed of head and thorax. Posterior abdominal segments strongly sclerotised dorsally to form a broadly oval shield, used to close gall opening. Sclerotised shield composed of dorsum of abdominal segments VII, VI and V (*Ph. oahuensis*) or VII–III (*Ph. cryptocaryae*); venter of these segments membranous. Posterior part of shield formed from flattened, strongly sclerotised anal lobes, each with spinose cerarian setae. Anal ring concealed between bases of anal lobes (in *Ph. oahuensis*) or at end of short anal tube (*Ph. cryptocaryae*); anal ring bearing 6 quite long setae, and with 2 rows of small pores. Vulva large and distinct. Antennae each 6 or 7 segmented; both apical and preapical segments with fleshy setae. Mouthparts typical for mealybugs. Legs either quite short and stout (*Ph. oahuensis*) or longer and slender (*Ph. cryptocaryae*); each trochanter with 2 campaniform sensilla on each side; tarsal and claw digitules capitate; claws each without a denticle; hind legs with translucent pores on femur and tibia in both species (mostly on dorsolateral and dorsal surfaces), also on trochanter and tarsus in *Ph. oahuensis*. Anterior dorsal ostioles present but poorly developed; posterior ostioles absent. Cerarii represented only by short, conical spinose setae on each anal lobe, either with spinose setae along entire posterior margin (*Ph. cryptocaryae*) or restricted to 2 on apex of each anal lobe (*Ph. oahuensis*). Circulus absent. Oral collar tubular ducts apparently absent in *Ph. oahuensis*; in *Ph. cryptocaryae*, these ducts present along posterior margins of segments in sclerotised shield but absent elsewhere. Setae sparse on head and thorax on both dorsum and venter but either becoming very abundant and longer on ventral abdomen, particularly posteriorly where more spinose (*Ph. cryptocaryae*), or sparse on abdomen and not spinose (*Ph. oahuensis*). Trilocular pores present on both dorsum and venter of head and thorax but absent from dorsal shield and both surfaces of anal lobes in both species, and from dorsum and venter of abdominal segments III–VII in *Ph. oahuensis*. Simple pores present wherever trilocular pores present, very sparse.

Comments. Ehrhorn (1912), in his original description of the type species, placed it tentatively in *Cissococcus* Cockerell, which he indicated by a question mark after the genus name. *Cissococcus* belongs to family Coccidae and is found only in South Africa (Hodgson *et al*. 2011). Beardsley (1984) also recorded *Ph. oahuensis* on *Urera sandwicensis* Wedd. (now *Touchardia sandwicensis* (Wedd.)) (POWO 2023; Wells *et al*. 2021) on Oahu, and Zimmerman (1948) noted a collection from Lanai, but no recent collections of *Ph. oahuensis* have been made from these islands and it may be that these populations are now locally extirpated (Janis Matsunaga, Hawai'i Department of Agriculture, pers. comm.). With the addition of the new species described below, the genus *Phyllococcus* now contains two endemic species from the Hawaiian Islands.

Phyllococcus oahuensis (Ehrhorn)

(Figs 1A & B, 2, 3)

Cissococcus? oahuensis Ehrhorn 1912: 149.
Phyllococcus oahuensis (Ehrhorn, 1912); Ehrhorn 1916: 236, change of combination.

Phyllococcus oahuensis was considered to be extinct by Moir (2021), but a population was found on Maui in 2007 and the leaf galls were photographed by Dr Karl Magnacca [on *Urera glabra*, -.viii.2007, Kahanaiki Gulch below Puu Kukui cabins, Maui, Hawaii] (Fig. 1). Subsequently, the species was collected in 2012 by Keahi Bustamente on *U. glabra* in the East Maui Mountains, and this material is described below. These Maui collections represent a new island record for *Ph. oahuensis*. Note that the recorded host, either as *Urera sandwicensis* or *U. glabra*, is now considered to be a synonym of *Touchardia sandwicensis* (Wedd.) (POWO 2023; Wells *et al*. 2021).

Material studied. Lectotype and paralectotypes: 1 slide containing 7 adult females with a single label: "Cissococcus? / oahuensis / n.sp. / on Urera sandwichensis [sic] / Tantalus / Oahu / EME 1.30.1911"; specimens in fairly good condition (but most slightly distorted by pressure of coverslip); the lectotype, here designated, is the specimen located nearest the edge of the circular coverslip, and is marked with an adjacent black ink spot (BPBM). The remaining 6 adult females on the same slide become paralectotypes.

Other material studied: 2 slides, each containing 1 adult female and 1 adult male: Hawaii, Mountains nr Koele, Lanai Island, June 1913, ex herbarium specimens of *Urera glabra*, coll. C.N. Forbes; det. J.W. Beardsley (good, but large air bubbles under the coverslips have displaced and tilted some of the specimens). Description below made from 2 slides, each containing 3 adult females labelled: Hawaii, West Maui Mountains, Maui, ex *Urera glabra* leaf galls, coll. Keahi Bustamente, 22.viii.2012, det. J. Garcia (good).

Note. Although the type series and the material identified by Beardsley were seen by GW, the description and illustrations were made from non-type specimens due to restrictions on the loan of the type slide to CH. We are, however, convinced that the specimens examined from West Maui Mountains are conspecific with those from Oahu.

Adult female

Field appearance and gall phenotype (Fig. 1). From Ehrhorn (1912: 149): "Galls in clusters on both sides of leaf but usually upper leaf surface preferred. Gall cone-shaped, somewhat curved and constricted near leaf surface and varying more-or-less in shape. At times, two or three will coalesce. Length about 3 mm and 1 mm at widest point." "Female elongate oval, tapering gradually caudad, about 1.5 mm long by 1 mm at cephalic end. Body a dirty yellow colour covered in slightly white secretion" (Ehrhorn 1912: 149). Note that the cone- or horn-shaped gall which usually protrudes from the upper leaf surface has the rounded gall aperture on the lower leaf surface (Figs 1, 2Z).

FIGURE 1. A. Galls of *Phyllococcus oahuensis* (Ehrhorn) on a leaf of *Touchardia sandwicensis*, found on Maui in 2007; **B**. Closer view of galls of *Ph. oahuensis*. Photographs by Karl Magnacca.

Slide-mounted adult female (Fig. 2) (based on 6 good specimens). Body broad and rounded anteriorly, gradually narrowing posteriorly, 2.1–3.4 mm long, 1.2–1.8 mm across prothorax; with a round-to-oval, strongly sclerotised dorsal shield covering posterior 3 abdominal segments. Anal lobes each rather triangular and pointed, apparently flattened, inner margins closely aligned at base but divergent towards apex; each heavily sclerotised dorsally, with 2 spinose cerarian setae on apex, each 15–18 µm long, plus a setose seta; lobe inner margin without setae; dorsal surface lacking setae but with sclerotised spinules along outer margins; ventral surface strongly sclerotised over posterior half, with a long seta placed more-or-less centrally, each seta 40–45 µm long, plus 3 or 4 shorter setae, each 8–13 µm long; much of lower surface covered in sclerotised spinules. Posterior ostioles absent from abdomen but anterior ostioles present, poorly developed and indistinct, each lacking trilocular pores and setae. Antennae each 6 or 7 segmented, each 260–282 µm long; when 7 segmented, segment III divided; setal distribution (7 segmented) as follows: scape, 4 hair-like; II, 3 hair-like; III, 4 hair-like; IV, 3 hair-like; V, 4 hair-like; VI, 5 hair-like + 1 large fleshy, and VI, 10–12 hair-like + 1 subapical + 3 apical fleshy. Legs well developed but short and stout; trochanters each bearing 2 campaniform sensilla on each surface; hind legs with translucent pores on both surfaces of trochanter, femur, tibia and tarsus; lengths of hind leg segments (in µm): coxa 109–135, trochanter + femur 185–202, tibia 96–105, tarsus 58–71; tarsal digitules capitate, with one digitule slightly broader than other; claw digitules capitate and exceeding tip of claw; claw fairly well developed, 16–20 µm long, moderately curved, without a denticle. Clypeolabral shield 125–135 µm long, relatively short and rounded; labium 90–100 µm long, clearly shorter than clypeolabral shield; labium 3 segmented. Spiracles: peritreme widths (in µm): anterior 30–33; posterior 34–38. Circuli absent. Cerarian setae absent apart from 2 on apex of each anal lobe. Vulva particularly large and obvious, situated ventrally between segments VII and VIII. Anal ring hidden, situated under base of anal lobes (B), about 50 µm wide, with 2 rows of small pores (not illustrated) and 6 long setae (each about 90 µm long). Eyespot well developed, each situated just lateral to scape; convex, without associated pores, 28–30 µm in diameter.

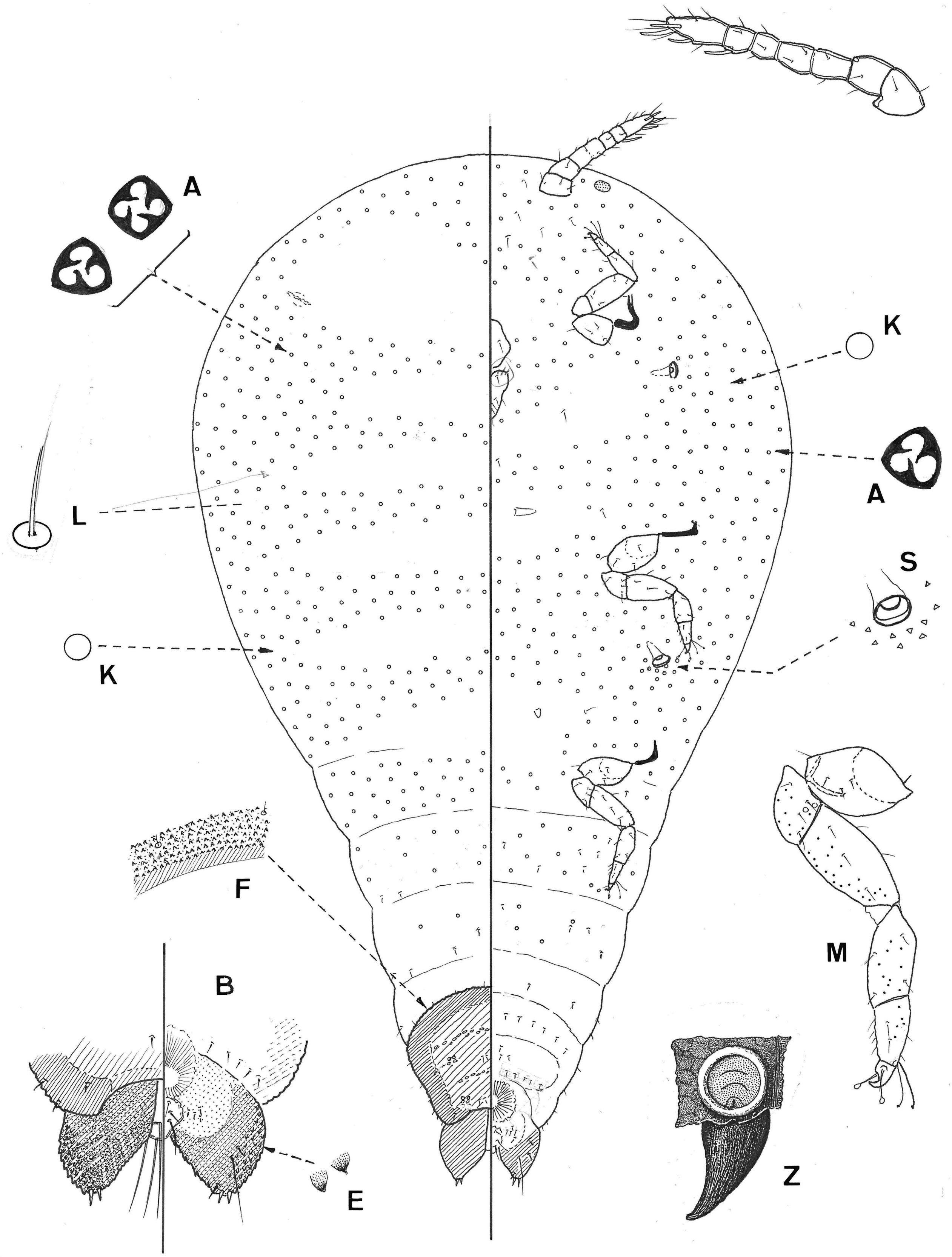

FIGURE 2. Adult female of *Phyllococcus oahuensis* (Ehrhorn). **A**. Trilocular pore; **B**. Dorsal and ventral views of anal plates; **E**. Spinules on anal plates and margins of dorsal shield; **F**. Margin of dorsal shield; **L**. Dorsal seta; **K**. Simple pores; **M**. Anterior view of hind leg; **S**. Spiracle; **Z**. Illustration of gall by Ferris (*in* Zimmerman 1948: 160, fig. 93).

Dorsum: mainly membranous but with a heavily sclerotised, almost round to oval shield or plate, 252–430 µm long and 245–345 µm wide; formed medially from abdominal segments IV–VII, with 2 intersegmental membranes visible on shield, each represented by dark lines with small oval clear areas (occasionally a narrow third line visible posteriorly, possibly representing part of segment VIII); shield raised above surrounding abdominal segments, with a strongly sclerotised border with numerous sclerotised spinules and occasional setae. Segments VI and VII each with a small group of areolations submedially. Anal lobes (B) described above. Anterior part of abdominal segment VIII probably represented dorsally by membranous folds under posterior margin of segment VII. Setae on shield all very short and setose, each about 5 µm long. Oral collar tubular ducts absent throughout dorsum. Trilocular pores (A) rather rounded, each 3.0–3.5 µm in diameter, present throughout head, thorax and abdominal segment I, becoming scarce on abdominal segment II and usually absent from more posterior segments. Simple pores (K) each about 2 µm wide, very sparse throughout, wherever trilocular pores present. Other types of pore absent. Dorsal setae (L) very short and setose, each 5–8 µm long, without raised basal sockets; very sparse.

Venter: membranous except for ventral surfaces of anal lobes, which are sclerotised posteriorly. Ventral setae short and setose, present on head and thorax, with a group of about 10 between antennae, each 15–25 µm long, setae sparsely present on rest of head and thorax; with 0 or 1 medial to each coxa. Abdominal segments anterior to vulva each with a transverse line of setose setae, more abundant than on more-anterior segments, each with normal setal socket; setae on either side of vulva each about 16–20 µm long. Trilocular pores (A) similar to but generally slightly more abundant than those on dorsum, present throughout on head, thorax and abdominal segments II and III, but absent more posteriorly; densest lateral to spiracles. Simple pores (Fig. 2K) as on dorsum. Multilocular and quinquelocular disc-pores and tubular ducts absent. Without a pair of narrow finger-like processes extending towards vulva, as noted in *Ph. cryptocaryae*.

Notes. The illustration here (Fig. 2) is very similar to that of Ehrhorn (1912) and Ferris (*in* Zimmerman, 1948) apart from the few new features, namely the presence of: (i) (poorly developed) anterior ostioles; (ii) simple pores on both the dorsum and venter, and (iii) translucent pores on the hind leg. Maui is a new island record. The species is probably viviparous. The first-instar nymph is illustrated in Ehrhorn (1912: [p. 151] Plate 5, fig. 4). One of the adult females found on herbarium material of the host collected in 1913 (coll. C.N. Forbes) on Lanai was found to contain a very early instar hymenopteran endoparasitoid, probably a chalcid (Hymenoptera: Chalcidoidea), possibly an aphelinid or encyrtid (Dr Andrew Polaszek (NHM) pers. comm.). This is the first record of a parasitoid of *Phyllococcus*.

Adult male (Fig. 3)

Note. The following description and illustration were made from a series of photographs taken of the two slide-mounted specimens (see "Other material studied", above). The measurements given in the text in *italics* are those provided by Beardsley (1960).

Slide-mounted material (n = 2). Macropterous; quite small, total body length about *1.25 mm*; antennae long, about half total body length (about *665 µm* long), with long fleshy setae (fs), each as long as or longer than width of antennal segments; body with few setae, all hair-like (hs), fleshy setae (fs) apparently absent from body [Beardsley states fs also present on head] but abundant on legs and antennae, each up to *36 µm* long; loculate pores present on margins of abdomen, each with 4 or 5 loculi [Beardsley says 3 as well]. Wings about 1.15 times as long as total body length, and about 0.4 times as wide as long.

Head: broadest across genae; probably a little longer than broad. Dorsum with mid-cranial ridge well developed, extending full length of head and fusing with postoccipital ridge posteriorly; median crest narrow, possibly showing a few reticulations (not shown); with a few setae plus (possibly) a few (4?) dorsal head pores (these indistinct) on either side of mid-cranial ridge. Preocular ridge well developed, extending from base of each scape dorsally around dorsal simple eyes and then posteriorly, eventually meeting mid-cranial ridge and forming part of a thin postoccipital ridge. Postocular ridge distinct, extending dorsally from each ocellus, passing posterior to each dorsal simple eye and fusing with postoccipital ridge; ocelli distinct, with what appears to be an interocular ridge that encircles each ocellus. Ocular sclerite mildly sclerotised, with a few reticulations around each dorsal simple eye but lacking setae; each dorsal simple eye round and *32 µm* wide. Each gena large, with a few setae but no obvious reticulations. Venter with mid-cranial ridge extending posteriorly between ventral simple eyes, with several setae and a few reticulations (not shown); lateral mid-cranial ridges well developed. Ventral simple eyes round, each *35 µm* wide, positioned quite far forward on head; probably with a few narrow reticulations and some ventral head setae anterior to each eye. Ocular sclerite weakly sclerotised. Preocular ridge not definitely identified, possibly short. Postocular ridge strongly developed, extending from posterior to each dorsal simple eye anterolaterally past each ocellus and then fusing with preocular ridge before extending posterolaterally to near mouth. Preoral ridge poorly developed. Cranial apophysis and mouth not detected.

Antennae: 10 segmented and filiform; *665 µm* long (ratio of total body length to antennal length 1 : 0.54). Scape approximately square, with pedicel arising anterolaterally. Segments III–X all rather irregular in width but each with mainly fs, most setae longer than width of segment, plus some shorter hs; number of setae per segment uncertain but at least 20; segments VIII and IX each with single long bristle, segment X with 3 bristles. Segment X and perhaps segment IX with capitate setae, number uncertain but probably at least 2 on segment X.

Thorax. Prothorax: dorsally with pronotal ridge well developed, long, extending ventrally and nearly touching proepisternum + cervical sclerite; pronotal sclerite possibly represented by a distinct ridge dorsolaterally; with a small group of 1 or 2 hs lateral pronotal setae just anterior to triangular plate. Post-tergite present, with some hs on each side (only one side visible). With 1 pair of medial pronotal setae. Sternum lightly sclerotised; median ridge poorly developed; transverse ridge well developed; with 1 or 2 prosternal setae on each side. Presence of anteprosternal setae uncertain but with perhaps 2 antemesospiracular setae on each side. Presence of pores on prothorax uncertain (Beardsley states 2 or 3 on each side but does not say whether dorsal or ventral).

Mesothorax: prescutum rather rectangular; sclerotised and lightly nodulated, approximately twice as wide as long; prescutal ridge well developed anteriorly but fading posteriorly; prescutal suture well developed; prescutum with several small pale pore-like areas that might be hs setal sockets. Scutum with median area sclerotised, not reticulated, distinctly wider than long; with 7–12 small pale pore-like areas on each side that might be hs scutal setae; lateral margins sclerotised but not reticulated; prealar ridge and triangular plate well developed; area lateral to scutellum rather square. Scutellum rectangular; without a scutellar ridge or foramen; with 2 or 3 pore-like areas (hs scutellar setae?) on each side; postnotal wing process thin and extending laterally. Tegula present, tegular setae not visible, possibly absent. Basisternum a little wider than long, without a median ridge; bounded anteriorly by a well-developed marginal ridge; posteriorly with a strong precoxal ridge; with perhaps 10 hs basisternal setae on each side; lateropleurite narrow, without an extension from marginal ridge along anterior margin; furca well developed, narrow waisted, arms very divergent and extending about 1/2 way to marginal ridge anteriorly. Mesopostnotum well developed; postnotal apophysis well developed. Area bounded anteriorly by scutellum and laterally and posteriorly by mesopostnotum membranous. Mesepisternum, subepisternal ridge and postalare not clear. Mesothoracic spiracle normal, without associated loculate pores. Postmesospiracular setae present, with 6 or 7 hs on each side anterior to marginal ridge of basisternum.

Metathorax: presence of metatergal setae unknown; metapostnotal sclerite not visible. Dorsal part of metapleural ridge not visible (but as hamulohalteres are present, it must be present). Posterior part of metapleural ridge well developed; episternum lightly sclerotised; presence of postmetaspiracular setae unknown; precoxal ridge well developed, extending medially; metasternal apophysis possibly present. Metepimeron sclerotised, but without setae. Metathoracic spiracle apparently normal. Presence and number of setae on metathorax unclear.

Wings: basal wing sclerites not visible. Wings hyaline, longer than total body length (ratio of length to width 1 : 0.25; ratio of total body length to wing length 1 : 1.11); alar lobe present; presence of alar setae unknown but 2 circular sensoria thought to be present just distal to where medial vein branches from radial vein. Hamulohalteres present, each with a single apical hamulus.

Legs: all legs with numerous, quite long fs and a few hs; metathoracic legs longest. Trochanter + femur: sensoria on each trochanter not visible, but with strong sclerotised ridges for articulation with femur; long trochanteral seta not differentiated; femur III with each fs about *33 µm* long. Tibia III with setae not becoming spur-like on distal third of leg; with 2 apical spurs on each protibia, perhaps 3 on each mesotibia and about 5 on each metatibia. Tarsi each 2 segmented, with proximal segment very short; tarsal spurs not differentiated; tarsal campaniform sensillum present; tarsal digitules not reaching to tip of claw; tarsus generally held at a distinct angle to tibia. Claws each long and thin, about as long as width of tarsus, almost straight, without a small denticle; claw digitules possibly each represented by a short, fine seta.

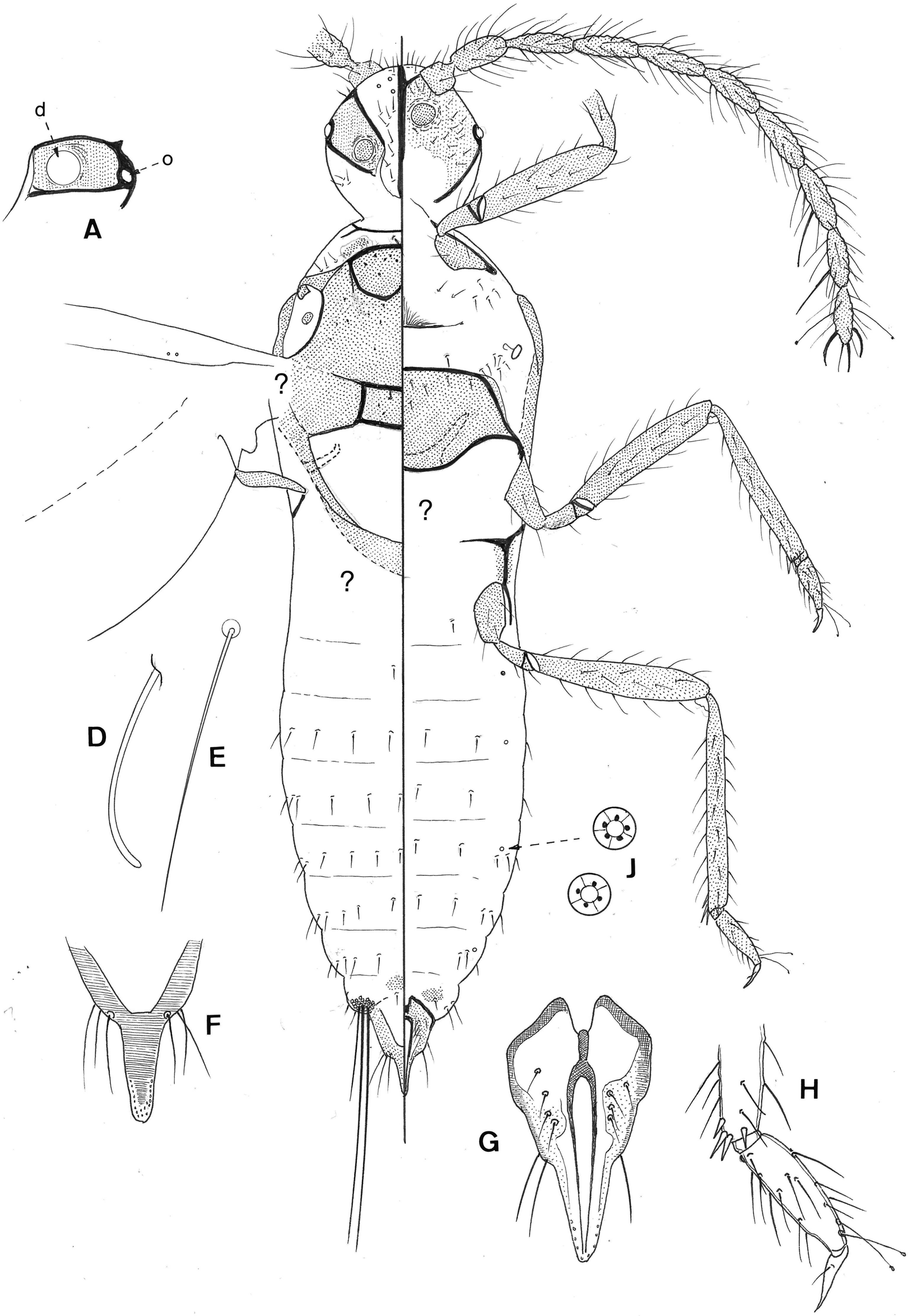

FIGURE 3. Adult male *Phyllococcus oahuensis* (Ehrhorn). **A**. Dorsal ocular sclerite, showing dorsal simple eye (d) and ocellus (o); **D**. Fleshy seta on leg; **E**. Hair-like seta on leg; **F**. Dorsal view of posterior half of penial sheath; **G**. Ventral view of penial sheath; **H**. Metatibia + tarsus; **J**. Loculate pores.

Abdomen: segments I–VII: tergites and sternites unsclerotised. Caudal extension of segment VII absent. Loculate pores only present laterally, visible on segments II, III, V and VII (Beardsley states 1 or 2 on most segments, with 3–5 on segment II); dorsal abdominal setae present in sparse rows across each segment, probably all hs; segments I–VII: 4–7 hs. Pleural setae: dorsopleural and ventropleural setae not separable but 4–5 on each side of most segments; what are thought to be small simple pores could be present on venter of many segments. Ventral abdominal setae (totals): II–VII 3–7. Ostioles not located.

Segment VIII: tergite lightly sclerotised medially, with 1 pair of hs dorsal abdominal setae; sternite with a small sclerotisation anterolaterally, each with a small hs; caudal extension small, segment rounded; 2 hs pleural setae present. Glandular pouches present, shallow, each with numerous loculate pores spreading out around glandular pouch; with 2 long glandular pouch setae, each about 3x longer than penial sheath, plus a third shorter seta, about as long as penial sheath, and another short seta.

Genital segment: penial sheath (ps) short, rather triangular, nearly twice as long as broad (*120 µm* long), with a fairly blunt apex. Dorsally with a broad triangular membranous extension (probably segment IX) with a vertical anal opening at posterior end; no other structures noted on dorsal surface. Ventrally, with basal ridge well developed; lateral processes of penial sheath indistinct but each side with 2 (perhaps 3) hs in this position plus 1 (or 2) other setae more anteriorly. Margins with 3 longer setae, possibly fs. Basal rod distinct, probably lying more-or-less vertically, at anterior end of aedeagus. Aedeagus parallel-sided at base but narrowing towards apex, where very needle-like.

Remarks. The taxonomic relationships of scale insects can be very difficult to determine based on the structure of the adult female, particularly where the adult female has been considerably modified, such as when a gall-inducer. However, apart from maybe having to modify their genitalia to reach the female within a gall, male scale insects are relatively uniform in structure. The structure of the adult male of *Ph. oahuensis* is typical of mealybugs and appears to have no obvious changes related to trying to mate with a gall-inducing female. Although the taxonomic value of many character-states on adult males is uncertain, in the key to known male pseudococcids (Hodgson 2020), the male of *Ph. oahuensis* keys out in the Pseudococcinae (rather than the Phenacoccinae).

Beardsley (1960) collected these adult males "from galls on leaves" of herbarium-mounted specimens, along with the adult females. Although Beardsley does not confirm whether the males he found were inside the female galls, or in their own galls, it is likely that both males and females of *Phyllococcu*s mature within a gall, and that those found by Beardsley had recently moulted to become adult. Ehrhorn (1912) also mentions finding males, so they may be quite common. It is notable that the penial sheath of these males is quite short. The sclerotised shield + anal lobes of the adult female plug the gall aperture so that the anus and vulva are close to the gall aperture, thus allowing the short aedeagus to reach the latter.

Phyllococcus cryptocaryae Percy, Watson & Hodgson, sp. n.

(Figs. 4D, E and F, 5)

Material examined. Holotype adult female: Cryptocarya mannii / 5 July 2014 / USA, Central Waianae / Mountains, Oahu, Hawaiian / Islands, 21.4574N, -158.0970W. / leaf gall / D. Percy leg. Hi65.2-14 / mounted singly on a slide (NHMUK). **Paratypes:** data as for holotype; 3 adult females, mounted singly on slides (2 NHMUK, 1 BPBM); 1 pharate second-instar female nymph on 1 slide, and 2 third-instar female nymphs, one containing a pharate adult female, mounted together on 1 slide (NHMUK).

Note. The four adult female specimens are all slightly damaged, lacking some legs or antennae, and with the labium distorted. Due to the heavy sclerotisation of the dorsal shield, it is not possible to determine the extent of the sclerotisation of the posterior venter but it is here considered that the underside of the anal lobes may also be sclerotised to some extent.

Adult female (Fig. 5)

Field appearance: Found in large subsurface chamber galls (Fig. 4E, F) with the aperture on the lower leaf surface and a raised dome on the upper leaf surface of *Cryptocarya mannii*. Each adult female lives within a chamber gall that is approximately ovoid. The gall projects on both upper and lower leaf surfaces. The opening of the gall is sealed by the sclerotised dorsal shield and anal lobes of the adult female. Wax secretions were not seen (Fig. 4D).

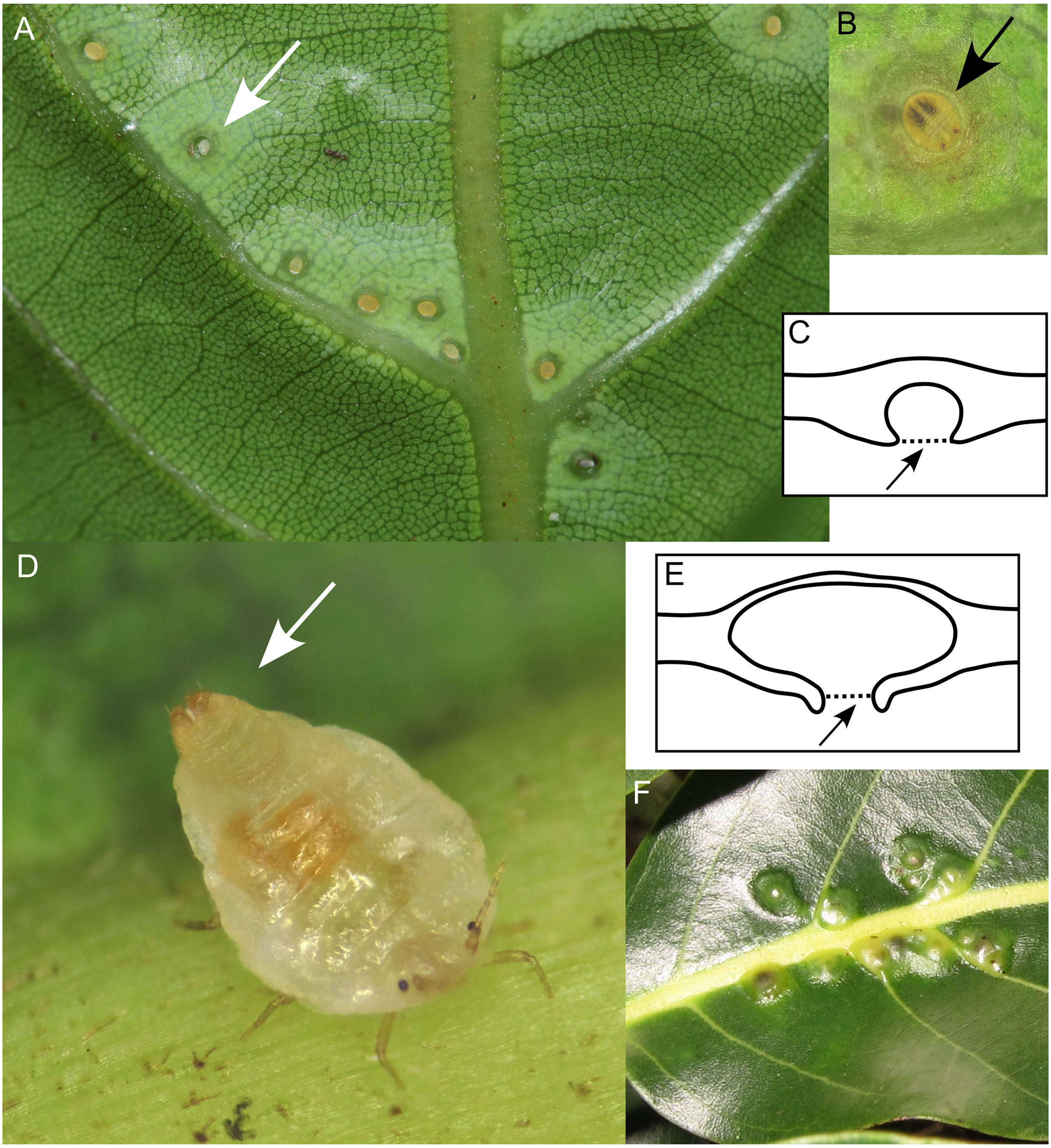

FIGURE 4. A. Galls of triozid psyllid, *Paurotriozana adaptata* Caldwell, distributed along midrib and veins on underside of leaves of *Cryptocarya mannii* (arrow indicates vacated gall cavity); **B**. *Pa. adaptata*, last-instar immature psyllid with dorsal surface close to surface of the gall; **C**. Illustration showing the shape of the psyllid gall in cross section (dotted line indicates position of the dorsal surface of the immature psyllid); **D**. Adult female *Ph. cryptocaryae* after removal from gall chamber (arrow indicates oval anal shield); **E**. Illustration showing the shape of the mealybug gall in cross section (dotted line indicates position of the dorsal surface of the anal shield); **F**. *Cryptocarya mannii* leaf showing protrusions on the upper leaf surface caused by the galls of *Ph. cryptocaryae*. Photographs by Karl Magnacca.

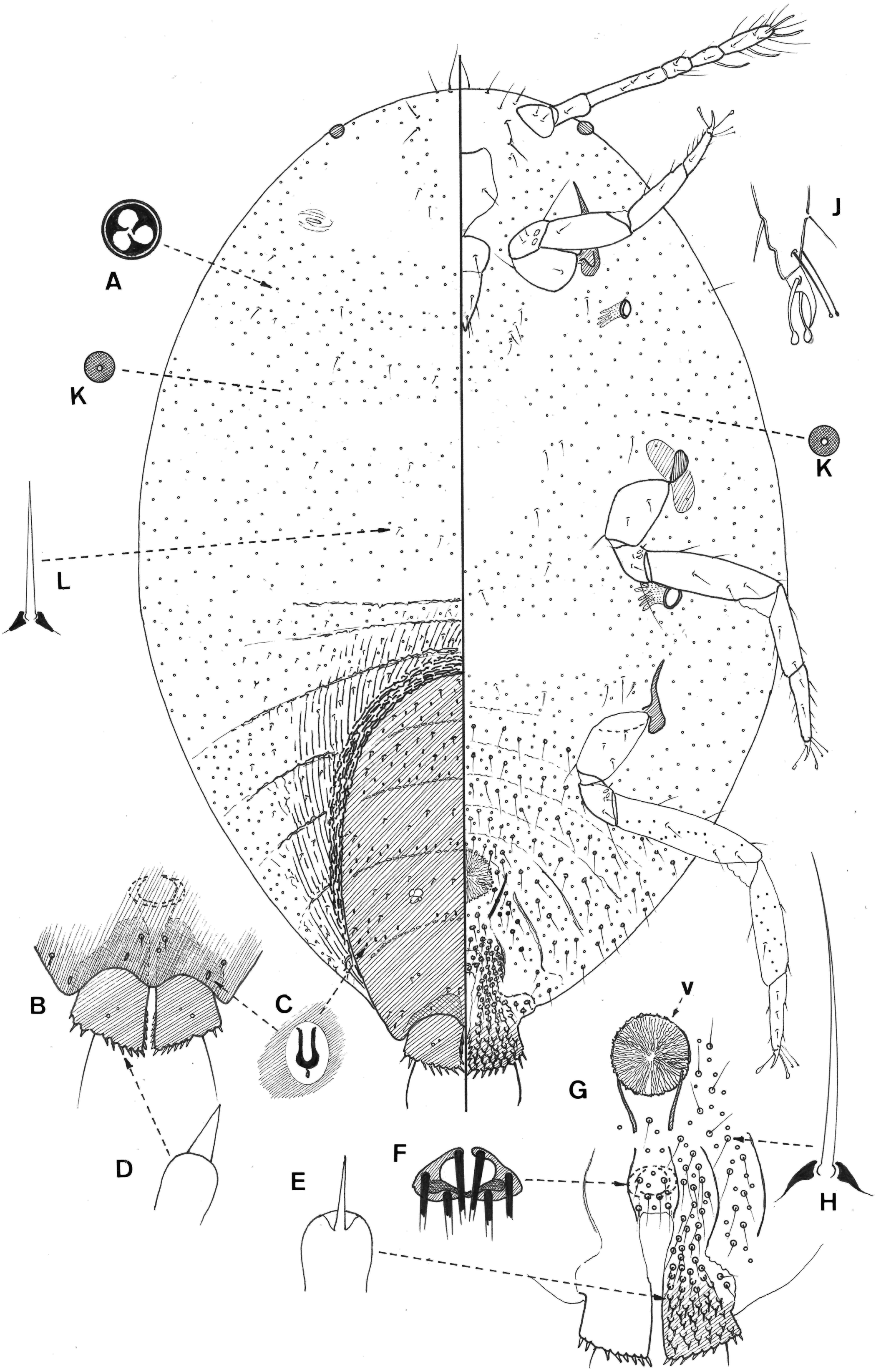

FIGURE 5. Adult female of *Phyllococcus cryptocaryae* Percy, Watson & Hodgson, **sp. n. A**. Trilocular pore; **B**. Dorsal view of anal plates; **C**. Oral collar tubular duct; **D**. Spinose seta along posterior margin of anal plate; **E**. Stiff seta on elongate, boss-like setal socket on ventral surface of anal plate; **F**. Shape of anal ring; **G**. Ventral view of posterior end of abdomen, showing anal lobes, position of anus and large vulva (v); **H**. Seta on posterior of abdomen with convex setal socket; **J**. End of tarsus plus claw; **K**. Simple pore; **L**. Dorsal seta.

Slide-mounted adult female (Fig. 5) (based on 4 damaged specimens). Body broadly oval to almost circular in mature specimens, 1.24 (1.15–1.45) mm long, 0.82 (0.82–1.33) mm wide, oval, with a strongly sclerotised dorsal shield covering most of abdomen; large clear areas present on dorsum, especially around the ostiole, and on venter of thorax; pores and setae absent in intersegmental areas. Anal lobes each approximately quadrate, with inner margins closely aligned but with spinose setae along posterior and inner margins, also on ventral surface. Ostioles poorly developed, not found on abdomen but a single ostiole found anteriorly on holotype, poorly developed and lacking trilocular pores and setae. Antennae (n = 3, other antennae broken off) normally 6 segmented, or 7 segmented with pseudoarticulation in segment III; total length about 340 (336) µm long; segment III approximately same length as or slightly longer than apical segment, sometimes partially divided. Antennal segment lengths in µm (including pseudoarticulation, present in only 1 specimen): scape (segment I), 69 (47–69); segment II, 48 (36–48); IIIa, 34 (34–60); IIIb, 52 (34–52); IV, 34 (34–38); V, 42; and VI, 87 (85–91); setal distribution as follows: scape, 4 (2 or 3) hair-like, 0 fleshy; segment II, 2 (2 or 3) hair-like, 0 fleshy; IIIa, 0 (or 1) hair-like, 0 fleshy; IIIb, 2 (2 or 4) hair-like, 0 fleshy (n = 3); IV, 2 (2 or 5) hair-like, 0 fleshy; V, 4 (2) hair-like, 1 large fleshy (n = 3); and VI, 10 (12 or 17) hair-like, 1 large and 3 small fleshy. Legs well developed, fairly slender, with coxae subequal in length; trochanters well developed, each bearing 2 campaniform sensilla on each surface; hind legs with translucent pores, numerous on posterior surface of femur, fewer on hind tibia; lengths of hind leg segments: coxa 127 (127–143), trochanter + femur 253 (253–279) (n = 3), tibia + tarsus 255 (255–257) (n = 2); tarsal and claw digitules capitate, equal in size, claw digitules exceeding tip of claw; claw fairly well developed, 26 (26–31) long (n = 3), moderately curved, without a denticle. Ratio of lengths of hind tibia + tarsus to hind trochanter + femur 0.92–1.01 : 1; ratio of lengths of hind tibia to tarsus 1.59–1.66 : 1. Labium long, only slightly shorter than clypeolabral shield; clypeolabral shield 145 (145–159) µm long (n = 3), relatively short and rounded; labium 3(?) segmented (basal segment not clearly visible), 120 (113–120) µm long. Spiracles quite large, peritreme widths in µm: anterior 35–40; posterior 40–45. Circuli absent. Cerarian setae absent (or represented by spinose setae along margins of anal plates). Vulva (v) particularly large and obvious, 93–108 across, situated ventrally between segments VII and VI. Anal ring (F) present at base of anal cleft, 60 (59–64) µm in diameter, with 2 rows of small pores (not illustrated) and 6 long setae (each about 85–100 µm); ring hidden under dorsal sclerotised shield (B), perhaps located at inner end of a short anal tube (G). Eyespots well developed, each situated just lateral to scape; convex, without associated pores, 32 (32–40) µm in diameter.

Dorsum: mainly membranous but with a heavily sclerotised, oval shield or plate, 475 (455–502) µm long and 343 (336–430) µm wide, formed medially from abdominal segments III–VII; 4 intersegmental membranes visible on shield, each represented by a dark line with small oval clear areas; shield raised above surrounding abdominal segments by a narrow band of sclerotised ridges. Segment VI with a small group of areolations submedially. More marginal areas of dorsal abdomen membranous initially, becoming somewhat sclerotised with maturity, sclerotisation spreading out from shield. Anal lobes (B) rather square, also heavily sclerotised, apparently flattened, without setae on dorsal surface but with 2 small pores; each anal lobe with about 8 spinose setae (D) along posterior margin, each situated on a raised boss (longest seta about 11 µm long, boss 8–10 µm long); also with a long, flagellate anal lobe seta towards outer margin, 49 (44–49) µm long, but sometimes shorter and more spinose; lobe inner margin also with about 4 or 5 spinose setae, each about 5 µm long, pointing somewhat posteriorly. Abdominal segment VIII probably represented dorsally by membranous folds under posterior margin of segment VII (cross-hatched area in B). Setae on shield all very short and setose, each about 8–10 µm long. Shield without trilocular pores but with small oral collar tubular ducts (C), all of same size, each with outer ductule about 3.0 µm long and 1.5 µm wide, these sometimes situated in a paler, less-sclerotised area of derm; present throughout anterior segments of shield but becoming restricted to along posterior margin on VII; tubular ducts absent from elsewhere on dorsum. Rounded, obscurely trilocular pores (A), each 3.0–3.5 (3.0–3.5) µm in diameter, present throughout but not abundant (but see discussion below). Simple pores (K), each about 2 µm wide, present very sparsely throughout. Other types of pore absent. Dorsal setae (L) flagellate, mostly each 20 (14–35) µm long, usually with a somewhat raised basal socket; very sparse.

Venter: membranous except for ventral surfaces of anal lobes, which are probably sclerotised. Slender flagellate setae present on head and thorax, with a group of about 16–18 between antennae, longest up to 65 µm long, generally with somewhat raised basal sockets; setae sparse on rest of head and thorax; with a group of 4 or 5 larger setae medial to each procoxa, 0 or 1 anterior to each mesocoxa, and a group of about 3 anterior to each metacoxa. Abdominal segments anterior to vulva each with a transverse band of flagellate setae, 2–4 setae deep, more abundant than anteriorly, but with setal sockets more strongly convex (H), setae becoming larger and setal sockets more convex posteriorly, particularly on segment VIII; setae on either side of vulva, each about 16–20 µm long; setae then tending to become shorter and more spinose further posteriorly, with sockets becoming more pronounced; setae on anal lobes narrow and stiff, each 12–16 µm long, with elongate, boss-like sockets each up to 12 µm long. Trilocular pores (A) similar to those on dorsum, present throughout (including on all abdominal segments) but absent from anal lobes; perhaps densest lateral to spiracles. Simple pores (K) as on dorsum. Multilocular and quinquelocular disc-pores and tubular ducts absent. Just anterior to anal ring are a pair of narrow finger-like processes (see G) which extend towards the vulva, each about 38–50 µm long; their homologies are unknown.

Remarks. A study of the third-instar female (see below) found that obvious ostioles were present between the two posteriormost segments of the dorsal shield, clearly indicating that the posteriormost segment of the shield is segment VII. The anal lobes of mealybugs are considered to represent segment VIII which, on normal mealybugs, extends anteriorly around the anal ring. This part of segment VIII is not visible on the dorsum of *Ph. cryptocaryae* but it is here considered to lie under segment VII on either side of the anal cleft (represented in Fig. 5B by a cross-hatched area). The pores found throughout the membranous part of the derm (both dorsal and ventral) are here considered to be rounded trilocular pores. However, their structure is extremely difficult to determine (even at high magnification), with some looking more like setal sockets, but others like small multilocular disc-pores. Occasionally some were found that appeared to be trilocular, as illustrated in Fig. 5A.

Phyllococcus cryptocaryae is the second species of *Phyllococcus* to be described. The morphology of the adult female differs from the type species, *Ph. oahuensis* (described above), in having the following character states (*Ph. oahuensis* character states given in parentheses): (i) body oval (tadpole-shaped, narrowing posteriorly); (ii) dorsal sclerotised shield composed of dorsum of abdominal segments III–VII + anal lobes (composed of segments V–VII + anal lobes); (iii) legs long and slender (short and robust); (iv) translucent pores restricted to femur and tibia of hind legs (also present on trochanter and tarsus); (v) oral collar tubular ducts present on sclerotised shield (absent); (vi) each anal lobe with 8 spinose conical setae along posterior margin (conical spinose setae restricted to 2 on apex); (vii) long setose seta on each anal lobe arising from posterior margin (arising from ventral surface); (viii) trilocular pores present on venter of almost all abdominal segments (only present on segments II–IV); (ix) ventral setae abundant on venter of posterior abdominal segments (very sparse); and (x) the gall is rounded and dome-shaped (horn-shaped, tapering to a point).

It seems likely that the heavily sclerotised dorsal shield in combination with the flattened, heavily sclerotised anal lobes is used to prevent access by predators and parasitoids. The anal lobes appear to fit closely into the rear margin of the sclerotised dorsal shield (as in Ferris' figure of *Ph. oahuensis*, see Fig. 2B), allowing the lobes to be opened and closed to permit ejection of honeydew. Whilst there are several significant morphological differences between *Ph. oahuensis* and *Ph. cryptocaryae*, the similarity of the structure of the sclerotised dorsal shield, and the distribution restricted to the Hawaiian archipelago, strongly suggests that these two species are congeneric and probably sister taxa but with substantial morphological divergence evident between the two species.

Third-instar female nymph (Fig. 6)

Note. There are two specimens: one is clearly pharate, with the body of the adult clearly visible, but this specimen is badly damaged and missing a large part of head and thorax; the other is not pharate, but has a twisted membranous thorax and head, making it difficult to distinguish dorsal from ventral derms. Locating structures such as the anterior ostioles was therefore not possible. It is here assumed that the distribution of the trilocular pores and setae is similar to that of the adult.

Slide-mounted specimens: very similar to a smaller and less-developed adult female. Body length about 1.25 mm, width about 0.46 mm; elongate oval, perhaps slightly more pointed at posterior end. Dorsal abdomen with an oval, strongly sclerotised shield or plate covering most of abdomen, about 365 µm long, 370–395 µm wide. Anal lobes apparently rather flat dorsally, with inner margins slightly divergent, each lobe triangular and pointed, 80 µm long, with 2 spinose cerarian setae (M) medially on dorsal surface (B); with 2–4 spinose setae along posterolateral margin (D) and 3 or 4 on inner margin; also with a long flagellate seta (about 60 µm long) on posterolateral margin (B); and with rather spinose setae on ventral surface (G). Antennae each 6 segmented, about 315 µm long, segments V and VI with large fleshy setae. Legs well developed, each with capitate tarsal and claw digitules (tarsal digitules

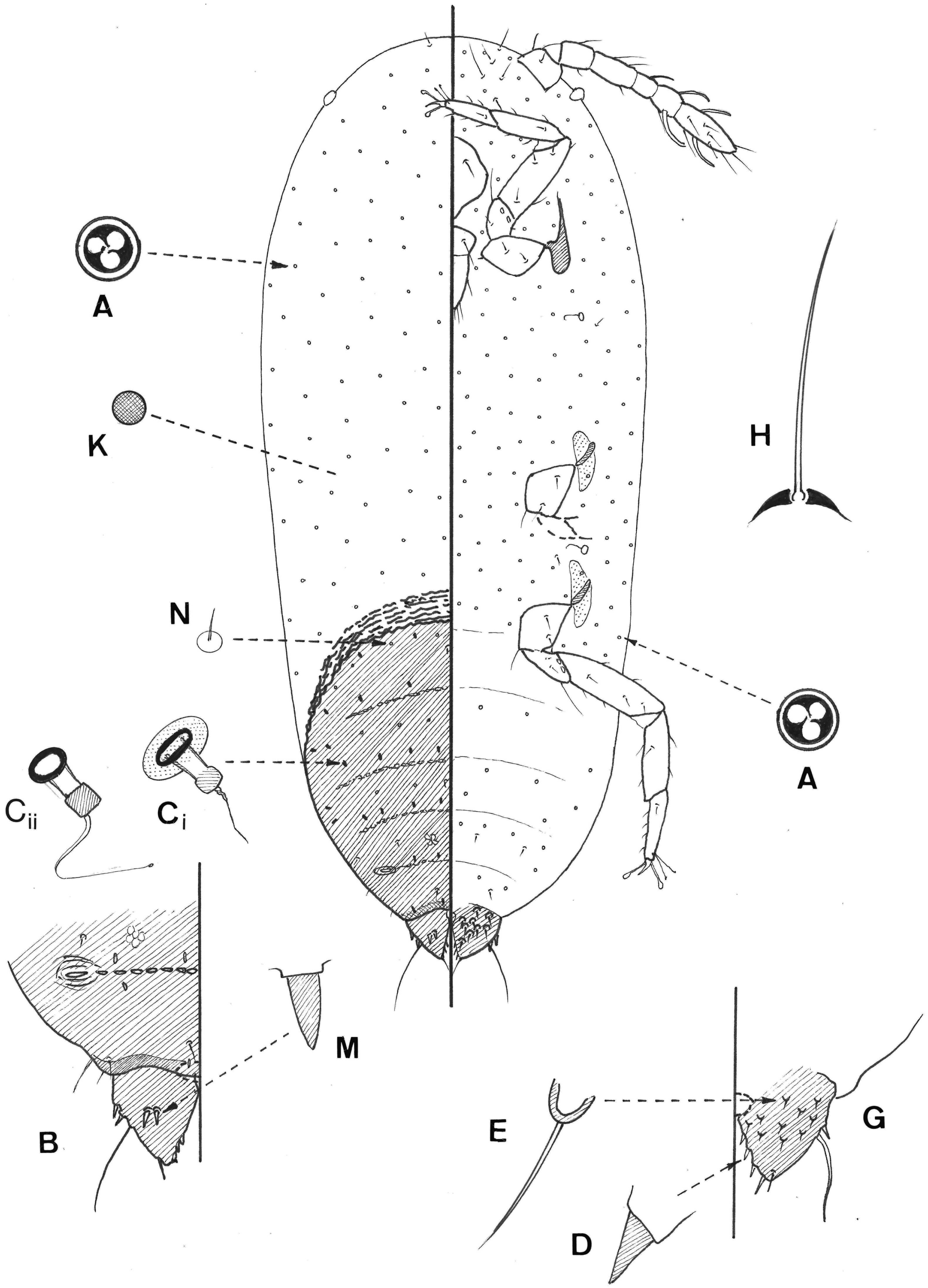

FIGURE 6. Third-instar female nymph of *Phyllococcus cryptocaryae* Percy, Watson & Hodgson, **sp. n.** **A**. Trilocular pore; **B**. Dorsal view of anal plates showing cerarian setae; **Ci**. Oral collar tubular duct on third-instar nymph; **Cii**. Oral collar duct on pharate adult female within second-instar nymph; **D**. Spinose seta along inner margin of anal plate; **E**. Seta on elongate setal socket on ventral surface of anal plate; **G**. Ventral view of posterior end of abdomen, showing position of anus; **H**. Ventral seta with convex setal socket; **K**. Simple pore; **M**. Spinose cerarian seta; **N**. Very small dorsal setae on shield.

missing but sockets present); claw without a denticle; segment lengths (µm): coxa 11, trochanter + femur 170, tibia 92, tarsus 88 and claw 23. Labium and clypeolabral shield distorted. Spiracles rather small, width of each peritreme 16–18 µm. Circuli absent. Cerarii represented by a pair of spinose setae, each about 13 µm long, on dorsal surface of each anal lobe. Anal ring with pores and 6 long setae; ring hidden beneath posterior margin of dorsal shield. Posterior ostioles present between segments VII and VI on sclerotised shield but anterior pair not detected; ostioles lacking both pores and setae. Eyespots well developed.

Dorsum: very similar to that of adult female, but sclerotised shield extending full width of abdomen; shield with very small setae (N), each only about 4 µm long, and oral collar tubular ducts (C) as on adult but structure of latter more clearly visible, each 6–7 µm long and about 1.5 µm wide, with a long inner filament; more lateral membranous areas of abdomen not visible (this part may be damaged); segment VI with a pair of submedial areolations. Morphology of anterior part of dorsum uncertain but probably with sparse trilocular pores, simple pores and flagellate setae as on venter.

Venter: very similar to that of adult female, membranous throughout but with venter of anal lobes probably sclerotised. Multilocular and quinquelocular disc-pores absent. Trilocular pores (A) sparse, possibly becoming even fewer on abdomen. Simple pores (K) present but very sparse. A few setae (H) present, mostly each 12–25 µm long, but those between antenna up to 100 µm long; some setae set on rather convex setal sockets, but those on abdomen anterior to anal folds not enlarged as on adult. Each anal lobe with about 10 rather stiff setae on ventral surface (G), each seta on a very convex setal socket.

Remarks. Clearly, by the third instar, the gall is already well developed and the shield-like dorsal sclerotisation is being used to plug the gall's orifice.

Second-instar female nymph

Note. Only a single, rather distorted, late pharate specimen available, which was too twisted to illustrate.

Slide-mounted specimen: body about 860 µm long and about 460 µm wide. Derm membranous throughout, lacking any signs of sclerotisation dorsally on abdomen and anal lobes. Derm with sparse small trilocular pores, smaller dark simple pores and setae, each 8–20 µm long. Membranous ostioles without pores or setae present at either end of intersegmental membrane between abdominal segments VI and VII. Antennae each 6 segmented, 260–275 µm long, possibly lacking a fleshy seta on segment V. Spiracles each with peritremes about 12–14 µm wide. Length of metathoracic leg segments (µm): coxa 85, trochanter + femur 165; tibia 115, tarsus 100 and claw 23 long; claw and tarsal digitules capitate; claw without a denticle.

Remarks. It is clear that the sclerotised shield on the dorsum of the abdomen does not develop until the third-instar nymph.

Ferris (*in* Zimmerman, 1948), when discussing the family placement of *Phyllococcus*, wrote: "Whilst the genus lacks the most characteristic features of the Pseudococcidae, namely dorsal ostioles, definite cerarii, circulus and distinctive tubular ducts, the presence of trilocular pores and the character of the antennae definitely indicate its assignment to this family". In the present study, we found that *Ph. cryptocaryae* has: (i) dorsal ostioles in the third-instar nymph (posteriorly), and adult female holotype (anteriorly) (ii) oral collar tubular ducts, and (iii) translucent pores on the hind femur and tibia. *Phyllococcus* clearly belongs to the Pseudococcidae therefore. It is worth noting that oral collar tubular ducts are also present in the abdomen of the third- and second-instar nymphs.

Host range. *Phyllococcus cryptocaryae* has only been found on *Cryptocarya mannii*, a tree endemic to the Hawaiian Islands and known only from the islands of Kauai and Oahu. It is likely that the mealybug is host-specific, like many gall-inducing insects, in which case it is highly endangered. Its host-plant species is on the IUCN Red List of Threatened Species, and although on Kauai the host is relatively abundant in several populations in numerous locations, only this one mature tree is currently known on Oahu (Morden *et al*. 2015). At least 10 trees on Kauai were checked recently (2015–2022) for galls (Dr Karl Magnacca, pers. comm.) but none were found there.

Biology. No males of *Ph. cryptocaryae* have been found so far but the male of *Ph. oahuensis* is described above. In mealybugs, the absence of multilocular disc-pores around the vulva (as is the case in both species of *Phyllococcus*) is often associated with vivipary and both species are probably viviparous.

Etymology. The new species is named after the genus of its host-plant, *Cryptocarya* R.Br., on which it induces leaf galls. The epithet is in the Latin genitive case, meaning "on *Cryptocarya*".

Galls

All the leaf cavity galls previously recorded from *Cryptocarya mannii* had been assumed to be induced by the triozid psyllid, *Paurotriozana adaptata* (Hemiptera: Psylloidea: Triozidae). These psyllid galls can be relatively numerous on the underside of leaves, often adjacent to the leaf midribs and veins (Fig. 4A) (Zimmerman 1948). The galls are typical of galls induced by a pit-galling triozid, with a relatively shallow circular cavity within which the immature insect is tightly encased with only the chitinised dorsal surface of the psyllid visible, more-or-less flush with the surface of the gall (Figs 4A, 4B, 4C). The vacated cavities of these psyllid-induced galls can also be seen containing the last instar immature exuviae (indicated by arrow in Fig. 4A). The galls induced by *Ph. cryptocaryae* appear to be less numerous and, although superficially similar to the psyllid galls in appearance, in particular with a similar-sized rounded gall opening on the lower leaf surface, are formed of a larger chamber within the leaf lamina (Fig. 4E), resulting in a more noticeably raised dome on the upper leaf surface (Fig. 4F). The galls induced by *Ph. cryptocaryae* are more lignified than those of the psyllid, with a raised lip around the gall opening (Fig. 4E), similar to that described and illustrated by Ferris (*in* Zimmerman 1948) around the opening of the gall of *Ph. oahuensis* (Fig. 2Z). When cut open, the largest of these chamber galls of *Ph. cryptocaryae* was found to contain only an adult female, with the gall orifice tightly plugged by the oval sclerotised anal shield (indicated by an arrow in Fig. 4D), and the surface of the shield just below the rim of the gall opening (Fig. 4E). Four galls were dissected.

Key to the adult females of *Phyllococcus* species

1. On *Touchardia sandwicensis* (Urticaceae). Gall triangular or "horn-shaped", narrowing towards apex (Fig. 1). Sclerotised dorsal shield composed of abdominal segments VII, VI and V only. Anal lobes each triangular and pointed, with 2 spinose setae on apex. Translucent pores on hind legs present on trochanter and tarsus as well as femur and tibia .... *Phyllococcus oahuensis* (Ehrhorn)

\- On *Cryptocarya mannii* (Lauraceae). Gall rounded or "domed", not narrowing significantly towards apex (Fig. 4 E). Sclerotised dorsal shield composed of abdominal segments VII–III. Anal lobes rather square, with spinose setae all along margin. Translucent pores on hind legs restricted to femur and tibia .... *Phyllococcus cryptocaryae* Percy, Watson & Hodgson, **sp. n**.

Discussion

The majority of gall-inducing scale insects (Coccomorpha) are found among the eriococcids (family Eriococcidae), a group that has diversified spectacularly in Australia (Cook & Gullan 2004; Gullan *et al*. 2005). Far fewer gall-inducing species are known among the mealybugs (Pseudococcidae) and, among the soft scales (Coccidae), only two species (*Cissococcus* species from South Africa) are known that induce a complex species-specific covering gall (Hodgson *et al*. 2011). In a review of gall-inducing coccoids, Beardsley (1984) noted that obligate gall-inducing mealybugs have rarely been recorded outside the Hawaiian Islands (see also Gullan *et al*. 2005), and a remarkable feature of the endemic Hawaiian mealybug fauna is the uncommonly high number of gall-inducing species, including the only mealybug species known to cause galls on pteridophytes (Beardsley 1984). He also believed that the gall-inducing habits in the Hawaiian Islands evolved independently several times (Beardsley 1984), driven by predator avoidance (Beardsley 1997). Cook & Gullan (2004) showed that multiple origins of the gall-inducing habit in the eriococcids was probably driven by selective advantages to the gall-inducing species. However, the selection strengths of the different advantages to gall induction, as well as the sequence of evolutionary steps in the transition to and maintenance of gall induction are still open to debate (Stone & Schönrogge 2003). In the scenario proposed by Beardsley, predation avoidance is the most likely initial driver for the evolution to gall induction, as well as potentially the different gall phenotypes, and thereafter the nutrient and microenvironment advantages that accrue from this habit may play a larger role in the persistence of the gall-induction habit.

Beardsley (1997) considered that the mealybug fauna of the Hawaiian Islands had been poorly studied at the close of the 20th century; and to date, few advances have been made on this group. He surmised that the scarcity of knowledge of endemic Hawaiian mealybugs was partly due to the species often being cryptic and occupying habitats such as living in plant galls, rolled leaves, under bark, and leaf sheaths of grasses, requiring careful and time-consuming examination (Beardsley 1997). The galls induced by *Ph. cryptocaryae* on *Cryptocarya mannii* had been observed previously but were assumed to be caused by the psyllid, *Paurotriozana adapata*. It was not until 2014, when DP dissected galls to obtain psyllid specimens, that the mealybug was discovered and the subtle differences in gall type between these two sternorrhynchan insects was noted. Beardsley (1984) also differentiated the Hawaiian mealybug gall-inducers into those species with less-specialised morphologies that caused simple galls, such as leaf-pocket and leaf-roll galls containing several individuals, frequently of both sexes and often of several developmental stages (e.g., the *Pseudococcus gallicola* Ehrhorn complex and *Pseudotrionymus* Beardsley species), versus the highly specialised group of gall-inducing species, such as *Phyllococcus oahuensis,* which induce a consistent species-specific gall phenotype typically containing a single individual.

Both in the context of sharing the same host plant and in the observed proximity of the different galls on the same leaves, this system of two gall-inducing sternorrhynchan insects, a psyllid and a mealybug, is remarkable. However, there is insufficient information about the phenology and potential synchronicity of these insects to permit us to infer how they interact, if at all. Of interest would be additional research on whether gall distribution and proximity in each of the species impacts the development and resource availability for the other species. Galls act as nutrient sinks (Chen *et al*. 2020), but little is known about the effects of multiple gall-inducing species co-occupying the same or adjacent plant organs, and the regulatory pathways involved in gall formation are still poorly understood (Takeda *et al*. 2021).

Interestingly, *C. mannii* is not the only endemic Hawaiian plant with co-occurring psyllid and mealybug gall-inducing species. The endemic woody plant *Metrosideros polymorpha* Gaudich. (Myrtaceae) (locally referred to as ohi'a) is host to the mealybug *Ohiacoccus cryptus* Beardsley, 1971, which Beardsley (1984) reported as causing pit galls on the host, as do a number of psyllid gall-inducing species in the genus *Pariaconus* (Percy 2017). Another notable similarity between these pit gall-inducing sternorrhynchan groups on *Metrosideros* is the preference in certain species for glabrous or pubescent morphotypes of the host plant (Beardsley 1971, Beardsley 1984, Percy 2017). There is another mealybug found on *Metrosideros* that does not induce galls itself, *Gallulacoccus tenorioi* Beardsley, 1971, but is morphologically specialised to inhabit abandoned psyllid galls (Beardsley, 1984). Resource partitioning among ohi'a-feeding psyllids has been proposed as a driver of speciation as well as potentially causing shifts in gall type and gall position (Percy 2017); but these ohi'a-feeding psyllids involve a radiation of congeneric species, rather than suborder-level species interactions as is the case here. It would be insightful to investigate and compare the interactions and potential resource competition between co-occurring mealybugs and psyllids, particularly as we now know of at least two hosts in the Hawaiian Islands that are possible study systems.

There is considerable concern for the long-term survival of both the psyllid, *Paurotriozana adaptata*, and the mealybug *Ph. cryptocaryae*. Neither of these endemic insect species are known outside Oahu; indeed, they are currently only known from the one remaining mature tree on Oahu. Examination of *C. mannii* trees on the island of Kaui did not locate any infestations of *Pa. adaptata* or *Ph. cryptocaryae* or evidence of galling on the leaves (Dr Karl Magnacca, pers. comm.). As the abundance of *Ph. cryptocaryae* appears even lower than that of the co-occurring psyllid, ongoing survival and conservation of *Ph. cryptocaryae* is considered highly tenuous, particularly considering attempts to propagate *C. mannii* on Oahu face considerable challenges (Morden *et al*. 2015).

Although Moir (2021) listed the related mealybug species and only other member of *Phyllococcus*, *Ph. oahuensis*, as extinct, previously unpublished records we report here of populations on Maui are a positive in an otherwise bleak conservation picture for this endemic mealybug genus. However, *Ph. oahuensis* has not been recorded in recent years from two islands where it was previously collected, Oahu and Lanai, and another trophic level can now be added to a possible local co-extinction scenario with our discovery of a parasitoid larva, almost certainly undescribed, in one of the *Ph. oahuensis* specimens collected on Lanai in 1913.

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Author contributions: DP undertook the field collecting, GW and CH prepared the descriptions, DP and CH prepared the figures and illustrations, all three authors wrote the paper.

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