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The genus *Acerocephala* and observations of the life history of *Acerocephala hanuuanamu* sp. nov. (Hymenoptera, Cerocephalidae) and its bark beetle host on the island of O‘ahu, Hawai‘i

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Abstract

The behavior of *Acerocephala hanuuanamu* **sp. nov.** found parasitizing *Cryphalus brasiliensis* under the surface of wood in *Ficus microcarpa* trees on the island of O‘ahu in Hawai‘i is deduced from observations in naturally occuring branches, and from direct observation using specially designed “phloem sandwich” observation chambers which consist of tree bark peeled through the phloem layer from freshly cut branches and sandwiched between a sheet of aluminum and a sheet of plexiglass. *Cryphalus brasiliensis* beetles, found living in large numbers in the phloem tissues in *F. microcarpa* trees, were collected and placed into these chambers. They tunneled into the wood and reproduced, producing an active colony of all life stages. *Acerocephala hanuuanamu* wasps were then placed into the system and their behavior observed. Typical behavior, aspects of which were recorded in video and still images, was as follows. A female *A. hanuuanamu* enters the tunnels of the bark beetles. She digs through the debris in the tunnels in a search for larvae and pupae. *Cryphalus brasiliensis* prepupae construct a hard pupal chamber around themselves before they pupate, and upon encountering a larva in the tunnels or the exterior of a pupal chamber with a pupa inside, she adeptly turns around in the tunnel to sting it, either inserting her ovipositor directly into the larva or by laboriously pushing it through the hard shell of the pupal chamber.

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When finished stinging, she withdraws her ovipositor slowly and carefully, often extracting tissue from the beetle immature as a sheath around her ovipositor. This structure remains projecting from the larva or pupa, and then the wasp turns around and host feeds through this structure, in the case of a pupa at a substantial distance through the wall of the pupal chamber. Oviposition occurs on larval stages and pupal stages. The egg hatches and the larva develops as an ectoparasitoid on the beetle. When finished feeding, it detaches and pupates in the tunnel. Mating behavior is also described. In addition to *C. brasiliensis* in *F. microcarpa*, *A. hanuuanamu* was also observed attacking C*ryphalus mangiferae* in mango (*Mangifera indica*) branches. *Acerocephala ihulena* **sp. nov.** was also found on O'ahu parasitizing *Eidophelus pacificus* in hau (*Hibiscus tiliaceus*) branches, and is described. The genus *Acerocephala* is revised given the perspective resulting from these two new species and aspects of functional morphology observed in the behavioral studies, *Acerocephala indica* **comb. nov.** is transferred to the genus, and a key to the genus is provided.

Keywords
Cerocephalinae, cryptoparasitoids, functional morphology, observation chamber, parasitoids

Introduction

The behavior and life history of insects that live inside wood or other plant parts can be difficult to observe. Mechanically opening up the plant material usually results in disrupting many of its inhabitants and their scattering, and it can be difficult to deduce their behavior prior to disruption. Simply placing the arthropods themselves or opened plant parts in a container for observation alters the environment substantially, and it can be unreliable to connect observed behavior in such circumstances with natural behavior. In this study we report observations of the behavior of a new species of cryptoparasitic wasp in tunnels constructed by its host beetles in an observation chamber as a semi-realistic representation of the environment in which we have found this species naturally.

This study is far from the only attempt at documenting the behavior of bark beetles and their natural enemies in concealed habitats. There is a history of making observation systems similar to the one constructed and used in this study, called "phloem sandwiches," which are variations on the idea of compressing natural wood or artificial diet between two hard sheets, at least one of which is clear to permit observation of its inhabitants (Beanlands 1966; Gouger et al. 1975; Nagel and Fitzgerald 1975; Kinn and Miller 1981; Salom et al. 1986; Grosman et al. 1992; Taylor et al. 1992; Aflitto et al. 2014; Sharma et al. 2016; Vega et al. 2017). These methods create an environment where wood boring beetles are able to construct their own tunnels and behavior within the tunnels can be observed. The environment in such systems is, however, still somewhat manipulated and not totally consistent with systems encountered in nature. In recent years, observations of wood boring insects in truly natural situations have also been successfully attempted. Alba-Alejandre et al. (2018) used a series of micro-CT scans to track the lives of coffee berry borer beetles, *Hypothenemus hampei* (Ferrari, 1867), inside coffee berries. Rezende et al. (2019) also used x-ray radiographs to track the movements of a thrips species thought to attack the coffee berry borer inside coffee

berries. These methods produced clear records of the biology and behavior of these insects, but only in static images.

This study focuses on *A. hanuuanamu* sp. nov. (Hymenoptera: Cerocephalidae) found attacking *Cryphalus brasiliensis* Schedl, 1976 (Coleoptera: Curculionidae: Scolytinae) on *Ficus microcarpa* L.f. trees on the island of Oʻahu in Hawaiʻi. In this study we reared *C. brasiliensis* in phloem sandwiches until overlapping generations composed of all life stages were present, then introduced the wasps and studied and recorded their behavior.

The discovery of this and another species results in perspective that allows for a revision of the genus *Acerocephala* Gahan. Cerocephalinae was first described by Gahan (1946) as a subfamily of Pteromalidae, *Acerocephala* described as part of this subfamily and two species included, *A. atroviolacea* and *A. aenigma*. The subfamily was later revised by Hedqvist (1969). Bouček (1988) added a third species to *Acerocephala*, *A. pacifica*, but stated that it was of uncertain generic identity, appearing substantially different from the other two previously described species which are morphologically very close. Cerocephalinae was then raised to the family level, as Cerocephalidae, by Burks et al. (2022). A key to genera of Cerocephalidae is provided by Bläser et al. (2015). All Cerocephalidae with known biological information are parasitoids of beetles in cryptic habitats (Bouček 1988).

Methods

Species descriptions

Specimens collected from wood and other plant parts were examined and photographed using a Leica MZ16 stereomicroscope or Macropod Pro imaging system. Specimens were also dissected, examined, and photographed using an Olympus CX31 compound microscope. Terminology relating to morphological characters follows Gibson (1997).

Morphometrics were measured as shown in Fig. 1, morphometrics of the head all measured in full face view or in lateral view, whichever was less obstructed by the antennae, except hea.l which was measured in lateral view. Acronyms in Fig. 1 and descriptions of the measurements, following Klimmek and Baur (2018), are as follows:

vac.l Full length of head; longitudinal line even with posterior of vertex to anterolateral corner of face (excludes mandibles).

vol.l Vertex-ocular line; longitudinal line even with posterior of vertex to even with top of compound eye.

vey.l Length of vertex to bottom of eye; longitudinal line even with vertex to even with bottom of compound eye.

vsc.l Length of vertex to scrobes; longitudinal line even with vertex to even with top of scrobal depression.

vto.l Length of vertex to toruli; longitudinal line even with vertex to even with center of toruli

eye.h Height of eye; posterior margin to anterior margin of compound eye.

mdb.l Length of mandible; straight line distance between protruding lateral corner at base of mandible and tip of mandible.

hea.b Breadth of head; maximum width of head including eyes

eye.d Eye distance; minimum distance between compound eyes on front of face

hac.d Width of head at anterolateral corner; distance between anterolateral corners of face.

msp.l Malar space; anterior margin of compound eye to anterolateral corner of face

wot.l Width of ocellar triangle; distance between outer margins of posterior ocelli.

pol.l Posterior ocellar line; shortest distance between inner margins of posterior ocelli.

ool.l Ocellar-ocular line; shortest distance from margin of posterior ocellus to margin of compound eye.

fcc.l Length of facial concavity; length of mesal line from even with anteriolateral corners of face to anterior of declivitous region comprising front of face, at posterior margin of projected clypeus.

cly.l Length of clypeal projection; length from anterior reach of clypeal projection to its base at the declivitous region at front of face.

hea.l Thickness of head; in lateral view, thickest part of head perpendicular to general plane of face and ventral surface of the head, typically at the level of the compound eyes for the species described.

prn.l Length of pronotum; base of pronotum on dorsomedian line to occipital foramen.

prn.b Breadth of pronotum; maximum width of pronotum measured in dorsal view.

msc.b Breadth of mesoscutum; width of mesoscutum just anterior of tegulae, measured in dorsal view.

tsa.l Length of transscutal articulation; in dorsal view, distance between intersections of transscutal articulation and axillar carina.

tsm.l Medial region of transscutal articulation; distance between where scutoscutellar lines join with transscutal articulation.

sct.l Length of scutellum; along median line, transscutal articulation to apex of scutellum and frenum.

mtn.l Length of metanotum; in dorsal view, distance along median line from apex of frenum to apex of metanotum.

ppd.l Length of propodeal disk; in dorsal view, distance along median line from metanotum to even with apex of propodeum.

pps.d Width of propodeal disk; in dorsal view, distance between propodeal spiracles.

gso.l Length of gaster excluding ovipositor; apex of petiole to apex of metasoma not including ovipositor or ovipositor sheaths.

ovi.l Length of ovipositor; apex of metasoma not including ovipositor or ovipositor sheaths, to apex of ovipositor or ovipositor sheaths.

Body length was obtained by adding the length of the head from the anterolatertal corner of the face to the occipital foramen, the occipital foramen to the anterior of the tegula, the anterior of the tegula to the petiole, and the petiole to the apex of the abdomen.

Morphometric measurements are reported in Suppl. materials 1, 2.

Repositories

Specimens are deposited in the following museums:

UHIM University of Hawai'i Insect Museum, Honolulu, Hawai'i, USA
BPBM Bernice Pauahi Bishop Museum, Honolulu, Hawai'i, USA
NMNH Smithsonian National Museum of Natural History, Washington DC, USA

"Phloem sandwich" observation chambers

(Fig. 10c, d)

An apparatus was constructed for the purpose of observing the parasitoids and their hosts in an environment resembling the below-bark environment in which they naturally occur (Fig. 10c, d). These observation chambers, a variation on the idea of a "phloem sandwich," consist of thin sheets of host wood; bark peeled from a branch through the phloem or cambium layer, sandwiched between a plexiglass sheet and an aluminum sheet. Adult *C. brasiliensis* were introduced to the wood through holes in the plexiglass, and if the conditions were appropriate, they would then tunnel into the wood and lay eggs. When the resulting larvae were at a stage suitable for parasitization, and as the colony developed further, *A. hanuuanamu* sp. nov. adults were introduced into the environment and their behavior was observed. The *C. brasiliensis* beetles this wasp uses as a host live typically in the thin layer of wood straddling the cambium, so a two-dimensional representation of their environment such as used here is likely a reasonably accurate representation of their actual habitat. Videos of behavior were recorded using a Dino-Lite Edge Digital Microscope and photos were taken using either the same Dino-Lite Edge or a Canon DLSR camera with a macro lens.

Construction of observation chambers and initiation of beetle colonies within them

The "phloem sandwich" style observation chambers used in this study are shown in Fig. 10c–f. The bottom layer of the sandwich is a 9.0 cm square of 1/16 inch (approximately 1.6 mm) sheet aluminum. Above it is a spacer made from a 9.0 cm square of 1/16 inch sheet aluminum with a rectangular hole 5.1 × 6.3 cm cut out of the middle. The top of the sandwich is a 9.0 cm square sheet of plexiglass. Holes were drilled at each corner through all three sheets, and 1/4 inch (approximately 6.35 mm) bolts were used to clamp the sheets together with a piece of host wood in the middle. Two additional small holes were drilled through the plexiglass to introduce beetles to the

chamber. This thickness of aluminum was chosen for the separator layer because it is slightly larger than the width of the *C. brasiliensis* beetles, which assured that beetles could move through the apparatus. Because the beetles were most interested in the phloem and cambium layer facing the plexiglass, they tended to make their tunnels up against the plexiglass and the full width of the tunnels were usually visible through it.

Using a knife and a chisel, *F. microcarpa* bark was carefully peeled off a branch down to the xylem layer. Branches with bark just slightly thicker than the 1/16 inch separator were chosen so the wood would be compressed tightly between the top and bottom of the sandwich, accounting for slight shrinkage when drying. The resulting sheets of bark were cut into pieces approximately 4.3 cm by 5.5 cm so that when placed in the aluminum forms there would be space for the beetles to travel around the perimeter. The freshly peeled bark was clamped between two ¾ inch × 5 ½ inch (1.9 cm × 14 cm) cedar boards with small holes drilled in them for airflow and left to dry for a few days. The wood, still clamped between the two cedar boards, was then autoclaved. This process is similar to steam bending wood, and as such, the bark would maintain its flat shape when the boards were unclamped and the wood was removed. The aluminum, nuts, bolts, and washers were also autoclaved, and the plexiglass was soaked and cleaned with a 70% ethanol solution before assembly. The parts were assembled quickly under a laminar flow hood to limit contamination. Parafilm or hot glue was used to seal any imperfections in the edges of the sandwich.

The correct stage of decay and water content of the wood is important for the beetles. The wood had been left to age and dry for a few days when clamped between the cedar boards, and was then reinfused with water during the autoclave treatment. After the boxes were assembled, the beetles were entered into them through the two small holes in the plexiglass sheets and then the holes were covered with tape. The beetles would often remain outside the wood for some time. The two larger holes in the aluminum on the bottom side of the boxes were initially left uncovered, resulting in gradual drying of the wood. Beetles entering the wood was assumed to indicate that the water content and age of the wood was appropriate for them, and when this was observed, tape was stuck over the holes to prevent further drying. If the wood seemed to get too dry, the tape was removed and a few drops of water added into the holes to absorb into the wood. Using these methods, approximately 10 separate colonies were produced. The apparatus was illuminated for observation using natural sunlight or fiber optic gooseneck microscope lights powered by a halogen lamp.

Observation in naturally infested wood

Ficus microcarpa branches containing bark beetles were observed in place by peeling off bark from branches still attached to the tree, or by cutting branches and dissecting them. To facilitate locating wood at a desired stage of decay, fresh branches were also cut, suspended off the tree, and later dissected. All such observations were taken from wood on a large *F. microcarpa* tree located in an unmaintained area of the campus of the University of Hawai'i at Mānoa at (21.2954°N, 157.8145°W, 15 m) (Fig. 10a),

or from other trees in the immediate vicinity. Additional host records were found by dissecting wood from a variety of tree species and locations as a part of a larger survey of bark beetle natural enemies on Oʻahu.

Results

Acerocephala Gahan, 1946

Redescription. Head subrectangular in face view, somewhat thin and elongate in side view, flattened dorsoventrally and not globose (vac.l/hea.l approximately 1.7 or greater). Anterolateral corner of head a distinct angle, sides of face either progressively widening to this corner or mildly curved mesally to reach it. Mandibles long and arcing (mdb.l/hea.b approximately 0.5 or greater), placed widely on face, their lateral corners at or nearly at anterolateral corners of face. Anterior of face a concave arc; clypeus, which has its base near the ventral side of this arc, may be visible in dorsal view projecting into the space between the mandibles. Compound eyes placed nearer back of head than front, so that vey.l/vac.l ≤ 0.5. Antennae inserted well anterior of compound eye, funicle with 5 or 6 segments in female. Scrobes deep and extend posteriorly well behind toruli. Scrobes separated by interantennal ridge that extends well behind the toruli to join with the upper face, the ridge flattened or mildly curved dorsally and protruding or not from plane of the face.

Forewing with or without callus on parastigma, but the callus, if present, without a tuft of setae. Wing membrane with slightly rippled texture and without setae on its surface; stigmal vein short, postmarginal vein short if present. Males of some species may be wingless.

Diagnosis and differential diagnosis. This genus can be distinguished within Cerocephalidae by the combination of elongate rectangular, thin head shape (vac.l/hea.l ≥ 1.7); anterolateral corner of face a distinct angle, and with long mandibles placed with their outer edges near the anterolateral corner of the face; antennae inserted distinctly anterior of compound eye; forewing without a tuft of thick setae on callus on the parastigma, or lacking a callus, and without setae extending from its membrane; clypeus may project into space between mandibles from near ventral side of arc that comprises the anterior of the face, dorsal plane of head lacking a distinct anterior projection into space between mandibles.

Within Cerocephalidae, this genus appears closest to *Choetospilisca* (Fig. 9), *Paralaesthia*, and *Muesbeckisia*. It can be distinguished from *Choetospilisca* by the elongate rectangular shape of the head in dorsal view and long arcing mandibles extending from just inside the anterolateral corner of face; and broad interantennal ridge joining to the plane of the upper face. (*Choetospilisca* with head more globose in side view; face broadly tapers anteriorly, and thick but shorter mandibles extending from well inside the lateral edge). The overall shape of the face is similar to *Paralaesthia*, but it can be

distinguished by the lack of a tuft of thick setae on the callus of the parastigma; at most a small projection of the clypeus into the space between the mandibles, which has its base on the ventral side of the arc that comprises the front of the face; scrobal grooves posterior to toruli deep and separated by a large, broad interantennal ridge connecting to the upper face; lack of a mesal groove on the upper face; funicle segments slightly nodose-bead like or transverse (*Paralaesthia* with thick setae emerging from the callus; lower face anteriorly extended into a large triangular region between the mandibles, its base extending from the dorsal plane of the face; a mesal groove running the length of the upper face; scrobes shallow and not extended greatly posterior to toruli, interantennal ridge small and similarly not of much consequence posterior to toruli; funicle segments elongate cylindrical). It can be distinguished from *Muesebeckisia* by the more elongate head shape and location of antennal insertion well below the anterior margin of the eyes, and broad interantennal ridge. (*Muesbeckisia* with head globose, eye reaching the anterior half of the face, and antennal insertion above anterior margin of eye).

Acerocephala indica comb. nov.

Choetospilisca indica Saraswat & Mukerjee, 1975

Remark. This species was only known from the holotype (female), slide mounted, from Yercaud, in the Eastern Ghats of Tamil Nadu, India. What appears to be the same species was found in the NMNH collection, a female and male point mounted with this collection data: "PUERTO RICO // Santa Isabel // 21-VIII-1991 // S. Medina-Gand //// ex mango // branch dying // of fire //// #91-9140 // Acerocephala // n. sp. // det. // E. Grissell 1991" (female) and "PUERTO RICO // Santa Isabel // 21-VIII-1991 // S. Medina-Gand //// ex mango // branch dying // of fire" (male). See Fig. 6 for photos, and key for distinguishing characters.

Acerocephala hanuuanamu Honsberger & Lorenzo-Elarco, sp. nov.

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Figs 1–3, 10a

Diagnosis. Females of this species can be distinguished from other known *Acerocephala* by the antenna with the first four funicular segments transverse and of similar size and shape, followed by a larger and subcircular fifth segment and the clava; interantennal ridge flush with face, not elevated in lateral view, and only slightly widened anteriorly; scrobes reaching more than half the length of the head; submarginal and marginal veins of forewing join smoothly with no callus; clypeus, to its apex, fills the space between the mandibles when mandibles are closed. Males are similar to females in characters of the head with the exception of the antennae, so can be distinguished from other known species by these characters as well.

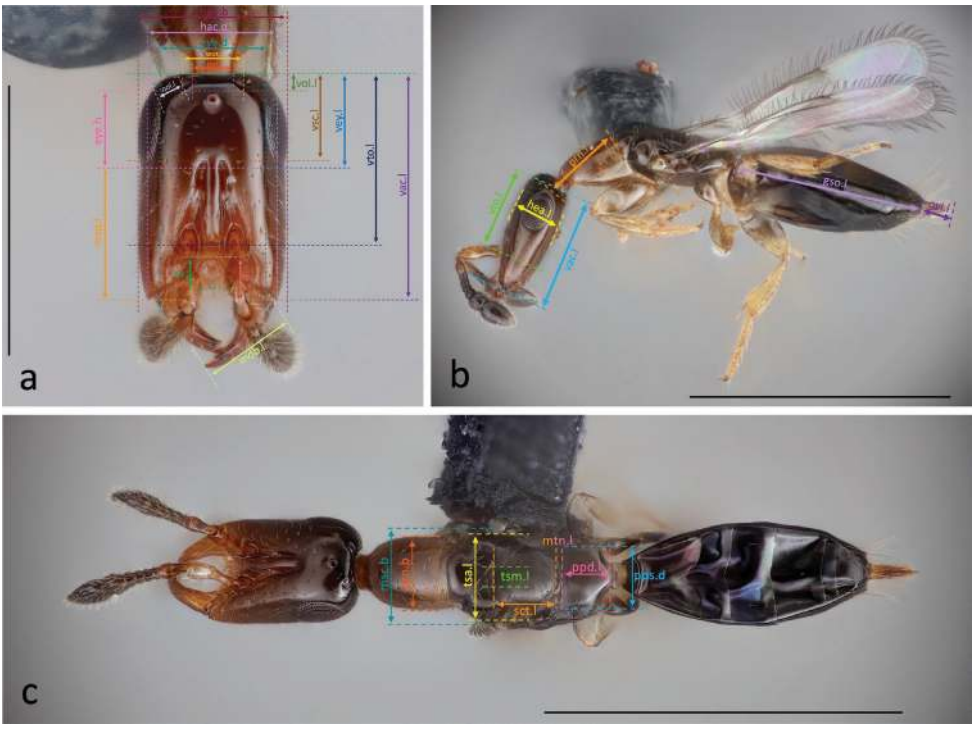


Figure 1. *Acerocephala hanuuanamu* sp. nov. (paratypes) showing morphometric measurements. Acronyms explained in text. Scale bars: 1 mm (**b, c**); 500 μm (**a**).

Differential diagnosis. Females are easily distinguished from *A. atroviolacea*, *A. aenigma*, and *A. pacifica* by the first four funicular segments much smaller and shorter than the fifth; overall gracility of the head and body; interantennal ridge not elevated from the face in lateral view (*A. atroviolacea*, *A. aenigma*, and *A. pacifica* with fifth funicular segment of similar size to preceding segments; body and head thicker and more robust; interantennal ridge elevated from the face in lateral view); and from *A. atroviolacea* and *A. aenigma* by lack of callus on the forewing (*A. atroviolacea* and *A. aenigma* with callus present).

A. hanuuanamu is closest to *A. ihulena* sp. nov. and *A. indica*. Females can be distinguished from *A. ihulena* and *A. indica* by interantennal ridge not elevated from the face in lateral view; first four funicular segments of similar size and distinctly smaller than the fifth; ovipositor sheaths only slightly exerted, extending less than 1/3 the length of the gaster; scutoscutellar grooves foveolate and meeting the transscutal articulation lateral of medial line (*A. ihulena* and *A. indica* with interantennal ridge elevated from the face in lateral view; fourth funicular segment slightly but distinctly larger than the first three; ovipositor sheaths distinctly exerted from the gaster, near half its length, dark brown at the apex and lighter near the base; scutoscutellar grooves a subcircular sulcus that reach the transscutal articulation mesally).

Description. Female (Figs 1, 2a–d, 3a–c, e–j, 10a; morphometric measurements in Suppl. material 1). ***Length*:** Variable, depending on size of host. On *C. brasiliensis* individuals range from 1.18–2.31 mm (Holotype 1.96 mm), the largest individual collected was 2.50 mm from *C. mangiferae*, a slightly larger beetle.

***Coloration*:** Head brown; slightly lighter anteriorly in lower face, basal part of mandibles, and scape and pedicel. Mesosoma brown, prothorax and apex of propodeum often somewhat lighter. Petiole yellow. Gaster dark brown except basoventrally where it is light brown, and the ovipositor sheaths which are light brown. Legs yellow-brown, pro- and metacoxae somewhat lighter in color than their respective tibiae.

***Head*:** Head subrectangular in full face view; more or less parallel sided, subtly widest across eyes, of nearly equal width at about half its length, and tapers very slightly to the anterolateral corner. Anterior of head, excluding the mandibles and projected clypeus, a strongly concave arc. Clypeus projected medially, subrectangular with slightly rounded base and longer than wide, to its apex occupies all the lateral space between the mandibles when mandibles are closed. Interantennal ridge flush with the face lateral of scrobes, not elevated dorsally from the face in lateral view; its anterior half, to about even with where the scrobes narrow, laterally carinate, dorsally smooth and slightly convex between the carinae; posterior to this non-carinate, more narrowly and evenly rounded, along the median line joining smoothly with the upper face. Lateral margins of scrobal depression just above the toruli extend approximately half the width of the face, lateral margins distinctly taper and at about half the length of the interantennal ridge where its carina ends; anterior of this the lateral margins are lightly carinate and the depressions deeper; posterior to this with rounded margins and the depressions become progressively narrower and shallow before they join with the upper face. Mandibles long and curved with three apical teeth; dorsal and middle tooth of a similar conical shape but with a deep groove between them, middle tooth projecting slightly more than dorsal tooth, ventral tooth projecting about twice this much relative to the middle tooth. Bottom of toruli adjacent to the dorsoventrally inclined arc that comprises the anterior of the face. Occipital carina just posterior to posterior ocelli, subcircular. Dorsal side of the face with smooth and shiny texture and with sparse setae, the setae increase slightly in length and density anteriorly, more densely placed short setae around the occipital carina. Ventral side of head generally flat with some longer setae posteriorly, median suture extends longitudinally from the mouthparts to the occipital carina, basal area near the suture indented slightly for about 2/5 the length of the head, the cuticle in this indent with reticulate texture, cuticle on ventral side of face otherwise smooth and shiny.

Antennal flagellum composed of 5 funicular segments and a subconical clava. First four funicular segments transverse cylindrical and of similar size and shape, 5th funicular segment subspherical and larger than the first four, clava is approximately 1.4 times as long as the first four flagellar segments, rounded subconical. All antennal segments with thin setae projecting at approximately 45 degrees, the first four funicular



Figure 2. *Acerocephala hanuuanamu* sp. nov. holotype ♀ (**a–d**) and allotype ♂ (**e–h**) **a, e** side view **b, f** head **c, g** anterior view of head showing mandibles **d, h** dorsal view. Scale bars: 1 mm (**a, d, e, h**); 250 μm (**b, c, f, g**).

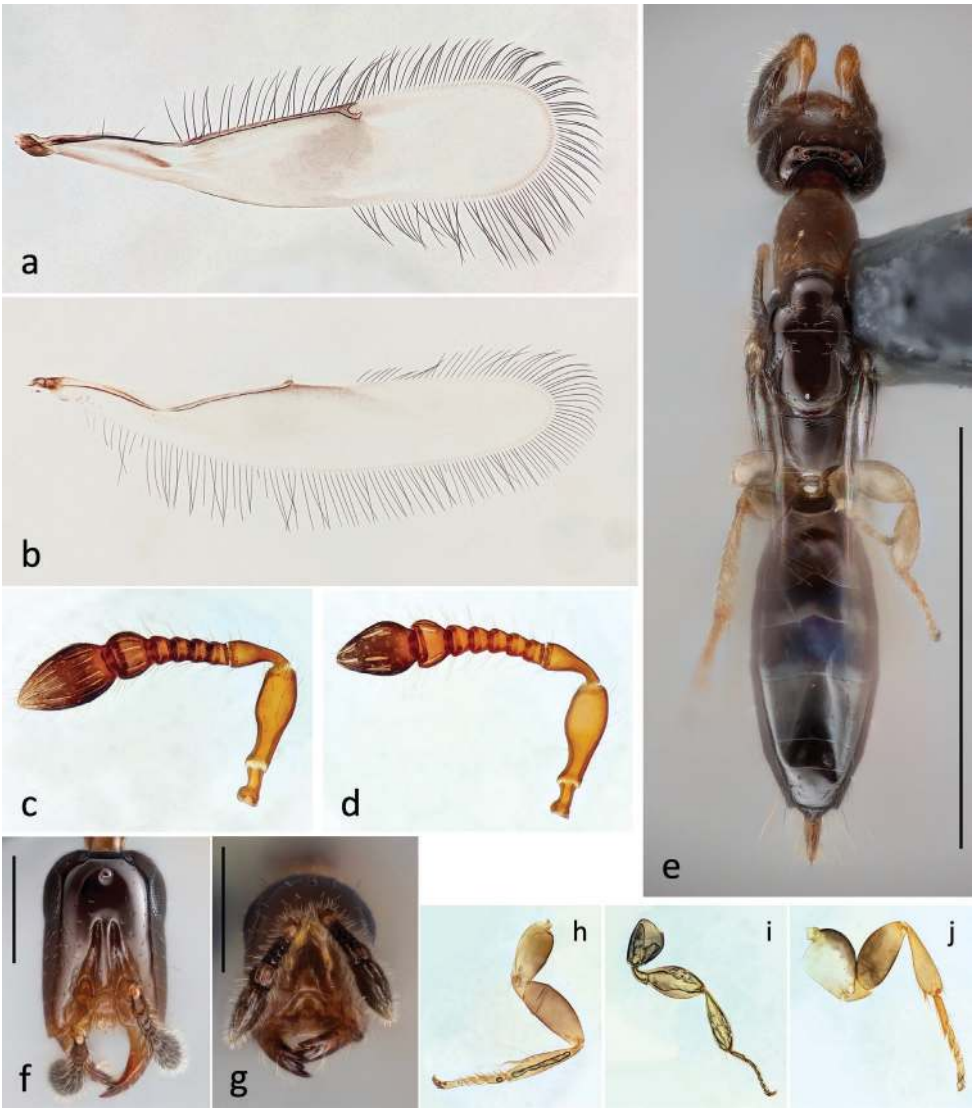


Figure 3. *Acerocephala hanuuanamu* sp. nov. **a** forewing ♀ **b** hindwing ♀ **c** antenna ♀ **d** antenna ♂ **e** dorsal view ♀ (paratype) **f** head ♀ (paratype) **g** anterior view of head showing mandibles ♀ (paratype) **h** foreleg ♀ **i** midleg ♀ **j** hindleg ♀. Scale bars: 1 mm (**e**); 250 μm (**f, g**).

segments with a single whorl of setae of length slightly less than the width of the segments, setae becoming progressively shorter towards the apex of the antenna. The 5th funicular segment with MPS and the clava with three whorls of MPS; the first four flagellar segments lack MPS. Mean length/mean width (Ratio) of antennal segments, length and width measured relative to length of F1 (n = 12): Scape 6.0/2.3 (2.7) ; Pedicel 3.4/1.7 (2.0) ; F1 1.0/1.5 (0.7) ; F2 0.9/1.5 (0.6) ; F3 1.0/1.6 (0.6) ; F4 1.1/1.8 (0.6) ; F5 2.5/3.0 (0.8) ; Clava 6.5/4.1 (1.6).

***Mesosoma*:** Long prothorax articulates with mesothorax, rotating from in line with the rest of the mesosoma to approximately 110 degrees. A light longitudinal carina present laterally on pronotal neck, pronotum otherwise smooth, lacking a transverse pronotal carina. Pronotal neck and collar smooth, collar with scattered mesal pointing setae except on its dorsal surface near the medial line where there are no setae. In dorsal view, pronotum very slightly widest near its middle, but at its widest distinctly narrower than the mesonotum. Transscutal articulation deep and well defined, straight until the lateral section where the sclerites incline vertically. Notauli and scutoscutellar suture both foveolate and visible relative to the otherwise smooth and shiny mesonotum, marked by punctures and a mild sulcus, setae on either side of the sutures, the notauli deepening anteriorly and giving the mesonotum a shouldered appearance. Lateral of the median line, notaulus and scutoscutellar suture meet the transscutal articulation at approximately a 45 degree angle and at approximately the same point, so the medial lobe of the mesoscutum and the scutellum run up against each other for a distance (see morphometric measurements). In dorsal view, scutoscutellar sutures are fairly straight until they meet the transscutal articulation, notauli are mildly curved. Posterior margin of scutellum evenly convex. Mesonotum smooth and glassy, free of setae except on either side of the notauli and on either side of the scutoscutellar suture, a few scattered setae on the axillae, and near posterior margin of the scutellum. Metanotum visible behind scutellum. Propodeum slightly wrinkled at its anterior margin and on the callus anterior of the spiracle, otherwise smooth and glassy, flat longitudinally and lightly rounded transversely. Propodeal spiracle slightly recessed in a small depression, paraspiracular sulcus a very slight and smoothly rounded depression continuing from the spiracular depression posteromedially and gradually fading. Sides of the propodeum slightly tapering posteriorly until above attachment of the rear coxae, where they abruptly taper to about 60 degrees from the anteroventral line, then curve to be slightly more longitudinally oriented toward their apex at the nucha, top of petiolar insertion flush with dorsal surface of propodeum. Setae near the lateral margins of propodeum: on callus anterior of the spiracle, on lateral margin where callus meets the metapleuron, and just above where the propodeum accommodates the hind coxal foramen. Mesopleuron with light reticulate texture, mesepisternum with setae.

***Wings*:** Forewing: Length of marginal vein approximately 1.15 × length of submarginal vein. Short postmarginal vein extends to approximately even with the stigma or somewhat less. Stigmal vein projects from marginal vein at slightly less than 45 degrees and has a slight curve apically. Three dorsal setae on marginal vein, basal one small and inconspicuous. Marginal setae begin at the base of marginal vein and continue around apex of wing with approximately consistent length to trailing edge approximately even with stigmal vein, just apical of retinaculum. Parastigma not swollen, submarginal and marginal veins joining smoothly and unperturbed with no swollen area or change in pigmentation; lacking any sign of a tuft of setae on the parastigma. Membrane subhyaline with slightly rippled texture and without setae; basally to end of venation lightly infuscated, the area near and posterior to stigma most shaded.

Hindwing: Venation with a concavity at approximately half the distance from the base to the hamuli, venation hyaline at the culmination of this concavity; anterior

margin of wing membrane extends more or less straight in this region so at the apex of the concavity the venation reaches nearly ½ the distance to the posterior of the wing membrane. Venation ends at the hamuli but the very anterior of the membrane in line with venation remains somewhat pigmented beyond the hamuli, to approximately 2/3 the length of the wing. Marginal setae present from the end of this pigmented region around to base of trailing edge of wing, longest around trailing edge where they are approximately ¾ the maximum width of the wing.

***Legs*:** Fore and rear coxae globose, subequal in size and shape though the fore coxa hides somewhat under the pronotum. Femora also globose, slightly larger than their respective coxae in the front and mid, legs, subequal in the back leg. Tibiae of similar length to their respective femora, also globose apically, but narrower basally. In all legs, first tarsal segment longest, 2nd through 4th segments sequentially decrease in length; 5th segment not including the claw intermediate between 1st and 2nd in front and middle legs, subequal to 2nd in back legs. Protibial spur deviates from straight with a jog of shape similar to a logistic function, its base set back on the tibia and extending just past base of first tarsal segment, tibia beneath the spur with protibial comb. Midleg and back leg with narrower, straight protibial spur extending from near the apex of the segment. Fore and midleg with the two basal tarsi of each leg spinose, spines fading on the apical segments; hindleg with spines smaller except for those at the apex of the tarsal segments. Tibiae with narrow setae and no additional spines, except for the very apex of the back leg.

***Metasoma*:** Petiole somewhat globose-vase shaped, the widest point marked by one or two lateral setae on a small knob; somewhat flat dorsally, overall of subequal length and width. First and second gastral segments emarginate medially, subsequent segments with straight posterior margin. Gaster in living individuals expands and contracts during feeding, use of the ovipositor, and movement; therefore the following applies to dried individuals. 1st and 4th gastral tergites longest, 3rd slightly shorter, 2nd substantially shorter than 3rd; 5th very short; 6th subequal in length to 2nd. Gaster not heavily sclerotized, shrivels slightly on drying. Gaster with few, small setae on first five segments, 6th with many setae, some short, some longer than the exserted ovipositor sheath, but rarely reaching past it due to their angle. Ovipositor sheaths also setose, and are slightly exserted; ovipositor thin and needle-like.

Male (Figs 2e–h, 3d; morphometric measurements in Suppl. material 1). ***Length*:** Typically, but not always, smaller than females developing in the same colony of hosts. As with the female, size depends on the size of the host, but the smallest individuals are nearly always male. Very variable, from 0.83–1.65 mm (allotype 1.60 mm).

Similar to female except: Wingless. Antennae with 6 funicular segments, similar to that of female except that the four similarly shaped basal flagellar segments in the female are five in the male, the sixth larger and subcircular; clava with two whorls of MPS. Mean length/mean width (Ratio) of antennal segments, length and width measured relative to length of F1 (n = 7): Scape 6.5/2.4 (2.7) ; Pedicel 3.7/1.8 (2.1) ; F1 1.0/1.4 (0.7) ; F2 1.1/1.5 (0.8) ; F3 1.1/1.6 (0.7) ; F4 1.2/1.8 (0.7) ; F5 1.4/2.1 (0.7) ; F6 2.1/2.9 (0.7); Clava 5.3/3.7 (1.5). Ocelli absent and compound eye smaller than in female, morphometrics of face otherwise similar, mandibles similar. Posterior region

of pronotum tapers slightly to fit around the narrower medial lobe of the mesoscutum. Notauli nearly meet on the medial line at the transscutal articulation, scutoscutellar suture meets transscutal articulation lateral to this, similar to the female. Pro- and mesoscutum smaller than in female, scutellum much shorter than in female, metanotum behind it appears in dorsal view nearly straight with nearly parallel anterior and posterior margins. Femora, tibiae, and tarsal segments somewhat stouter than in female, but their relative lengths remain similar. Posterior margin of propodeal disk with scattered setae. Gaster shorter, apically truncated-looking in dry specimens.

Materials examined. ***Holotype*** (Fig. 2a–d): ♀; Hawaiian Islands, Oʻahu, Mānoa; 21.2946°N, 157.8136°W; 2.viii.2022; below bark of *Ficus microcarpa* branch (deposited in UHIM).

Allotype (Fig. 2e–h): ♂; Hawaiian Islands, Oʻahu, Mānoa; 21.2946°N, 157.8136°W; 2.viii.2022; below bark of *Ficus microcarpa* branch (UHIM).

Paratypes**:** 65♀, 54♂. Hawaiian Islands, Oʻahu, Mānoa; 21.2946°N, 157.8136°W; 2.viii.2022; below bark of *Ficus microcarpa* branches; 57♀, 52♂ (19♀, 18♂ UHIM; 19♀, 17♂ BPBM; 19♀, 18♂ NMNH) • Hawaiian Islands, Oʻahu, Mānoa; 21.3060°N, 157.8092°W; 15.xii.2020; below bark of *Artocarpus altilis* branch; 2 adult ♀ and 1 pupa glued to point (UHIM) • Hawaiian Islands, Oʻahu, Mānoa; 21.5604°N, 157.8765°W; 31.i.2020; below bark of *Mangifera indica* branches; 3♀, 1♂ (1♀, 1♂ UHIM; 1♀ BPBM; 1♀ NMNH) • Hawaiian Islands, Oʻahu, Mānoa; 21.2954°N, 157.8145°W; 27.vii.2018; below bark of *Ficus microcarpa* branches; 3♀, 1♂ (1♀, 1♂ UHIM; 1♀ BPBM; 1♀ NMNH).

Other materials examined. Hawaiian Islands, Oʻahu, Mānoa; 21.2952°N, 157.8141°W; 3.xii.2020; below bark of *Trema orientalis* branch; wasp ex tunnels inhabited by the beetle; 1 ♀ and 1 *C. brasiliensis* adult glued to point (UHIM).

Etymology. The species name is Hawaiian, hanuʻuanamū (lit., flowing between caves of the insect). This species constructs a feeding tube to host-feed through the walls of the pupation chamber constructed by its host. Hanuʻu represents the continuous action of ebb, flow, and exchange of fluid through the connection bridging the cavern (ana) and the wasp, and ana mū recognize the system of tunnels and caverns constructed by the host insect (mū), reminiscent of lava chambers.

Known distribution. This species is known from the island of Oʻahu in Hawaiʻi, where it is likely adventive.

Known hosts. *Cryphalus* spp., including *C. brasiliensis* and *C. mangiferae*.

Acerocephala ihulena Honsberger & Lorenzo-Elarco, sp. nov.

https://zoobank.org/4C02F85F-8AA5-4847-95F6-01C3C4235F5A

Figs 4, 5

Diagnosis. Females of this species can be distinguished from other known *Acerocephala* by the antenna with the first three funicular segments transverse and of similar size and shape, the fourth segment slightly but distinctly larger, the fifth larger and subcircular;

internantennal ridge elongate-oval in dorsal view, elevated from face in lateral view; submarginal and marginal veins of forewing join smoothly with no callus; clypeus projected between the mandibles subrectangular and apically mildly bidentate; ovipositor sheaths exerted from gaster, approximately half its length, apically dark brown and basally lighter.

Differential diagnosis. Females are easily distinguished from *A. atroviolacea*, *A. aenigma*, and *A. pacifica* by the first four funicular segments transverse and much smaller and shorter than the fifth; the overall gracility of the head and body; and the elongate-oval shape of the interantennal ridge (*A. atroviolacea*, *A. aenigma*, and *A. pacifica* with fifth funicular segment of similar size to preceding segments; body and head thicker and more robust; interantennal ridge in dorsal view triangular or wedge shaped); and from *A. atroviolacea* and *A. aenigma* by lack of callus on the forewing (*A. atroviolacea* and *A. aenigma* with callus present).

Females can be distinguished from *A. hanuuanamu* by the fourth funicular segment slightly but distinctly larger than the first three; interantennal ridge elevated from the plane of the face; ovipositor exerted from the gaster approximately half its length, dark brown apically and lighter basally; scutoscutellar lines sulcate and form a consistent arc to meet the transscutal articulation along the mesal line (*A. hanuuanamu* with the fourth funicular segment indistinctly larger than the first three; interantennal ridge flush with the face lateral of the scrobes; ovipositor only slightly exerted from the gaster; scutoscutellar lines foveolate and meet the transscutal articulation lateral of the mesal line).

Females can be distinguished from *A. indica* by the shape of the interantennal ridge, in *A. ihulena* elongate-oval and reminiscent of the nose of a proboscis monkey (*A. indica* with interantennal ridge blunt wedge-like, widening posteriorly with somewhat straight margins); by the anterior of the face excluding the clypeus distinctly concave in *A. indica* (nearly straight between the anterolatral corners of the face in *A. ihulena*); and by the stigmal vein of the forewing, *A. ihulena* with the stigmal vein very short, only incompletely separating the stigma from the marginal/postmarginal veins (*A. indica* with stigmal vein short, but a distinct vein-like constriction between the marginal/postmarginal vein and the stigma).

Description. Female (Figs 4a–d, 5a–g; morphometric measurements in Suppl. material 2). ***Length*:** Can be expected to vary depending on the size of the host; the 7 individuals collected range from 1.52–1.84 mm (Holotype 1.80 mm).

***Coloration*:** Head brown, slightly lighter anteriorly in lower face, basal part of mandibles, and scape. Mesosoma orange, prothorax somewhat lighter. Gaster dark brown, slightly lighter basally, and ovipositor sheaths yellow in their basal 2/3 and brown apically. Legs yellow, pro- and metacoxae sometimes nearly translucent.

***Head*:** Head subrectangular in full face view; more or less parallel sided, but subtly widest across eyes, of nearly equal width at about three quarters its length, and tapers slightly to the anterolateral corner; vertex between posterior ocelli nearly straight, broadly rounded laterally to eyes. Anterior of head excluding mandibles and projected clypeus a mildly concave arc. Clypeus projected medially, somewhat square in shape and mildly bidentate, occupies about half the lateral space between the mandibles when mandibles are closed. Interantennal ridge widest at about half its length, shape elongate-

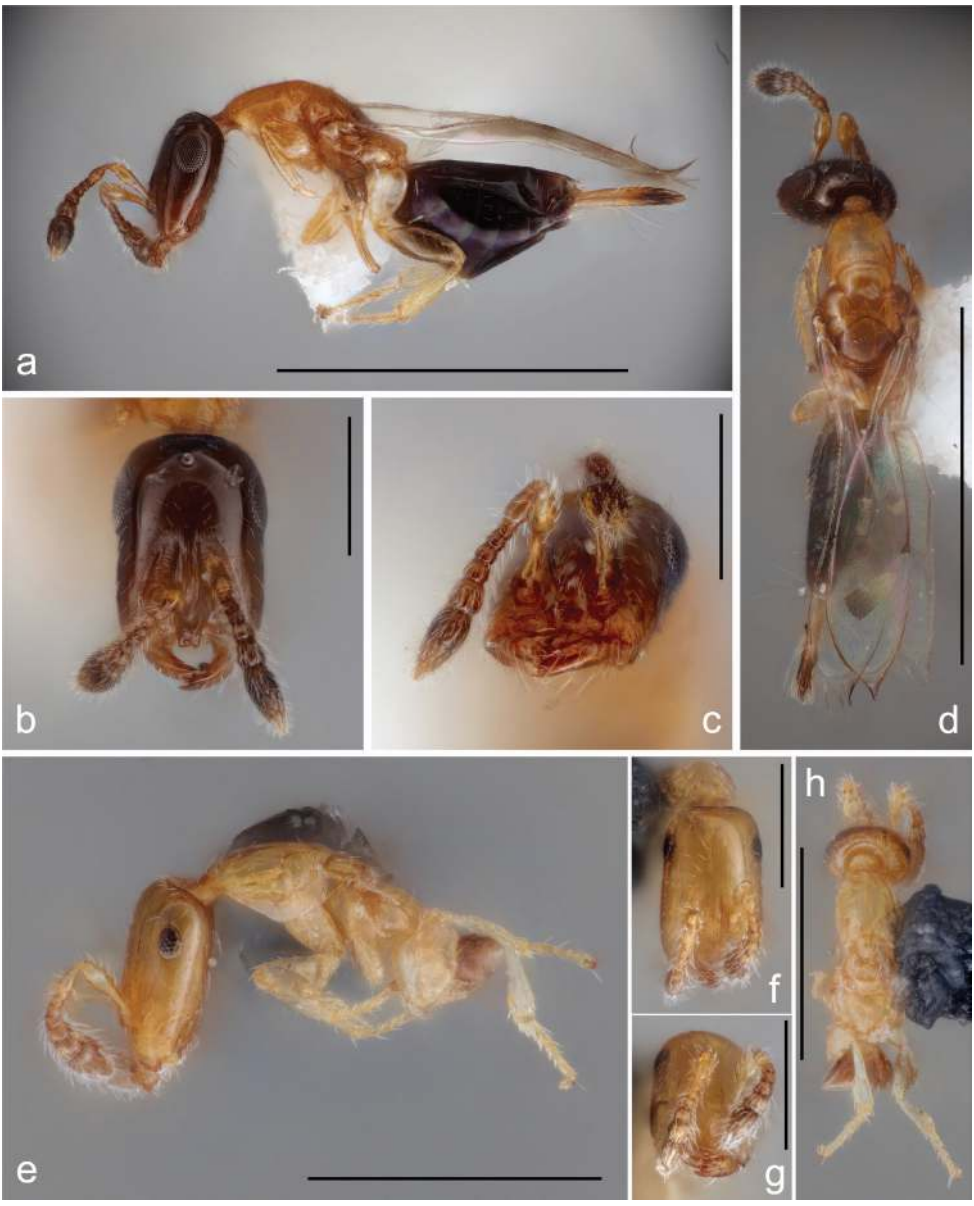


Figure 4. *Acerocephala ihulena* sp. nov. holotype ♀ (**a–d**) and allotype ♂ (**e–h**) **a, e** side view **b, f** head **c, g** anterior view of head showing mandibles **d, h** dorsal view. Scale bars: 1 mm (**a, d**); 500 μm (**e, h**); 250 μm (**b, c, f, g**).

oval, similar to that of a proboscis monkey; carinate laterally, medially between the carinae slightly convexely rounded with light longitudinal striations; slightly elevated from the level of the face lateral of scrobes, in lateral view of head extends tangential to curve of face at its thickest point disregarding the interantennal ridge, and continues



Figure 5. *Acerocephala ihulena* sp. nov. **a** head (paratype ♀) **b** antenna (♀) **c** side view (paratype ♀) **d** forewing (♀) **e** hindwing (♀) **f** dorsal view (paratype ♀) **g** anterior view of head showing mandibles (paratype ♀) **h** head (paratype ♂) **i** anterior view of head showing mandibles (paratype ♂) **j** dorsal view (paratype ♂). Scale bars: 1 mm (**c, f**); 250 μm (**a, g–j**).

straight more or less parallel with ventral profile of the head, giving the head approximately equal thickness over its length while the face lateral of scrobes thins towards the mandibles. Interantennal ridge begins a gradual descent to the mouthparts posterior to the toruli, and at about even with middle of the toruli, somewhat abruptly curves downward, to connect with the projection of the clypeus, at an approximate 60 degree angle to the overall plane of its dorsal surface. Lateral margins of scrobal depression a consistent arc, narrowing posteriorly, and slightly carinate; scrobes decrease in depth posteriorly. Mandibles long and curved with three apical teeth; dorsal and middle tooth of a similar conical shape but with a deep groove between them, middle tooth projecting only very slightly more than dorsal tooth, ventral tooth joined to middle tooth more closely and projecting a short way beyond it. Occipital carina just posterior to posterior ocelli, subcircular. Texture smooth and shiny with sparse setae, on the dorsal

side setae concentrated on the gena anterior of the compound eyes and on the face just above the scrobes, a few longer setae dorsally around the occipital carina, ventral side of head posterior of the indented region also with longer setae. Bottom of toruli adjacent to the dorsoventrally inclined arc that comprises the anterior of the face. Ventral side of head generally flat, median suture extends longitudinally from the mouthparts to the occipital carina, basal area near the suture indented slightly for about 2/5 the length of the head, cuticle posterior of this indent of rougher texture than cuticle within it.

Antennal flagellum composed of 5 funicular segments and a subconical clava. First three funicular segments transverse cylindrical, progressively becoming subtly conical, and of similar size, 4th is slightly rounded and slightly but distinctly larger than first three, 5th is subspherical and larger than the 4th; clava is approximately 1.4 times as long as the first four flagellar segments together, rounded subconical. All antennal segments with thin setae projecting at approximately 45 degrees, first four funicular segments each with a single whorl of longer setae of length subequal to the width of the segments, setae becoming progressively shorter towards apex of antenna. 5th funicular segment and claval segments with MPS, clava with 3 whorls of MPS, first four flagellar segments lacking MPS. Mean length/mean width (Ratio) of antennal segments, length and width measured relative to length of F1 (n = 7): Scape 6.8/1.7 (4.0); Pedicel 2.9/1.4 (2.0); F1 1.0/1.2 (0.8); F2 0.9/1.2 (0.7); F3 1.0/1.4 (0.7); F4 1.3/1.8 (0.7); F5 2.1/2.6 (0.8); Clava 5.8/3.2 (1.8).

***Mesosoma*:** Long prothorax articulates with mesothorax. A light longitudinal carina present laterally on pronotal neck, pronotum otherwise smooth, neck distinct from collar but lacking transverse pronotal carina. Pronotal neck with light transversely ridged texture, and collar smooth; collar with scattered mesal pointing setae except on its dorsal surface near the median line where there are no setae; one or two longer setae on its ventral side, of similar length to those on the ventral side of the head. Pronotum distinctly widest at its middle, but at its widest distinctly narrower than mesonotum in dorsal view, at its maximum width a little less than 3/4 the width of mesoscutum not including the tegulae. Transscutal articulation straight, inclines to vertical at its lateral edges. Notauli and scutoscutellar suture both well defined sulci; mesoscutum and scutellum lacking setae medially, a few setae present near the notauli, scutoscutellar suture, and transcutal articulation. On each side of the median line, notaulus curves to meet the transscutal articulation in the vicinity of 60 degrees, and scutoscutellar suture arcs to meet the transscutal articulation along the medial line, so medial lobe of mesoscutum runs up against transscutal articulation but scutellum is separated from it by the axillae except at its middle point (see morphometric measurements). Posterior margin of scutellum evenly convex. Mesonotum smooth and glassy, free of setae except on either side of the notauli and on either side of the scutoscutellar suture, a few scattered setae on the axillae and near the posterior margin of the scutellum. Metanotum visible behind scutellum. Propodeum slightly wrinkled at its anterior margin but otherwise smooth and glassy, flat longitudinally and lightly rounded transversely. Propodeal spiracle slightly recessed in a small depression. Sides of propodeum slightly tapering posteriorly until above the attachment of the rear coxae, where its dorsal margin bends to

run nearly transversely except for at the nucha which is bumped out posteriorly, top of petiolar insertion flush with disk of propodeum. Setae near lateral margins of the propodeum: on callus anterior of the spiracle, and on lateral margin where the callus meets the metapleuron. Mesopleuron with light reticulate texture, mesepisternum with setae.

***Wings*:** Forewing: Length of marginal vein approximately 1.1 × length of submarginal vein. Stigmal vein very short, hardly separating stigma from marginal vein, postmarginal vein also very short or absent, appearing together with stigmal vein as a slightly thickened apex of the marginal vein. Marginal vein without dorsal setae. Marginal setae begin at base of marginal vein and continue around apex of the wing with approximately consistent length to trailing edge approximately even with stigmal vein, just apical of the retinaculum. Parastigma not swollen, submarginal and marginal veins joining smoothly and unperturbed with no swollen area or change in pigmentation; lack of any sign of a tuft of setae on the parastigma. Membrane subhyaline with a slightly rippled texture and without setae.

Hindwing: Venation with a concavity at approximately half the distance from the base to the hamuli; anterior margin of wing membrane extends more or less straight in this region so at the apex of the concavity the venation reaches nearly ½ the distance to the posterior of the wing membrane. Venation ends at hamuli but the very anterior of the membrane in line with venation remains somewhat pigmented beyond the hamuli, to approximately 2/3 the length of the wing. Marginal setae present from the end of this pigmented region around to the base of the trailing edge of the wing, longest around trailing edge and posterior margin where they are approximately 3/4 the maximum width of the wing.

***Legs*:** Fore and rear coxae globose, rear coxa larger than fore coxa, mid coxa smallest. Femora also globose, slightly larger than their respective coxae in front and mid legs, of similar size but more elongate in back legs. Tibiae of similar length to their respective femora, also globose apically, but narrower basally. In all legs, first tarsal segment longest, 2nd through 4th segments sequentially decrease in length; 5th segment not including the claw subequal to 1st in front legs, subequal to the 2nd in mid and back legs. Protibial spur deviates from straight with a jog of shape similar to a logistic function, its base set back on tibia and extending near middle of the first tarsal segment, tibia beneath spur with a protibial comb.

***Metasoma*:** Petiole somewhat narrower medially than basally or apically, one or two lateral setae on a small knob near its middle; overall somewhat longer than wide. In dried individuals, 1st gastral tergite longest; 4th tergite a little more than half the length of 1st; 2nd and 3rd subequal and about half the 4th; 5th very short; 6th a little shorter than 4th. Gaster not heavily sclerotized, shrivels slightly on drying. Gaster with few, small setae on first five segments, 6th with many setae, some short, some longer and reaching about half the length of the exerted ovipositor sheaths. Dried individuals have hypopygium distinct. Ovipositor sheaths substantially exserted from apex of gaster, setae basally present on only ventral side, medially and apically present; longest setae at about half its length, reaching approximately the apex of the sheaths; ovipositor thin and needle-like.

Male (Figs 4e–h, 5h–j; morphometric measurements in Suppl. material 2). ***Length*.** Only two individuals collected, allotype 1.14 mm, paratype 0.85 mm.

Similar to female except: Wingless. Antennae with 6 funicular segments, basal four segments of relatively consistent size, fourth through sixth increasing in size; clava with two whorls of MPS. Mean length/mean width (Ratio) of antennal segments, length and width measured relative to length of F1 (n = 2): Scape 9.1/2.7 (3.4) ; Pedicel 4.3/2.3 (1.9) ; F1 1.0/1.8 (0.6) ; F2 1.2/1.9 (0.6) ; F3 1.1/1.9 (0.6) ; F4 1.4/2.1 (0.7) ; F5 2.1/3.2 (0.7) ; F6 2.9/4.1 (0.7); Clava 6.9/4.7 (1.4). Ocelli absent and compound eye smaller than in female, face very subtly widest about even with middle of scrobes, morphometrics of face otherwise similar, mandibles similar. Body size relative to head size smaller than in female. Posterior region of pronotum tapers slightly to fit around the narrower medial lobe of the mesoscutum. Notauli meet on medial line anterior of transscutal articulation, scutoscutellar suture meets transscutal articulation lateral to this. Pro- and mesoscutum smaller than in female, scutellum much shorter than in female, metanotum behind it appears in dorsal view with nearly straight posterior margin but partially covered by the scutellum medially. Femora, tibiae, and tarsal segments somewhat stouter than in female, but their relative lengths remain similar. Posterior margin of propodeal disk with scattered setae. Gaster shorter, truncated-looking apically in dry specimens.

Materials examined. ***Holotype*** (Fig. 4a–d): ♀; Hawaiian Islands, Oʻahu, Mānoa; 21.5571°N, 157.8783°W; 24.vii.2018; ex *Hibiscus tiliaceus* branches (deposited in UHIM).

Allotype (Fig. 4e–h): ♂; Hawaiian Islands, Oʻahu, Mānoa; 21.5571°N, 157.8783°W; 11.xii.2019; pupating next to *Eidophelus pacificus* dessicated larva in *E. pacificus* tunnel in *H. tiliaceus* branch (deposited in UHIM).

***Paratypes*:** 12♀, 1♂. Hawaiian Islands, Oʻahu, Mānoa; 21.5571°N, 157.8783°W; 24.vii.2018; ex *Hibiscus tiliaceus* branches; 7♀ point mounted, 1♀ slide mounted (2 point mounted, 1 slide mounted UHIM; 2 BPBM; 3 NMNH) • Hawaiian Islands, Oʻahu, Mānoa; 21.5571°N, 157.8783°W; 17.x.2018; ex *Hibiscus tiliaceus* branches; 2♀ point mounted (1 BPBM; 1 NMNH) • Hawaiian Islands, Oʻahu, Mānoa; 21.5571°N, 157.8783°W; 2.xii.2019; ectoparasitoid on *E. pacificus* larva found under bark of *H. tiliaceus* branch; 1♀ (BPBM) • Hawaiian Islands, Oʻahu, Mānoa; 21.5571°N, 157.8783°W; 11.xii.2019; pupating next to *Eidophelus pacificus* dessicated larva in *E. pacificus* tunnel in *H. tiliaceus* branch; 1♂ (NMNH) • labeled "Tapatapao // Upolu, Samoa // vii-13-40 //// 1000' //// Beating dead branches //// EC Zimmerman Collector"; 1♀ (BPBM).

Etymology. The species name is Hawaiian (lit., yellow nose). The nose-like interantennal ridge appears to be a good distinguishing character in the genus. In this species the interantennal ridge is distinguished from that in other *Acerocephala* by its elongate-oval shape with carinate edges and light longitudinal striations, reminiscent of a banana cut in half longitudinally. Ihulena is a play on ihu (nose) and iholena, a short and rounded variety of banana brought by Polynesian ocean voyagers and grown in Hawaiʻi.

Known distribution. This species is known from the island of Oʻahu in Hawaiʻi, and the island of Upolu in Sāmoa. It is likely adventive in Hawaiʻi.

Known hosts. Found developing as an ectoparasitoid of an *Eidophelus pacificus* (Schedl, 1941) (Coleoptera: Scolytinae) larva in tunnels under the bark of a *Hibiscus tiliaceus* L. log in Kahana Bay, Oʻahu, 21.5571°N, 157.8783°W, 15 m (Fig. 17b, c). Also found pupating next to dessicated larvae of *E. pacificus* in otherwise uninhabited larval feeding tunnels in the same logs (Fig. 17a, b).

Key to world known *Acerocephala* spp. females

(See Figs 1–8 for photos)

1 Callus on parastigma of forewing; antennal funicle 6-segmented; mandibles 4-dentate **2**

– Submarginal vein of forewing joins smoothly to marginal vein without a callus or especially thickened region; antennal funicle 5-segmented (males may be 6-segmented); mandibles 3-dentate **3**

2 Interantennal ridge truncate anteriorly, in side view abruptly becomes vertical relative to the plane of the face; scrobal grooves reach to approximately even with the middle of the compound eyes ..... ***A. atroviolacea*** (Fig. 8a–e)

– Interantennal ridge rounded anteriorly, in side view gently sloped as it nears the clypeus; scrobal grooves reach to approximately even with the anterior margin of the compound eyes ..... ***A. aenigma*** (Fig. 8f–h)

3 First two antennal funicle segments distinctly longer than wide; head widest at eyes and at anterolateral corner, head below eyes progressively widens to the anterolateral corner ..... ***A. pacifica*** (Fig. 7)

– At least first 3 funicle segments distinctly shorter and compressed relative to distal funicle segments, subequal length and width or transverse; head widest across eyes and at about half its length, tapers slightly as it approaches the anterolateral corner **4**

4 First four funicle segments of similar shape and size, much smaller and compressed compared to the fifth which is more round; scrobes reach past half the length of the face; interantennal ridge not elevated, flush with face lateral of scrobes; ovipositor sheaths only slightly exerted from apex of gaster, less than 1/3 the length of the gaster; scutoscutallar grooves meet the transscutal articulation lateral of the median line, so the scutellum runs up against the mesoscutum for a short distance ..... ***A. hanuuanamu*** (Figs 1–3, 10a)

– First three funicle segments small and compressed, the fourth and fifth distinctly progressively larger and more rounded; interantennal ridge slightly elevated relative to the face lateral of the scrobes; ovipositor sheaths distinctly exerted from apex of gaster, nearly half or more its length; scutoscullar grooves arc to meet the transscutal articulation along its midpoint, so the scutellum is only directly next to the mesoscutum at this midpoint, and is separated from it laterally by the axillae..... **5**

5 Internantennal ridge elongate-oval shape, narrowed anteriorly and posteriorly relative to its middle; anterior of the face between the anterolateral corners

excluding the projected clypeus nearly straight; stigmal vein very short, so the stigma is nearly contiguous with the marginal/postmarginal veins though it may narrow somewhat between them .....***A. ihulena*** (Figs 4, 5)

– Interantennal ridge blunt-wedge shaped, progressively widening posteriorly with somewhat straight margins; anterior of the face between the anterolateral corners excluding the clypeus distinctly concave; stigmal vein somewhat longer, distinctly separating the stigma from the marginal/postmarginal vein .....***A. indica*** (Fig. 6)

Note: Males are only known for *A. hanuuanamu*, *A. ihulena*, *A. indica*, and *A. aenigma*, so males of other species must be found before distinguishing characters are determined with certainty. Males of *A. hanuuanamu*, *A. ihulena*, *A. indica*, and *A. aenigma* are, however, very similar to females in characters of the head with the exception of the antennae in all four species, and the smaller eye and lack of ocelli associated with aptery in *A. hanuuanamu*, *A. ihulena*, and *A. indica*; the overall shape of the head and the interantennal ridge very similar between the sexes. If this pattern holds for other species, males may likely be identified using these same characters of the head as well, listed in the key. Males are wingless in *A. hanuuanamu*, *A. ihulena*, and *A. indica*, and winged similar to the females in *A. aenigma*, so wings and the associated development of the mesosoma, along with characters of the gaster associated with their sex, may be expected to differ.

Behavior of *C. brasiliensis* and *A. hanuuanamu* in phloem sandwiches

Cryphalus brasiliensis **beetle galleries in** ***F. microcarpa*** **wood**

Some of the *C. brasiliensis* beetles placed in the phloem sandwiches bored into the wood and excavated somewhat irregular subovate chambers, much wider than the entry tunnel, in which they laid their eggs (as in Fig. 12a, see also Fig. 11b for the corresponding stage of development in natural wood). Adult beetles were observed to actively clean the inside of these chambers by pushing debris out of the entrance to the tunnel with their elytral declivity. Larvae hatching from their eggs chewed tunnels around the perimeter of the chamber and then progressed generally along the grain of the wood, often moving as a whole in somewhat of a comb pattern but with staggered progress. On one occasion, an adult beetle was observed using its head and prothorax to vigorously and repeatedly push a newly emerged larva, the behavior continuing for a minute or two. The purpose of this behavior was unclear to us, but two possibilities may be (1) an attempt to assist the larva in starting its own feeding tunnel off the main gallery, or (2) a transfer of symbiotic organisms to the larva. If the view boxes were suddenly exposed to high levels of light, adults were observed to become somewhat agitated and occasionally cannibalize their eggs. We did not observe any clear differences in the behavior of immature beetles when exposed to different levels of light.

Moving through the beetle galleries
(Video 1 (https://vimeo.com/717186840))

Female *A. hanuuanamu* entered wood in the phloem sandwiches through holes drilled by the beetles. After entering the tunnels, adult beetles with eggs or larvae deeper in their tunnels were observed to actively attempt to block the wasp from progressing past them deeper into the tunnel. A beetle did so by sharply moving its posterior to block attempts

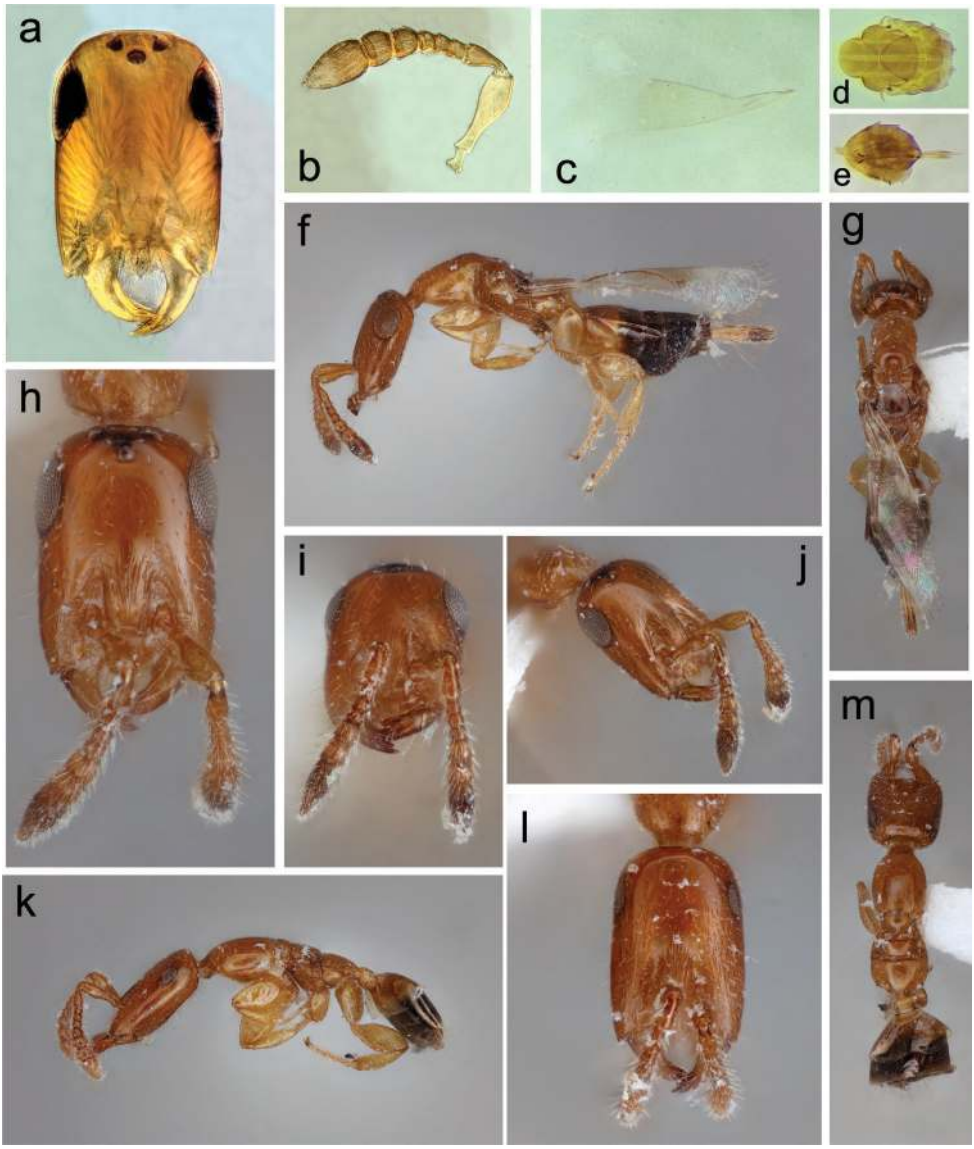


Figure 6. *Acerocephala indica*. Holotype ♀ (**a–e**); non-type ♀ (**f–j**); non-type ♂ (**k–m**) **a, h, l** head **b** antenna **c** forewing **d** mesosoma (dorsal view) **e** gaster **f, k** side view **g, m** dorsal view **i** anterior view of head showing mandibles **j** head.

by the wasp to go around. Wasps were observed to grab the elytral declivity or posterior of the abdomen of beetles with their mandibles when attempting to pass them, though this was not observed to actually help them progress past the bark beetle. Physically encountering an adult beetle in an open area, either in a spacious gallery or outside wood, not in the confined space of a tunnel, resulted in the wasp quickly moving away. Such avoidance behavior was potentially for good reason, as when wasps and beetles were placed together in a confined space such as a tube, it was not uncommon to see wasps missing their entire gaster which, though this was never actually observed, was presumably bitten off by the beetles.

The beginnings of some tunnels bored by the larvae were very narrow due to the small size of the larvae in their early development, though small larvae were also observed to sometimes work in small groups of two or three larvae that would move through the wood side by side and create a wider tunnel (e.g. Fig. 12c and the two larvae on the right side in Fig. 12a). Though *A. hanuuanamu* adults vary substantially in size depending on size of the host on which they develop, even some of the smallest female wasps were not able to fit through these smaller larval tunnels. As time progressed, more space opened up as beetle larvae and adults developed and created



Figure 7. *Acerocephala pacifica*. Holotype ♀ (**a–c**) and paratype ♀ (**d–g**) **a, g** side view **b, d** dorsal view **c, e** head **f** view of head showing mandibles. All photos taken by Lisha Jasper and Jeremy Frank at BPBM.

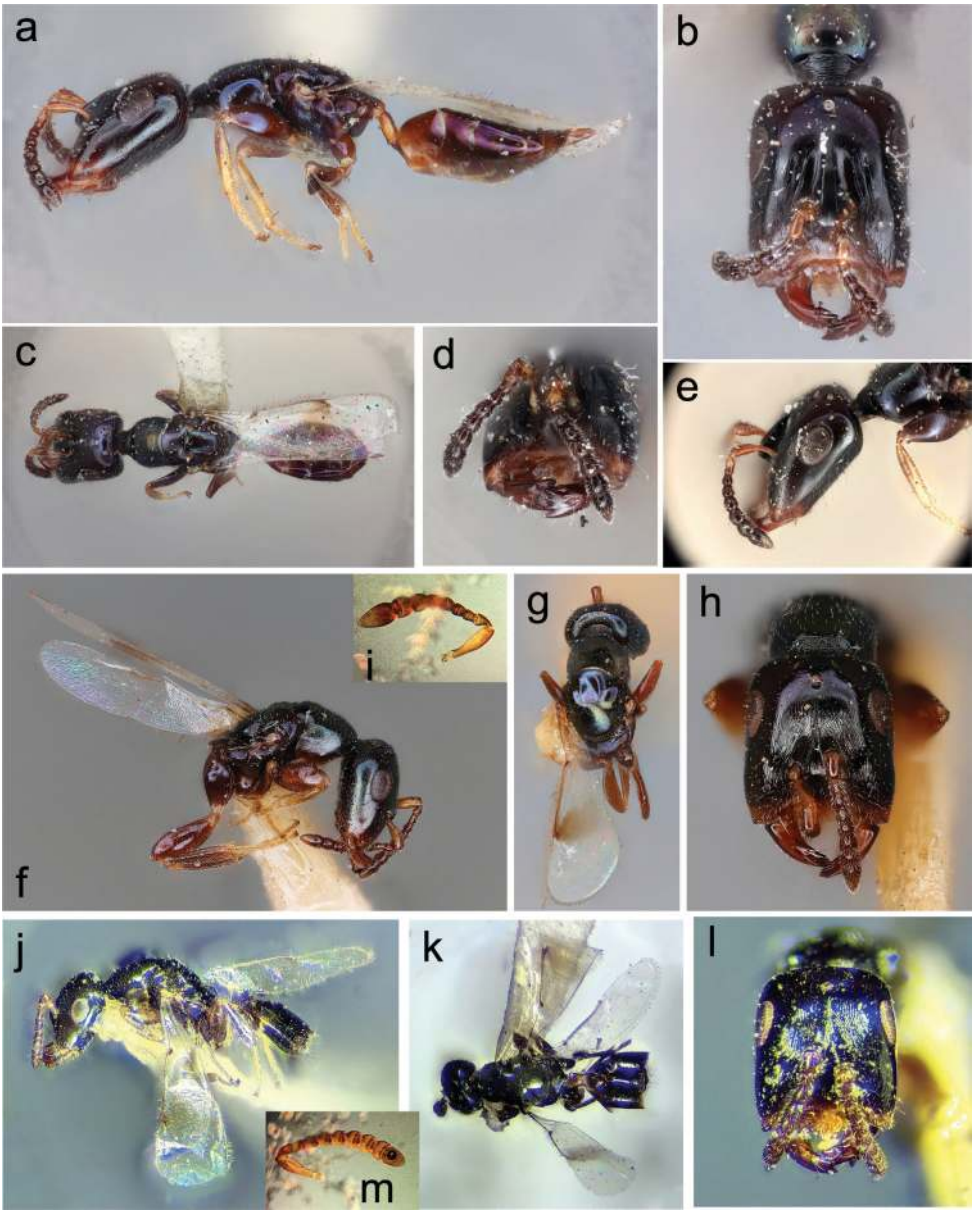


Figure 8. *Acerocephala atroviolacea* and *Acerocephala aenigma*. *Acerocephala atroviolacea* paratype ♀ (**a–e**); *A. aenigma* holotype ♀ (**f–h**) (photos from NMNH database); *A. aenigma* allotype ♂ (**j–l**) **a, f, j** side view **b, h, l** head **c, g, k** dorsal view **d** anterior view of head showing mandibles **e** side view of head showing antenna **i** *A. aenigma* antenna (paratype ♀) **m** *A. aenigma* antenna (paratype ♂).

tunnels in the wood, and individual, isolated tunnels formed a network of intersecting tunnels. Observations in both naturally infested wood (see Fig. 11d, e) and the phloem sandwiches (see Fig. 10d) showed that this dynamic would progress until eventually almost all the inner bark had been consumed and the outer bark was only loosely at-



Figure 9. *Choetospilisca tabida* holotype ♀ (**a–e**) and allotype ♂ (**f–i**) **a, f** side view **b, i** dorsal view **c** antenna **d, g** head **e, h** anterior view of head showing mandibles.

tached to the xylem layer. In a developed tunnel network such as this with a population of host beetles, *A. hanuuanamu* adults were able to move around with much more ease, encounter more potential hosts and fewer one-way tunnels blocked by adult beetles, and seemed to have the most success.

Such tunnel systems often contained frass and debris from the beetles' excavation, sometimes packed somewhat densely, and the wasps would dig through it in pursuit of hosts. *Acerocephala hanuuanamu* has remarkably large mandibles, for which one use was to facilitate this digging behavior. Females progressed through debris-filled tunnels by grabbing a chunk of debris with the mandibles, wrestling it loose, and then passing it within reach of the front legs. Then using all her legs in sequence she would quickly roll it back behind her abdomen in a running motion. In this way, the wasp was able to travel through the tunnels in a way reminiscent of a bubble in a tube of liquid: surrounded on all sides and moving material around its margins to progress through.

Acerocephala hanuuanamu females having entered a tunnel seemed to be able to sense the approximate location of potential host larvae they could not directly see, shown by apparent deliberate motion in its direction, though the sensory mechanisms involved were not clear.

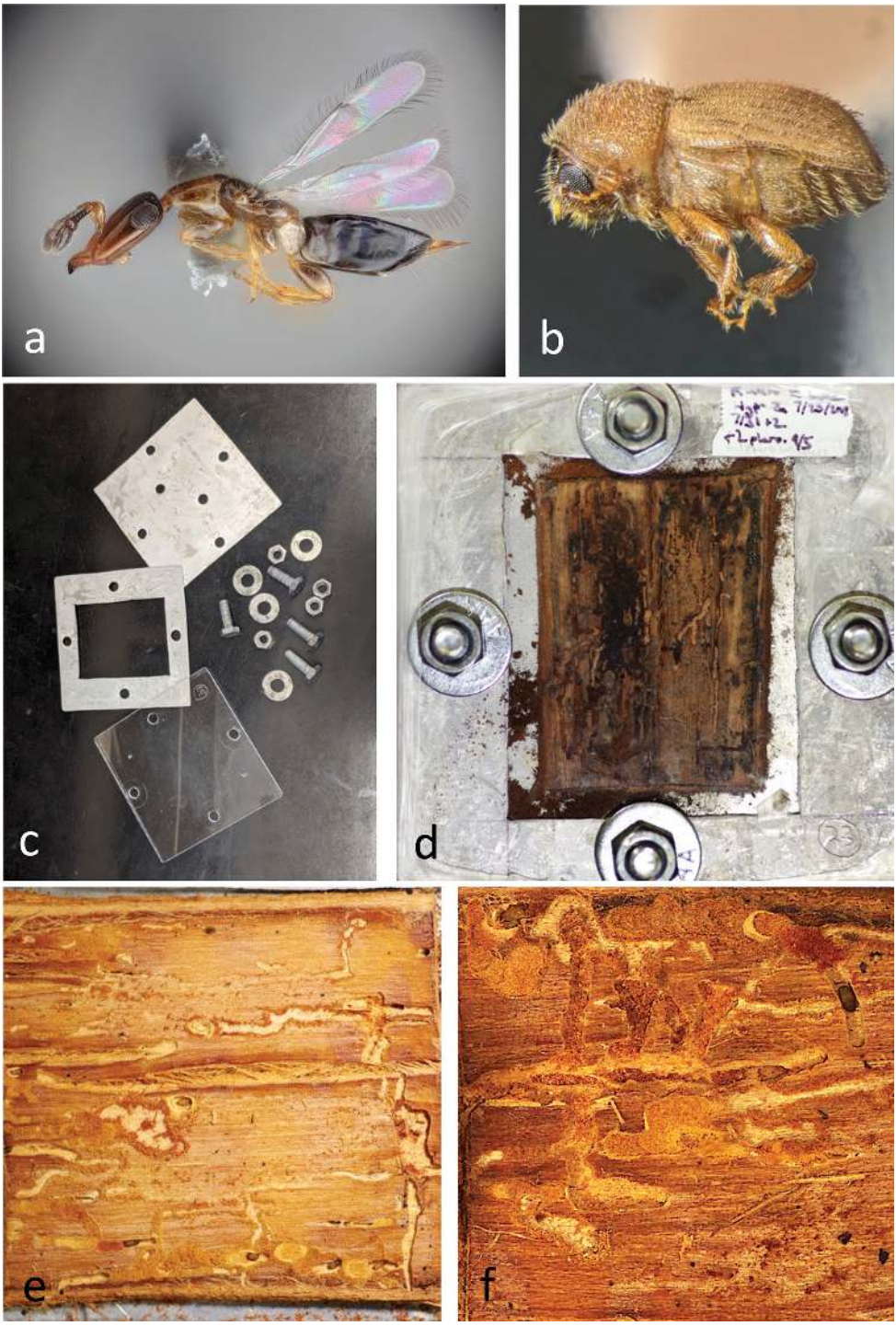


Figure 10. *Acerocephala hanuuanamu*, *Cryphalus brasiliensis*, and the phloem sandwiches **a** *A. hanuuanamu* ♀ **b** *C. brasiliensis* ♀ **c** parts of phloem sandwich style observation chamber **d** phloem sandwich with colonies of *C. brasiliensis* in *F. microcarpa* wood **e, f** closeups of additional phloem sandwiches.

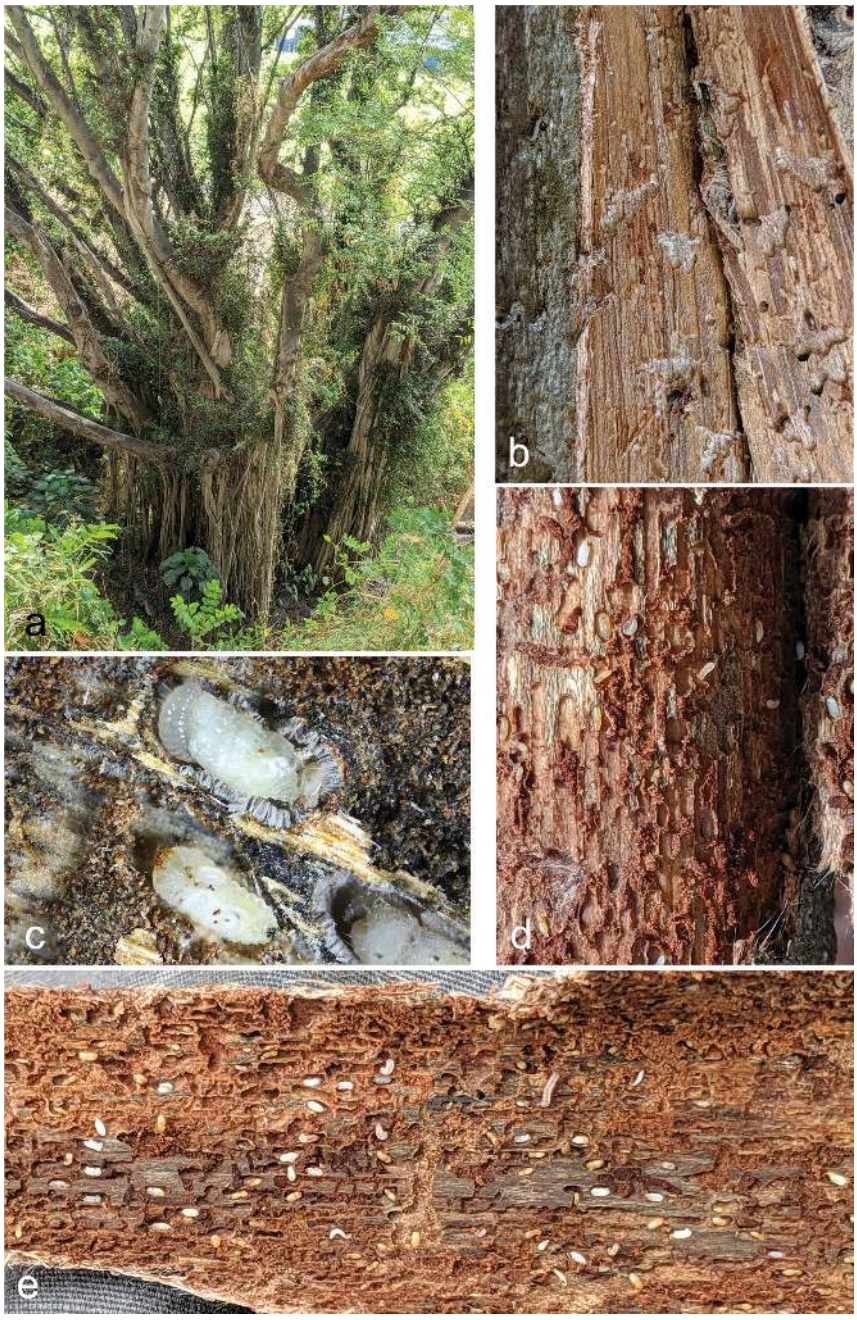


Figure 11. *Ficus microcarpa* wood where observations of behavior in a natural system were made. Photographs of wood are from naturally infested branches taken after peeling off the bark **a** the *F. microcarpa* tree from which most branches were collected and observations were made, in an unmaintained area of the University of Hawai'i at Mānoa **b** wood in an early stage of colonization by *C. brasiliensis* beetles **c** three *C. brasiliensis* beetle immatures, each parasitized by a feeding *A. hanuuanamu* larva **d** *Ficus microcarpa* branch with bark peeled off, showing *C. brasiliensis* tunnel systems and beetles, and *A. hanuuanamu* larvae, prepupae, and pupae **e** same as (**d**) except the bark layer of the branch.

Turning around
(Fig. 13; Videos 1 (https://vimeo.com/717186840), 2 (https://vimeo.com/716967741))

One amazing feat of agility accomplished by *A. hanuuanamu* with regularity is their ability to turn around in the tight confines of a tunnel, often not much wider than the wasp itself. The wasp first articulates its neck to face its head down, then bends its prothorax down, and in doing so slides its head under the rest of the as-of-yet unmoved posterior parts of its mesosoma. Bending its body along its points of articulation and pushing on its own body with its legs while doubled over to assist its progress, the prothorax is followed by the rest of the mesosoma and finally by the flexible gaster, ending with the wasp being in more or less the same location but facing the opposite direction. This maneuver is carried out very fluidly and quickly, and usually takes less than a few seconds, but sometimes longer if the wasp appears not to have a strong purpose for its movement. The fluidity in this snake-like maneuver is in part made possible by the head, the prothorax, and the rest of the mesosoma all being subequal in length, and the ability of the prothorax to articulate with the rest of the mesosoma. A similarly long,

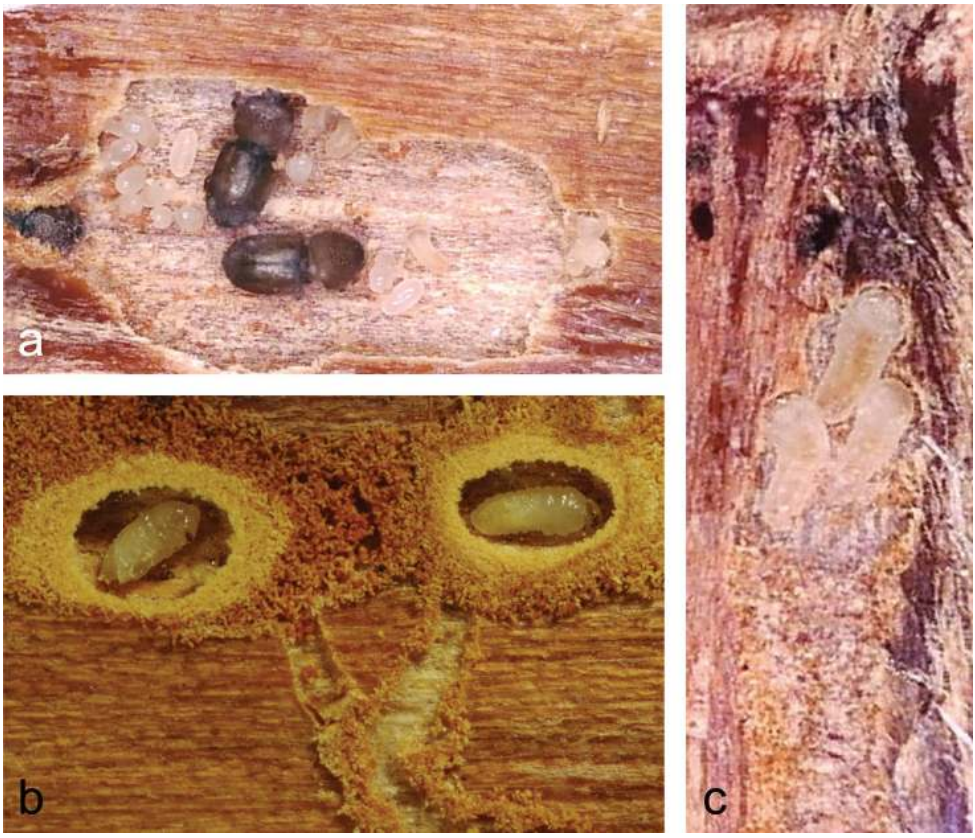


Figure 12. *Cryphalus brasiliensis* in phloem sandwiches **a** *C. brasiliensis* adults in a gallery with eggs and newly hatched larvae feeding and creating tunnels on the margins of the gallery **b** *C. brasiliensis* pupa and prepupa in hard pupal chambers they constructed **c** *C. brasiliensis* larvae feeding and moving through wood.

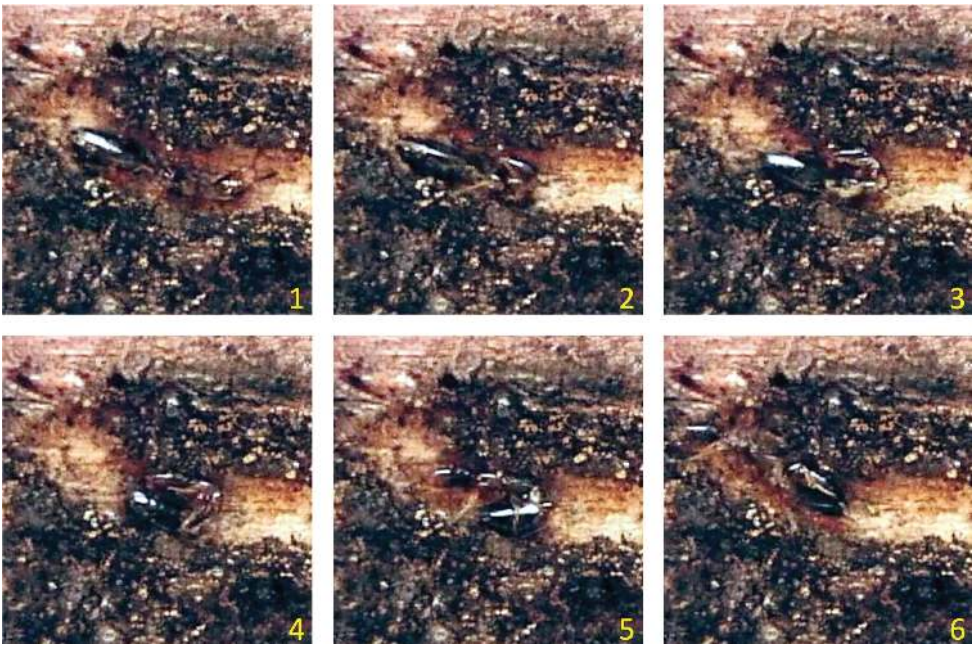


Figure 13. *Acerocephala hanuuanamu* turning around in *C. brasiliensis* tunnels in a phloem sandwich: sequence showing this agile maneuver frequently used to reverse orientation in the tunnels.

articulating prothorax is a character found in other unrelated taxa, such as much of the Bethylidae, which also typically attack their hosts in concealed environments. The agility in a tunnel system or tight space that this trait confers could potentially be what has resulted in this convergence.

Parasitism and host feeding on larvae in tunnels and construction of a feeding tube

(Figs 14–16; Videos 1 (https://vimeo.com/717186840), 2 (https://vimeo.com/716967741))

When a host larva was encountered in the tunnels, the *A. hanuuanamu* female would antennate upon it. Special attention was seemingly placed on the frass and debris around the larva, suggesting that this is a cue for host location, host acceptance, or both. Once a host was identified, the wasp would then turn around using the previously described turning maneuver and back up in the direction of the larva, moving its body backward in pulses and extending its ovipositor. Sometimes the wasp would contact the larva with its ovipositor, but other times it would not, and turn around to reexamine the larva with its antennae. The wasp seemed very cautious when encountering the larva, especially when backing up into it, presumably because of the danger presented by its mandibles. If the ovipositor made contact with the larva, the wasp would fully extend it into the body of the larva (Fig. 14a). The wasp would typically remain with its ovipositor inside the larva for approximately 15 minutes. During this time, the larva would gradually cease motion, the wasp apparently having injected it with a paralytic venom.

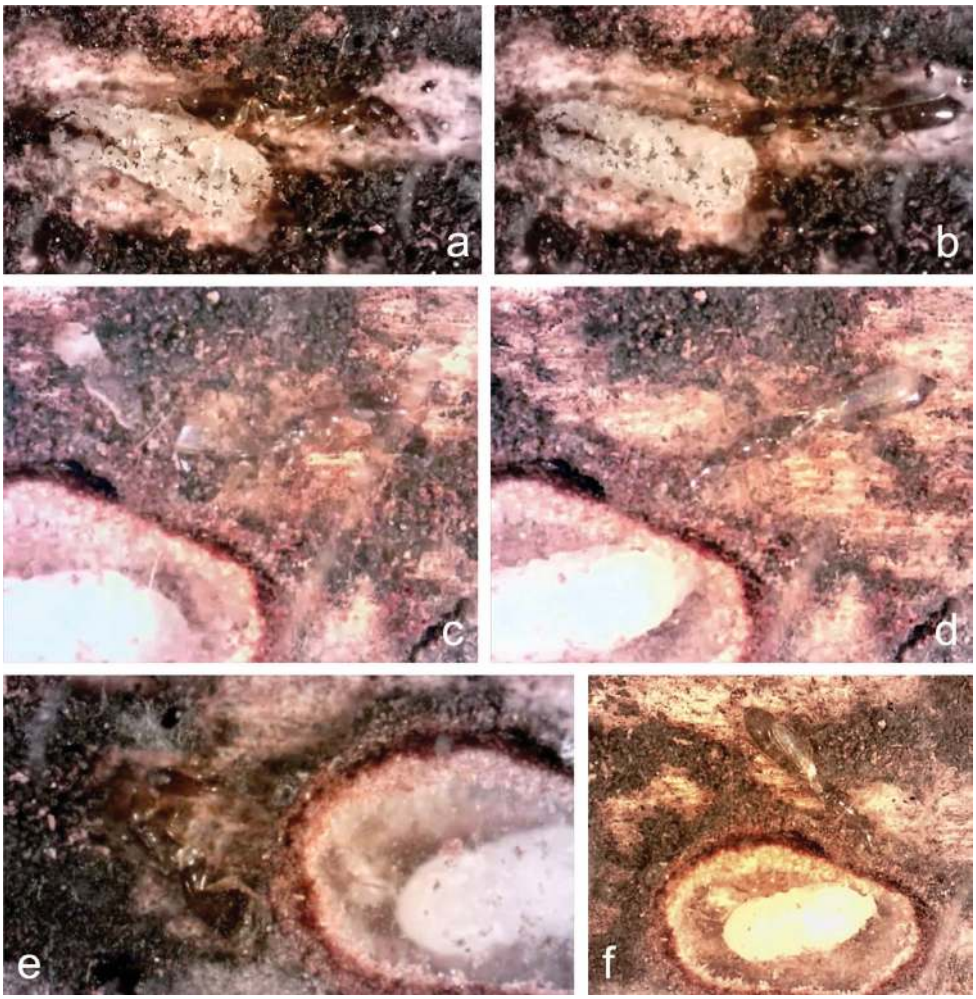


Figure 14. *Acerocephala hanuuanamu* stinging *C. brasiliensis* and host feeding in phloem sandwiches **a** stinging a *C. brasiliensis* larva. The ovipositor is visible extending nearly the length of the wasp's gaster within the larva **b** subsequent host feeding on the same larva as in (**a**), on the same spot where it stung the larva **c** stinging a *C. brasiliensis* pupa through its hard pupal chamber after excavating the loose debris outside the chamber. The ovipositor is visible in the empty space between the chamber wall and the pupa **d** subsequent to stinging the pupa in (**c**), host feeding through the wall of the pupal chamber. Part of the feeding tube is marginally visible protruding from the pupa as a small bump between the pupa and the interior of the chamber wall, on the part of the pupa most proximal to the mouth of the wasp **e** probing with the ovipositor to find the pupa inside the chamber. The ovipositor is visible extending towards the pupa within the chamber. This attempt by the wasp was unsuccessful due to the position of the pupa within the chamber **f** an additional subsequent feeding event by the same wasp on the same pupa. The gaster is distended and the liquid periodically excreted by the wasp as it feeds is visible just past the end of the wasp's gaster.

When finally removing its ovipositor from the larva, the wasp would do so slowly and carefully. In a few observed instances as it withdrew from the larva, tissue from inside the body of the larva was visibly pulled out as a sheath around the ovipositor.

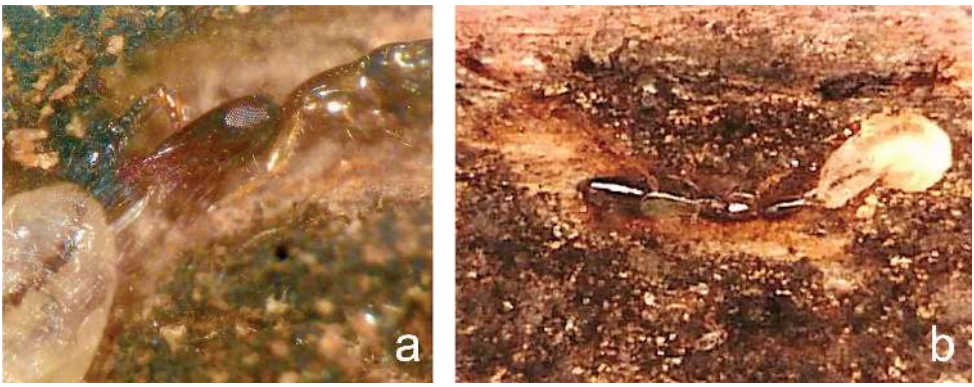


Figure 15. Feeding tube constructed by *Acerocephala hanuuanamu* after stinging, in phloem sandwiches **a** close-up of a tube constructed on a larva as the wasp host feeds **b** tube is visible extending from the posterior end of the larva near the wasp's mouth. Such tubes constructed for feeding through the hard shell of the pupal chamber are also marginally visible in Fig. 14d, f.

This sheath would remain projecting from the larva after the wasp had extracted its ovipositor. The wasp would then turn around in the tunnel and put its mouthparts on that projection, and host feed on the larva through it, evidently having produced a drinking straw (Fig. 15). On occasions when construction of such a straw was not observed, the wasp would still put its mouthparts precisely on the place where it had stung the larva. The wasp would remain in this position, host feeding typically for about 15 minutes. The wasp's body would be still but its mouthparts could be seen moving slightly, and it would periodically expel a clear liquid from its abdomen (Fig. 14b). This liquid is likely to be excess fluid excreted for the purpose of concentrating nutrients from the host within the body of the wasp. Eventually the wasp would stop feeding and would then often turn around again, sting the larva for a similar amount of time as it had initially, and then feed again. This process was often observed to be repeated three or four times on the same larva. Stinging was always observed to result in death of the beetle immature. The wasp would most often leave the larva without laying an egg, and sometimes it would eventually lay an egg on the same larva upon which it had host-fed.

Feeding and oviposition through a pupal chamber
(Video 2 (https://vimeo.com/716967741))

Cryphalus brasiliensis prepupae were observed to build a hard pupal shell around themselves made from bonded tunnel debris before they pupated (Fig. 12b). Upon approaching a pupal chamber, wasps were clearly able to sense the presence of a host and were stimulated to excavate the loose material in the vicinity of the pupal chamber and dig into the hard pupal shell as far as possible. This process of excavating appeared to be very laborious and was observed to last over an hour on occasion. Due to the toughness of the wall, which seemed to increase in strength near its inner boundary, the wasps were not

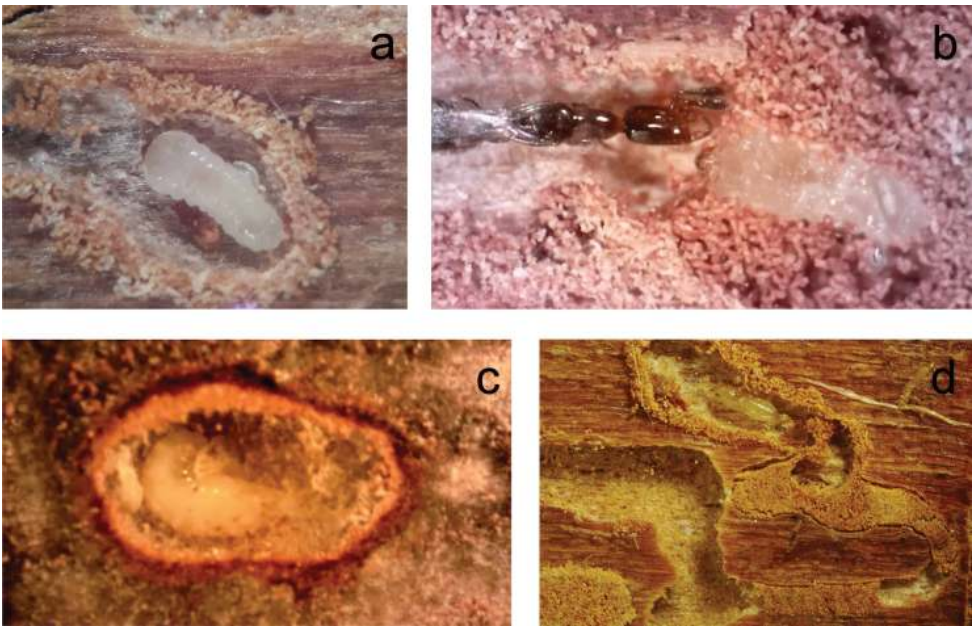


Figure 16. Development of *A. hanuuanamu* on *C. brasiliensis* in phloem sandwiches **a** small *A. hanuuanamu* larva on a *C. brasiliensis* larva **b** *A. hanuuanamu* female remaining motionless near a developing larva on its *C. brasiliensis* host for a long period of time as if guarding it **c** *A. hanuuanamu* larva inside a *C. brasiliensis* pupal chamber having consumed all the hemolymph of its host. This is the same pupal chamber as pictured in Fig. 14c–f, the wasp having oviposited on the pupa subsequent to stinging and host feeding on it multiple times **d** *A. hanuuanamu* pupa inside *C. brasiliensis* tunnels.

observed to break all the way through the shell to the pupa or prepupa inside. After progressing as far as it deemed practical, the wasp would stop digging, turn around, place its back legs on the wall of the pupal shell with its gaster pointing towards the inside of the chamber, extend its ovipositor, and use its body to push its ovipositor through the shell. This was a lengthy process. After pushing and pushing, the ovipositor would finally break through to the other side (Fig. 14c). The wasp would then flex the ovipositor, probing the space in an attempt to contact the larva or pupa inside. Great flexibility and control over its ovipositor was observed (Fig. 14e; Video 2 (https://vimeo.com/716967741)). If able to contact and penetrate the pupa or prepupa inside, it would sting it for about 15 minutes, and then eventually remove its ovipositor, slowly and carefully as it did when stinging a larva, simultaneously pulling the pupa or prepupa into contact with the wall of the chamber. The wasp would then turn around and put its mouthparts on the exact place where it had drilled through the pupal chamber. Physically separated from the pupa by the wall of the pupal chamber, it would then begin feeding, again through a tube it had made (Fig. 14d, f). This was observed multiple times. That it was actually feeding successfully was clear: its abdomen would progressively distend and periodically excrete clear liquid, and the pupa would noticeably progressively shrink in size. A feed-

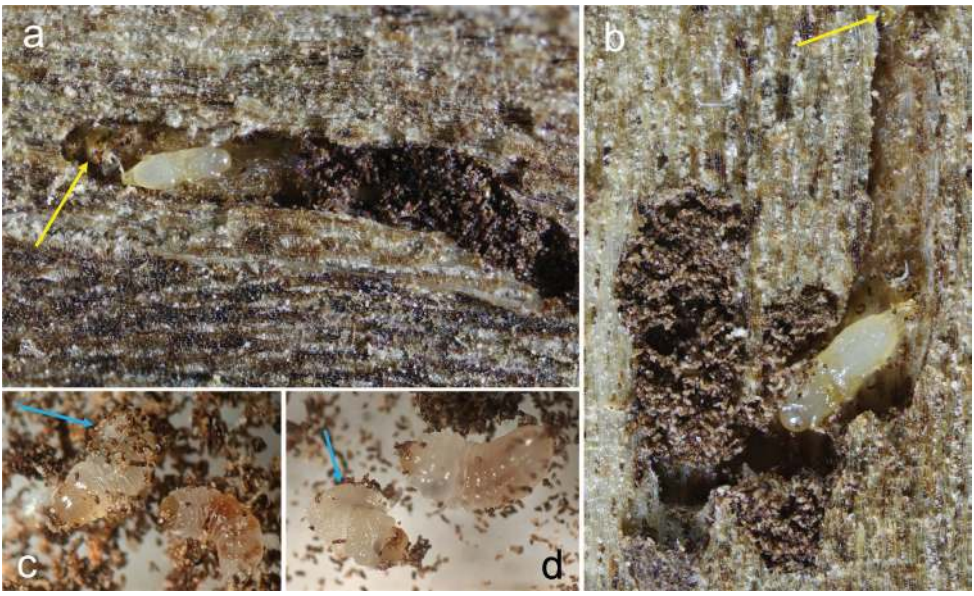


Figure 17. *Acerocephala ihulena* development. Photos are from naturally infested wood taken after peeling off bark **a** *A. ihulena* male (paratype) pupa in an *E. pacificus* tunnel under the bark of *H. tiliaceus* wood, having developed on the desiccated *E. pacificus* larva next to it (indicated by yellow arrow) **b** *A. ihulena* female (paratype) pupa found in the same branches, also having developed on the now desiccated *E. pacificus* larva (indicated by yellow arrow) **c, d** *E. pacificus* larvae from tunnels under the bark of *H. tiliaceus*, with larval *A. ihulena* males developing as ectoparasitoids (parasitoid larvae indicated by blue arrows).

ing straw was never observed directly due to its position within the material, but it was clearly utilizing one as it was feeding from a distance through the wall. Occasionally a small bump was observed on the pupa or prepupa where it was in contact with the wall (Fig. 14d, f), presumably comprising the proximal part of the feeding tube. Wasps were observed repeating this drilling and feeding behavior multiple times on the same pupa before oviposition, the egg having also passed through its ovipositor and the narrow hole it had drilled through the wall of the pupal chamber.

Oviposition and development

An egg was never directly observed coming out of the ovipositor but was often later observed on a larva or pupa, often the same one on which a wasp had previously host fed. The surface of the eggs appears to be adhesive, and eggs were either stuck directly to the larva or pupa, or were placed in the tunnel adjacent to it. A wasp larva emerging from the egg would attach to the beetle larva or pupa (Fig. 16a, b), and over the next 2 or 3 days the wasp larva would suck the hemolymph out of the beetle larva or pupa, transferring more or less all of it to its own body, leaving the shriveled cuticle of its host (Fig. 16c). It would then detach and later pupate (Fig. 16d, Video 3 (https://

vimeo.com/717187250)). The adult wasp would thus emerge in the tunnel or pupal chamber. Interestingly, though this was never observed in action, emergent adult wasps seemed to be able to make their way out from the inside of the beetle pupal chambers.

Mating
(Video 4 (https://vimeo.com/717187205))

A female and male were observed on two occasions to encounter each other and mate. Upon encounter, the wasps slowed their pace and touched antennae to antennae, maintaining that position for a few seconds. The female seemed to relax and the male moved onto the dorsal part of her abdomen, and then curled his abdomen around the female's abdomen to copulate. The act of copulation took in the vicinity of one minute. The wasps then remained near each other, the male often contacting the body of the female with the antennae, the female remaining calm and slow. This sequence of events, including both copulation that appeared successful and attempts that did not seem mechanically successful, were repeated multiple times until the female moved away.

Both times mating was observed, it was outside the piece of wood in the open area of the observation chamber. This should not necessarily be taken to imply that mating takes place external to the wood in nature, though. The place it occurred both times was in frass/debris piles pushed out by the beetles during construction and maintenance of their tunnels. Mating was likely observed there because the chance of males and females encountering each other in the region outside the tunnels was high given that it was a somewhat open space and there were often wasps present in that region.

Observation in naturally infested wood

In *F. microcarpa*
(Fig. 11)

Cryphalus brasiliensis beetles seem to be some of the first colonizers of the environment below the surface of *F. microcarpa* wood at the location studied on O'ahu (Fig. 11a). They drill through the bark and form tunnels straddling the phloem and xylem layers of the wood, but can also be found entirely in the phloem layer on branches with thicker bark. For healthy wood cut from the tree in the studied environment, initial colonization of wood typically happens 3–5 weeks after it is separated from the tree. As multiple generations of beetle adults and larvae feed and tunnel through the wood, the tunnels become increasingly dense, often forming networks covering nearly the whole phloem layer underneath the bark. The beetles then begin to leave the branch at around this stage, and the bark often begins to separate from the rest of the branch, the phloem layer having largely been removed by the beetles. In sections of branches still connected to the tree that seemed to have been somewhat abruptly cut off from the vascular system of the tree, *C. brasiliensis* beetles were present in large numbers throughout the phloem layer for a period of time similar to those in the cut branches.

They were also found to infest older branches at the junction between the dead section and where sap was still flowing. In these, it was difficult to tell whether the beetles were overcoming the immune defenses of the tree in that area and contributing to death of the wood progressively down the branch, or only progressing to the point where the wood had already stopped sap flow for other reasons.

Where there were reproducing *C. brasiliensis* in these trees, it was common to find both female and male *A. hanuuanamu* traveling in their tunnels, especially where there was a high density of *C. brasiliensis* larvae and pupae. In fact, in branches both disconnected from the tree and still attached to the tree, it was rare to find *C. brasiliensis* without at least females of these wasps also present. This suggests that the female wasps are efficient at locating wood newly infested by *C. brasiliensis*, and likely that they can do so by flying. The ectoparasitic larvae and pupae of *A. hanuuanamu*, reared to confirm their identity, were often found in the tunnels and pupal chambers built by *C. brasiliensis* beetles. Parasitoid larvae were found developing on both early and late instar larvae, which was reflected in the great size variation found in both female and male *A. hanuuanamu*. Parasitized larger larvae seemed to be substantially more common, which implies a preference for larger larvae given that these wasps are idiobionts. The parasitism rate seemed very high in some places; many pupal chambers or larval tunnels ending with parasitized beetle immatures or wasp prepupae or pupae (Fig. 11d, e). Two other ectoparasitoids were observed also parasitizing the *C. brasiliensis* beetles. These were an *Ecphylus* sp. (Braconidae) that oviposits into larvae and pupae through the bark, whose pupae could be distinguished morphologically or by the pupal cocoon they build when they pupate, and *Cerocephala dinoderi* Gahan, 1925, which was much more rare than *A. hanuuanamu* or the *Ecphylus* sp., and whose ectoparasitic larvae were observed feeding on *C. brasiliensis* larvae. The cerambycid *Pterolophia bigibbera* (Newman, 1842) was also common in this wood, and was parasitized by *Rhaconotus vagrans* (Bridwell, 1920) (Braconidae), *Sclerodermus immigrans* Bridwell, 1918 (Bethylidae), and *Allobethylus ewa* (Bridwell, 1920) (Bethylidae).

Additional hosts of *Acerocephala hanuuanamu*

In addition to *C. brasiliensis* in *F. microcarpa*, *A. hanuuanamu* was also found parasitizing *Cryphalus mangiferae* Stebbing, 1914 in mango branches (*Mangifera indica* L.) in the area of Kahana Bay on Oʻahu island (21.5604°N, 157.8765°W), and a *Cryphalus* sp. in breadfruit (*Artocarpus altilis* (Parkinson) Fosberg) branches in Mānoa Valley on Oʻahu island (21.2954°N, 157.8145°W). Identities were confirmed by rearing of parasitoid larvae, and when bark beetle larvae could be clearly associated with the adult beetles in the tunnels. *Acerocephala hanuuanamu* was also found emerging from breadfruit fruits with *Cryphalus negrosensis* Browne, 1979, which presents another putative host because the beetle was in high numbers and the only scolytid emerging from the fruits, though this was not confirmed through observation and rearing of parasitized beetles. Adults were also found with *C. brasiliensis* in *Trema orientalis* (L.) Blume branches in Mānoa Valley (21.2952°N, 157.8141°W).

Discussion

Aspects of the behavior of *Acerocephala hanuuanamu*

Some aspects of the behavior of *A. hanuuanamu*, as viewed in the phloem sandwiches, were remarkable. Adult *C. brasiliensis* were observed to actively attempt to block the wasps from passing them in the tunnels. *Acerocephala hanuuanamu* were observed to move through tunnels packed with debris by removing chunks in their direction of travel with their large mandibles and using their legs to pass the material posterior to their bodies. They fluidly and adeptly turned around in narrow tunnels, demonstrating the morphological advantage of a long articulating prothorax also found convergently in other unrelated lineages of cryptoparasitoids such as bethylids. Stinging and host feeding behavior was observed, including, possibly most remarkably, the use of the ovipositor to construct a feeding tube that allowed the wasps to host feed at a distance on pupae through the hard shell of a pupal chamber.

Implications about taxonomic position of the new species given functional aspects of morphology

Especially in taxa where there are few known species, morphological characters of phylogenetic significance are not always immediately clearly differentiated from characters variable within the taxa, nor are meaningful groupings of species into clades. The species here are close to previously described *Acerocephala* species but also differ somewhat, and thus their placement within existing genera, or if a new genus should be constructed, is not immediately obvious. In the original description of *Acerocephala*, Gahan (1946) described the genus consisting of *A. aenigma* and *A. atroviolacea* (in part by a 4-dentate mandible, forewing with callus on the parastigma but lacking a tuft of setae on the callus, long mandibles, and a 6-segmented antennal funicle in females), and considered *Acerocephala* close to the monotypic *Paralaesthia*, sharing a similarly elongate subrectangular head, but distinguished it by the mandible teeth, callus of the forewing lacking setae, and lack of a mesal groove extending the length of the frons. Hedqvist (1969) described the monotypic *Muesebeckisia* as also close to *Acerocephala*, distinguishing it by the mandible teeth and lack of callus on the forewing. Use of the keys provided by Hedqvist (1969) and Bläser et al. (2015) would guide both of the species described here to *Choetospilisca* (Fig. 9) given the number and shape of the antennal funicle segments, and lack of a setose callus on the forewing. Bouček (1988) grouped *A. pacifica* from Australia in with the two previously described *Acerocephala* from the Americas, identifying differences from these species in the antennae, shape and placement of features on the head, callus on the forewing, and characters of the meso- and metasoma, but it was not determined necessary to describe a new genus for it. The family Cerocephalidae as a whole is thought to generally be cryptoparasitic on wood boring insects concealed within the wood. The only known host association previously reported within these putatively related genera is *A. atroviolacea*, which is thought to parasitize a scolytid in

pine cones. The two species described here are similarly parasitoids of scolytids, these in the phloem layer under tree bark and potentially also in fruits. Here, observed aspects of functional morphology and behavior, in combination with the spectrum of habitats among tunnel systems of scolytids and other wood-borers, are used to propose hypotheses about traits that may be conserved and traits that may vary among closely related species. These hypotheses are then used to explain the present revision of the genus.

In observations of the behavior of *A. hanuuanamu* two functions of the antennae were of particular note. 1. When the wasp presses its mouthparts against a substrate as it searches for the spot through which to host feed, whether the opening of a feeding tube passing through the wall of a pupal chamber, or on the cuticle of a larva, it uses the antennae to gently probe the area around and between its mandibles and projection of the clypeus to sense where to place its mouthparts to feed (Videos 1 (https://vimeo.com/717186840), 2 (https://vimeo.com/716967741)). 2. In excavating a path through the debris-filled tunnel systems, the antennal club was placed at the apex of the mandibles to inform the manipulation of the debris using the mandibles, and possibly also to sense promising directions of travel for host searching inferred from chemical characteristics of the debris particles (Video 1 (https://vimeo.com/717186840)). Additionally, when debris was picked up by the mandibles, the antennae rested on top of the particle as if further sensing its characteristics. Antennae can, in general, be predicted to be most mobile, with the least amount of movement of the scape and pedicel resulting in greatest movement of the terminal antennal segments, when the scape is positioned approximately perpendicular to the plane of the face and the pedicel is bent at 90 degrees. In *A. hanuuanamu* the antennal segments are of such length that, when in this position, the club of the antenna reaches near the apex of the mandibles. Therefore, the length of the antennae coincides with their observed function in sensing the vicinity of the mouthparts to inform host feeding and excavation of debris.

Other than as a mechanism to hold the mandibles and move debris being held by the mandibles, the head was not observed to be directly used in digging in *A. hanuuanamu*; that is, it was not used to push material or as a wedge to open up space. The thinness and gracility of the head was observed to be important for the action of turning around within the tight opening excavated by the wasp. If the head were thicker, the tunnel would have to be larger to accommodate its size underneath the mesosoma, and would make turning around in the tight space more difficult.

There is substantial diversity in debris particle size, density, and tunnel geometry among bark beetles and other wood borers; for example, the converging feeding chambers produced by *Ips typographus* (Linnaeus, 1758), clean linear tunnels typical of Xyleborini, and debris-filled linear tunnels produced by cerambycid larvae. In the *C. brasisilensis* tunnel systems observed in this study, the debris is of relatively small particle size. In generations subsequent to the initial colonizers, the tunnel system develops into a network of tunnels that have grown together to form a two-dimensional expanse of debris that the parasitoid must dig its way through to pursue hosts. *Cryphalus brasiliensis* pupae also construct hard chambers that are difficult to penetrate. The previously discussed aspects of morphology of *A. hanuuanamu* were observed to be useful for navigating the specifics

of this host-habitat system: the length of the antennae appeared useful in informing host feeding, debris manipulation, and travel through the tunnels using the mandibles and legs; and the thin head and long articulating prothorax was useful for turning around in the tight spaces opened up during its travel through the debris.

In other species that exist in different host-habitats below the surface of wood, the methods of passing through the tunnel systems to find their hosts may be different, and this would likely be reflected in morphological differences. *Acerocephala pacifica*, *A. atroviolacea* and *A. aenigma* have longer antennae and more stout heads. What follows is speculative, but longer antennae could be useful in more open tunnel systems not as packed with debris as in *C. brasiliensis* tunnels, as longer antennae would be able to sense a larger area around the wasp to inform its direction of movement in the dark tunnels. The stouter head could be used as a wedge to open a path for movement through tunnel debris less dense than that found in *C. brasiliensis* tunnels, and the protruding interantennal ridge would protect the antennae while doing so. In the species with longer antennae, *A. atroviolacea*, *A. aenigma*, and *A. pacifica*, when the scape is folded back into the scrobes, the antenna reach just about the apex of the mandibles, possibly allowing for sensing and manipulation of debris by the mandibles concurrent with the utilization of the head as a wedge. In *C. brasiliensis* tunnels, longer antennae or a larger head would be of little use, and likely a hinderance, because the density of the debris would typically prevent a wide area for exploration by long antennae, and the size of the debris is small enough that it is manipulable using the mandibles; use of the head as a wedge would presumably only cause the particles to jam and would not effectively open a path for movement. For *A. hanuuanamu* in *C. brasiliensis* tunnels, searching for a host appears to be a tactile process of digging through small particles in a direction informed by chemical cues in the particles. In linear tunnel systems, in contrast, there is no option for direction of travel except forward or backwards through the tunnel, and thus less directional decision making needs to happen. This, combined with debris of larger grain size, or less debris, would make longer antennae and a stouter head possibly more useful for exploring more open space and moving through tunnels that contain debris some of which is too large to be picked up using the mandibles.

Therefore, parasitism of hosts that are related but differ in characteristics of their tunnels such as tunnel geometry, frass/debris size, and other aspects of host biology such as the creation of a hard pupal chamber in *C. brasiliensis*, may incur heavy selection on characters such as length of antennae, head size, size and protrusion of the interantennal ridge, and to some extent size of mandibles. These characters, while they should not be disregarded, should be used with some caution in making phylogenetic implications above the level of species. Other characters not observed to be as functionally relevant based on subtle habitat differences may be better clues to higher taxonomic relationships. Here are some considerations:

1. The antennae of *A. hanuuanamu*, *A. ihulena*, and *A. indica* have the basal three or four funicular segments much shorter than those of *A. pacifica*, *A. atroviolacea*, and *A. aenigma*. Interestingly, the basal funicular segments of *A. pacifica*, and to some ex-

tent also *A. aenigma* and *A. atroviolacea*, may be viewed as a nodose version of those in *A. hanuuanamu*, *A. ihulena*, and *A. indica*, the terminal portion of the segments of similar shape; that is, if the neck of the first segments were much shortened and the segments otherwise remained the same, antennae of the species with elongate antennae would appear similar to those with the compressed funicle segments. It is plausible that this variation could be in evolutionary response to their function in debris manipulation and host feeding described above, where the optimal length of the antennae depends on characteristics of the host-habitat system such as grain size, grain density, tunnel geometry, and the logistics of host feeding given the existence of pupal chambers or lack thereof. *A. hanuuanamu* and *A. ihulena* are the species for which we know host-habitat environments. The characteristics of the *C. brasiliensis* system in *F. microcarpa*, and *E. pacificus* in *H. tiliaceus* wood, are similar expanses of small grain-size debris in tunnels having grown together. These could be predicted to be best manipulated and traversed using the mandibles in combination with shortened antennae.

The number of flagellar segments has been used in keys to cerocephalid genera (Hedqvist 1969; Bläser et al. 2015) and also appears to be different in the overall more robust *A. atroviolacea* and *A. aenigma* (females 6-segmented) as compared to *A. hanuuanamu*, *A. ihulena*, *A. indica*, and *A. pacifica* (females 5-segmented). Slide mounted antennae of *A. hanuuanamu*, *A. ihulena*, *A. indica*, and *A. aenigma* females were examined, and the clava of *A. hanuuanamu*, *A. ihulena*, and *A. indica* were found to have three distinct whorls of MPS (Figs 3c, 5b, 6b), suggesting that they are formed from 3 fused segments, giving the total number of ancestral flagellar segments at 8. The clava of female *A. aenigma* appeared to be composed of two fused segments based on the distribution of MPS (Fig. 8i), thus also giving a total number of flagellar segments at 8. Therefore the number of ancestral segments appears to be conserved among all the species, the difference being that one of these segments is in the clava of *A. hanuuanamu*, *A. ihulena*, and *A. indica* while separate from the clava in *A. aenigma*. Males of *A. hanuuanamu*, *A. ihulena*, and *A. indica* also have a 6-segmented funicle and a clava that appears to be composed of 2 segments based on the whorls of MPS (Figs 3d, 6k), and thus the same original number of funicle segments as in the female. *A. aenigma* males had one more segment, with 6 funicular segments and a clava formed from two clearly distinct segments, the apical one with two whorls of MPS (Fig. 8m). Overall, the number of antennal segments therefore does not give a good indication that at least *A. aenigma* is phylogenetically distant from the species with one fewer funicular segment, and because of the overall similarity between *A. aenigma* and *A. atroviolacea*, the same can be said for the group as a whole.

Therefore, length of the antennae given the morphology of the funicular segments and that length is putatively under strong selection for the host-habitat environment, and number of funicular segments, does not appear to clearly separate the species into distinct higher taxa.

2. While the overall shape of the head in full face view is similar among the species, there are differences in head thickness. These are largely a result of the elevation of the interantennal ridge and overall robustness of the head, which may be subject

to selection as in the above discussion, based on host environment. *A. atroviolacea* and *A. aenigma*, and to some extent, *A. pacifica*, are more robust wasps with a greatly protruding interantennal ridge. These are also the species with longer antennae. These characters together would be consistent with the putative adaptation to manipulating larger grain-size debris in less densely packed tunnel systems, possibly using the head as a wedge. The elevation of the interantennal ridge occurs over a gradient among species, some being more lifted (*A. atroviolacea*, *A. aenigma*, *A. pacifica*), *A. hanuuanamu* flush with the face lateral of the scrobes, *A. ihulena* and *A. indica* intermediate. These characters of the shape of the head are thus used with caution to distinguish clades above the level of the species.

3. As discussed by Bouček (1988), the petiole is substantially longer in *A. aenigma* and *A. atroviolacea* than it is in *A. pacifica*. The other species now known have petiole similarly shorter. The shape of the petiole is, however, somewhat conserved. It is thus likely of little phylogenetic significance above the species level.

4. Males of *A. hanuuanamu*, *A. ihulena*, and *A. indica* are wingless and have smaller body size, while males of *A. aenigma* are fully winged and sized similar to the females (males of *A. pacifica* and *A. atroviolacea* are unknown). In the agaonid subfamily Sycophaginae, aptery in males is known to be variable among and sometimes within genera likely dependent on life history strategies including brood size and likelihood of being able to mate without leaving the plant material (Cruaud et al. 2011). Given that such variability in life history is likely also within *Acerocephala*, possibly partially dependent on density and tunneling strategies of hosts (e.g. *A. hanuuanamu* found along with its hosts often in high density and in interconnected tunnel systems, and with apterous males), male aptery and body size relative to the female does not provide a clear reason to split the genus.

5. An exception to the above considerations that give little reason to divide this genus is the presence or absence of a callus on the parastigma of the forewing. A callus is present in *A. atroviolacea* and *A. aenigma*, but absent in *A. hanuuanamu*, *A. ihulena*, *A. pacifica*, and *A. indica*. Characteristics of the callus or lack of a callus appear to be good generic characters within Cerocephalidae. While only *A. atroviolacea* and *A. aenigma* have a defined callus, some very subtle variation among individuals was observed in *A. hanuuanamu* as to a slight thickening of the parastigma in some individuals. *A. pacifica* in other characters seems intermediate between the more robust *A. atroviolacea* and *A. aenigma* and the other species, but lacks a callus. Therefore, presence or absence of a callus does not seem to clearly separate the species, especially when other characters are considered as well.

Thus while there are differences among species in the genus, some of which may suggest grouping into clades, all seem to best be placed in *Acerocephala*, the differences appearing not at the level for which we view a new genus to be necessary. *A. atroviolacea* and *A. aenigma* are both larger wasps and overall appear closely related, and are the only two with a callus. In general, characters of the species included in the putatively related genera *Choetospilisca*, *Paralaesthia*, and *Muesbeckisia* are distinctly

different and fall well outside such a range of variation between the species placed here in *Acerocephala*. Collection of more species, of which there are undoubtedly many in the world-–cryptoparasitoids within wood are typically little known–will likely illuminate these considerations better.

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Supplementary material 1

***Acerocephala hanuuanamu* sp. nov. morphometric measurements**

Authors: David N. Honsberger, Maya Honsberger, J. Hau'oli Lorenzo-Elarco, Mark G. Wright

Data type: csv

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Supplementary material 2

***Acerocephala ihulena* sp. nov. morphometric measurements**

Authors: David N. Honsberger, Maya Honsberger, J. Hau'oli Lorenzo-Elarco, Mark G. Wright

Data type: csv

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