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Revision of the Hawaiian endemic leaf-mining moth genus *Philodoria* Walsingham (Lepidoptera: Gracillariidae): its conservation status, host plants and descriptions of thirteen new species

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Abstract

Philodoria Walsingham, 1907 is a threatened, Hawaiian endemic genus of leaf-mining gracillariid moths that feeds as larvae on many threatened and endangered Hawaiian endemic plants. These moths are poorly studied and species lack detailed descriptions of morphology, distribution data, and natural history information of adults and immatures. Based on extensive fieldwork from 2013 to 2016, and examination of museum specimens, we describe or redescribe 51 species, 13 which are new species and provide biological and distribution data for 41 species. The 13 new species and their host plants are: *P. alakaiensis* Kobayashi, Johns & Kawahara, **sp. n.** (Asteraceae: *Dubautia* sp.), *P. funkae* Kobayashi, Johns & Kawahara, **sp. n.** (Asteraceae: *Wilkesia gymnoxiphium*), *P. haelaauensis* Kobayashi, Johns & Kawahara, **sp. n.** (Urticaceae: *Pipturus albidus*, *P. rockii*, *Pipturus* sp.), *P. hesperomanniella* Kobayashi, Johns & Kawahara, **sp. n.** (Asteraceae: *Hesperomannia arborescens* and *H. swezeyi*), *P. keaensis* Kobayashi, Johns & Kawahara, **sp. n.** (host unknown), *P. keahii* Kobayashi, Johns & Kawahara, **sp. n.** (Asteraceae: *Remya mauiensis*), *P. knudseniiella* Kobayashi, Johns & Kawahara, **sp. n.** (Asteraceae: *Dubautia knudsenii* subsp. *nagate* and *D. latifolia*), *P. lama* Kobayashi, Johns & Kawahara, **sp. n.** (Ebanaceae: *Diospyros sandwicensis* and/or *D. hillebrandii*), *P. limahuliensis* Kobayashi, Johns & Kawahara, **sp. n.** (Malvaceae: *Hibiscus waimeae* subsp. *hannerae*), *P. napaliensis* Kobayashi, Johns & Kawahara, **sp. n.** (Ebanaceae: *Diospyros sandwicensis* and/or *D. hillebrandii*), *P. obamaorum* Kobayashi, Johns & Kawahara, **sp. n.** (Urticaceae: *Pipturus albidus*, *Pipturus* sp.), *P. opuhe* Kobayashi, Johns & Kawahara, **sp. n.** (Urticaceae: *Urera kaalae* and *U. sandvicensis*) and *P. platyphylliella* Kobayashi, Johns & Kawahara, **sp. n.** (Asteraceae: *Dubautia platyphylla*). Types of 30 species were examined, lectotypes of 16 species are designated, and a key to all *Philodoria* species and all Hawaiian leaf-mining moths are provided. We also present a new Hawaiian name for *Philodoria*, which we call *Hunelele ʻelilau*, meaning "tiny flier, leaf excavator", referring to their life history and behavior. *Philodoria* feeds on five herbraceous and woody host plant families, and 41 species persist in localized populations in Hawaii as of 2016. Twelve species (*P. alakaiensis, P. funkae, P. haelaauensis, P. hespermanniella, P. kauaulaensis, P. keaensis, P. keahii, P. knudsniiella, P. limahuliensis, P. platyphylliella, P. sciallactis, P. wilkesiella*) appear to be severely threatened, as these species are rare or feed exclusively on plants that are endangered or rare. We were unable to document 10 species (*P. costalis, P. lipochaetaella, P. micropetala, P. nigrella, P. nigrelloides, P. opuhe, P. pipturiana, P. pipturicola, P. pittosporella, P. spilota*) after many efforts to sample in or near their historical habitats. We believe these species may be extinct. Given their restricted distribution and the fact that many species feed on rare and endangered plants, there is a risk that many more *Philodoria* species may go extinct unless immediate conservation measures are taken.

Key words: endangered, Hawaiʻi, host plant, *Hunelele ʻelilau*, leaf-miner, microlepidoptera, natural history, parasitoids, systematics, taxonomy, threatened, Yponomeutoidea

Introduction

The Hawaiian Islands are one of the most geographically isolated archipelagos and harbor thousands of unusual, highly threatened endemic species. Many lineages that successfully colonized Hawaii diversified because they were faced with with limited competition and had few natural predators (Funk & Wagner 1995). There are many examples of Hawaiian radiations, and due mainly to habitat loss, over 530 Hawaiian animal and plant species are listed as either endangered or threatened under the federal and state Endangered Species Acts (U.S. Fish and Wildlife Service 2019). Approximately 94% of Hawaiian insects are endemic (Evenhuis & Eldredge 1999), and more than 38% of native Hawaiian plants are threatened (Howarth 1995). Phytophagous insects that rely on endemic Hawaiian plants are especially at risk as they depend on the survival of their native host plants.

Philodoria Walsingham, 1907, a genus with 32 previously described species of endemic Hawaiian leaf-mining micromoths in the subfamily Ornixolinae, is one of these lineages. All species in the genus have larvae that feed on native Hawaiian plants, and larvae are reported on up to six plant orders (Asterales, Apiales, Ericales, Malvales, Myrtales and Rosales). Among these orders, Asterales (Asteraceae: *Dubautia*) and Rosales (Urticaceae: *Pipturus*) appear as dominant hosts (Swezey 1954; Zimmerman 1978a). Approximately 80% of *Philodoria* species feed on a single plant host species, and more than three-quarters of these species are restricted to a single Hawaiian island

(Zimmerman 1978a). Most of these estimates were made decades ago, and a comprehensive survey of *Philodoria* larval host plant associations has not been conducted in over half a century.

Similarly, nearly all systematic research on *Philodoria* was conducted in the early part of the twentieth century. The *Insects of Hawaii* series by Zimmerman (1978a) provided a synthesis of *Philodoria* and its species, but this source primarily served as a summary of earlier work by Walsingham (1907) and Swezey (1910–1946). *Philodoria* can be distinguished from other ornixoline genera by three adult morphological characters: (1) a hindwing with small frenular costal bristles (Zimmerman 1978a), (2) a dorsal flap extending from the posterior margin of male tergum VIII, and (3) lamella antevaginalis that is sclerotized and semicircular (Kobayashi *et al*. 2018). One adult morphological trait, the size of maxillary palpus, was used to divide the genus into subgenera (Zimmerman 1978a). However, a molecular phylogenetic analysis by Johns *et al.* (2016) rejected the subgeneric concept, as the two proposed subgenera, *Philodoria* Walsingham 1907 and *Eophilodoria* Zimmerman, 1978, were paraphyletic in their analysis and morphological characters used to classify them were inferred as homoplasious. Although Johns *et al*. (2016) provided the first phylogenetic analysis of *Philodoria* species, their study was limited to eleven species and three genes, and some phylogenetic relationships were weakly supported.

Johns *et al*. (2018) significantly expanded taxon and gene sampling to 33 *Philodoria* species and 507 loci and conducted a divergence time estimation analysis to examine the timing and pattern of *Philodoria* colonization in relation to their host plants. These authors estimated that *Philodoria* originated on the now partially sunken Hawaiian islands of Laysan or Lisianski, approximately 21 Ma, and were associated with host plants in the families Ebenaceae, Malvaceae, or Primulaceae. Since then, Kobayashi *et al*. (2018) described two new *Myrsine* feeding *Philodoria* species, *P*. *kauaulaensis* and *P*. *kolea*, expanding the number of described species. Despite their significant contribution to the evolution of *Philodoria*, sixteen species in the phylogeny of Johns *et al*. (2018) still lack formal names.

The primary goal of the present paper is a revision of *Philodoria* to synthesize the scattered systematic and biological data with new information from our research, and assign species names where needed. Our study provides for the first time, detailed information on the taxonomic history, biology, and distribution of all 51 recognized *Philodoria* species along with illustrations of genital structures, photographs of immature stages, and type specimens with corresponding labels. Fourty one species were reared during this study, and mine images of these species are presented. We also revise the definition of the genus, discuss its classification based on morphological characters, and examine patterns of host plant associations on an existing molecular phylogeny. Ninety eight parasitoid wasps were reared from immature stages of at least 15 *Philodoria* species; many of these wasps are figured. We also provide recommendations for *Philodoria* species with the highest conservation concern for inclusion in the IUCN Red List (IUCN 2019).

Materials and methods

Pinned adult specimens from museum collections. We examined 280 existing types and 200 non-type pinned specimens in the Natural History Museum (NMUK), the Bernice Pauahi Bishop Museum (BPBM) and the National Museum of Natural History Smithsonian Institution (USNM). Some newly collected specimens are deposited in the Florida Museum of Natural History, Gainesville, FL (FLMNH). Abbreviations and addresses for these museums are:

BPBM Bernice P. Bishop Museum, Department of Zoology, 1355 Kalihi Street, Honolulu, Hawaii 96818, USA.

FLMNH McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, USA.

NHMUK Natural History Museum, Department of Zoology, Cromwell Road, London SW7 5BD, United Kingdom.

USNM National Museum of Natural History, Smithsonian Institution, 10th St. & Constitution Ave. NW, Washington, DC 20560, USA.

The "Type material" and "Additional material" sections of each species account in the present paper includes the original wording of specimen labels. We chose this approach so that readers can see how the original label data were

written and in order to limit the potential for incorrect interpretation by our study. We are sensitive to Hawaiian names and their cultural importance, but we have chosen not to include Hawaiian diacritical marks in order to retain consistency with historical information on specimen labels. NHMUK/BMNH specimen numbers are listed without a space or hash symbol (#) to limit ambiguity. We report scientific plant names on labels, and plant taxonomy follows the Plant List (www.theplantlist.org). Finally, we present in Table 1 a list of E. C. Zimmerman's *Philodoria* genitalia slides and their code numbers, as we refer to these slides throughout the manuscript.

Specimens newly collected from fieldwork. In total, 673 specimens were collected from fieldwork conducted between 2013–2016 from 42 locations on the islands of Kauai, Oahu, Molokai, Lanai, Maui and Hawaii (Fig. 1, Table 2). These specimens were collected as larvae in mines or occasionally, as cocoons that were found on mined leaves. Larvae and pupae were reared in 420 ml plastic cups (129 mm in diameter at top and 60 mm in depth) at 20 ± 5°C under a photoperiod condition in the laboratory of 13–16L (hours light) 8–12D (hours darkness). A small piece of damp cotton was added to each rearing cup to prevent plant desiccation.

One hundred and eighty-four adults that emerged from our rearing efforts were immediately mounted (and spread, when possible) and preserved as a dry pinned specimen. For reared specimens, labels state the adult emergence ('em') and/or date of storage in 99% ethanol or RNA stabilization reagent (labeled 'stored'). In addition, 131 adult specimens which were preserved in 99% ethanol or an RNA stabilization reagent (RNAlater solution, Thermo Fisher Scientific) but were not sequenced for the studies of Johns *et al.* (2016, 2018) were examined for their morphology. These 131 specimens were transferred out of solution, air-dried for 15–20 hours, and their wings and legs placed on a 18 mm round micro coverslip (Fig. 2). A 15 mm square cover glass was placed over the coverslip and secured with 4 droplets of wood glue (Konishi Co., Ltd., Japan). This assembly was subsequently glued to a small rectangular piece of label paper so that it could be mounted to an insect pin (Fig. 2E–I). Of the 131 specimens, 34 had their head and thorax pinned to a small piece of mounting foam with their wings and legs on coverslips (Fig. 2E, G–I).

A total of 98 parasitoid wasps emerged from our rearing efforts. All parasitoid wasps were collected from rearing containers and transferred to a 1.5 ml Eppendorf tube containing 99% ethanol. Data on the parasitoid's host moth and associated plant species (when known) were recorded. All parasitoids are currently stored in a -80°C freezer in the collections of the FLMNH.

Imaging and dissection. Descriptions that we provide here are focused on the adult stage and leaf mines. Photographs of leaf mines were taken primarily in the field using a Canon EOS 60D and 5D MKIII digital camera. Some leaf mines were scanned using an EPSON Perfection V600 Photo scanner for visualization. Observations and measurements were made under a Leica M2 16 dissection microscope at 71–115× and a Leica S6E microscope at 6.3–40× with the aid of a micrometer scale. The size of the adult body (palpus of head, wingspan, forewing, genitalia structures) and immature stages (length of larva, pupa, leaf mine) were measured. Images of adults were captured using an Olympus E-330 camera and Moticam 580 5.0 MP. Images from various depths were stacked using the Helicon Focus 6.22; all of which were taken with equipment at the FLMNH. SEM images were taken by sputter-coating the specimen or region of the specimen with a 60:40 mixture of gold-palladium on a HITACHI SU1510 (Hitachi Ltd., Tokyo, Japan), with a lanthanum hexaboride (LaB6) source, at an accelerating voltage of 15 kV at the Osaka Prefectural University, Japan. All images were then edited with Adobe Photoshop Elements 9 into final figures.

Two hundred and seventy-five genital dissections were made. For genitalia dissections, the entire abdomen was removed and heated for 3–4 min in 10% aqueous KOH, transferred to a dish with 70% ethanol, and residual scales and soft parts were removed. Genitalia were stained in acetocarmine for 0.5–1h, dehydrated in a series of dishes containing 70−100 % ethanol and mounted in Canada balsam on a glass slide. A few specimens that were collected initially were stained with Chlorazol Black E (1% solution in 70 % ethanol). We generally follow the wing pattern nomenclature of Walsingham (1907) and Zimmerman (1978a) labeled in here in Figure 3. Terms for genitalia follow Kobayashi *et al*. (2018) and "gnathos" is employed to indicate the sclerotized V-shaped transverse band joining the ventral base of the tegumen.

TABLE 1. *Philodoria* slides preparated by E.C. Zimmerman, stored in the Bernice P. Bishop Museum, Honolulu, Hawaii, USA. The column "Type" indicates the specimen designation by the original author (whether it is a paratype or not), along with indication of the body part of the specimen, when known. "P" in that column indicates the existence of a hand-written red "P" on the slide, but does not necessarily imply that the sample is from a type specimen.

Species name	The slide label set by E.C. Zimmerman	Sex	Slide number	Collection data	Type	BPBM number	Figure number	Current designation
P. auromagnifica Walsingham, 1907	*P. auromagnifica* Walsingham, 1907	M	Z-XII-20-62-5	Kahana, Oahu, 1-1-28, O.H.Swezey, *Suttonia*			Fig. 61A–D	
P. auromagnifica Walsingham, 1907	*P. auromagnifica* Walsingham, 1907	F	Z-XII-20-62-6	Wailuqe, Oahu, 1-11-25 Swezey	P		Fig. 61E–G	
P. basalis Walsingham, 1907	*P. basalis* Walsingham, 1907	F	Z-XII-20-62-4	Wals, Kohala Mts, Hawaii 9-4-19	P		Fig. 61H	
P. costalis Swezey, 1934	*P. costalis* Swezey, 1934	M	Z-XII-20-62-2	Makaha, 3000ft, [Oahu], 4.15.34, O.H. Swezey, *Pipturus*	Paratype	4269	Fig. 61I–N	Paralectotype of *P. costalis*
P. lysimachiella Swezey, 1928	*P. lysimachiella* Swezey, 1928	M	Z-XII-20-62-1	Hapapi, Waianae Mts, Oahu, 1-16-27, O.H. Swezey, *Lysumachia*	P	4270	Fig. 62A–E	
P. molokaiensis Swezey, 1928	*P. molokaiensis* Swezey, 1928	F	Z-XII-20-65	Kawela, 3700, 12-23-25 Mol., *Lysimachia*, O.H. Swezey Collector	Paratype, wing vein	4271	Fig. 62H	Paralectotype of *P. molokaiensis*
P. molokaiensis Swezey, 1928	*P. molokaiensis* Swezey, 1928	F	Z-XII-19-62-26	Kawela, Molokai, 3700ft, 12-23-25 ex *Lysimachia*, O.H. Swezey	Paratype, genitalia		Fig. 62F, G	Paralectotype of *P. molokaiensis*
P. knudseniiella Kobayashi, Johns & Kawahara, **sp. n.**	*Philodsoria* sp.? not *naenaeiella* (Swezey, 1940)	F	Z-I-10-66-A	Kumuwela, Kauai, 3-10-28, O.H. Swezey Collector ex Unknown			Fig. 62I, J	Paratype of *P. knudseniiella*
P. hesperomanniella **sp. n.**	*P. naenaeiella* (Swezey, 1940)	F	Z-V-17-61	Pupukea, Oahu, 12-17-33, *Hesperomania*		4261	Fig. 63A, B	Paratype of *P. hesperomanniella*
P. obamaorum **sp. n.**	*P. neraudicola* (Swezey, 1920)	M	Z-1-26-61(3)	S. of Hilo, Hawaii, 7-25-21, O.H. Swezey, *Pipturus*	Paratype	4257	Fig. 63E–G	Paratype of *P. obamaorum*
P.obamaorum **sp. n.**	*P. neraudicola* (Swezey, 1920)	F	Z-V-18-61	S. of Hilo, Hawaii, 7-25-21, O.H. Swezey, *Pipturus*			Fig. 63C, D	Paratype of *P. obamaorum*
P. splendida Walsingham, 1907	*P. splendida* Walsingham, 1907	M	Z-XII-19-62-20	Waialae Nui, Oahu, 2-16-19	P		Fig. 64G–I	
P. pipturiella Swezey, 1923	*P. pipturiella* Swezey, 1923	F	Z-XII-1962-22	Palikea, Waianae, Mts, Oahu, 2-3-35, O.H. Swezey, ex *Pipturus*	P	4273	Fig. 64E, F	
P. haelaauensis **sp. n.**	*P. pipturicola* Swezey, 1915	M	Z-XII-19-62-23	Wailuku, Maui, 2000ft, 12-9-22, Swezey coll. *Pipturus*	P		Fig. 64A–D	Paratype of *P. haelaauensis*
P. haelaauensis **sp. n.**	*P. pipturicola* Swezey, 1915	F	Z-XII-19-62-24	Wailuku, Maui, 2000ft, 12-9-22, Swezey coll. *Pipturus*	P	215	Fig. 63H	Paratype of *P. haelaauensis*

TABLE 2. Localities that were survedy for *Philodoria* during the course of this study. Localities correspond to the map in Figure 1.

	Island	Locality	Longitude (N)	Latitude (W)	Elevation (m)
1	Kauai	Alakai	22.1473	159.6088	1100–1200
2	Kauai	Kokee	22.1508	159.6369	1200
3	Kauai	Limahuli	22.1867	159.5864	700–800
4	Kauai	Blue Hole	22.0716	159.4953	1400–1500
5	Oahu	Kaena Point	21.5726	158.2753	10
6	Oahu	Kaala Boardwalk	21.504	158.146	1000–1200
7	Oahu	Palikea	21.4077	158.0984	400–500
8	Oahu	Waiaai Trail	21.4207	157.9082	300–400
9	Oahu	Nuuanu Pali	21.3627	157.791	400
10	Oahu	Konahuanui	21.34–21.35	157.78–157.81	400–500
11	Oahu	Mt. Tantalus	21.3394	157.8108	400–500
12	Oahu	Kaau Crater	21.3328	157.7758	500
13	Oahu	Hawaiiloa	21.3243	157.7418	500
14	Molokai	Mokio	21.20–21.22	157.20–157.24	40–100
15	Molokai	Waiehu Sea Cliff	21.1611	156.8446	800
16	Molokai	Olokui	21.1354	156.8506	1200–1300
17	Molokai	Kamakou Boardwalk	21.1184	156.9049	1200–1300
18	Molokai	Kamakou	21.11–21.13	156.92	1000–1300
19	Molokai	Kaluaaha	21.095	156.8386	800
20	Lanai	Kanepuu	20.8743	156.9753	500
21	Maui	Flemming Arboretum Trail	20.9762	156.6193	500
22	Maui	Waihee Ridge Trail	20.9481	156.544	400–500
23	Maui	Eke	20.9379	156.5801	800–900
24	Maui	Waihee Dunes Mclt	20.9342	156.5046	10–50
25	Maui	Haelaau	20.91–20.93	156.59–159.62	1200–1400
26	Maui	Waihee valley	20.9045	156.5762	1300–1500
27	Maui	Iao valley	20.88	156.54–156.57	400–600
28	Maui	Makawao Forest Reserve	20.80–20.82	156.24–156.26	1100–1300
29	Maui	East Wailuaiki Stream	20.7995	156.1418	600
30	Maui	Waikamoi	20.7826	156.2304	1800
31	Maui	Kula Forest Reserve	20.6724	156.3402	1500–1600
32	Maui	Kahikinui Forest Reserve	20.6834	156.248	2000
33	Maui	Nakula Natural Area Reserve	20.6815	156.232	1800
34	Maui	Ulupalakua Ranch	20.66289	156.3321	1700
35	Hawaii	Upper Hamakua Ditch trail	20.0523	155.6398	800
36	Hawaii	Laupahoehoe Natural Area Reserve	19.9349	155.2956	1200
37	Hawaii	Mauna Kea, Hale Pohaku	19.7669	155.4508	3000
38	Hawaii	Puu Makaala Nar	19.4813	155.2794	1200–1400
39	Hawaii	Kaumana Trail	19.45	155.21–155.19	1600
40	Hawaii	Volcanoes National Park	19.4138	155.238	1000–1200
41	Hawaii	Mauna Ulu Havo	19.3653	155.2161	800–950
42	Hawaii	Punaluu Beach	19.1336	155.5062	10–50

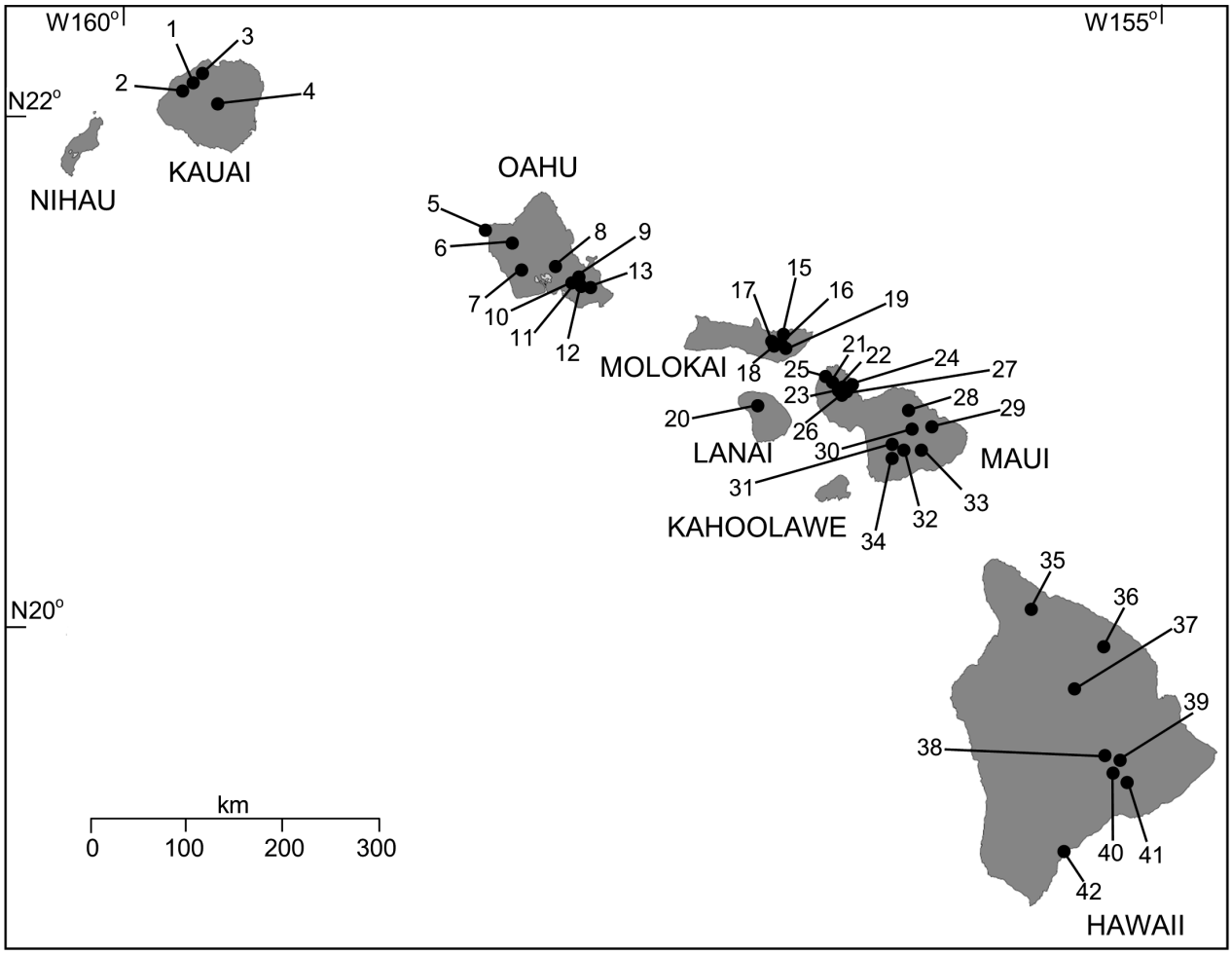

FIGURE 1. Map of the Hawaiian Islands showing the location of *Philodoria* collection sites. Numbers correspond to localities listed in Table 2.

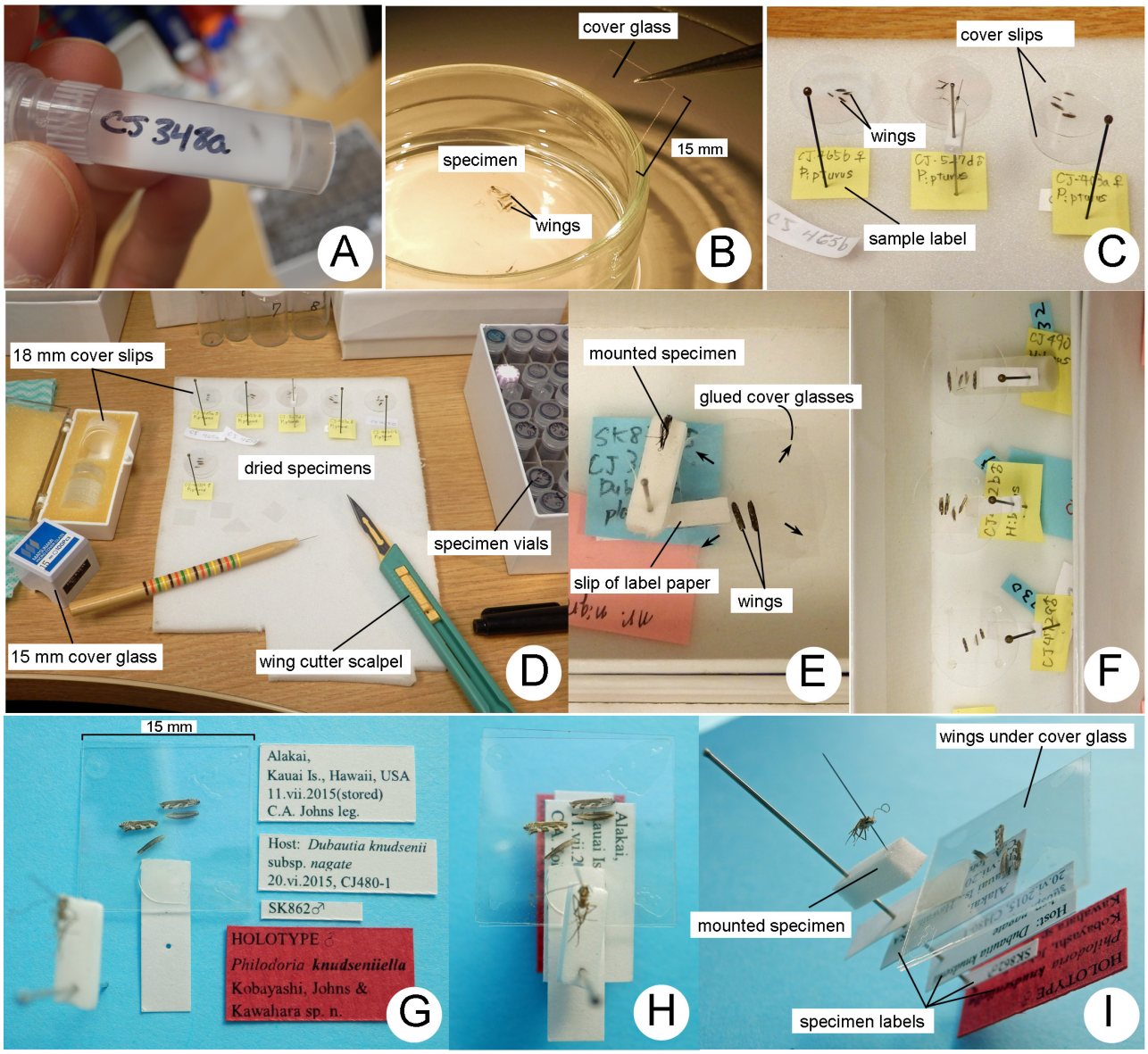

FIGURE 2. Steps applied to set and mount damaged specimens. **A** Specimen vial containing tissue preserved in 99% ethanol, **B** Wings, legs, antennae from vial transferred to a dish and then on to a cover glass, **C** Transfer of structures to cover slips, and left to dry at room temperature for 15–20 hours, **D** Dried specimens and specimen tools, **E** Mounted specimen on minuten and wings mounted to cover slip, the four corners of cover glass are gluded (shown as arrows), **F** Mounted wings on pins in unit tray, **G** Holotype of *Philodoria knudseniiella* and its labels, **H** Labeled holotype, viewed from above, **I** Same as H, lateral view.

Results

Subfamily Ornixolinae Kuznetzov & Baryshnikova, 2001

Genus *PHILODORIA* Walsingham, 1907

Hawaiian Name: ***Hunelele ʻelilau***

Figs. 3–95, 97.

Philodoria Walsingham, 1907: 717. Zimmerman 1978a: 644–718, figs. 427–481; Johns *et al*. 2016: 66–67.

Synonymy

Subgenus *Eophilodoria* Zimmerman, 1978: 659, fig. 432. Type species: *Philodoria succedanea* Walsingham, 1907.
Subgenus *Philodoria* Zimmerman, 1978: 659, figs. 433–434. Type species: *Philodoria marginiestrigata* (Walsingham, 1907).

Original description: "Antennae a little longer than the forewings, simple, without pecten. Labial Palpi long, curved, drooping, divergent, smooth; terminal joint almost as long as the median. Maxillary Palpi obsolete. Haustellum well-developed. Ocelli present. Head and thorax smooth. Forewings narrow, elongate, lanceolate: neuration 12 veins all separate; 2, 5 and 6 weak; 7 to costa. Hindwings narrow, lanceolate, acute; cilia 3 1/2: neuration 7 veins (3 and 4 coincident); 2 and (3 +4) stalked; cell open between 4 and 5; 5 and 6 stalked out of 7; 8 short. Abdomen slender. Legs, hind tibiae smooth.

This genus is closely allied to *Gracilaria*, Hw., but differs in the absence of the maxillary palpi." (Walsingham 1907: 717).

Type species. *Philodoria succedanea* Walsingham, 1907 by original description.

Systematic history. The systematic history of the genus was reviewed by Johns *et al.* (2016). In summary, the genus was placed originally in the Tineidae by Walsingham (1907), and incorrectly assigned to the Glyphipterygidae by Meyrick (1912a). Walsingham characterized the genus from others as lacking a maxillary palpus. Genera he thought were closely related, *Gracillaria* and *Elachista,* have a maxillary palpus and/or blackish forewing. Swezey (1910b, 1913bc, 1915, 1920, 1928, 1940 & 1946) and Meyrick (1928) similarly assigned species within *Philodoria* with a developed maxillary palpus to other genera, i.e. *Parectopa* and *Gracillaria*. Meyrick (1928) placed some *Philodoria* species described by Walsingham as *Gracillaria* in the Gracillariidae. Zimmerman (1978a) taxonomically reviewed Hawaiian Gracillariidae and placed some species assigned to other genera in *Philodoria*. Zimmerman also divided the genus into two subgenera, *Philodoria* (*Eophilodoria*) and *Philodoria* (*Philodoria*) based on the length of the maxillary palpus. Recently, Johns *et al*. (2016) synonymized the subgenus *Eophilodoria* Zimmerman 1978 with the genus *Philodoria* Walsingham, 1907. *Philodoria* has been treated as a genus of the *Parectopa* group, subfamily Gracillariinae (Kumata *et al*. 1988; Davis & Robinson 1998; De Prins & De Prins 2005). Recently, Kawahara *et al*. (2017) placed *Philodoria* in the subfamily Ornixolinae Kuznetzov & Baryshnikova, 2001 based on a phylogeny that utilized 22 genes and 94 gracillariid species. Johns *et al.* (2018) published the first molecular phylogeny of *Philodoria* utilizing 507 loci and 33 *Philodoria* species. They estimated the origin of the genus to the now partially sunken Hawaiian islands of Laysan or Lisianski, approximately 21 Ma, and hypothesized that the ancestral moth was likely associated with host plants in the families Ebenaceae, Malvaceae or Primulaceae. While the study of Johns *et al.* (2018) was a major breakthrough in understanding the evolutionary patterns of *Philodoria*, many of the species included in that study did not have formally assigned names and species boundaries were never formally examined. Two species of *Philodoria* were described by Kobayashi *et al.* (2018) but many more remained undecribed until the present revision.

Diagnosis. *Adults*. The association of this genus to Ornixolinae is substantiated by the presence of three autapomorphies for the subfamily: 1) the presence of moderately long, four-segmented maxillary palpi; 2) forewing with three branches of the medial vein and two branches of the cubital vein (Fig. 38); and 3) an ostium bursae opening at the seventh sternum in female (Fig. 40E, F). However, 17 *Philodoria* species possess very reduced four-segmented maxillary palpi, of which the apical two segments are very small and indistinct (Figs. 34A,D, 37A, B) or nearly absent (Figs. 34B, C, 35).

Diagnostic features of the genus include: forewing with lustrous and metallic apical portion; hindwing with small frenular costal bristles; in the male, a dorsal flap extending tergum VIII; in the female, terminus of ductus bursae tubular and sclerotized; corpus bursae with a pair of lateral signa that are either a pair of spines or series of small spines; inception of ductus seminalis at the posterior part of corpus bursae. Larvae and pupae were not examined in the present study and therefore do not include a diagnosis for them..

Redescription: Adult (Figs. 3–6, 34–40). Head and frons smooth. Haustellum well-developed. Ocelli and chaetocemata absent (despite Walsingham's [1907] claim that ocelli are present, *Philodoria* lack ocelli). Maxillary palpus developed, 4-segmented (Figs. 34E, F, 36) or reduced 2-segmented and obscure small 3rd and 4th segments (Fig. 34A, D), sometimes greatly reduced, vestigial, obsolete (Figs. 34B, C, 35). Labial palpus developed, upcurved, 3-segmented. Antenna about 1.0–1.5 length of forewing. Thorax smooth. Legs slender, smooth. Basal color of forewing dark lustrous and metallic, fuscous or brown. Forewing pattern (Fig. 3) consisting of orange ocherous patches with white bands or spots (Fig. 3A, B) or oblique white to brown streaks (**cs**$_{1–3}$ and **ds**$_{1–3}$) (Fig. 3C, D). Hindwing a little shorter in length than forewing.

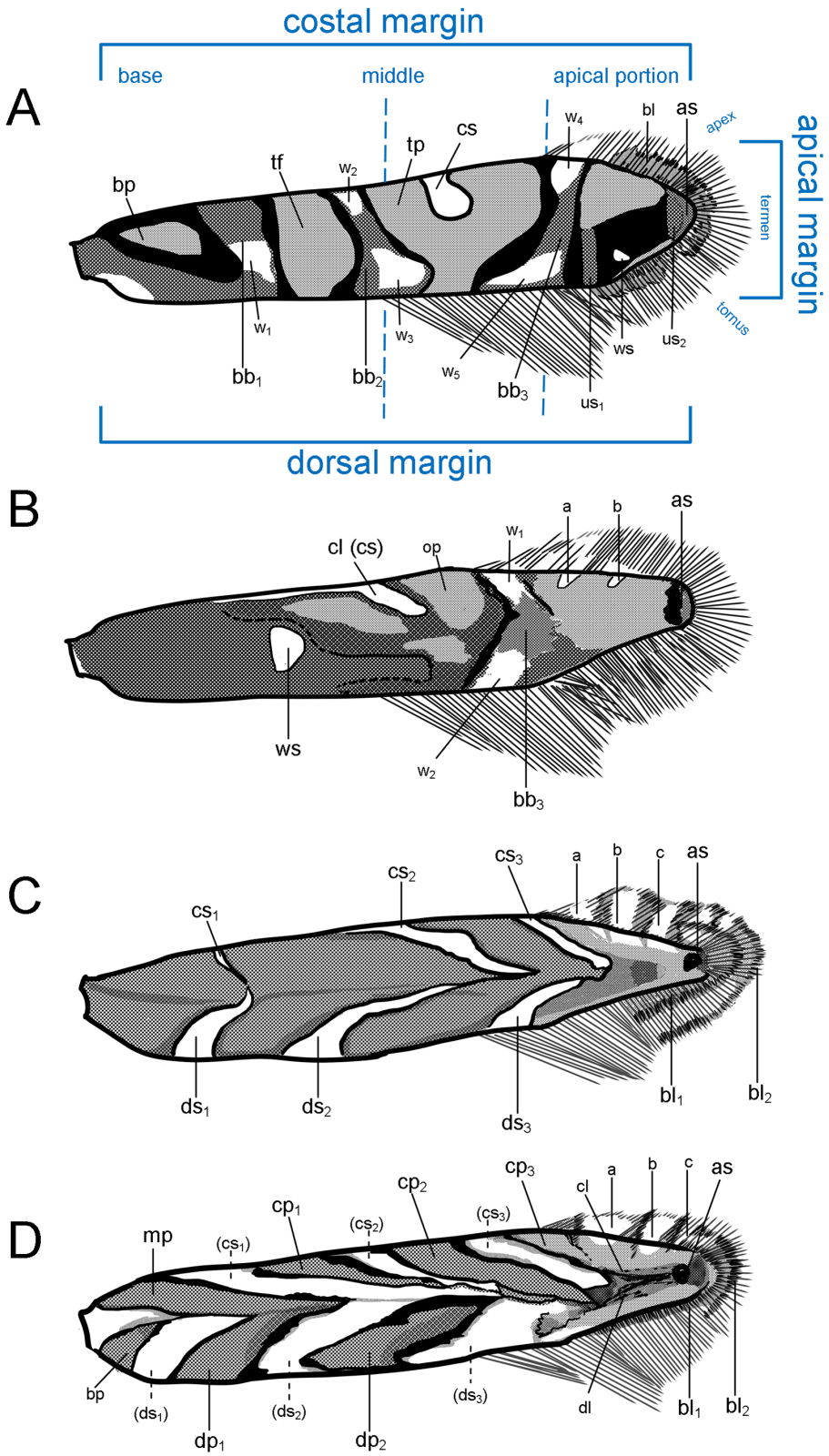

FIGURE 3. Nomenclature adopted in this study for the characterization of the four major *Philodoria* forewing pattern types (A-D). After Kobayashi *et al.* (2018). **A** tf and tp present, **B** wp present at the middle, tf absent and tp obscure, **C** $cs_{1\sim3}$ and three ds present, **D** cp and dp present and cs and ds indistinct. a, b, c: white line on costal cilia, as: apical spot, $bb_{(1–3)}$: bronze color band, bp: basal patch, $bl_{(1–2)}$: basal line, cl: costal line, $cs_{(1–3)}$: costal streak, cp: costal patch, $ds_{(1–3)}$: dorsal streak, $dp_{(1–3)}$: dorsal patch, op: orange patch, mp: median patch, tf: transverse fascia, tp: transverse patch, us: uplight spot, $w_{(1–5)}$: white color band, ws: white spot.

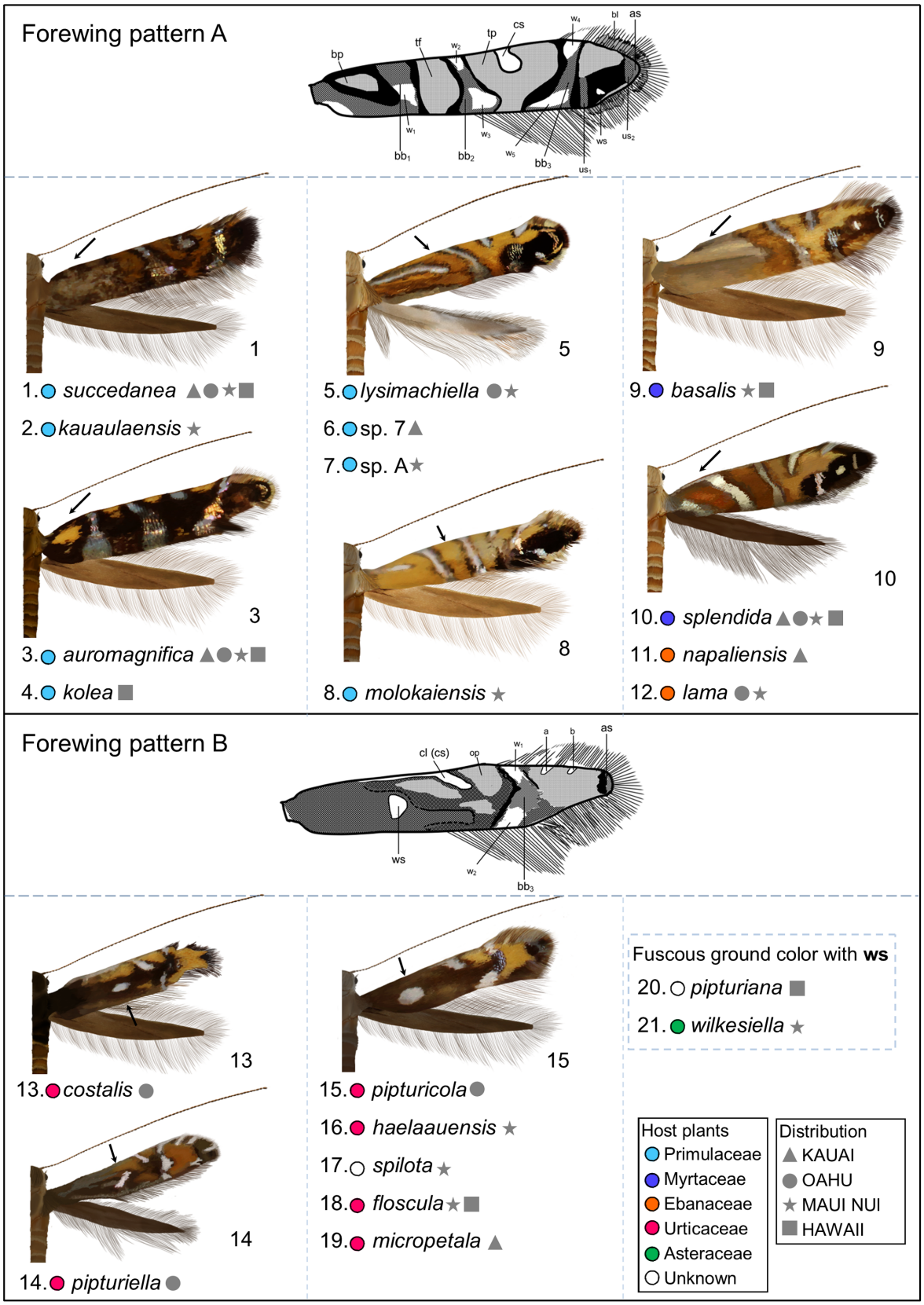

FIGURE 4. Forewing pattern of *Philodoria* species that have a reduced maxillary palpus (Forewing pattern type A and B of Fig. 3). Numbers at the bottom right of each moth image refer to the corresponding species below the image. Additional species that have similar forewing pattern are listed below each moth wing morph type, but not illustrated. **A** Species with forewing pattern type A, those with orange tp are numbered 1–12. **B** Forewing pattern type B those with ws and obscure tp are numbered 13–19. Arrows indicate diagnostic characters of species. These are: bp or base (1, 3, 9, 10), tf (5, 8), ws (13–15).

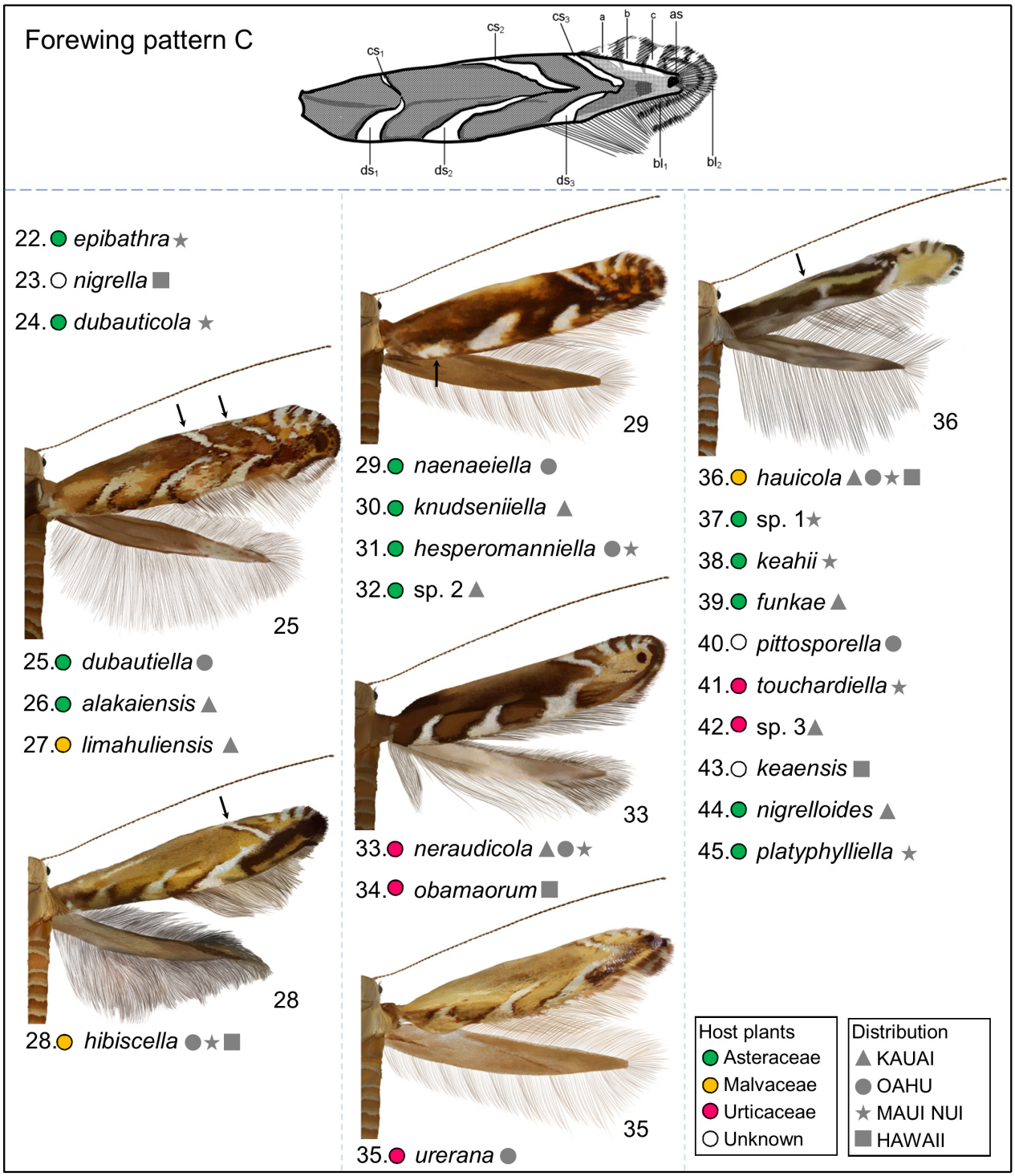

FIGURE 5. *Philodoria* species with forewing pattern type C. These species have white streaks and a developed maxillary palpus. Numbers at the bottom right of each moth image refer to the corresponding species below the image. Additional species that have similar forewing pattern are listed below each moth wing morph type, but not illustrated. Arrows indicate diagnostic characters: cs (25, 28), ds_1 (29), lemon-yellow streak (36).

Wing venation (Figs. 38, 62H). Forewing lanceolate, with thirteen veins (Fig. 38A). Sc along costal fold, ending at one-third of costa; R1 from base to ending at the middle of costa; branched R2 at two-third of the wing; R3, R4 and R5 from end of cell to costa; M1, M2, M3 and CuA1 from end of cell to tornus; CuA2 rather week, at about two-thirds of the wing; CuP weak, from base and reaching dorsal area; A1+2 from base to beyond midde of dorsum. Hindwing lanceolate, with eight veins (Fig. 38B); Sc along anterior margin, ending at one-fourth of costa with about

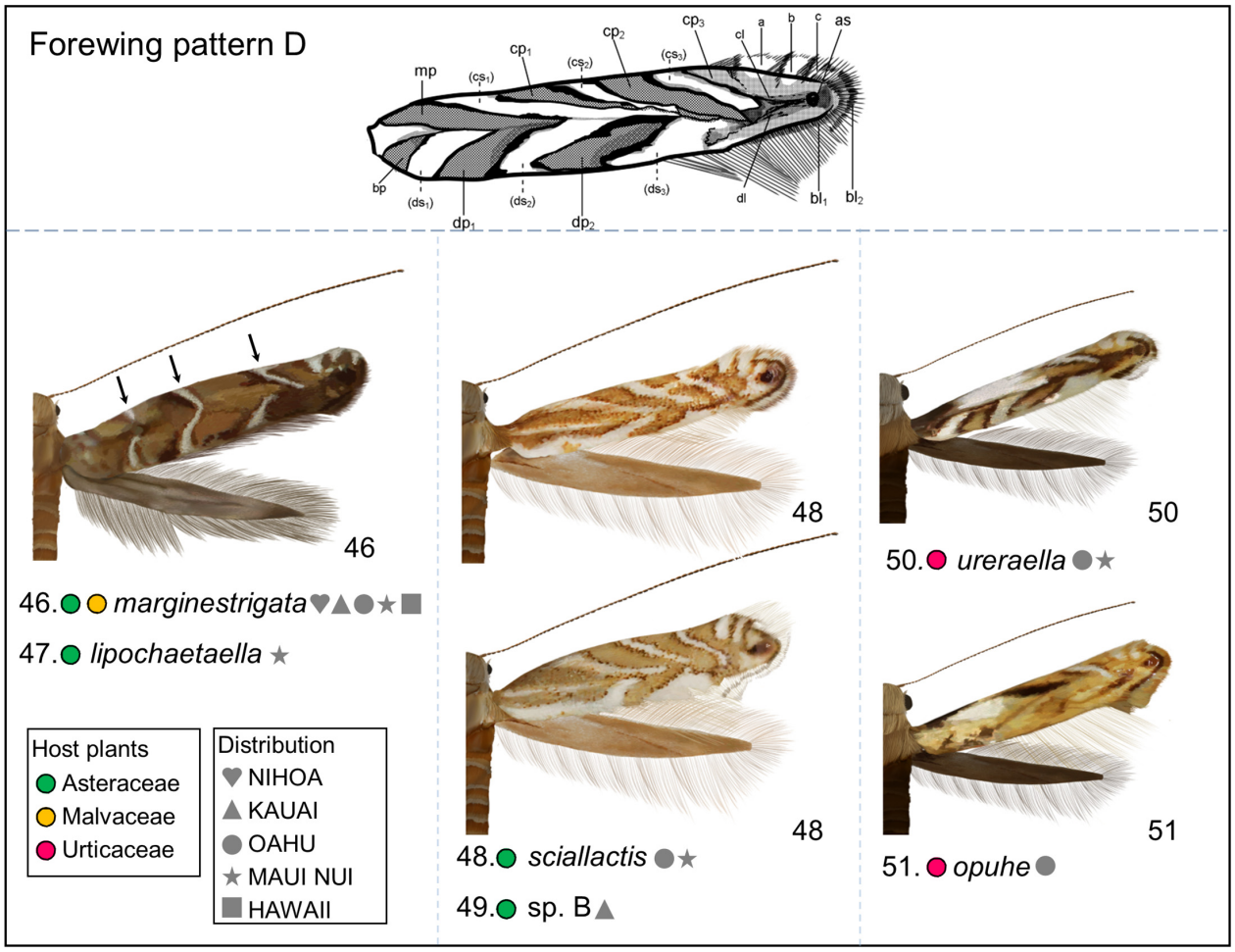

FIGURE 6. *Philodoria* species with forewing pattern type D. These species have a brown patch and developed maxillary palpus. Numbers to the bottom right of each moth image refer to the corresponding species below the image. Additional species that have similar forewing pattern are listed below each moth wing morph type, but not illustrated. Arrows indicate diagnostic characters: cs_{1-3} (46).

four small frenulums; R1 weak, along anterior margin, ending at near the middle of the wing; RS from base to reaching apex; branched M1 and M2; CuA from base to ending at the middle of dorsum; branched M3; CuP from base to ending at one-fourth of dorsum.

Abdomen. Tergum smooth without spiniform setae. Male 8th abdominal segment (Fig. 39) with one or two pairs of coremata; a dorsal flap extending tergum VIII, elongate, triangular, covered with slender, round and flat scales (Fig. 39, 40D).

Male genitalia (Fig. 40A–C) Uncus absent. Tegumen as long as valva in length (Fig. 40B). Tuba analis membranous with weakly sclerotized subscaphium; gnathos V-shaped transverse band, terminal margin weakly joining subscaphium and anterior process connecting ventral base of tegumen (Fig. 40B). Valva elongate, at the middle, tapering along costal margin (Fig. 40C), some species have broad valva with a process; small spines at the apex, surrounded by a set of long setae; a set of short median sized spines arranged on the basal region. Vinculum U-shaped; saccus developed. Phallus tubular, slender; vesica with cornuti; coecum developed (Fig. 40A).

Female genitalia (Fig. 40E–H) Apophyses anteriores and apophyses posteriores slender. Ostium bursae broad, opening at the middle of 7th abdominal segment (Fig. 40E); antrum cup-shaped with a pair of lateral lobes; lamella antevaginalis semicircular and sometimes sclerotized; ductus bursae slender, tubular, posterior section very slender and membranous, curved inside of body and median section weakly sclerotized and flattened (Fig. 40E, F); anterior section tubular sclerotized, terminus of ductus bursae biforked in ventral view and flanked pairs of sclerotized wrinkles reaching anterior end of corpus bursae; inception of ductus seminalis on the posterior part of ductus bursae; corpus bursae pyriform; signa both lateral, a pair of spines or many series of small spines (Fig. 40G, H).

Distribution. United States: Hawaiian Islands (Nihoa, Kauai, Oahu, Molokai, Lanai, Maui and Hawaii [Big Island]).

Host plants. Asteraceae, Ebanaceae, Malvaceae, Myrtaceae, Primulaceae and Urticaceae.

Biology. (Figs. 79–95). *Philodoria* larvae mine leaves of Hawaiian endemic plants in at least 20 genera and 52 species. Of these, 16 plant species are herbaceous. The larva forms a slender linear or serpentine mine on the adaxial side of the host leaf, and gradually expands its mine as it feeds and the mine later becomes the form of a blotch. Larvae of nearly all *Philodoria* species are presumed specialists on one plant genus (for example, 16 *Philodoria* species were recorded from one plant species), except for *P. neraudicola P. sciallactis* and *P. splendida*, that utilize two genera in one plant family. *Philodoria marginestrigata* is unusual in that it utilizes five genera in two plant families. Twenty-seven species are known to create a cocoon outside of the mine, usually pupating on the surface of the leaf. Three species, *P. dubautiella, P. marginestrigata*, and *P. wilkesiella* pupate within larval mines (Fig. 88A; Swezey 1913: 279; Zimmerman 1978a: 685).

Natural enemies. (Table 3, Figs. 98–110). Natural enemies, other than parasitoids, are not well known. Eighteen parasitoid species from four families have been recorded from 14 *Philodoria* species (Yoshimoto 1965; Zimmerman 1978a), these are: Bethylidae: *Sierola planiceps*, *S. philodoriae*, *S. pulchra*, *Sierola* sp.; Braconidae: *Mirax* sp., *Pholetesor bedelliae*; Eulophidae: *Cirrospilus* sp., *Closterocerus* sp., *Diglyphus begini*, *Diglyphus* sp., *Euderus metallicus*, *Neochrysocharis formosus*, *Pauahiana maculatipennis*, *P. metallica*, *Pnigalio externa*, *Sympiesis vagans*, *Zagrammosoma flavolineatum*; Pteromalidae: *Lyrcus tortricidis*. We reared and examined 98 parasitoid wasps that emerged from 15 *Philodoria* species.

Remarks. A total of 51 species are described or redescribed in the present study (See Table 4 and discussion). In addition, some potentially unnamed species have been reported, for example, a "*Philodoria* (*Philodoria*) species" on Maui associated with *Clermontia* (Campanulaceae) (Zimmerman 1978a), and two unidentified "*Philodoria* (*Eophilodoria*) species" on the island of Hawaii (Big Island) associated with *Myoporum* (Scrophulariaceae) (Mines by Swezey 1954:136) and *Pisonia* (Nyctaginaceae) (See Swezey 1954:167) respectively. We observed small mine-like markings on *Pisonia* on Maui and Oahu, and window-like leaf mines in *Clermontia* on East and West Maui, but these mines contained no larvae and it is unclear whether these are made by *Philodoria.* We also could not observe *Philodoria* leaf mines on *Myoporum*, despite there being records of *Philodoria* on this plant. *Myoporum* leaves from Maui and Hawaii (Big Island) had leaf mines, but those were made by agromyzid flies.

Etymology: According to Walsingham (1907), the scientific name "*Philodoria*" has the meaning "bounteousness." It remains unknown what aspect of the moths this word refers to. We present a Hawaiian common name because there are many Hawaiian names for endemic plants and animals, yet this group of moths lacks one. Early Western entomologists in Hawaii did not record Hawaiian names of the many living plants and animals nor did they often take advantage of native guides in their entomological explorations. Roughly translated, *hunelele* means "tiny flier" (*hune* + *lele*) which reflects the microlepidopteran nature of these moths. The second part *'elilau* means "leaf excavator" and alludes to the leaf mining habits of the larval form. We encourage anyone who works with *Philodoria* species to use this name when referring to the genus in the vernacular.

Key to Hawaiian leaf mining moths including *Philodoria*

1. Tentiform mine . . . . . ***Cremastobombycia lantanella*** Busck¶ (Gracillariidae, Lithocolletinae), all Hawaii islands, host: *Lantana* spp.
- Short, tortuous linear, spiral mine, about ~30 mm length **2**
- Long (tortuous) linear or blotch mine **3**
2. Mature larva (3rd~ instar) is external feeding, nibbling the leaf tissue and skeletonizing it . . ***Bucculatrix thurberiella*** Busck¶ (Bucculatricidae), Oahu, host: *Gossypium tomentosum* (endemic Hawaiian cotton).
- Mature larva is leaf-mining, and mines leaf tissue forming several blotch mine. . . . . ***Bedellia*** Stainton (Bedelliidae), all Hawaiian Islands, host: Convolvulaceae, Liliaceae, Poaceae, Urticaceae. Hawaiian *Bedellia* include many unnamed species¶.
3. First instar larva is sap-feeding, forming whitish linear mine **4**
- Larva tissue-feeding, forming linear or serpentine to blotch mines; cocoon usually situated outside of mine . . . . . ***Philodoria*** Walsingham (Gracillariidae, Ornixolinae)
4. Cocoon situated outside of mine, usually on surface of leaf **5**
- Cocoon situated within end of mine, larvae mining leaves of Rutaceae (*Citrus* spp.). . . . . ***Phyllocnistis citrella*** Stainton (Gracillariidae, Phyllocnistinae)

5. Late instar larva tissue feeding, cones created by rolling leaf . . . . . ***Caloptilia*** Hübner[¶]
- On *Diospyros hillebrandii* and *D. sandwicensis* (Ebenaceae), Oahu. . . . . ***C. mabaella*** (Swezey) (Fig. 73D)
- On *Myrica faya* (Myricaceae), Hawaii (Big Island). . . . . ***Caloptilia* sp.** nr. *schinella*[†](= *coruscans* (Walsingham))
- Late instar larva tissue feeder in blotch mine elongated along the leaf edge; the leaf edge at the blotch is narrowly folded down; on *Terminalia catappa* (Combretaceae), Oahu. . . . . ***Ketapangia*** sp.

[*]This key, where only mines and/or cocoons have been examined, but not larvae or adults, can serve only as a partial aid to determination.

[¶]Zimmerman (1978a); [†]Markin (2002); Perreira and Yee (2016)[§].

Key to adults

(Adults of *Philodoria* sp. 2 and *P.* sp. 3 are unknown and are thus excluded from this key.)

- Forewing shiny, metallic bronze with ocherous to orange patches (Fig. 3A) . . . . . **A**
- Forewing brown to fuscous with orange patches and a white spot near middle of wing (Fig. 3B). . . . . **B**
- Forewing brown with one to three costal white streaks and two to three dorsal white streaks (Fig. 3C) . . . . . **C**
- Forewing white with costal ocherous patches and three dorsal ocherous patches (Fig. 3D). . . . . **D**
- Forewing brownish fuscous to black with white patches (Figs. 12, 13) . . . . . **E**
- Forewing leaden gray, externally with fuscous brown (Fig. 7F) . . . . . ***P. kolea***

(A).

1 Basal patch (**bp)** absent; basal half of forewing leaden gray color (Fig. 8C–F). . . . . ***P. basalis***
- **bp** present **2**
2 A bright orange transverse fascia (**tf**) at 3/4 in middle interrupted with blue patch; an orange medial transverse patch (**tp**), narrowing towards dorsum, (Fig. 7C) . . . . . ***P. kauaulaensis***
- An orange transverse patch beyond middle to costal 3/4, narrowing towards dorsum, extending to dorsal 2/3, with white costal spot (Fig. 7A, B, D, E, 8A, B, 9) **3**
3 A black **bp** along costal fold; a fuscous patch near apex (Figs. 7A, B) . . . . . ***P. succedanea***
- An orange **bp** along costal fold, fringed with blackish scales (Fig. 7E); a fuscous patch with dark orange scales at apex . . . . . ***P. auromagnifica***
- An ocherous **bp** from near base of costal fold to dorsal 1/4 (Fig. 9). . . . . ***P. splendida*** (Fig. 9A, B, 73B), ***P. lama* sp. n.** (Figs. 9C, 73E, F), ***P. napaliensis* sp. n.** (Fig. 9D)[§]

[§] It is difficult to identify three species: *lama*, *napaliensis*, and *splendida* from forewing pattern, see key to genitalia and diagnosis of species.

- An ocherous to oraenge **bp** containing two longitudinal streaks **4**
4 An ocherous-orange **tf** from costal 1/3 to dorsal 1/2; **bp** from base to 1/3 (Figs. 8B, 73A) . . . . . ***P. molokaiensis***
- **tf** absent 5
5 **bp** from base to 1/2; $\mathbf{bb}_2$ completed (Fig. 8A); Oahu . . . . . ***P. lysimachiella***[#]
- Basal 1/4 forewing unknown, but orange patch reach 1/2; $\mathbf{bb}_2$ interrupted at middle by an orange patch (Fig. 26G); Kauai . . . . . ***P.* sp. A**

[#] ***P.* sp. 7** has similar forewing pattern, but basal 1/4 of forewing missing and damaged.

(B).

1 **ws** at near middle of the wing, not reaching dorsal margin (Fig. 3B) **2**
- **ws** reaching dorsal margin (Fig. 74B) **3**
2 **ws** oval (Fig. 10C). **4**
- A small oblque **ws** at near middle of the wing; Oahu (Fig. 11A–D) . . . . . ***P. pipturicola***
3 **ws** large, about 3x in diameter than that of *costalis*; $\mathbf{w}_2$ widening toward the wing margin; Oahu (Fig. 10B, C). . . ***P. pipturiella***
- White spot small; two white bands almost the same size; Oahu (Fig. 10A) . . . . . ***P. costalis***
4 **ws** almost erect line; Kauai (Fig. 10F) . . . . . ***P. micropetala***
- **ws** bent toward apex; Hawaii (Big Island) (and Maui) (Figs. 10D, E, 11E, F) **5**
5 **cs** and $\mathbf{w}_1$ rather narrowing; Hawaii (Big Island) and Maui (Figs. 10D, E, 26M) . . . . . ***P. floscula***
- **cs** and $\mathbf{w}_1$ rather broad; Hawaii (Big Island) (Figs. 11E, F, 26K, L, 74). . . . . ***P. haelaauensis* sp. n.**

(C).

1 A lemon-yellow streak from costal fold to 2/5, obliquely, at 3/5 to the middle (Figs. 20C, 77A). . . . . ***P. hauicola***
- Three white costal streaks ($\mathbf{cs}_{1-3}$) present; white streaks are very narrow (Figs. 23A–C, 77E, F) . . . . . ***P. marginestrigata***
- Two white costal streaks ($\mathbf{cs}_2$ and $\mathbf{cs}_3$) present (Figs.14, 15) **2**
- One white streak ($\mathbf{cs}_3$) present (Figs.16–22). **4**
2 A white longitudinal streak in basal half of wing (Fig. 14A). . . . . ***P. dubauticola***
- A broad white streak at costal fold; a transverse fascia at 3/4 ($\mathbf{cs}_3$ + $\mathbf{ds}_3$) (Fig. 22A, B) . . . . . ***P. keaenisis* sp. n.**
- Not so, $\mathbf{ds}_1$ present or brown in basal half **3**
3 $\mathbf{ds}_1$ absent; $\mathbf{cs}_2$ rather short, not reaching the middle of wing (Figs. 14F, 15A–E). . . . . ***P. alakaiensis* sp. n.**
- $\mathbf{ds}_1$ present; $\mathbf{cs}_2$ reaching the middle of wing (Figs. 14B–D, 15F, G). . . . . ***P. dubautiella***, ***P. limahuliensis* sp. n.**[**]

** *P. limahuliensis* has more dark color forewing.

4 Three white dorsal streaks ($\mathbf{ds}_{1-3}$) present respectvely **5**

- **ds**$_2$ connecting basal patch on dorsum (**ds**$_1$) **8**
- **ds**$_1$ absent; a small white costal spot at near base; blue to fuscous patch at apical portion (Figs. 22D, 75D–G) . . . . . ***P. platyphylliella* sp. n.**

5 **ds**$_1$ is small white patch (Fig. 16C, D); **ds**$_3$ rather small . . . . . ***P. naenaeiella***
- **ds**$_1$ is triangular-shaped streak (Fig. 21E); **ds**$_3$ rather small (See also key of *P. nigrella*) . . . . . ***P. touchardiella***
- **ds**$_1$ reaching the middle of wing **6**

6 Base to apex of **ds**$_1$ and **ds**$_2$ are almost same in width; **ds**$_3$ is triangular-shaped white patch (Fig. 19C–E) ***P. obamaorum* sp. n.**
- **ds**$_{1, 2}$ are slightly widend at dorsum; **ds**$_3$ is nearly triangular-shaped white patch (Fig. 19A, B) . . . . . ***P. neraudicola***
- **ds**$_{1–3}$ are widened at dorsum (Figs. 16A, B, 17, 18, 75B, C, 77B–D, 78E, F) **7**

7 Rather narrowing **ds**:
- Apical portion orange with fuscous scales at center and a large **as**; ocherous color forewing (Figs. 16A, B, 77B–D). . . . . ***P. hibiscella***
- Apical portion pale lemon-yellow with a small **as**; brounish fuscous to brown color forewing (Figs. 20A, B, 78E, F). . . . . ***P. urerana***
- Rather wider **ds** from dorsum to the middle; apical portion with blue patch (Figs. 17, 18, 75B, C). . . . . ***P. hesperomanniella* sp. n., *P. knudseniiella* sp. n.**

8 **ds**$_1$ is narrowing white band (Figs. 20F, 76). **9**
- **ds**$_1$ is weakly triangular (Fig. 21B, D) **10**

9 A fuscous patch at dorsum 3/4; dark brown color forewing (Fig. 76) . . . . . ***P.* sp. 1**
- A fuscous patch at 3/4, not reaching dorsal margin; ocherous color forewing (Fig. 20F) . . . . . ***P. keahii* sp. n.**

10 Apical portion fuscous; bronze brown color forewing (Fig. 21A, B) . . . . . ***P. funkae* sp. n.**
- Apical portion light ocherous brown, but damaged; light ocherous brown color forewing (Fig. 21D). . . . . ***P. pittosporella***

(D).

1. A fuscous costal line from base to about 1/2 (Fig. 25C, D) . . . . . ***P. opuhe* sp. n.**
- **cp**$_1$ absent (Figs. 25A, B, 78D). . . . . ***P. ureraella***
- **cp**$_1$ present; **dp**$_1$ indistinct, connecting **mp** (**ds**$_2$ connecting **ds**$_1$) (Figs. 23D–G, 24, 78A–C) **2**

2 **dp**$_2$ and **dp**$_3$ not meeting . . . . . ***P. lipochaetaella*** (Figs. 23D–G, 24A), ***P. sciallactis*** (Figs. 24B–G, 78A–C)
- **dp**$_2$ and **dp**$_3$ meeting at median line (Fig. 24H) . . . . . ***P.* sp. B**

(E).

1 An oval white spot about the middle of wing (Fig. 12A–C) **2**
- An oval white spot absent (Figs. 12D, 13). **3**

2 A longitudinal white streak from base to 1/3; an oblique white costal spot at 2/3, recurves to the costa (Fig. 12A–C) . . . . . ***P. pipturiana***
- A white costal spot at 2/3, not curve (Zimmerman 1978a: fig. 467) . . . . . ***P. spilota***

3 Two or three costal spots (Fig. 12D) . . . . . ***P. wilkesiella***
- A costal streak (**cs**$_3$) at 3/4 (Fig.13) **4**

4 Dorsal streaks (**ds**$_{1–3}$) rather wider at dorsal base; **ds**$_1$ indistinct or along dorsal margin (Fig. 13A–C) . . . . . ***P. epibathra***
- **ds**$_{1–3}$ rather narrow; **ds**$_1$ reaching the middle of wing (Fig. 13D, E). . . . . ***P. nigrella***
- **ds**$_{1–3}$ rather narrow; **ds**$_1$ is very small white patch (Zimmerman, 1978a: fig. 466; Fig. 22C) . . . . . ***P. nigrelloides***

Key to male genitalia

(Males of *P. funkae* sp. n., *P. kauaulaensis*, *P. keaensis* sp. n., *P. micropetala*, *P. nigrelloides*, *P. spilota*, *P.* sp. 1–3, *P*. sp. A and B are unknown.)

- Valva broad and having a short dorsal process (Fig. 41) . . . . . **A**
- Valva oblong, broad at basal part and tapering from the middle along the costal margin (Figs. 44, 47, 50, 53). . . . . **B**

(A).

1 A dorsal process digitiform covered with fine setae (Fig. 41A–H) **2**
- A dorsal process knob-like, densely covered with minute spines (Fig. 41I–N). . . . . ***P. basalis*, *P. splendida*, *P. lama* sp. n., *P. napaliensis* sp. n.**

2 Saccus short, about 200 μm long and tapering toward the point (Fig. 42E–G) **3**
- Saccus long, about 250–300 μm long and slightly wide at the point in ventral view (Fig. 42A–D) **4**

3 A dorsal process short and slender; saccus rather slender (Figs. 41E, 42E) . . . . . ***P. lysimachiella***
- A dorsal process short and broad toward at apex; saccus digitiform (Fig. 41F, G, 42F) . . . . . ***P.* sp. 7**

-. . . . . A dorsal process very long and slender (Fig. 41H), extending at dorsal base; saccus rather broad (Fig. 43G) . . . . . ***P. molokaiensis***

4 Saccus slender, curved toward dorsum (Fig. 41A); vinculum small and inflexed on the ventral side (Fig. 42A). . ***P. succedanea***
- Saccus broad and straight; vinculum large and inflexed on the ventral side (Fig. 42B–D) **5**

5 Valva slightly narrowing in middle with terminally rounded dorsal process (Fig. 41B, C). . . . . ***P. auromagnifica***
- Valva with short, pointed dorsal process (Fig. 41D) . . . . . ***P. kolea***

(B).

1 Two pairs of coremata in 8th segment (Fig. 39C, D) **2**

-	One pair of coremata in 8th segment (Fig. 39A, B)	**3**
2	Valva 500–550 µm long, slender; dorsal margin of valva 2x width of apical portion of valva, slightly angled (Fig. 44E–H)	***P. haelaauensis* sp. n.**
-	Valva 590 µm long, slightly rounded at apex, narrowing at middle; dorsal margin of valva 3x width of apical portion of valva (Fig. 47E)	***P. alakaiensis* sp. n.**
3	Saccus very long, 230 µm in length (Fig. 48B)	***P. epibathra***
-	Saccus short, ~150 µm in length	**4**
4	Valva digitiform (Fig. 50F)	**5**
-	Valva tapering along costal margin from the middle	**6**
5	Saccus very slender, needle-shaped:	
-	Phallus short and broad with two series of spiny minute cornuti in vesica (Fig. 52D)	***P. hauicola***
-	Phallus short and broad with indistinct cornuti in vesica (Zimmerman 1978a: Fig. 451)	***P. nigrella***
-	Phallus unknown (Zimmerman 1978a: fig, 449)	***P. lipochaetaella***
6	Phallus with two series of spiny minute cornuti in vesica	**7**
-	Phallus with indistinct cornuti in vesica	**8**
7	Valva 400–570 µm long, rounded at apex with dorsal magin of basal portion rounded (Fig. 44A, B, I, J; Zimmerman, 1978a: fig. 469); phallus short, about 400 µm long (Fig. 46A, E; ; Zimmerman, 1978a: fig. 469).	***P. costalis*, *P. pipturiella*, *P. floscula***
-	Valva 500–550 µm long slender; dorsal margin of valva slightly angled (Fig. 44C, D)	***P. pipturicola***
-	Valva 480–600 µm long, rather straight, thick, and stick shaped from base 2/5 to apex (Fig. 47A, H); phallus pointed at apex (Fig. 48A, H)	***P. wilkesiella*, *P. naenaeiella***
-	Valva length unknown, similar to above two species and *P. hesperomanniella* sp. n.; Saccus very slender (Zimmerman, 1978a: 465).	***P. pipturiana***
-	Valva 480–500 µm long; saccus and coecum half length of these of *P. neraudicola* (Figs. 50C, D, 51B) .	***P. obamaorum* sp. n.**
-	Valva about 540 µm long, slightly narrowing at middle; saccus pointed at apex in ventral view (Figs. 50A, B, 51A)	***P. neraudicola***
-	Valva 780 µm long, widened at basal portion with slender apical portion curved to inner side; saccus digitiform (Figs. 47I, 48I)	***P. knudseniiella* sp. n.**
8	Valva short, 400–500 µm long	**9**
-	Valva oblong, 500~ µm long	**10**
9	Valva 430 µm long, slightly narrowing at 2/3 and rounded at apex; saccus short and triangular in ventral view (Figs. 50G, 51E)	***P. keahii* sp. n.**
-	Valva 440–460 µm long, slender at apical half and slightly curved dorsally; dorsal margin of basal portion angular (Figs. 50J–M, 53A, B)	***P. marginestrigata*, *P. sciallactis***
10	Valva 560–580 µm long, costal margin of valva slightly curved dorsally, slightly tapering at apex (Fig. 47C, D):	
-	Saccus short digitiform, rather broad (Fig. 48C)	***P. dubauticola***
-	Saccus short digitiform, rather slender (Fig. 48D)	***P. dubautiella***
-	Valva 660 µm long, widened at basal portion with slender apical portion curved to ventral side; saccus triangular (Figs. 47J, 48J)	***P. hesperomanniella* sp. n.**
-	Valva 630–700 µm long; saccus slender and digitiform; phallus straight; phallobase sinuous (Figs. 47F, G, 48F, G, 49F, G)	***P. hibiscella*, *P. limahuliensis* sp. n.**
-	Valva 690 µm long; saccus slender and needle-shaped in ventral view; phallus straight (Figs. 50E, 51C, 52C)	***P. urerana***
-	Valva 570 µm long, slightly sinuous from basal 2/5 to apex; saccus rather long and stick-shaped in ventral view; phallus straight (Figs. 50H, 51F, 52F)	***P. touchardiella***
-	Valva 590 µm long; saccus digitiform in ventral view; phallus straight (Figs. 50I, 51G, 52G)	***P. platyphylliella* sp. n.**
-	Valva 540 µm long, apical half digitiform and slightly curved toward outer margin; saccus very slender and needle-shaped in ventral view; phallus nearly straight (Figs. 53C, 54B, 55B)	***P. ureraella***
-	Valva 620 µm long, apical half digitiform and slightly curved toward outer margin; saccus triangular or digitiform in ventral view. Phallus rather thick, slightly sinuous in lateral view (Figs. 53D, 54C, D, 55C).	***P. opuhe* sp. n.**
-	Valva length unknown, apical half slender and slightly curved toward inner margin; Saccus short and pointed at apex in ventral view. Phallus straight (Zimmerman 1978a: fig. 452)	***P. pittosporella***

Key to female genitalia

(Females of *P. limahuliensis* **sp. n.**, *P. napaliensis* **sp. n.**, *P. nigrella*, *P. pipturiana*, *P. pittosporella*, *P. platyphylliella* **sp. n.**, *P*. sp. 2, 3, 7, and *P*. sp. B are unknown. The female of *P. micropetala* is known except that its corpus bursae and ductus bursae are missing)

1	Signa present with spines	**2**
-	Signa absent; corpus bursae smooth or with some lines consisting of wrinkles running longitudinally, some sclerotized.	**8**
2	Lamella antevaginalis large sclerotized plate	**3**
-	Lamella antevaginalis weakly sclerotized; antrum cup-shaped with a slender pair of lateral lobes	**4**
3	Spines on signa large, triangular; lamella antevaginalis trapezoid (Fig. 56I, J).	***P. molokaiensis***

- Spines on signa short, linear; lamella antevaginalis trapezoid, rather narrowing at posterior end (Fig. 56H) . . . . . ***P.* sp. A**
- Spines on signa large claw-shaped (Fig. 56G) . . . . . ***P. lysimachiella***
- Spines on signa oblong and podlike (Fig. 40G, H, 56K, L) . . . . . ***P. basalis***, ***P. splendida***, ***P. lama* sp. n.**

4 End of ductus bursae membranous **5**
- End of ductus bursae sclerotized, bifurcated **7**

5 Signa small and narrow with minute spines; lateral lobes of antrum short (Fig. 56F) . . . . . ***P. kolea***
- Signa spiny pyriform with minute spines (Fig. 57F; Zimmerman 1978a: fig. 480) . . . . . ***P. haelaauensis* sp. n.**, ***P. spilota***
- Signa rather broad, sinouous, linear; lateral lobes long and slender (Fig. 57G) . . . . . ***P. floscula***
- Signa with a pair of large spines **6**

6 Spines long and slender (Fig. 56A, B) . . . . . ***P. succedanea***
- Spines on signa small and rounded (Fig. 56D, E) . . . . . ***P. kauaulaensis***
- Spines on signa blunt (Fig. 56C) . . . . . ***P. auromagnifica***

7 Signa small and podlike with minute spines (Fig. 59L) . . . . . ***P. hauicola***
- Signa two short lines with minute spines (Figs. 58H, 59J) . . . . . ***P. hibiscella***, ***P. touchardiella***
- Signa very small with a pair of slender minute spines (Fig. 59K) . . . . . ***P. keaensis* sp. n.**
- Signum very small with a minute spine (Fig. 60A–C) . . . . . ***P. marginestrigata***

8 Ductus bursae short, about 300 µm in length; lamella antevaginalis inflexed on posterior margin (Fig. 57A–E) . . . . . ***P. costalis***, ***P. pipturiella P. pipturicola***
- Ductus bursae short, about 300 µm in length; lamella antevaginalis semicircular (Fig. 58A) . . . . . ***P. wilkesiella***
- Ductus bursae long, 400~µm in length (Figs. 58B–G, I–M, 59A–I, 60D–F) . . . . . ***P. alakaiensis* sp. n.**, ***P. dubauticola***, ***P. dubautiella***, ***P. epibathra***, ***P. obamaorum* sp. n.**, ***P. hesperomanniella* sp. n.**, ***P. funkae* sp. n.**, ***P. keahii* sp. n.**, ***P. knudseniiella* sp. n.**, ***P. lipochaetaella*, *P. naenaeiella***, ***P. neraudicola***, ***P. nigrelloides*, *P. opuhe* sp. n.**, ***P. sciallactis*, *P. ureraella***, ***P. urerana***, ***P.* sp. 1**[¶]

[¶] Females of the 18 species have the following similar characters: lamella antevaginalis weakly sclerotized, widening toward anterior margin of A7; Ductus bursae posterior extremity widening and membranous, and middle part weakly sclerotized, round and flat; terminus of ductus bursae tubular, biforked. Corpus bursae pyriform or oblong; signa absent; paired rows consisting of wrinkles running longitudinally. See also key to adults and male genitalia for species identification.

Key to leaf mines and larval host plants

Family **Asteraceae**

Genus ***Argyroxiphium***
- Early instars create a mine that is linear between the major leaf veins, the late stage mine form is unknown; cocoon situated within the end of the mine (Fig. 88A); on *A. grayanum*; Maui . . . . . ***P. wilkesiella***

Genus ***Dubautia***
- Early instars create a mine that is linear along leaf margin and making it a near complete oval; on *D. menzesii*; Maui (Fig. 8-7E, F) . . . . . ***P.* sp. 1**
- Slender linear mine lengthwise in the leaf and tortuous:
  On "*Dubautia*"(= *D. plantaginea*?) and *D. laxa*; Maui (Fig. 88B–F) . . . . . ***P. dubauticola***
  On *D. plantaginea* and *D. laxa*; Oahu . . . . . ***P. dubautiella***, ***P. naenaeiella*** (Fig. 88G, H)
- Linear to blotch mine:
  On *D. platyphylla*; Maui (Fig. 87G–I) . . . . . ***P. platyphylliella* sp. n.**
- Mine unknown:
  On *D. laxa* Molokai . . . . . ***P. epibathra***
  On *D. knudsenii* subsp. *nagate* and *D. latifolia*; Kauai . . . . . ***P. knudseniiella* sp. n.**
  On *Dubautia* sp. (*D. laxa* or *D. paleata*); Kauai . . . . . ***P. alakaiensis* sp. n.**
  On *Dubautia* sp.; Kauai . . . . . ***P. nigrelloides***
  On *Dubautia* sp.; Kauai? . . . . . ***P. marginestrigata***

Genus ***Hesperomannia***
- At early stages the mine is sinuous linear along leaf margin, later becomes a large blotch mine:
  On *H. arborescens,* and *H. swezeyi*; Oahu, Maui (Fig. 89) . . . . . ***P. hesperomanniella* sp. n.**
  On *H. lydgateyi*; Kauai (Fig. 90) . . . . . ***P.* sp. 2**

Genus ***Lipochaeta***
- Blotch mine along leaf margin; pupation external in cocoon; on *L. rockii*; Molokai (Fig. 91D–F) . . . . . ***P. sciallactis***
- Mine unknown:
  On *L. lavarum*; Maui . . . . . ***P. lipochaetaella***
  On *L. connata* var. *acris*; Kauai . . . . . ***P.* sp. B**
  On *L. rockii*; pupation external in cocoon within mine; Molokai . . . . . ***P. marginestrigata***

Genus ***Melanthera***
- Blotch mine along leaf margin; pupation external in cocoon; on *M. integrifolia* and *M. kamolensis*; Oahu, Molokai, Maui (Fig. 91A–C, G) . . . . . ***P. sciallactis***

Genus ***Remya***

- Linear to blotch mine; on *R. mauiensis*; Maui (Fig. 91H, I) . . . . . ***P. keahii* sp. n.**

Genus ***Xanthium***

- Mine unknown; on *X. echinatum*, *X. strumarium, Xanthium* sp.; Oahu. . . . . ***P. marginestrigata***

Genus ***Wilkesia***

- Blotch mine at the leaf tips; on *W. gymnoxiphium*; Kauai . . . . . ***P. funkae* sp. n.**

Family **Ebenaceae**

Genus ***Diospyros***

Slender linear to irregular blotch mine; pupation in "taco"-like oval cocoon (Fig. 83A–C, E); on *D. sandwicensis* and/or *D. hillebrandii*:

- Oahu, Lanai, Maui (Fig. 83). . . . . ***P. lama* sp. n.**
- Kauai. . . . . ***P. napaliensis* sp. n.**

Family **Malvaceae**

Genus ***Abutilon***

- Mine unknown; on *A. incanum*, *A. molle*, *A. menziesii*; Kauai?[a], Oahu, Molokai . . . . . ***P. marginestrigata***

[a] Kauai records of this species were from "larvae mining various plant" (Walsingham, 1907: 722)

Genus ***Hibiscus***

- Elongate blotch mine along leaf margin (Fig. 93A, B, D); on *H. arnottianus*, *H. rosasinensis*, *H. arnottianus* subsp. *immaculatus* and *H. tiliaceus*; Oahu, Maui, Molokai, Hawaii (Big Island). . . . . ***P. hibiscella***
- Linear to blotch mine (Figs. 92, 93F); on *H. tiliaceus*; Kauai, Oahu, Maui, Hawaii (Big Island). . . . . ***P. hauicola***
- Mine unknown; on *H. waimeae* subsp. *hannerae*; Kauai. . . . . ***P. limahuliensis* sp. n.**

Genus ***Sida***

- Tortuous linear mine (Fig. 93C); on *S. cordifolia, S. fallax*, *S. meyeniana*, *S. rhombifolia*; Nihoa, Kauai, Oahu, Molokai, Lanai ***P. marginestrigata***

Family **Myrtaceae**

Genus ***Metrosideros***

Slender linear to blotch mine; pupation in "taco"-like oval cocoon (Fig. 81B, J–M):

On *M. polymorpha* and other *Metrosideros.* sp.; Maui, Hawaii (Big Island) (Fig. 81) . . . . . ***P. basalis***

On *M. polymorpha* (Fig. 82A, D, E), *Syzygium* sp. (Fig. 82B, C, F); Kauai, Oahu, Molokai, Lanai, Hawaii (Big island). . . . . ***P. splendida***

Family **Primulaceae**

Genus ***Lysimachia***

Slender linear to blotch mine:

On *L. hillebrandii* var. and *L. maxima*; Molokai (Fig. 80A, B, D, E) . . . . . ***P. molokaiensis***

On *Lysimachia hillebrandii*; Oahu . . . . . ***P. lysimachiella***

On *L. kalalauensis*; Kauai . . . . . ***P.* sp. 7**

On *Lysimachia* sp.; Maui (Fig. 80C, F) . . . . . ***P.* sp. A**

Genus ***Myrsine***

1 Beginning of mine spiral (Fig. 79E); on *Myrsine lanaiensis*, *M. lessertiana, M. sandwicensis*; Maui . . . . . ***P. kauaulaensis***

- Start of mine linear or tortuous linear. **2**

2 Reddish brown long linear mine following leaf vein (Fig. 79A–D, F, G), mature larva mine of fallen leaf (Fig. 79G); on *M. knudsenii*, *M. lessertiana*, *M. linearifolia*, *M. sandwicensis*; Kauai, Oahu, Lanai, Maui, Hawaii (Big Island) . . . . . ***P. succedanea***

- Brown tortuous linear mine, mature larva in *in situ* leaf **3**

3 Mines on leaves on mature plants (tree height: >1 m); on *M. lessertiana*, *M. sandwicensis* and *M. wawraea*; Kauai, Oahu, Molokai, Hawaii (Big Island) (Fig. 79H). . . . . ***P. auromagnifica***

- Mines on fresh leaf of seedling (Fig. 79I–K); on *M. lessertiana*; Hawaii (Big Island) . . . . . ***P. kolea***

Family **Urticaceae**

Genus ***Neraudia***

Mine unknown; on *Neraudia melastomifolia*; see biology of ***P. neraudicola***

Genus ***Pipturus***

1 Tortuous linear to blotch mine; frass line linear (Figs. 84–86) **2**

- Blotch mine; the frass gathered in center (Fig. 85E, 86C); on ***Neraudia melastomifolia***, *Pipturus albidus*, *Pipturus* sp.; Kauai? (See Remarks), Molokai, Oahu, Maui . . . . . ***P. neraudicola***
- Mine unknown; on *Pipturus* sp. :

Oahu . . . . . ***P. costalis***, ***P. pipturiella***

Kauai. . . . . ***P. micropetala***

Hawaii (Big Island) . . . . . ***P. pipturiana***

2 At early stages the mine is tornuous linear, later becomes a blotch mine (Figs. 84):

On *Pipturus* sp.; Oahu . . . . . ***P. pipturicola***

On *P. albidus*, *P. rocki*, *Pipturus* sp.; Maui, Molokai . . . . . ***P. haelaauensis* sp. n.**

- Early stage the mine unknown, later becomes a blotch mine; on *P. albidus*, *Pipturus* sp.:
  Hawaii (Big Island) . . . . . ***P. obamaorum* sp. n.**
  Maui, Hawaii (Big Island) . . . . . ***P. floscula***
  We collected numerous *Philodoria* mines from several *Pipturus* species: we observed tortuous linear to blotch mines on the leaves of *P. albidus* (Fig. 86A), *Pipturus* sp. 1 (Fig. 85A), *Pipturus* sp. 4 (Fig. 85B), and *Pipturus* sp. 2 (Fig. 85C). We could not examine adult specimens because adults did not emerge from rearing efforts, and we were unable to identify larvae to species.

Genus ***Touchardia***

- Broad linear mine; on *T. latifolia*; Molokai, Maui (Fig. 94) . . . . . ***P. touchardiella***
- Mine unknown; on *T. latifolia*; Kauai . . . . . ***P.* sp. 3**

Genus ***Urera***

- At early stages, the mine is slender, linear or tortuous linear, later becomes a blotch mine (Fig. 95A, B); on *U. sandvicensis*, *U. glabra*; Oahu. . . . . ***P. urerana***
- Slender, tortuous linear mine (Fig. 95D, E); on *U. sandvicensis*, *U. glabra*; Oahu, Maui. . . . . ***P. ureraella***
- At early stages, the mine is small roundish and blotch, later becomes an irregular blotch mine; on *U. kaalae*, *U. sandvicensis*; Oahu . . . . . ***P. opuhe* sp. n.**

Taxonomy

Philodoria succedanea Walsingham, 1907

Figs. 7A, B, 26A, 34A, 39A, 41A, 42A, 43A, 56A, B, 79A–D, F, G.

Philodoria succedanea Walsingham, 1907: 717–718; pl. 25, fig. 19; Zimmerman 1978a: 718: figs. 433, 435, 467, 472; Kobayashi *et al*. 2018: 118–126, figs. 2A–D, 5A–D, 6A–D, 7E, F, 8A, 9, 14A.

Type locality. Olinda, Haleakala (Maui).

Type material. Lectotype ♀, Olinda, 4000 ft., Haleakala, MAUI, Hawaiian Is. iv.1894, Perkins. 26695 [Walsingham specimen number]|PHILODORIA SUCCEDANEA Wlsm. Fn. Hawaii. I TYPE ♀ descr. figd.|Walsingham Collection. 1910-427.| NHMUK010305341. Paralectotypes 17 (2♂ 1♀ 14 sex unknown; NHMUK ones are all from above Walsingham accession and 'PARATYPE' below is short for 'PHILODORIA SUCCEDANEA Wlsm. PARATYPE' as printed on large black-margined labels, with the 5-digit Walsingham specimen numbers whose first digit is '2' borne on the locality label): 1 ♂, Haleakula 4000 ft. MAUI, Hawaiian Is. V. 1896|Perkins. 28505|PHILODORIA SUCCEDANEA Wlsm. Fn. Hawaii. I TYPE ♂|BM ♂ Genitalia slide no. 2755|NHMUK010305341. 1♀ 2 sex unknown: Haleakala, 5000ft, MAUI, Hawaiian Is., v.1896, Perkins. 28355|PARATYPE 3/17|NHMUK010862804|; 28230|PARATYPE 4/17♀|BPBM 34324; 28236|PARATYPE 5/17|BPBM 34321. 4 sex unknown: Haleakula -4000 ft. Maui, v. 1896, Perkins. 28492|PARATYPE8/17; 28493| PARATYPE 9/17|BPBM 34320|; 28494|PARATYPE10/17|NHMUK010862806; 28495| PARATYPE 11/17|NHMUK010862807. 1 ♂ 7 sex unknown, same data and locality as lectotype: 26696|NHMUK010862803; 26661|PARATYPE1/17|BPBM34325; 26667| PARATYPE2/17|BPBM 34222; 28511|PARATYPE12/17|NHMUK010862808; 28512|PARATYPE13/17|NHM UK010862809; 28513|PARATYPE14/17|NHMUK010862810;28514|PARATYPE15/17♂|NHMUK010862811;28552|PARATYPE 16/17|BPBM 34323.

Diagnosis. *Philodoria succedanea* is very similar to *P. auromagnifica*. Both species feed on *Myrsine*, but the former is distinguished by the bright orange patches and black triangular shaped **bp** in the forewing (Fig. 7A, B); the male genitalia which has broad valva, slender and long saccus curving toward dorsal margin (Figs. 41A, 42A); the female genitalia which has signa with slender and long spines (Fig. 56A, B) (Kobayashi *et al*. 2018).

Adult (Fig. 7A, B, 26A, 34A). Wingspan 9–10 mm in type series. **Male genitalia** (Figs. 39A, 41A, 42A, 43A) and **Female genitalia** (Fig. 56A, B). See also Kobayashi *et al*. (2018).

Distribution. Kauai, Oahu, and Lanai: (Kobayashi *et al*. 2018), Maui (Walsingham 1907) and Molokai and Hawaii (Big Island) (Zimmerman 1978a).

Host plants. Primulaceae: *Myrsine lessertiana* A. DC. and *M. sandwicensis* A. DC. (Johns *et al*. 2016), *M. linearifolia* Hosaka and *M. knudsenii* (Rock) Hosaka (Kobayashi *et al*. 2018), *Myrsine* sp. (Zimmerman 1978a).

Biology. (Fig. 79A–D, F, G) Kobayashi *et al*. (2018: 123, 126, Figs. 8A, 9, 14A) reported leaf mine, pupal cocoon and resting posture of the adult.

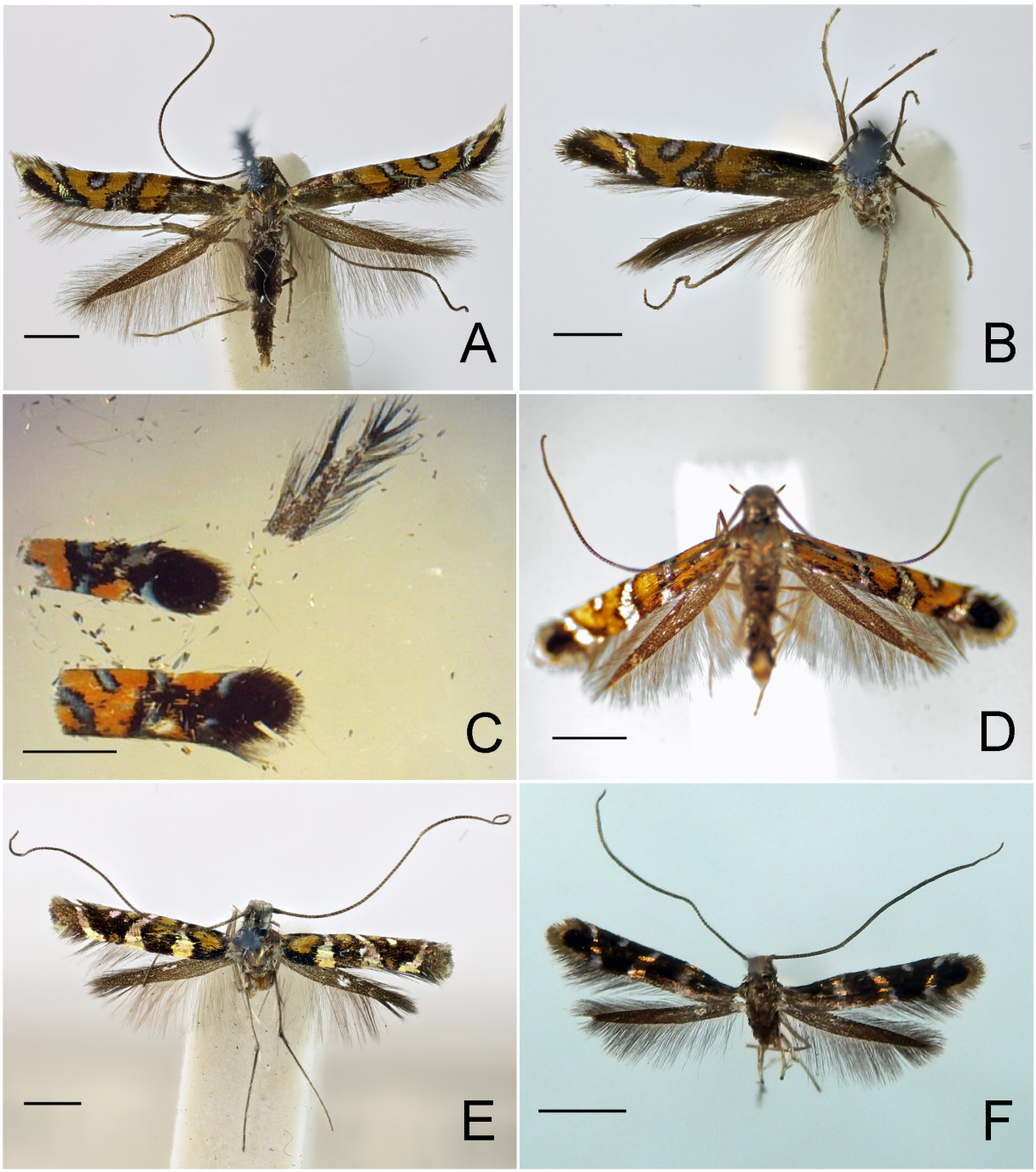

FIGURE 7. Adults of *Philodoria* species. **A** *P. succedanea* Walsingham, 1907 lectotype female, **B** Paralectotype male, **C** *P. kauaulaensis* Kobayashi, Johns & Kawahara, 2018 holotype female, **D** *Philodoria* sp. nr. *P. auromagnifica* male Kauai, **E** *P. auromagnifica* Walsingham, 1907 holotype male, **F** *P. kolea* Kobayashi, Johns & Kawahara, 2018 holotype male. Scale bar 1 mm.

Philodoria kauaulaensis **Kobayashi, Johns & Kawahara, 2018**

Figs. 7C, 56D, E, 79E.

Philodoria kauaulaensis Kobayashi, Johns & Kawahara, 2018: 126–129, figs. 5I, J, 7H, 10, 14B.

Type locality. Kauaula (Maui).

Type material. Holotype ♀, Kauaula, Maui, 18.viii.2014 (stored in 99% ethanol), C.A. Johns leg., host: *Myrsine lanaiensis*, 31.vii.2014, CJ-381, SK690 in BPBM.

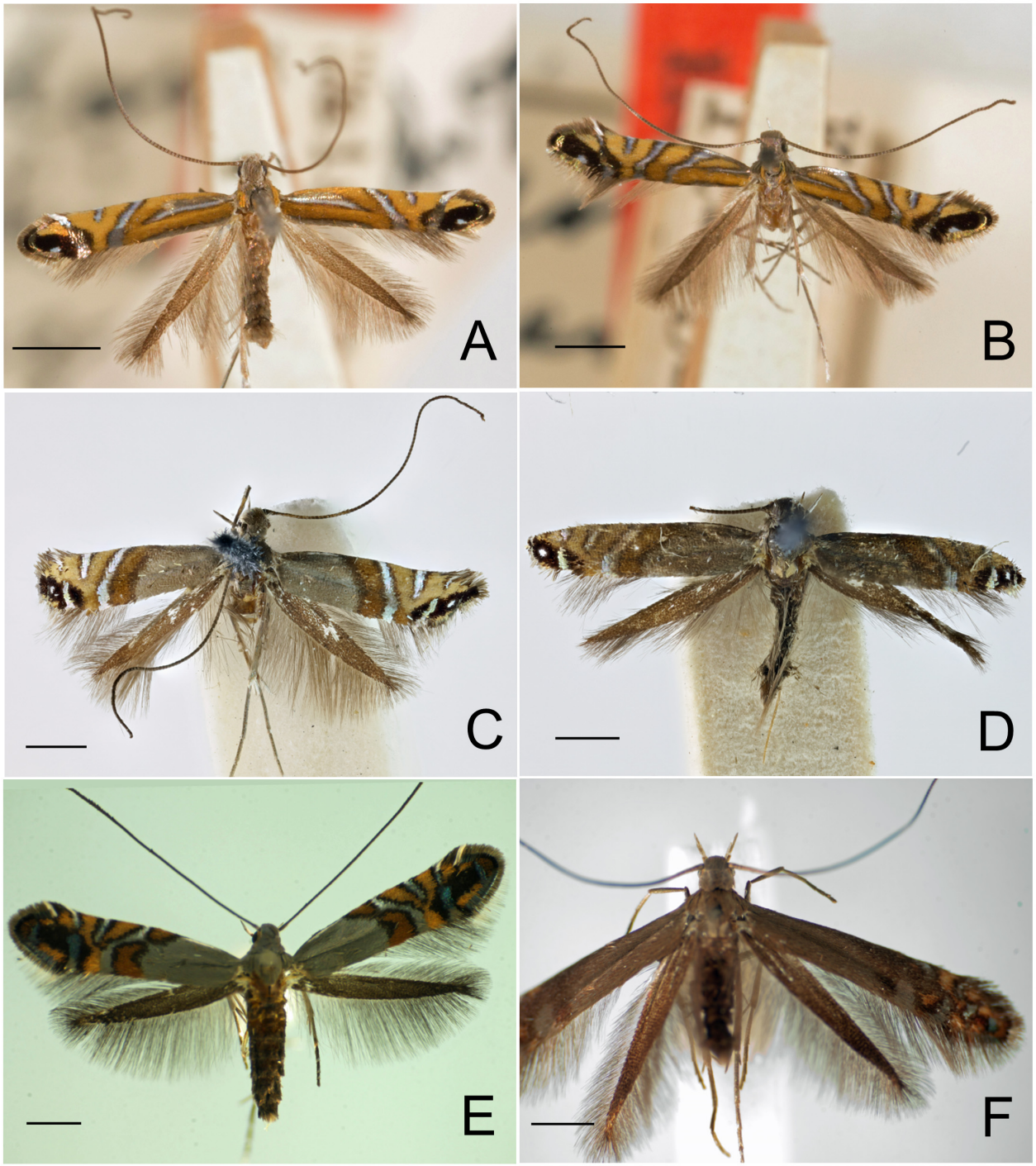

FIGURE 8. Adults of *Philodoria* species. **A** *P. lysimachiella* Swezey, 1928 lectotype male, **B** *P. molokaiensis* Swezey, 1928 lectotype male, **C** *P. basalis* Walsingham, 1907 lectotype male, **D** Paralectotype male, **E** Female, Hawaii (Big Island), **F** Male, Hawaii (Big Island). Scale bar 1 mm.

Diagnosis. The forewing pattern is similar to that of *P. succedanea*, but differs from the latter by having broad orange transverse fasciae and a white and bronze band near the apical portion of wing, in the middle interrupted by a blue patch (Fig. 7C) (Kobayashi *et al*. 2018).

Adult (Fig. 7C). Forewing length 2.4 mm, basal part of forewing missing.

Male genitalia. Unknown and **Female genitalia** figured (Fig. 55D, E). See also Kobayashi *et al*. (2018).

Distribution. Maui.

Host plants. Primulaceae: *Myrsine lanaiensis* Hillebr., *M. lessertiana* A. DC. and *M. sandwicensis* A. DC.

Biology. (Fig. 79E). Kobayashi *et al*. (2018: 128, fig. 10, 14B) reported the leaf mine and pupal cocoon.

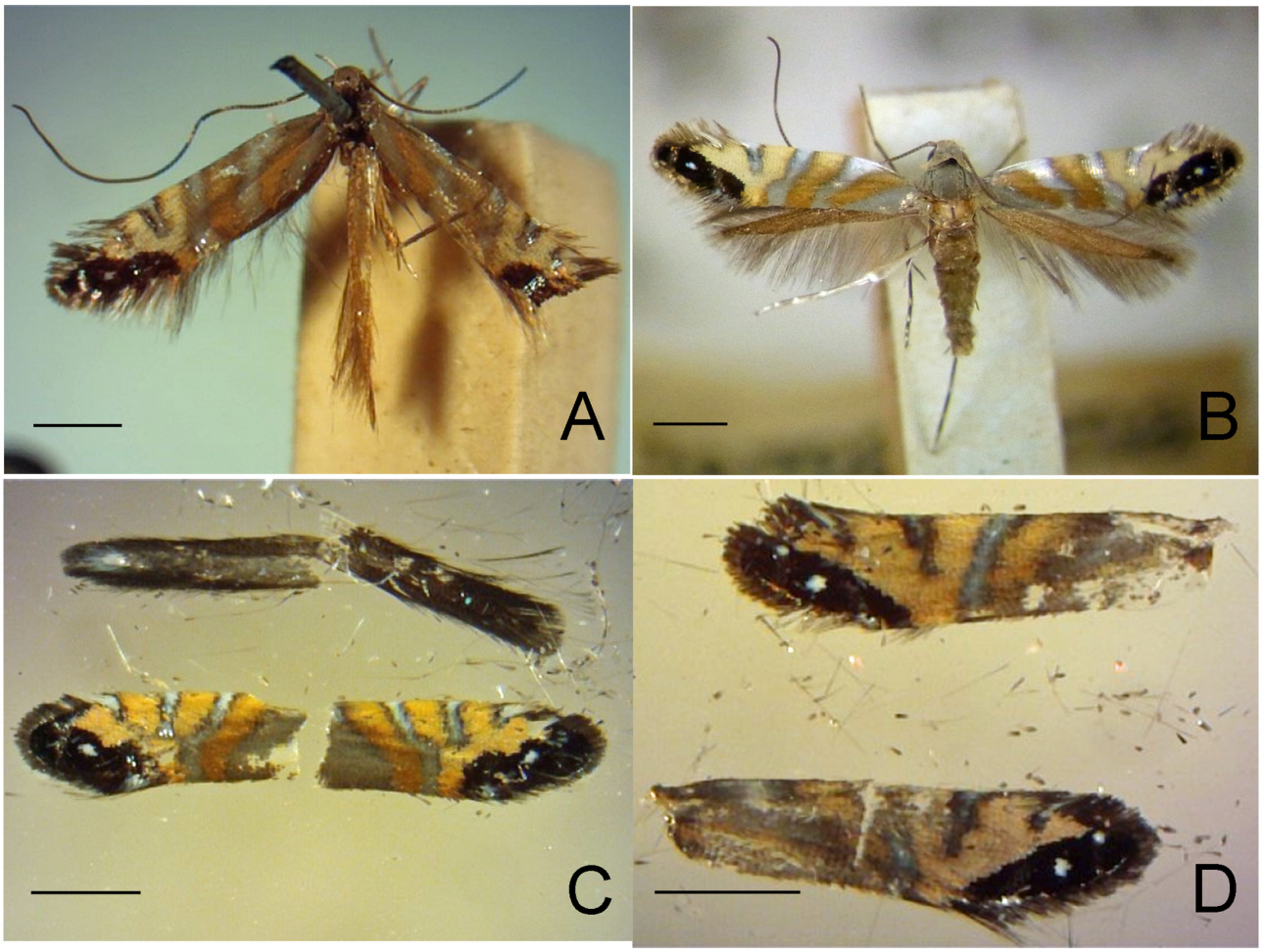

FIGURE 9. Adults of *Philodoria* species. **A** *P. splendida* Walsingham, 1907 lectotype male, **B** Female, Oahu, **C** *P. lama* **sp. n.** holotype male, **D** *P. napaliensis* **sp. n.** holotype (sex unknown). Scale bar 1 mm.

Philodoria auromagnifica Walsingham, 1907

Figs. 7E, 26B, 41B, C, 42B, C, 43B, C, 56C, 61A–G, 79H.

Philodoria auromagnifica Walsingham, 1907: 718, pl. 25, fig. 20; Swezey 1913b: 223; Zimmerman 1978a: 695, figs. 461, 468, 474; Kobayashi *et al*. (2018): 130–132, figs. 2E, F, 5E–H, 6E–H, 7G, 8B, 11, 14C.

Type locality. mountains, 2000 ft near Honolulu (Oahu).

Type material. Holotype ♂, Mts. 2000 ft near Honolulu, Oahu, 25.x.1892, Perkins. 25857|BM slide no. 472|Walsingham Collection. 1910–427.|NHMUK010305330| in NHMUK.

Diagnosis. Very similar to *P. succedanea*, but distinguished from it by the dark brownish orange patches and brownish orange basal patch in the forewing; a fuscous patch with dark orangish scales in the apical portion (Fig. 7E); in the male genitalia by the rather long valva narrowing in the middle, vinculum large, inflexed on the ventral side, broad and straight saccus (Figs. 41B, C, 42B, C); in the female genitalia by signa with rather blunt spines (Fig. 55C) (Kobayashi *et al*. 2018). See also diagnosis of *P. succedanea*.

Adult (Fig. 7E). Wingspan 8 mm in holotype. **Male genitalia** (Figs. 41B, C, 42B, C, 43B, C, 61A–C) and **Female genitalia** figured (Figs. 56C, 61G). See also Kobayashi *et al*. (2018).

Distribution. Kauai (Kobayashi *et al*. 2018), Oahu (Walsingham 1907), Molokai (Swezey & Bryan 1929), and Hawaii (Big Island) (Zimmerman 1978a).

Host plants. Primulaceae: *Myrsine lessertiana* A. DC. and *M. sandwicensis* A. DC. (Johns *et al*. 2016), *M. wawraea* (Mez) Hosaka (Kobayashi *et al*. 2018), *Myrsine* sp. (Swezey 1913a).

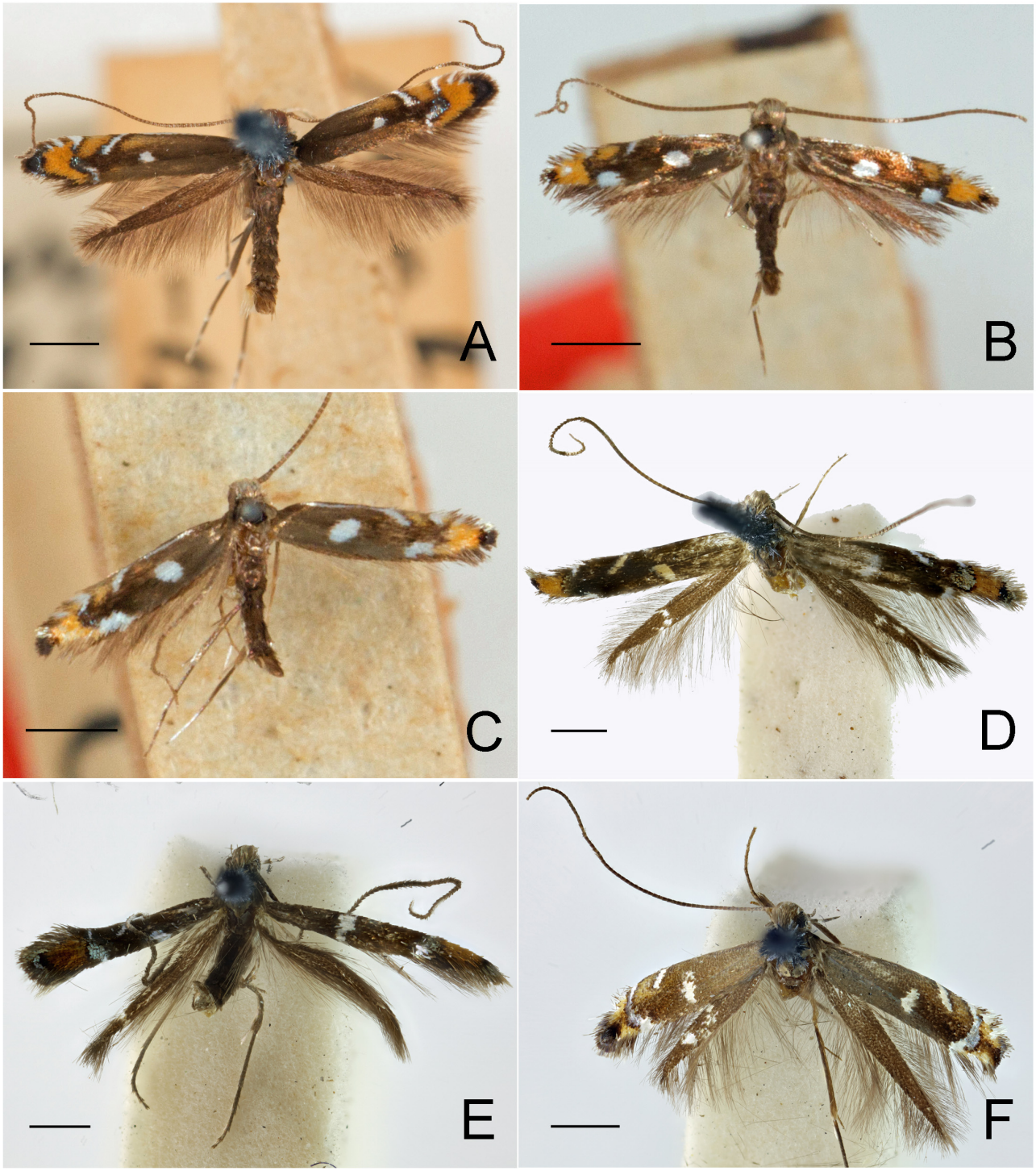

FIGURE 10. Adults of *Pipturus* feeding *Philodoria* species. **A** *P. costalis* Swezey, 1934 lectotype male, **B** *P. pipturiella* Swezey, 1923 lectotype male, one of two cotypes (upper specimen) on the same mount, **C** Paralectotype male on the same mount as of lectotype (lower specimen), **D** *P. floscula* Walsingham, 1907 lectotype female, **E** Paralectotype male, **F** *P. micropetala* Walsingham, 1907 holotype female. Scale bar 1 mm.

Biology. (Fig. 79H). Kobayashi *et al*. (2018: 131, figs. 8B, 11, 14C) reported the leaf mine and pupal cocoon.
Parasitoids. Eulophidae: *Euderus metallicus* (Ashmead, 1901) (Zimmerman 1978a).

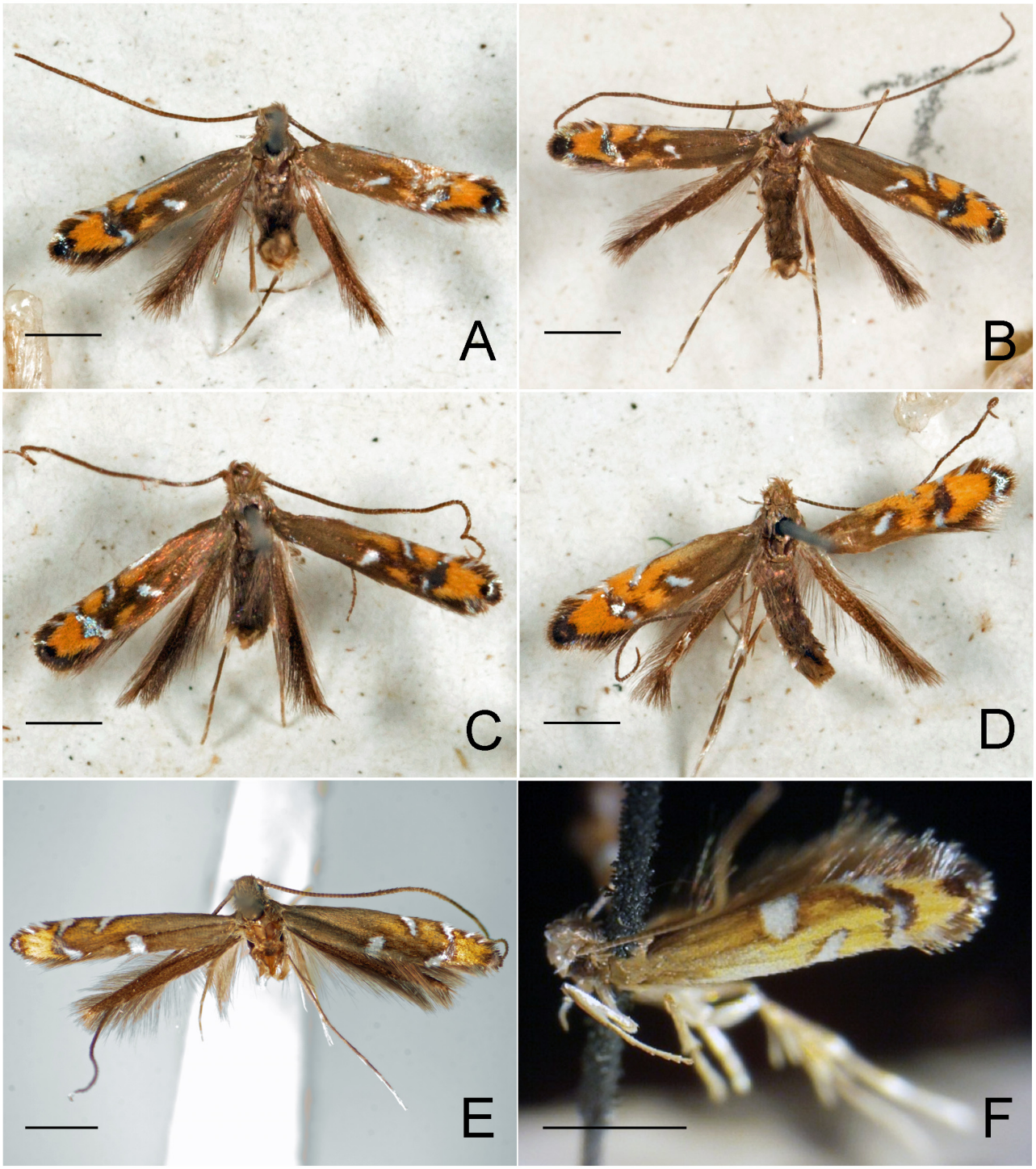

FIGURE 11. Adults of *Pipturus* feeding *Philodoria* species. **A** *P. pipturicola* Swezey, 1915 paralectotype male, one of four cotypes (upper left specimen) on the same mount, **B** Lectotype male (upper right specimen on mount), **C** Paralectotype female (lower left specimen on mount), **D** Paralectotype female (lower right specimen on mount), **E** *P. haelaauensis* **sp. n.** male, **F** Paratype female. Scale bar 1 mm.

Philodoria kolea **Kobayashi, Johns & Kawahara, 2018**

Figs. 7F, 34B, C, 35, 41D, 42D, 43D, 56F, 79I–K.

Philodoria kolea Kobayashi, Johns & Kawahara, 2018: 132–137, 3, 5K, L, 7A–D, I, 12, 13, 14D

Type locality. Hawaii Volcanoes National Park (Big Island).

Type material. Holotype ♂, Hawaii Volcanoes National Park, Hawaii (Big Island), 25.iv.2016, A. Kawakita leg., host: *Myrsine lessertiana* (understory shrub), Gen-Bank accession no. MF804825, IO-322, SK851 in BPBM. The type series was mounted from emerged adult moths.

Paratypes, in BPBM: 1♀, Kaumana Trail, Hilo, Hawaii (Big Island), 28.iv.2016, em., C.L.-Vaamonde & C. Doorenweerd leg., host: *Myrsine* sp., 20.iv.2016 (Cocoon), HILO016, SK634♀. 1♀, Thurston lava tube (Nahuku), Hawaii Volcanoes National Park, Hawaii Is., 13.v.2016, em., S. Kobayashi leg., host: *Myrsine lessertiana*, 25.iv.2016 (larva), SKH-05-1, SK632♀; 1♀, same locality and data as holotype, IO-323, SK852; 2♀, same locality as holotype, 2&24.v.2016, em., C.L.-Vaamonde & C. Doorenweerd leg., host: *Myrsine lessertiana*, 22.iv.2016 (larva), HILO020/SKH-15, SK630♀, 631♀.

Diagnosis. Among *Philodoria* species having similar fuscous forewing coloration (i.e., *P. epibathra* (Walsingham), *P. nigrella* (Walsingham) *P. pipturiana* Swezey, and *P. wilkesiella* Swezey (See Zimmerman 1978a)), *P. kolea* is distinguished by the white and bronze color bands on the forewing (Fig. 7F). The forewing pattern and genitalia are similar to those of other *Myrsine* mining species, *P. auromagnifica* and *P. succedanea*, but *P. kolea* completely lacks the orange markings (Fig. 7F).

Adult (Fig. 7F, 34B, C, 35). Wingspan 6.7 mm in holotype, 6.6, 8.5 mm in paratypes. **Male genitalia** (Figs. 41D, 42D, 43D) and **Female genitalia** (Fig. 56F). See also Kobayashi *et al*. (2018).

Distribution. Hawaii (Big Island) (Kobayashi *et al*. 2018). **Host plants.** Primulaceae: *Myrsine lessertiana* A. DC. (Kobayashi *et al*. 2018).

Biology. (Figs. 79I–K). Kobayashi *et al*. (2018: 136–137, figs. 12, 13, 14D) reported the leaf mine and pupal cocoon.

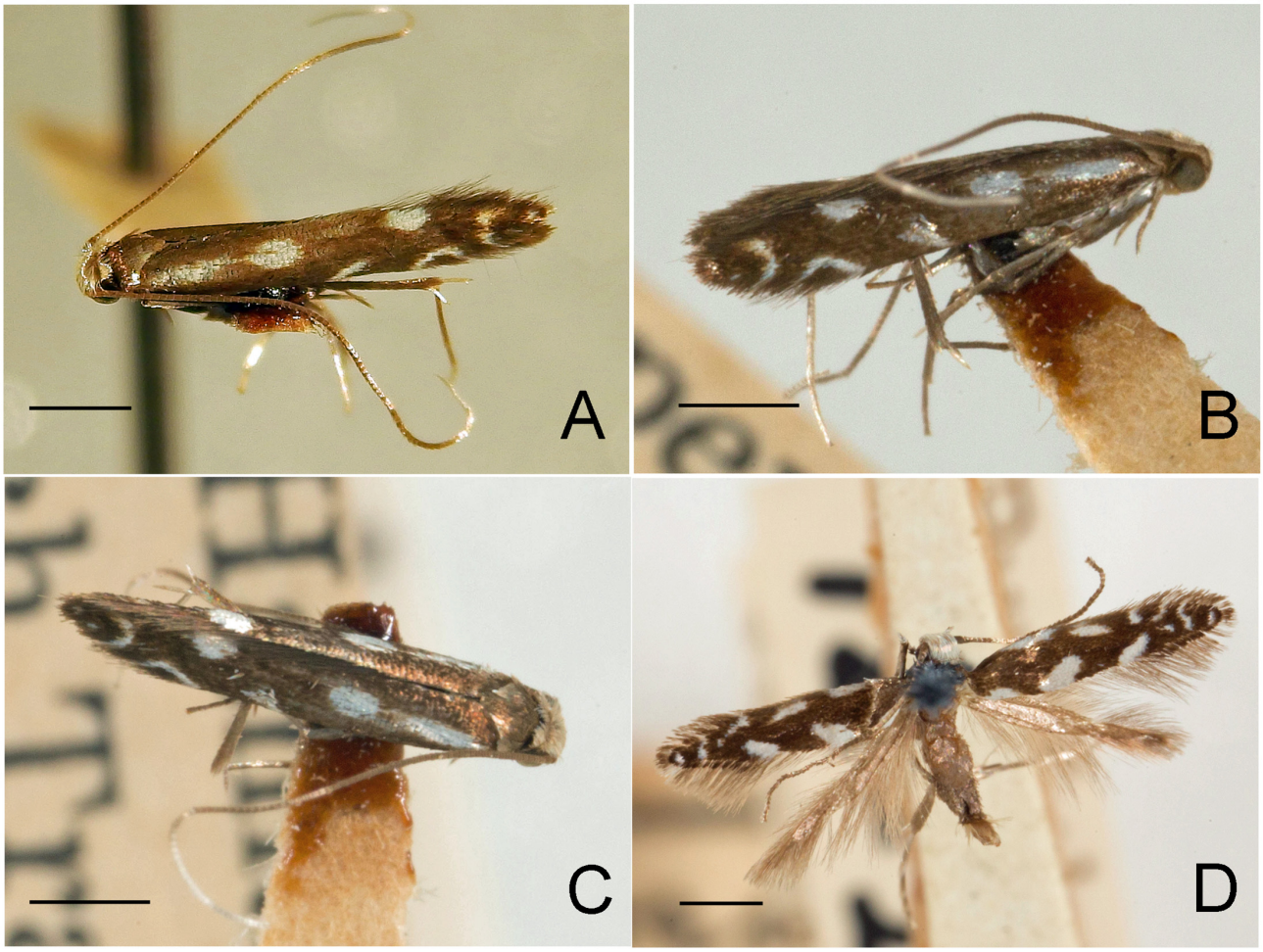

FIGURE 12. Adults of *Philodoria* species. **A** *P. pipturiana* Swezey, 1923 lectotype male, left lateral view, **B** Same right lateral view, **C** Same dorsal view, **D** *P. wilkesiella* Swezey, 1940 lectotype male. Scale bar 1 mm.

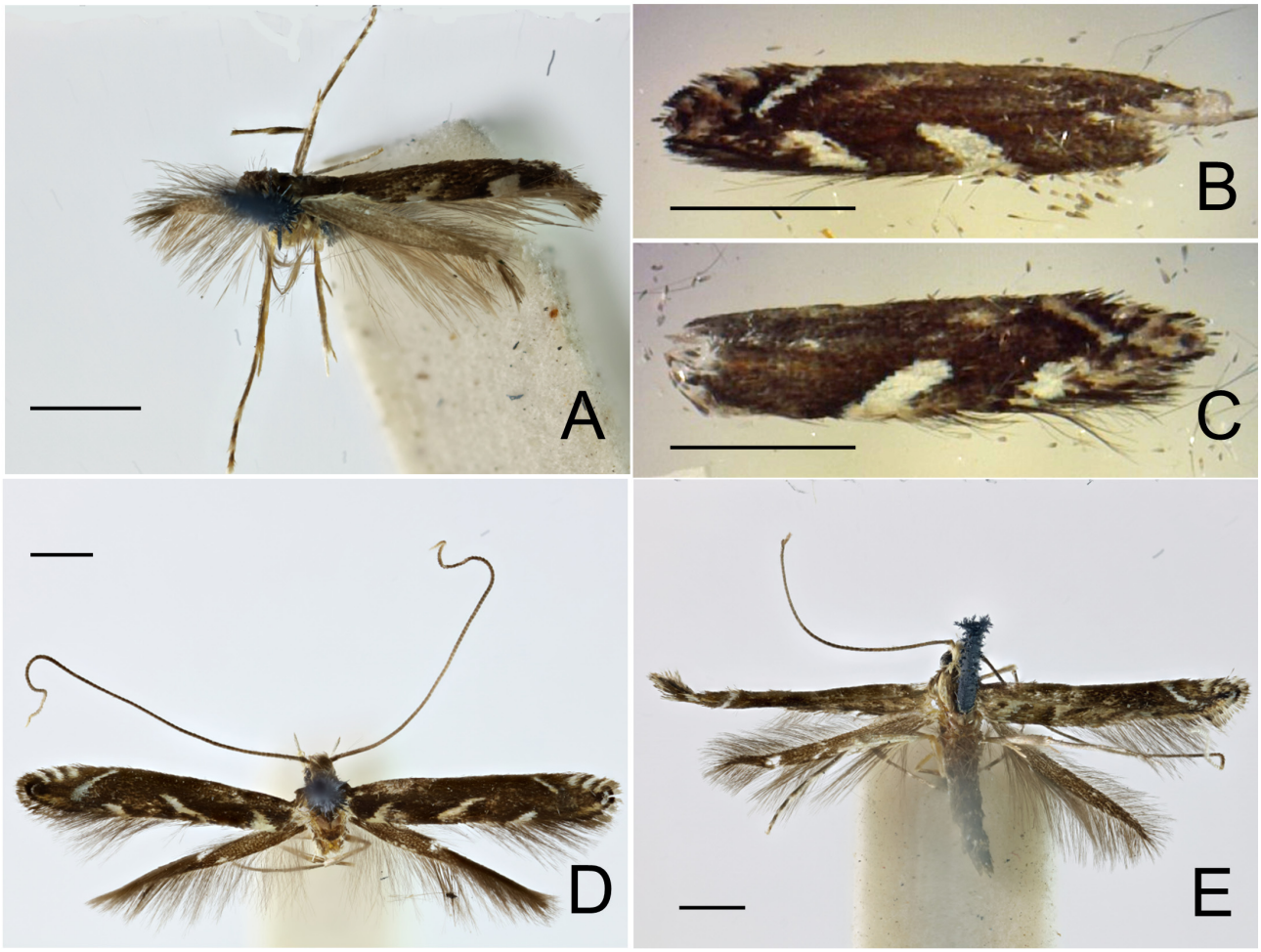

FIGURE 13. Adults of *Philodoria* species. **A** *P. epibathra* (Walsingham, 1907) holotype female, **B** Same, left forewing, host *Dubautia* sp., CJ492, Molokai, **C** Same, right forewing, **D** *P. nigrella* (Walsingham, 1907) lectotype male, **E** Paralectotype male. Scale bar 1 mm.

Philodoria sp. 7 of Johns *et al*. (2018)

Figs. 39B, 41F, G, 42F, 43F.

Philodoria sp. 7: Johns *et al*. 2018: fig. 2.

Material examined. 2♂, Kokee, Kauai, 2.vii.2015 (stored), C.A.Johns leg., host: *Lysimachia kalalauensis*, 15.vi.2015, CJ451ab, SK754♂, SK755♂ in BPBM. Not much remains of these two specimens: 1 specimen, 'CJ451a', mounted by placing two wings without mountant under a coverslip: half of right forewing and the half of one hindwing; 1 specimen, 'CJ451b', mounted by placing three wings without mountant under a coverslip: 3/4 left forewing and two half of hindwings.

Additional material. 3 adults (CJ-451/AHE_20) entirely sacrificed for molecular analysis (Johns *et al*. 2018: fig. 2): they are same series and data as the two adults mentioned above (CJ451ab).

Diagnosis. Similar to *P. lysimachiella* Swezey, but the male genitalia differed slightly, i.e. the specimens have rather broad dorsal process of valva and round saccus (Figs. 41F, G, 42F).

Adult. Head, antenna, thorax, and legs unknown. Forewing shiny, metallic bronze with ocherous-orange patches, basal 1/4 missing and damaged: a large **tp** after the middle to costal 3/4, distinctly narrowing in the dorsum, extending to dorsal 2/3, containing white **cs**; one white band on the middle of the first bronze color band (**bb_2**), another on costa to the middle of second band (**bb_3**), dorsally suffused with shining black scales.

Male genitalia (Figs. 39A, 41F, G, 42F, 43F) (n=2). Capsule 960–970 µm. Tegumen same length as valva;

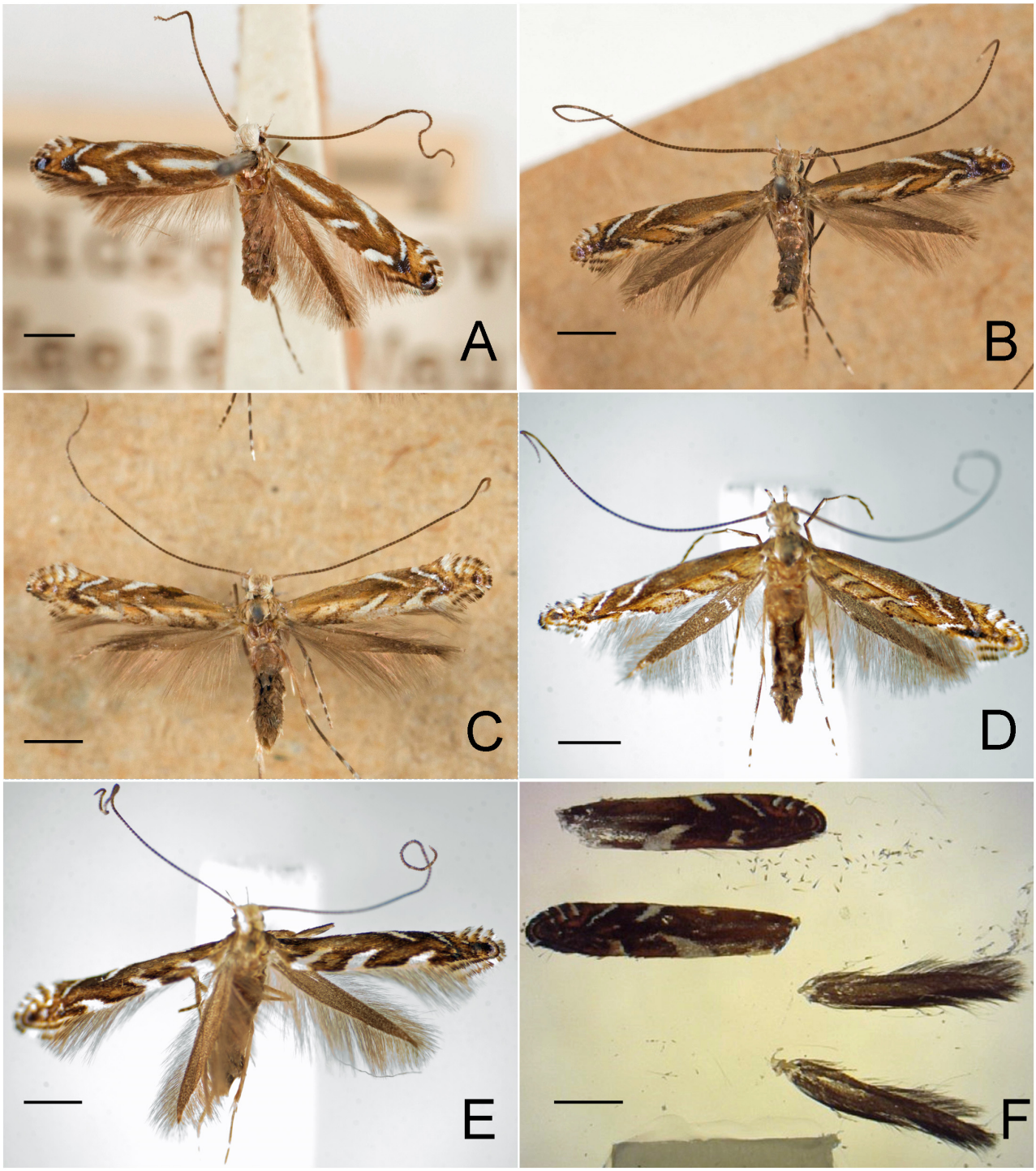

FIGURE 14. Adults of *Philodoria* species that have two costal streaks (cs_1 and cs_2). **A** *P. dubauticola* Swezey, 1940 lectotype female, **B** *P. dubautiella* (Swezey, 1913) lectotype male one of two cotypes on the same mount (upper specimen), **C** Paralectotype female (lower specimen), **D** Female, Oahu, **E** *P.* sp. nr. *P. dubautiella* male, Kauai, **F** *P. alakaiensis* **sp. n.** holotype male. Scale bar 1 mm.

valva 610–640 µm long, very broad, having a dorsal process, rounded toward apex (Fig. 41F, G). Saccus short and digitiform in ventral view (Fig. 42F). Phallus 700 µm long and almost straight in lateral view with two series of minute cornuti in vesica (Fig. 43F).

Female genitalia Unknown.

Distribution. Kauai. **Host plants.** Primulaceae: *Lysimachia kalalauensis* Skottsb.

Biology. Unknown, but it is presumably similar to that of *P. molokaiensis*.

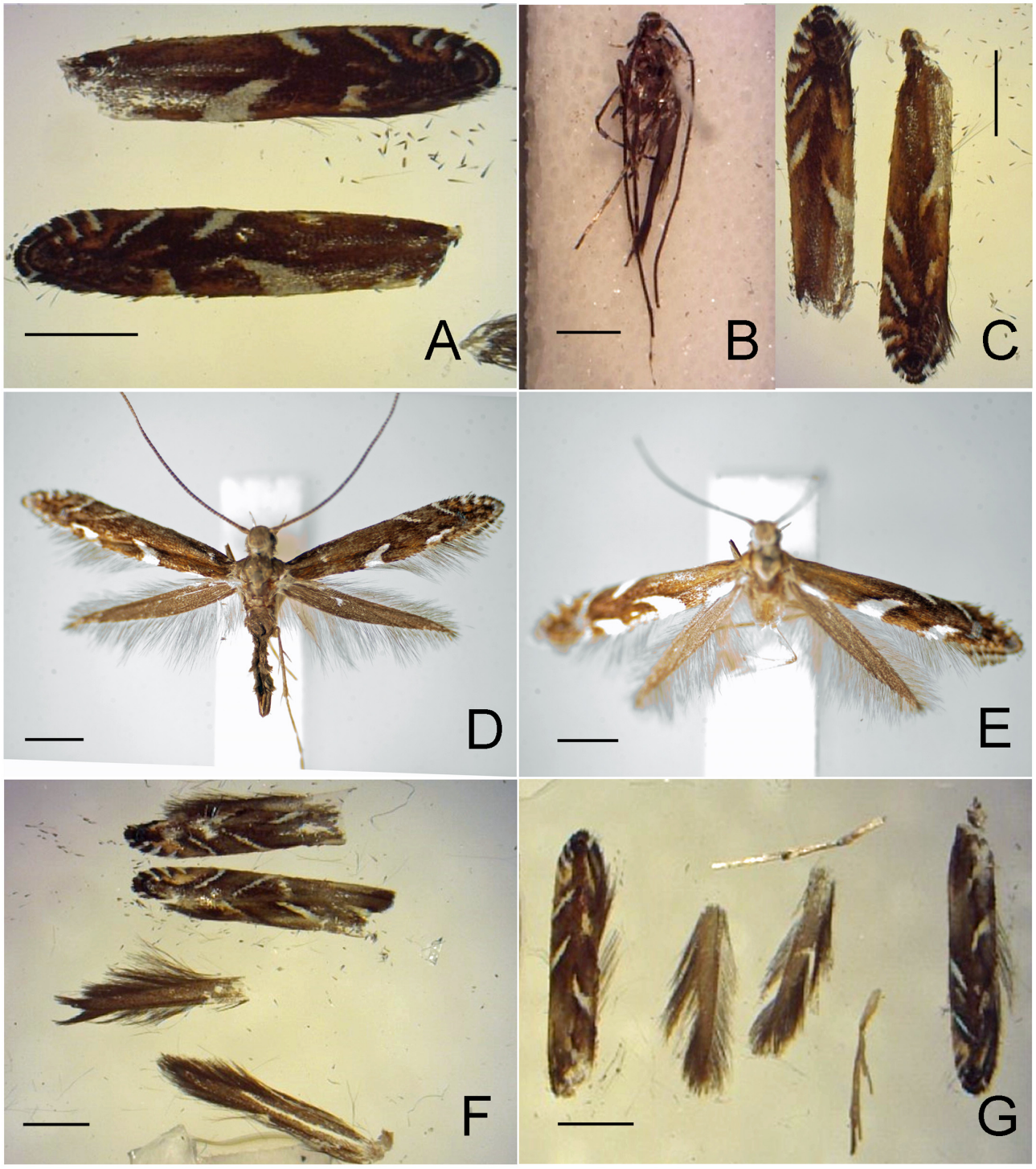

FIGURE 15. Adults of *Philodoria* species that have two costal streaks (cs_1 and cs_2). **A** Forewings of *P. alakaiensis* **sp. n.** holotype male, **B** Paratype male, **C** Same as B, forewings, **D** Paratype male (BMNH(E)1621107) in NHMUK, **E** Paratype female (BMNH(E)1621109) in NHMUK, **F** *P. limahuliensis* **sp. n.** holotype male, **G** Paratype male. Scale bar 1 mm.

Remarks. Swezey (1928: 28) mentioned in a description of *P. molokaiensis* that "leaf mines have been collected on two occasions on *Lysimachia hillebrandii* on the high plateau of Kauai, but no moths were reared from them; probably when reared at some future time this will be another closely related species". This Kauai *Lysimachia* miner might be *P.* sp. 7. We investigated two Kauai endangered *Lysimachia* populations. *L. daphnoides* in Alakai swamp and an individual plant of *L. iniki* that fell off of the headwater cliff wall at Blue Hole, but no leaf mines were found. *L. iniki* only occurs on the high cliff walls and is extremely difficult to access. We observed leaf mines on *Lysimachia glutenosa* at Kokee, but never found any fresh mines with larvae. Four (sex unknown) adults were

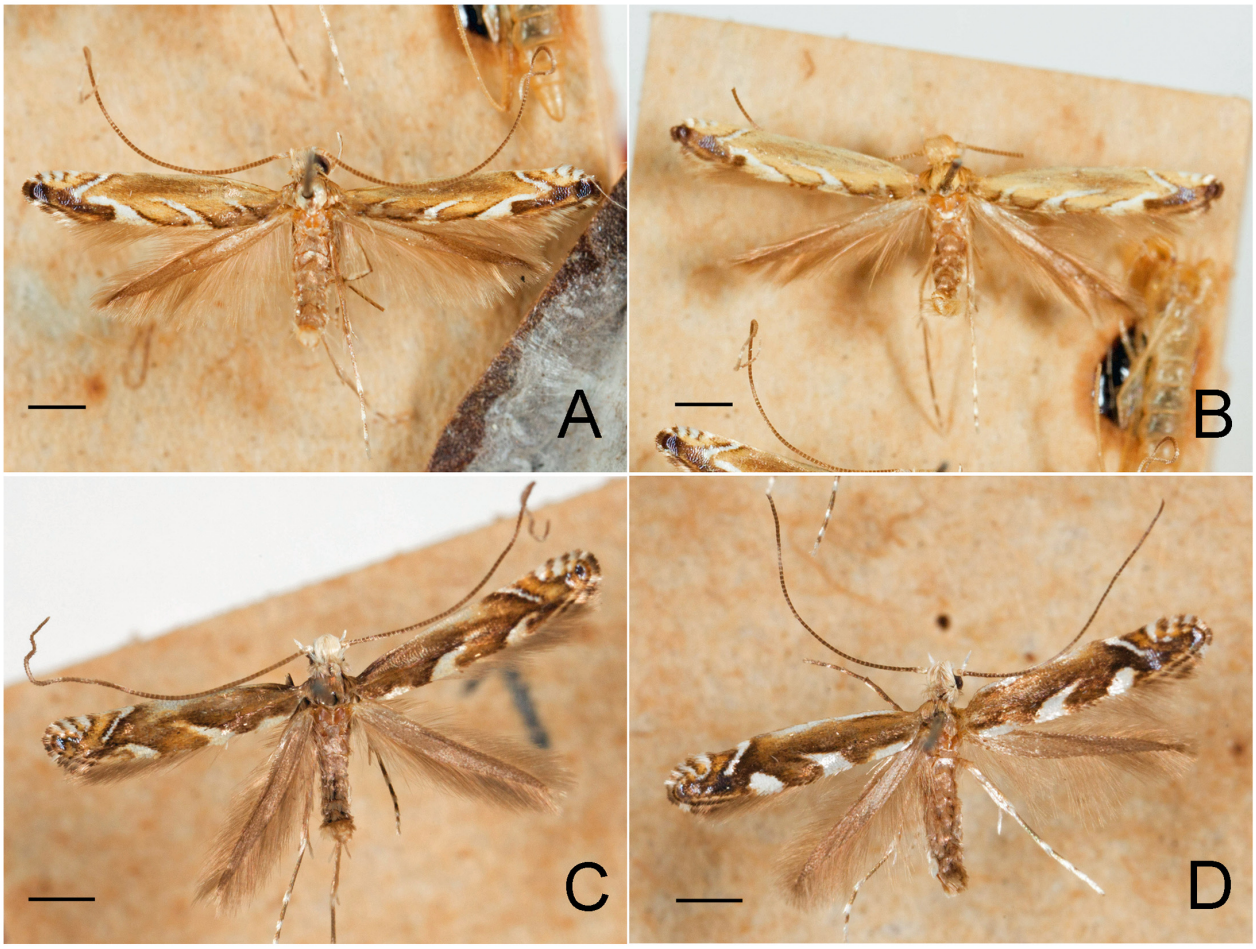

FIGURE 16. Adults of *Philodoria* species. **A** *P. hibiscella* (Swezey, 1913) lectotype male, one of two cotypes on the same mount (upper specimen), **B** Paralectotype female (lower specimen on mount), **C** *P. naenaeiella* (Swezey, 1940) lectotype male, one of two cotypes on the same mount (upper specimen), **D** Paralectotype female (below holotype specimen on mount). Scale bar 1 mm.

reared from *L. glutenosa* at Kalalau, 9.viii. 2014 (stored), K. Bustamente leg., CJ345 /AHE_10, but they were sacrificed for molecular analysis. Both host plant species noted above should be further examined for possible undocumented *Philodoria* mines.

Philodoria lysimachiella Swezey, 1928

Figs. 8A, 26H, 37B, 38, 41E, 42E, 43E, 56G, 62A–E.

Philodoria lysimachiella Swezey, 1928: 188; Zimmerman 1978a: 708, figs. 463, 469.

Type locality. Puu Hapapa, Waianae Mountains (Oahu).

Type material. Lectotype ♂, Windward slope of Puu Hapapa, 2000 ft, half a mile south from Kolekole Pass, Waianae Mts., Oahu, 16.i.1927, O.H. Swezey Collector, *Lysimachia* [*rotundifolia*], |Holotype| *Philodoria lysimachiella* Swezey Det. by O. H. Swezey| Type no. 4270, in BPBM (here designated). Paralectotype 5♂, 2♀, same data and locality as holotype, |Paratype| 34188|♂ genitalia slide Z-XII-20-62-1| BPBM34189♀, BPBM 34190♀, BPBM 34191♂, BPBM 34192♂ and 2♂ in USNM. Described from nine specimens: the holotype was originally in the collection of the Hawaiian Entomological Society; paratypes in author's collection, Bishop Museum and the U.S. National Museum. We found eight "types" in the BPBM and USNM. The holotype was not specified in the description, and the so-labeled holotype and paratype are to be considered syntypes under Article 73.2 of the Code (ICZN 1999), and any one is therefore eligible for designation as lectotype under Article 74 of the Code (ICZN

1999). The syntype labeled, 'Holotype' is formally designated here as lectotype (Fig. 8A). The remaining syntype is the paralectotype.

Additional material. 2♂, 3♀, 3 (sex unknown), Waianae (21.501325, -158.16538), Oahu, 28.iii.2016 (stored), K. Bustamente leg., host: *Lysimachia hillebrandii*, 9.xi.2015/KMB01,CJ530 / SK654♀, SK655♀, SK656♂, SK657♂, SK751(wing vein); deposited in BPBM.

Diagnosis. Very similar to *P. molokaiensis* Swezey feeding on same host plant, *Lysimachia*, but is distinguished by the median white streak reaching from base to near middle of wing and the lacking an oblique transverse fascia (**cl** + **bb$_2$**) from the base via costal fold, curved at costal 1/4 to dorsal 1/2 in the forewing (Fig. 8A) and the broad valva with short slender dorsal process and the rather slender pointed saccus in the male genitalia (Figs. 41E, 42E); oval-shaped lamella antevaginalis rather small and signa with rather small spines in the female genitalia (Fig. 56G).

Redescription: Adult (Figs. 8A, 26H, 37B, 38). Wingspan 6.7–7.7 mm in paratypes; forewing length 2.5 mm in holotype, 3.0–3.7 mm in paratypes. Head light gray; frons white; maxillary palpus reduced; labial palpus white, slightly grayish externally on the apical half of middle joint, terminal joint blackish in front (Fig. 37B). Antenna light gray, white below on basal third, very long, about 1.5 x length of forewing. Thorax light gray, patagium ocherous-orange. Forewing shiny, metallic bronze with ocherous-orange patches: a large oblique patch from base to 1/2, containing two longitudinal streaks, a median white one from base to near middle of wing lying slightly in front of the fold, bent dorsally in the outer 1/4; another bronze one same length, on the dorsal margin; a large **tp** after the middle to costal 3/4, distinctly narrowing in the dorsum, extending to dorsal 2/3, containing white **cs**; one white band on the middle of the first bronze color band (**bb$_2$**), another on costa to the middle of second band (**bb$_3$**), dorsally suffused with shining black scales; apical portion with a fuscous patch extending toward the termen and apex with a bronze **as** with orange-ocherous color encroaching on the apex and a small white spot at tornus; cilia light gray, with a white spot at beginning of costal cilia, remainder of cilia with black scales at base. Hindwing light gray, slightly infuscated towards apex, cilia light gray. Abdomen light gray, white beneath. Legs mostly light gray, white beneath.

Male genitalia (Figs. 41E, 42E, 43E, 62A, B) (n=1). Capsule 900 µm. Tegumen 0.5–0.6 x length of valva; valva 480–500 µm long, very broad, apically rounded and having a slender dorsal process (Fig. 41E). Saccus short and tapering toward the point (Fig. 42E). Phallus 780–800 µm long and sinuous at phallobase in lateral view with two series of spiny minute cornuti in vesica (Fig. 43E).

Female genitalia (Fig. 56G) (new record) (n=2). 1290 µm long. Ostium bursae small; antrum slender, cylindrical; lamella antevaginalis 200 µm, well-developed, oval-shape. Corpus bursae 600 µm long; paired signa with a pair of claw-shaped spines.

Distribution. Oahu (Swezey 1928).

Host plants. Primulaceae: *Lysimachia hillebrandii* Hook. f. (Swezey 1928).

Biology. Unknown, but it is presumably similar to that of *P. molokaiensis*.

Remarks. Leaf mines were once collected from *Lysimachia* along a ridge of Kalihi Valley on Oahu, but no adult moths were reared from them (Swezey 1928). Tim Kroessig (pers. comm.) found *Philodoria* leaf mines on *L. remyi* ssp. *subherbacea*, which were collected in Wai'anae mountains, Oahum, , but larvae from these mines were not reared.

Philodoria* sp. A near *P. lysimachiella

Figs. 26G, 56H.

Material examined. 6♀, 1 (sex unknown), Halehaku, Ko'olau Gap, Maui, 9.viii.2014 (stored), K. Bustamente leg., 20.7767N, 156.2076W, host: *Lysimachia* sp., CJ346a–e [CJ346a / SK753♀ & ♀, CJ346b / 2 ♀, CJ346d / sex unknown (no abdomen)]; deposited in BPBM. Seven specimens were examined, all of which have parts of their body missing. Because specimens are incomplete, we refrain from formally describing this species until a complete specimen becomes available. What remains of seven specimens are: 1 specimen with only 75% of forewing and hindwing remaining, wings without mountant under a coverslip (CJ346a / SK753); 5 specimens with only wings and abdomen remaining; sample CJ346d which has wings unmounted and damaged in four separate vials (CJ346a–e). The head, antenna, thorax, and legs for all samples were sacrificed for molecular analysis.

Diagnosis. The forewing pattern is similar to *P. lysimachiella* (Fig. 26G), but *Philodoria* sp. A is distinguished by a bronze color band (**bb$_2$**) interrupted at middle by an orange patch and female genital characters are differed

by the trapezoid lamella antevaginalis rather narrowing at posterior part and shorter cup-shaped antrum and short spines on signa (Fig. 56H).

Adult (Fig. 26G). See Material examined and diagnosis sections.

Male genitalia. Unknown.

Female genitalia (Fig. 56H) (n=1). 1520 µm long. Ostium bursae large; antrum short, cup-shaped; lamella antevaginalis 360 µm, trapezoid, rather narrowing at posterior part, inflexed on the posterior margin. Corpus bursae 700 µm long; paired signa each with a short linear spine.

Distribution. Maui.

Host plants. Primulaceae: *Lysimachia* sp. This host plant may be a new species discovered by Keahi Bustamente and Hank Oppenheimer (K. Bustamente & H. Oppenheimer pers. comm.)

Biology. Unknown.

Remarks. We observed *Philodoria* leaf mines on *L. remyi* in Iao Valley on West Maui (Fig. 80C, F). These larvae form white linear mines with a dark brown frass line on the adaxial leaf surface, similar to that of *P. molokaiensis*. Unfortunately, adults did not emerge from our rearing efforts, and therefore cannot confirm for certain that these were the mines of *P. lysimachiella*.

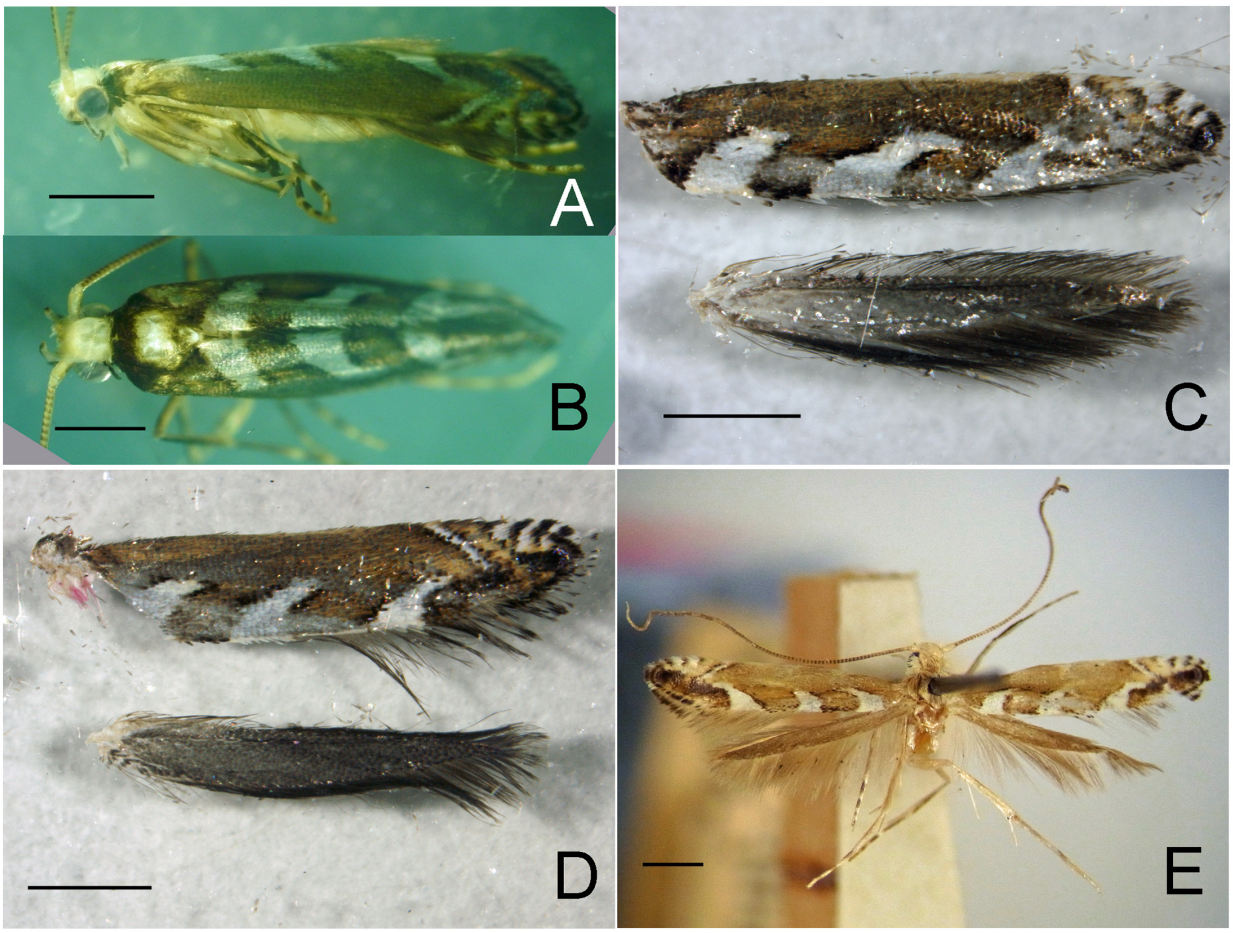

FIGURE 17. Adults of *Philodoria knudseniiella* **sp. n. A** holotype lateral view (CJ480/SK862), **B** Same, dorsal view, **C** Same, right wings, **D** Paratype female right wings (CJ480/SK863), **E** Paratype female (34241 BPBM slide Z-I-10-66-A). Scale bar 1 mm.

Philodoria molokaiensis Swezey, 1928

Figs. 8B, 26F, 41H, 42G, 43G, 56I, J, 62F–H, 73A, 80A, B, D, E.

Philodoria molokaiensis Swezey, 1928: 188–189; Zimmerman 1978a: 709, figs. 464, 470, 478.

Type locality. Kawela (Molokai).

Type material. Lectotype ♂, Kawela, 3700ft, Molokai, 23.xii.1925, O.H. Swezey Collector, *Lysimachia* [*hillebrandi* var.], |Holotype| *Philodoria molokaiensis* Swezey Det. by O. H. Swezey| ♀ paratype & ♂ holotype abdomen sent ECZ 7?-17-61| Type no. 4271, slide no. Z-XII-20-65 in BPBM (here designated). Paralectotype ♀, same data and locality as lectotype, Z-XII-19-62-26 in BPBM. Described from two specimens. Swezey considered them as holotype and paratype, as indicated on their specimen labels. However, because the holotype was not specified in the original description, the so-labeled holotype and paratype are all to be considered syntypes under Article 73.2 of the Code (ICZN 1999), and any one is thus eligible for designation as lectotype under Article 74 of the Code (ICZN 1999). The syntype labeled 'Holotype' is here designated as lectotype (Fig. 8B), and the other syntype is the paralectotype.

Addtional material. (2♂, 2♀). **Molokai**: 2♀, Kamakou, 16–20.i.2014 (stored), C.A. Johns leg., host: *L. hillebrandi* var., CJ229 / SK668♀ (20.xii.2013 em., wing and abdomen), CJ239 / SK669♀ (abdomen); 2♂, Kawela, 26.vii.2015 (stored), K. Bustamente leg., host: *L. maxima*, KMB01, 20150317, CJ509 / SK667♂ (wing and abdomen), SK666♂ (abdomen); deposited in BPBM.

Diagnosis. Forewing with two longitudinal streaks of ocherous-orange on distal area of thorax and the patagium is light gray instead of ocherous-orange as in *P. lysimachiella* Swezey (Swezey 1928) (Fig. 8B, 73A). See also diagnosis of *P. lysimachiella*.

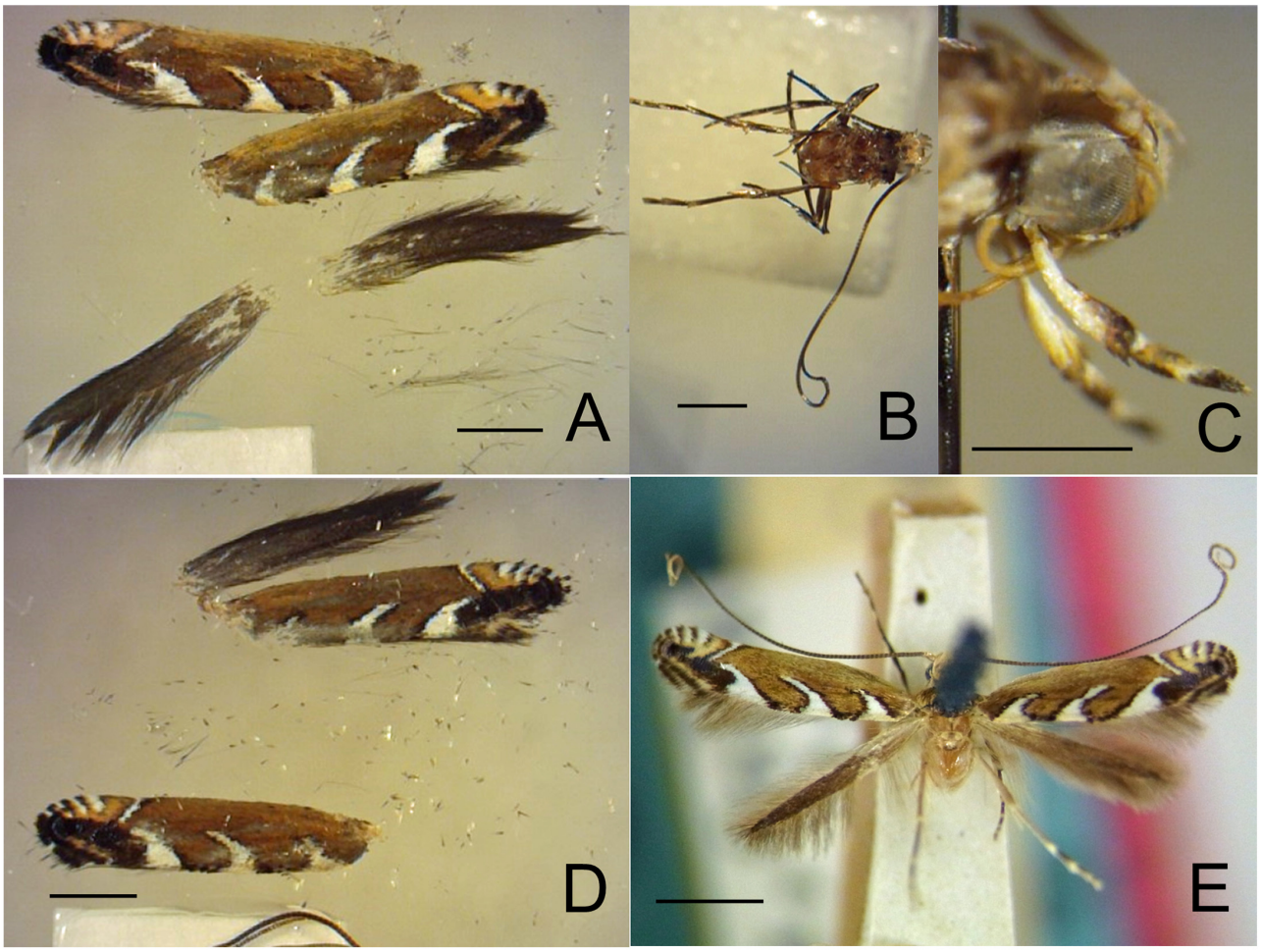

FIGURE 18. Adults of *Philodoria hesperomanniella* **sp. n. A** Wings of holotype male, **B** Same, head and thorax, dorsal view, **C** Same, head lateral view, **D** Paratype female, Maui, collected by O. H. Swezey, E Paratype female, Oahu (BPBM no.34224). Scale bar 1 mm.

Redescription: Adult (Figs. 8B, 73A). Wingspan 9 mm in lectotype; forewing length 3.2 mm in paralectotype. Head light gray; frons white; maxillary palpus reduced; labial palpus white, slightly brownish externally on the base. Antenna light gray, white below on basal third, about 1.3x length of forewing. Thorax ocherous-orange on each side of disk, patagium light gray. Forewing shiny metallic bronze with ocherous-orange patches: a large

oblique patch from base to 1/3, containing two longitudinal streaks; a median white one narrowing toward apex, another same length, on the dorsal margin; **tf** from costal 1/3 to dorsal 1/2; a large **tp** after the middle to costal 3/4, distinctly narrowing in the dorsum, extending to dorsal 2/3, containing white **cs**; one white band (**w_1**) on the middle of first bronze color band (**bb_1**) from the base via costal fold, curved at costal 1/4 to dorsal 1/2; others on costa to the middle of **bb_2** and **bb_3**; apical portion with a fuscous patch extending toward the termen and apex with a bronze **as** with orange-ocherous color encroaching on the apex and a small white spot at tornus; cilia light gray, with a white spot at beginning of costal cilia, remainder of cilia with black scales at base. Hindwing light gray, slightly infuscated towards apex, cilia light gray. Accessible abdomen that we had in poor condition, pale brownish gray, preserved in 99% ethanol. Legs mostly gray, distal segment white.

Male genitalia (Figs. 41H, 42G, 43G) (n=2). Capsule 970 µm. Tegumen 570 µm long and 0.9 x length of valva; valva 640–650 µm long, very broad and long apically extended and having a slender and very long dorsal process (Fig. 41H). Saccus short and thick, apically blunt (Fig. 42G). Phallus 710 µm long and nearly straight and gradually wider in phallobase (Fig. 43G).

Female genitalia (Figs. 56I, J, 62F) (n=2). 1260 µm long. Ostium bursae large; antrum rather short; lamella antevaginalis 340 µm, trapezoid, large inflexed on the posterior margin. Corpus bursae 630 µm long; paired signa with a pair of large triangular-shaped spines.

Distribution. Molokai (Swezey 1928).

Host plants. Primulaceae: *Lysimachia hillebrandii* var. (Swezey 1928) and *L. maxima* (R. Knuth) H. St. John: new record. *L. maxima* is very rare plant, only two small populations remain on Molokai, listed as an endangered plant species in the United States.

Biology. (Fig. 80A, B, D, E). Larvae form a slender linear mine on the adaxial leaf surface, and mines gradually expand as the larvae feed and grow (Fig. 80A, B). One mine per leaf. The late instar larva is pale yellow-green (Fig. 80D). Pupation occurs in the cocoon outside of the mine, usually on the abaxial leaf surface; a pupal cocoon is pale grayish ocherous and near ellipsoid (Fig. 80E).

Parasitoids. Chalcidoidea spp. (including at least three species from CJ201), Euplemidae sp.: new record (Fig. 99E–L).

Philodoria basalis Walsingham, 1907

Figs. 8C–F, 26C, 34D, 37A, 40E–H, 41I, 42H, 43H, 61H, 81.

Philodoria basalis Walsingham, 1907: 720, pl. 5, fig. 24; Zimmerman 1978a: 695, figs. 468, 475.

Type locality. Olinda (Haleakala), 4000 ft (Maui).

Type material. Lectotype ♀ (="Type ♂ (26666) Mus. Wlsm" in original description), Olinda, 4000ft, Haleakala, Maui, iv. 1894, Perkins 26666, B.M. ♀Genitalia slide no. 3952 | PHILODORIA BASALIS, Wlsm. Fn. Hawaii. I. TYPE ♂ descr. fig[d].| Walsingham Collection. 1910—427.| NHMUK010305331 in NHMUK (here designated). Paralectotype ♂, same locality as holotype, v. 1896, Perkins 28541 | *Philodoria basalis* ♂ Wlsm PARATYPE 1/1 descr. fig[d].| Walsingham Collection. 1910—427.| NHMUK010305332 in NHMUK. Described from two specimens: 'Type ♂ (26666)' and 'paratype' from Maui. This may indicate that Lord Walsingham considered them as holotype and paratype, as indicated on the specimen label. But because a holotype was not specified in the description, the so-labeled holotype and paratype are to be considered syntypes under Article 73.2 of the Code (ICZN 1999), and any one is thus eligible for designation as lectotype under Article 74 of the Code (ICZN 1999). The syntype 'Type ♂ (26666)' (= ♀) is here designated as lectotype (Fig. 8C), and the other syntype is the paralectotype.

Additional material. 41 (17♂, 20♀, 4 sex unknown). **Maui**, in BPBM: 1♀, 2 (sex unknown), Keanae, 22.viii.1918, BPBM34151; 1 (sex unknown), Makawao forest Reserve, 7.v.2013 (stored), C.A. Johns leg., host: *Metrosideros polymorpha*, 13.iv.2013, CJ112, KT982411; 2♂, 2♀, Makawao For. Res., Flume Rd. 1296 m, N20.80720 W 156.25259, 10–11.v.2013(UV Bucket trap 1), A. Prestes & W. Haines leg., SK635–638. **Hawaii** (Big Island): 1♂, S. Kona, 8.viii.1919, O.H. Swezey Collector, "Ohia", BPBM34148; 1♀, Upper Hamakua Ditch Trail, Kohala Mts., 4.ix.1919, O.H. Swezey Collector, "Ohia Lehua", Z-XII-20-62-4 ("Slight vari"), BPBM34152; host: *M. polymorpha* in BPBM: 1♂, Kohala Watershed Partnership, 4.vi.2015 (stored), C.A. Johns leg., 18.v.2015, CJ416, SK775♂; 2♂, 1♀, Puu Makaala Natural Area Reserve, Hawaii, 30.v.&13.vi.2015 (stored), C.A. Johns leg., 7.v.2015, CJ410, CJ430 / SK776♂, CJ431 / SK778♂; 4♂, 12♀, 1 (sex unknown), same locality, 3.v.–6.vi.2016

em., A.Y. Kawahara leg., 1.v.2016, SKH-09-1 / SK615♀, SK616♀, 617♀; 1♂, Volcanoes National Park, Thurston Lava Tube, 24.v.2016em., C.L.-Vaamonde & C. Doorenweerd leg., 22.iv.2016, HILO019; 4♂, 2♀, Same locality, 16–28.v.2016em., A.Y. Kawahara leg., 27.iv.2016(larva); 3♂, 1♀, same locality, 28–29.iv.2016 (light trap). In NHMUK: 1♂, Hawaii 1300', S. Hilo Distr., Waiakea F. R., Stainback Highway, 21.vi.1976, K. & E. Sattler, B.M.1976-605, *Philodoria* sp. 11 (Hawaii) Sattler Coll., D. C. Lees Sep. 2016, BMNH(E)1621300; 1♂, Hawaii 1300', S. Hilo District, Upper Waiakea F. R., Stainback Highway, 9.vii.1976, K. & E. Sattler, B.M.1976-605, *Philodoria* sp. 11 (Hawaii) Sattler Coll., D. C. Lees Sep. 2016, BMNH(E)1621134; 1♂, Hawaii 2800', Kau District, Ocean View, 20.vi.1976, K. & E. Sattler, B.M.1976-605, *Philodoria* sp. 10B cf *splendida* (Hawaii [=Big Island]) Sattler Coll., D. C. Lees Sep. 2016, BMNH(E)1621065; 1♂, Hawaii 6200', Kau District, Kahuku Ranch, Punaluu Kahawai, 4.viii.1976, K. & E. Sattler, B.M.1976-605, *Philodoria* sp. 15 (Hawaii [=Big Island]) Sattler Coll., D. C. Lees Sep. 2016, BMNH(E)1621320; 1♂1♀, Kilauea, Hawaii (Big Island), at light (= light trap), 20&21.v.1915, A. Busck Collector, deposited in USNM.

Diagnosis. A leaden gray patch covers the entire lower (anal vein) portion of forewing (Fig. 8C–F). The male genitalia has a broad valva with a short dorsal process, a rather broad and shorter capsule, and a broad phallus. The female has a sclerotized lamella antevaginalis and oblong pod-shaped signa similar to those of *P. splendida* Walsingham and *P. lama* **sp. n.**

Redescription: Adult (Fig. 8C–F, 34D). Wingspan 8–10 mm; forewing length 4.5 mm in holotype, 3.8–4.3 mm in the additional specimens examined. Head leaden gray; frons white; maxillary palpus reduced; labial palpus white (Fig. 34D, 37A). Antenna grayish fuscous. Thorax: grayish fuscous. Forewing leaden gray suffused with pale brown patches enclosing dark gray fascia; **tf** from costal 1/3 to dorsal 1/2, **tp** after the middle to apical portion, distinctly narrowing near the dorsum, containing two short, shining, steel gray costal spots; apical portion with large jet-black terminal patch from tornus to apex, containing two upright steel-gray spots near its opposite extremities; a single bright silvery dot in its middle; a very narrow ocherous line along the base of tornus; cilia shiny, leaden gray with a blackish fringe line; two white costal streaks, longer streak extends to apex; terminal cilia often black. Hindwing tawny black; cilia tawny gray. Abdomen grayish fuscous above, banded with white beneath. Legs pale graysih fuscous, spurs white.

Male genitalia (Figs. 41I, 42H, 43H): new record (n=4). Capsule 750 µm. Tegumen 1.1–1.2 x length of valva; valva 500 µm long, rather broad and having a knob-shaped dorsal process; dorsal process densely covered with minute spines ventrally and on inner margin (Fig. 41I). Saccus rather short, broad, slightly narrowing in the middle (Fig. 42H). Phallus 650 µm long, rather broad; two series of cornuti large and developed in vesica (Fig. 43H).

Female genitalia (Fig. 40E–H, 61H; Zimmerman 1978a: fig. 474) (n=3). 1450 µm long. Ostium bursae broad; antrum very short and wide; lamella antevaginalis 200 µm, semicircular (Fig. 40F, H). End of ductus bursae broad, connecting in dorsal portion of anterior part of corpus bursae; corpus bursae about 1000 µm long; anterior end of corpus bursae weakly sclerotized; some lines consisting of wrinkles running longitudinally, some sclerotized; paired signa oblong and podlike with a series of minute spines (Fig. 40G, H).

Distribution. Maui (Walsingham, 1907) and Hawaii (Big island) (Zimmerman 1978a).

Host plants. Myrtaceae: *Metrosideros polymorpha* Gaudich. (present study), *Metrosideros* sp. (Zimmerman 1978a).

Biology. (Fig. 81). Zimmerman (1978a: 695) reported the cocoon and mature larval habit based on Swezey's observations. We observed larvae on multiple occasions. Early instar larvae form a slender, linear mine on the adaxial leaf surface that gradually expands into a larger blotch mine as the larva feeds and grows (Fig. 81A, G). Mines ~5 cm in length, brownish pale green; older mines turn dark brown to pale grayish ocherous and redish brown (Fig. 81B). One or two mines per leaf (Fig. 81E). The larva nearly always causes the leaf to dehisce from the plant, leading to the mined leaf to fall to the ground. Fully grown larvae exit the mine, and cut an oval ring into the upper (adaxial) epidermis of the bloch mine (Fig. 81J). The oval epidermis is folded by the final instar larva by using silk to pulling two ends of the outer surface of the epidermis, creating a "taco"-like cocoon (5.0–6.0 mm in length and 1.5–2.0 mm in width), which hardens and becomes bronze-colored over time (Fig. 81B, K–M). The taco often falls out of the oval cut-out in the leaf and falls beneath the leaf litter (Fig. 81C), but can occasionally remain attached (Fig. 81C, D, F). We suspect it may help avoid parasitoids and other predators while being in a humid environment. The penultimate and final instar larvae are approximately 4–5 mm long and pale yellow (Fig. 81H, I). During the day, adults rest on adaxial side of leaves of *Melicope* species, Rutaceae (not a *Philodoria* host plant) at Mt. Kaala on Oahu.

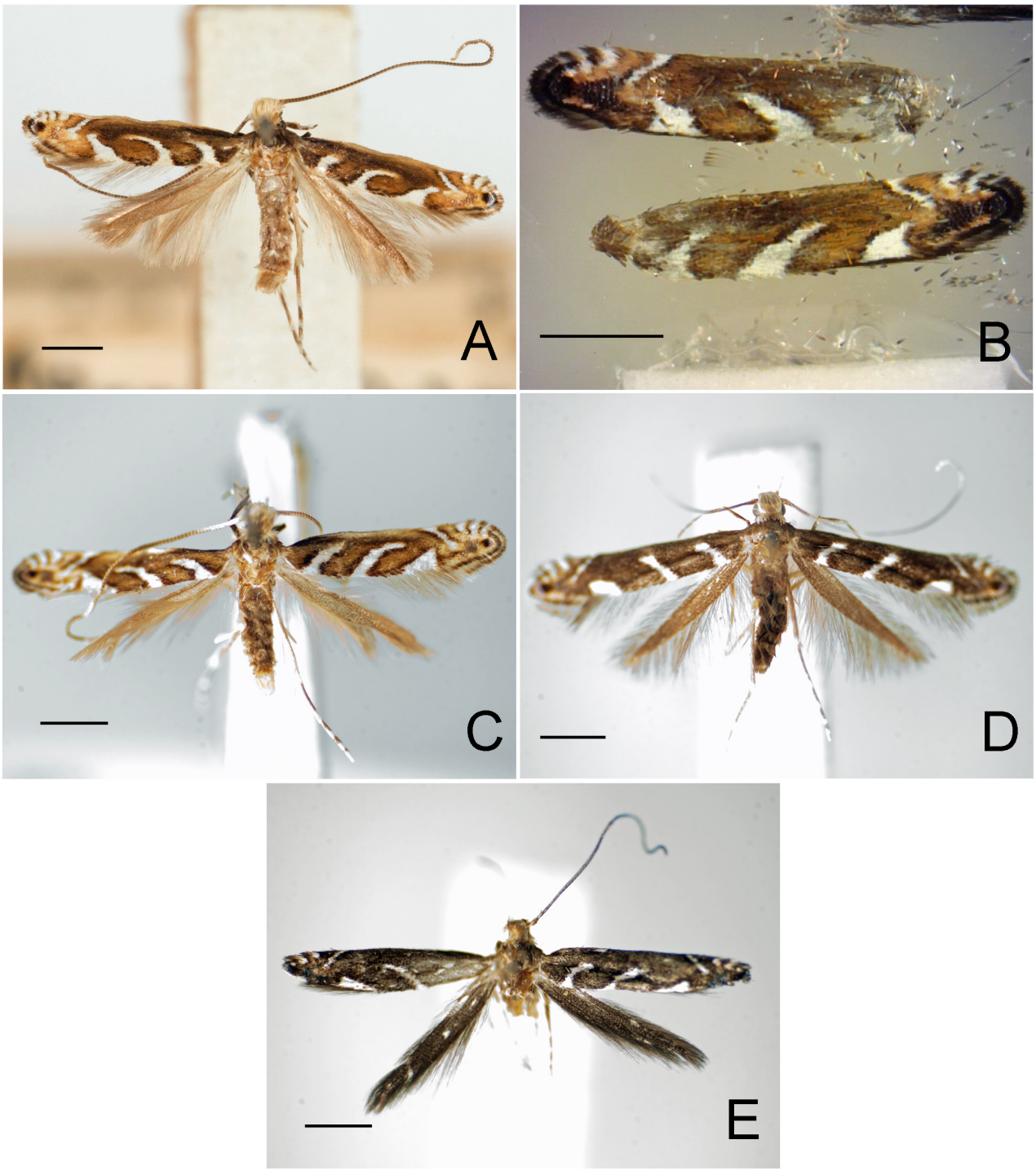

FIGURE 19. Adults of *Philodoria neraudicola* (Swezey, 1920) and *P. obamaorum* **sp. n. A** *P. neraudicola* lectotype male, **B** Forewings of lectotype female, host *Pipturus albidus*, Maui, **C** *P. obamaorum* holotype male, **D** Paratype female, E Female (CLV017). Scale bar 1 mm.

Parasitoids. Eulophidae: *Euderus metallicus* (Ashmead, 1901) (Zimmerman 1978a).

Remarks. We identified one adult moth (Coll ID CJ-112 / GenBank accession no. ID KT982411) as *P. basalis*, based on a leaden gray patch covering the entire lower portion of forewing, from which whole bodies were sacrificed for molecular analysis (Johns *et al*. 2016). William Haines (pers. comm.) collected >10 adults of this species in UV Bucket trap at one night in Makawao Forest Reserve, Maui (10–11.v.2013).

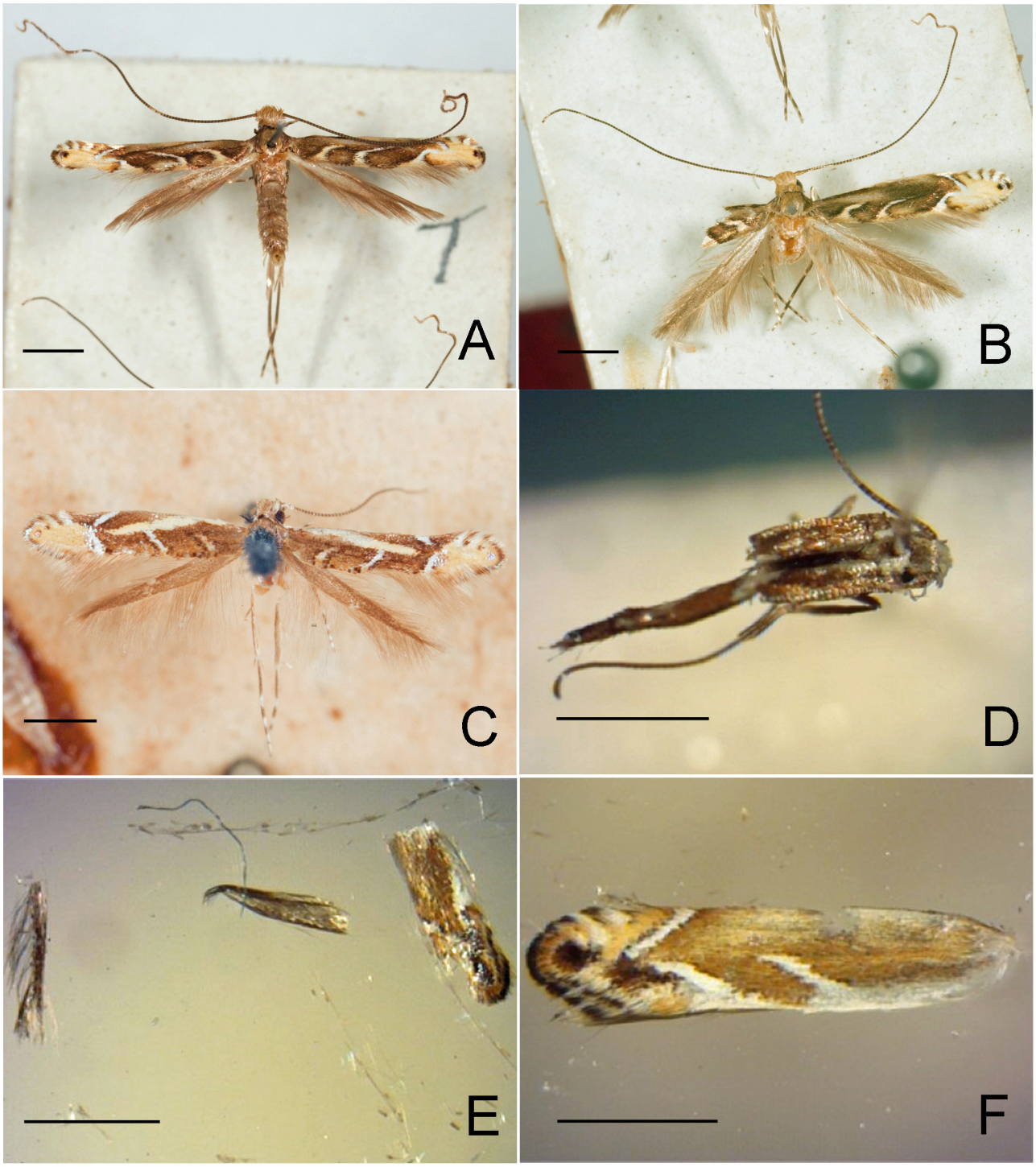

FIGURE 20. Adults of *Philodoria* species. **A** *P. urerana* (Swezey, 1915) lectotype female, one of two cotypes on the same mount (upper specimen), **B** Paralectotype (sex unknown, lower specimen on same mount as A), **C** *P. hauicola* (Swezey, 1910) lectotype male, **D** *P. keahii* **sp. n.** holotype male, **E** Wings of holotype, **F** Left forewing of paratype female. Scale bar 1 mm.

Philodoria splendida **Walsingham, 1907**

Figs. 9A, B, 26D, E, 41J, K, 42I, J, 43I, J, 56K, 64G–I, 66C, D, 73B, C, 82.

Philodoria splendida Walsingham, 1907: 719–720, pl. 25, fig. 23; Swezey 1913b: 223; Zimmerman 1978a: 718, figs. 466, 471, 477, 481.

Type locality. Lanai, 2000ft.

Type material. Lectotype ♂, Lanai, 3000ft, ii.1894, Perkins 26452 |♂ genitalia on slide 101, Oct.17.1940| Philodoria splendida ♂ Wlsm PARATYPE 2/9| Fauna Hawaiiensis Collection| No. 34284 Hawaiian Coll. BISHOP Museum in BPBM (here designated). Paralectotype 2 (1♂, 1 sex unknown). 1 (sex unknown), Lanai, 2000ft, vii.1894, Perkins 26493 | Philodoria splendida Wlsm PARATYPE 3/9| in BPBM; 1♂, Kauai Mts., 3000–4000ft, vi.1894, Perkins 27188, | Philodoria splendida ♂ Wlsm PARATYPE 9/9| in BPBM. Described from ten specimens: 'type ♂ (26430) and nine 'paratypes' from Kauai, Oahu, Molokai and Lanai. Given the manner in which the descriptions were written, Walsingham likely considered them as the holotype and paratypes, as indicated on their specimen labels. However, because a holotype was not specified in the description, the so-labeled types and paratypes are to be considered syntypes under Article 73.2 of the Code (ICZN 1999), and any one of them is thus eligible for designation as lectotype under Article 74 of the Code (ICZN 1999). We could not find 'type ♂ (26430)' from 2000 ft., Lanai, xii.1894 and six syntypes: 1 (sex unknown), Halemanu, 4000 ft, Kauai, v.1895; 1 (sex unknown), Waianae Mts., 2000 ft., iv.1892, beaten from "Lefua" (*Metrosideros polymorpha*?); 1 (sex unknown), Mts., near Honolulu, 2000 ft., 25.x.1892; 1 (sex unknown), Kalae, 1500 ft., v.1893; 1 (sex unknown), Mts., about 4000 ft., 9.vi.1893; 1 (sex unknown), 3000 ft., Lanai, ii.1894. Zimmerman (1978a: 701, fig. 466) provided the last photograph for the 'holotype' (=type ♂ (26430)) in the NHMUK. The current curator of NHMUK, D.C. Lees informed us that the 'holotype' of *P. splendida* is not stored in the designated location of the NHMUK. We selected a lectotype from three syntypes (Fig. 9A), and the remaining syntypes are paralectotypes.

Additional material. 28 (14 ♂, 11 ♀, 3 sex unknown). **Kauai**: 1♂, Kauai Na Pali, Kona Forest Reserve, Alakai Swamp trail, 3800', 29ix.1973, K. & E. Sattler, B.M.1973-498, *Philodoria* sp. 12 (Kauai) Sattler Coll., color slide 140, D. C. Lees Sep. 2016, BMNH(E)1621068. **Oahu**: 1♂, Waianae, 5.i.1913, ex *Metrosideros polymorpha*, SK697♂, BPBM 34316; 1♂, Waianae, 5.i.1913, ex Ohia (= *M. polymorpha*) in USNM;1♂, 1♀, Lauiluli, 25.x.1914, "Ohia Lehua" (= *M. polymorpha*), BPBM 34312; 3♂, 1♀, Malamalama, 8.x.1916, "Ohia Lehua", 34293–34295, ♂ ♀slide aB Aug26 1941 in USNM; 1♀, Konahuanui, 2300ft, 9.v.1943, Resting on Cladium, EC Zimmerman Collector, BPBM 34319; 1♀, Kalihi, Coll. O.H.S, "Ohia Lehua", BPBM34311; 1 (sex unknown), Olympus, Coll. O.H.S, no. "35" in USNM.1♂, Waialae, Nui, 16.ii.1919, Z-XII-19-62-20♂ in BPBM. 1 (sex unknown), Kaala Road, 23.iv.2013 (stored), C.A. Johns leg., Adult on *Melicope clusiifolia*, 21.iv.2013, CJ049, KT982402 in BPBM; 1♂, 2♀, Kanahuanui, 30.i.&4.ii.2014 (stored), C.A. Johns leg., host: *M. polymorpha*, 3.i.2014, CJ246ab, CJ247, SK780♂, 781♀, 773♀ in BPBM. In NHMUK: 1♂, Oahu 4000', Waianae Range, Ma Kaala, 4.ix.1976, K. & E. Sattler, B.M.1976-605, *Philodoria* sp. 10D (Lanai, Mauai, Oahu) *splendida*? Sattler Coll., D.C. Lees, Sep. 2016, BMNH(E)1621292; 1♀, Oahu 2200', Waianae Range, above Makua Valley, 11.ix.1976, K. & E. Sattler, B.M.1976-605, *Philodoria* sp. 10C cf *lysimachiella* (Oahu) Sattler Coll., D. C. Lees. Sep. 2016, BMNH(E)1621295. **Lanai**: 1♂, 2750', Munro Trail, 2.x.1976, Philodoria sp. 10D (Lanai, Mauai, Oahu) splendida? Sattler Coll., D. C. Lees Sep. 2016, BMNH(E)1621678 in NHMUK; **Maui**: 1♂, Haelaau, 17.xii.1928, O.H. Swezey, 34289 in BPBM; 1♂, 1♀, 1 (sex unknown), Flemming Arboretum Trail, [3.v.2013 (stored), C.A. Johns leg., host: *M. polymorpha*, 12.iv.]2013, SK621♀, SK696♂, CJ105 (sex unknown) / KT982410 in BPBM. 1♀, W. Mauai, 3000', W. Maui Forest Res., Kaulalewelewe (Puu Kukui Trail), 26.viii.1976, K. & E. Sattler, B.M.1976-605, Philodoria sp. 10D (Lanai, Mauai, Oahu) splendida? Sattler Coll., D. C. Lees Sep. 2016, BMNH(E)1621208 in NHMUK; ***Syzygium* sp.**, C.A. Johns leg., in BPBM: 2♀, Limahuli, Kauai, 21.vii.2015 (stored), 20.vi.2015, CJ488ab, SK748♀, SK752♀; 1♂, Waiaai Trail, Oahu, 30.vii.2014 (stored in RNAlater solution), 5.vii.2014, CJ312, SK747♂ (only abdomen).

Diagnosis. This species and *P. lama* **sp. n.** have a brownish ocherous basal oblique fascia on forewing (Figs. 9A, B, 73B, C). Genital features very similar to those of *P. basalis* and *P. lama*, but distinguished by a rather slender dorsal process of valva in male. Kauai specimens (CJ488, male unknown) on *Syzygium* sp. have similar forewing pattern (Fig. 26D, E) and female genitalia, but the Oahu specimen (CJ312, thorax sacrificed for molecular analysis) have thickened dorsal process with slightly curved dorsal side (Fig. 41K) and slender saccus (Fig. 42J).

Redescription: Adult (Figs. 9A, B, 26D, E, 73B, C). Wingspan 8–9 mm in type series; forewing length 4 mm in holotype, 3.9 mm in paratype. Head dark brown; frons white; maxillary palpus reduced; labial palpus white, externally fuscous at apical portion. Antenna grayish fuscous. Thorax leaden gray. Forewing shining, pale leaden gray with dark brownish ocherous patches enclosing gray fascia: **bp** from near base of costal fold to dorsal 1/4; **tf** from costal 1/3 to dorsal 1/2, **tp** after the middle to apical portion, distinctly narrowing in the dorsum, containing two short, shining, steel gray costal spot; apical portion with large jet-black terminal patch from tornus to apex, containing two upright steel-gray streaks near its opposite extremities; a single bright silvery dot in its middle; a very narrow ocherous line along the base of tornus; cilia shiny, leaden gray with a black fringe line; two white costal lines,

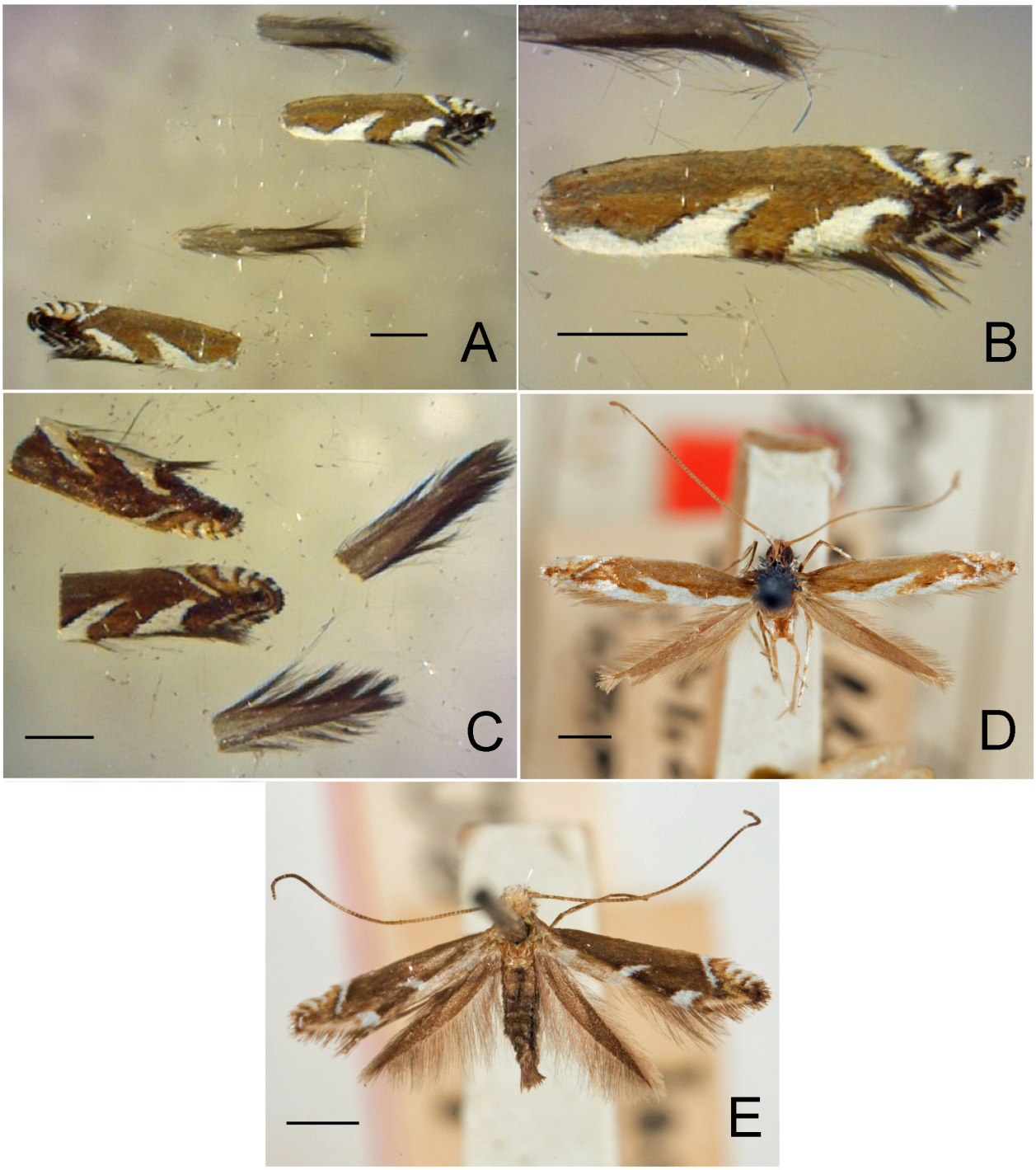

FIGURE 21. Adults of *Philodoria* species. **A** Wings of *P. funkae* sp n., holotype female, **B** Right forewing of holotype shown in A, **C** Wings of paratype female, **D** *P. pittosporella* (Swezey, 1928) holotype male, **E** *P. touchardiella* (Swezey, 1928) lectotype female. Scale bar 1 mm.

long one extend apex; terminal cilia often black. Hindwing coppery brown; cilia tawny. Abdomen tawny brown, silver below. Legs grayish fuscous, with white spots on tarsal joints and at distal end of tibiae; spurs white.

Male genitalia (Figs. 41J, K, 42I, J, 43I, J, 64G, I) (n=3). Capsule 830 µm. Tegumen same length as valva and rather wide; valva 490 µm long, similar to *P. basalis* except dorsal process rather slender (Fig. 41J). Saccus broad and straight (Fig. 42I). Phallus 660 µm long, sinuous in lateral view; cornuti large and well developed apically (Fig. 43I).

Female genitalia (Fig. 56K) (n=4). 1400 µm long. Lamella antevaginalis 200 µm in length. Corpus bursae 800 µm long. Similar in the appearance to *P. basalis*.

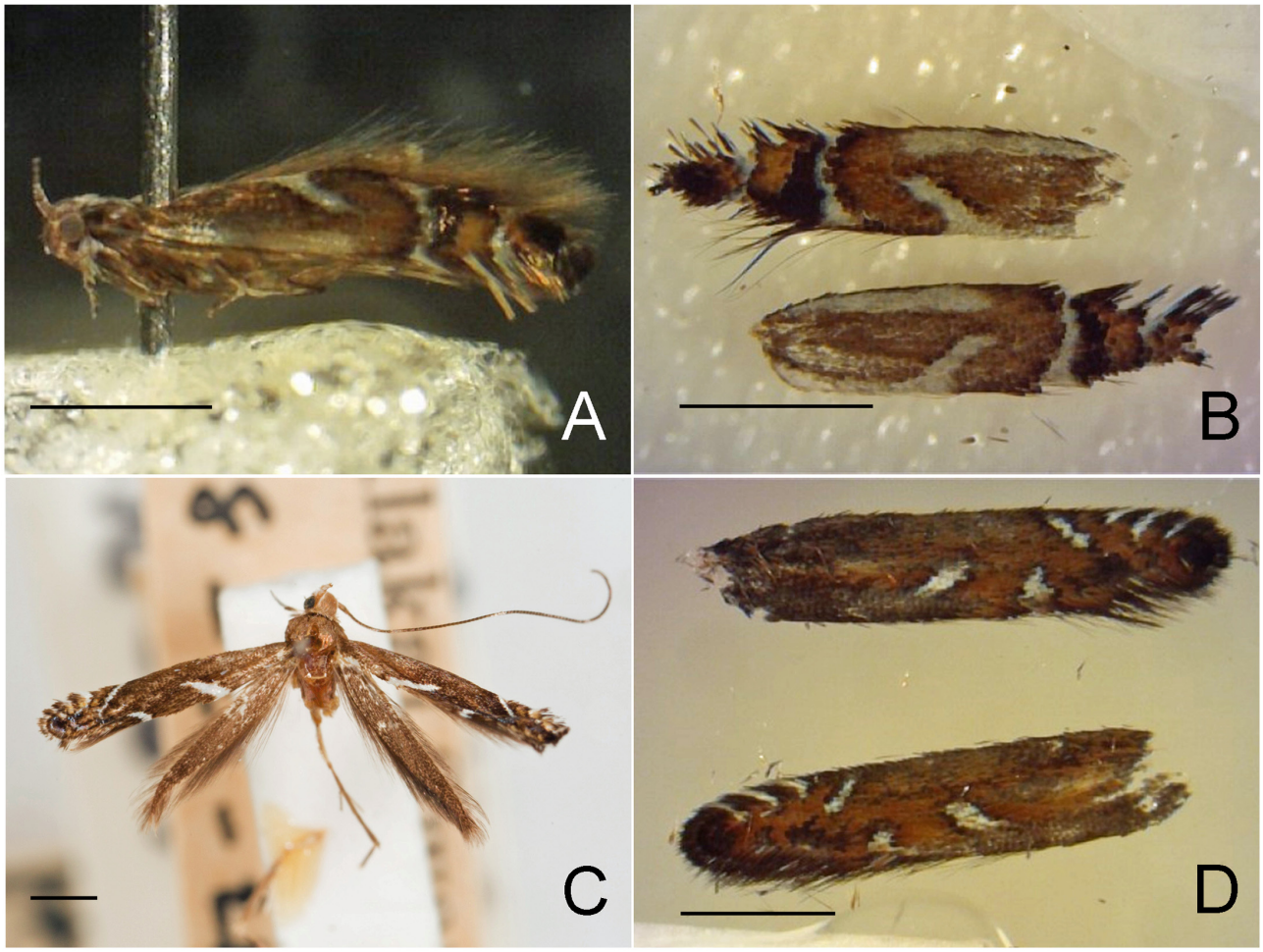

FIGURE 22. Adults of *Philodoria* species. **A** *P. keaensis* **sp. n.** holotype female, lateral view, **B** Forewings of holotype, **C** *P. nigrelloides* (Swezey, 1946) holotype female, **D** Forewings of *P. platyphylliella* **sp. n.** holotype male. Scale bar 1 mm.

Distribution. Kauai, Oahu, Molokai, Lanai (Walsingham 1907), and Hawaii (Big Island) (Zimmerman 1978a).

Host plants. Myrtaceae: *Metrosideros polymorpha* Gaudich. (Walsingham, 1907), *Syzygium* sp.: new record.

Biology. (Figs. 66C, D, 82). Swezey (1913b: 223) reported the "taco" like cocoon and mature larval habit, which are similar to that of *P. basalis*. The biology is poorly studied, but it is presumably similar to that of *P. basalis*. In general, larvae form slender linear mine on the adaxial leaf surface (Fig. 82E), which gradually expands as lavae feed and grow (Fig. 82A). One or two mines per leaf. We often observed the fallen mined leaves under the host plant (Fig. 66C, D) with late instar larvae in the mine and/or pupae in a taco cocoon on or near the leaf.

Parasitoids. (Fig. 101G, H). Bethylidae: *Sierola philodoriae* Fullaway, 1920; Eulophidae: *Pauahiana metallica* Yoshimoto, 1965 (Zimmerman 1978a).

Remarks. We identified two adult moths (Coll ID CJ-049 / GenBank accession no. ID KT982402 and CJ-105 / KT982410) as *P. splendida*, based on the presence of a brown basal oblique fascia on forewing and host plant, from which whole bodies were sacrificed for molecular analysis (Johns *et al*. 2016).

***Philodoria napaliensis* Kobayashi, Johns & Kawahara, sp. n.**
Figs. 9D, 41M, N, 42L, 43L.

Philodoria sp. 4; Johns *et al*. 2018: fig. 2.

Type locality. Nâ Pali Trail (Kauai).

Etymology. The specific epithet, *napaliensis* is derived from the type locality, Nâ Pali (pronounced 'Nah-Pah-lee') Coast.

Type examined. Holotype (sex unknown), Na Pali Trail, Kauai, 13&21.vii.2015 (stored), C.A. Johns leg., host: *Diospyros sandwicensis*, 24.vi.2015, CJ491a (abdomen missing) in BPBM. Paratype 2♂, same locality and data as holotype, CJ482 / SK767♂, CJ491b / SK745♂ (apex of tegumen broken); deposited in BPBM. Three specimens are incomplete but they have features that are distinctive enough to allow this species description. What remains of three specimens were: holotype mounted by placing three wings without mountant under a coverslip: two full forewings slightly damaged at base and small apical region of one hindwing; two paratypes: a specimen mounted by placing four wings without mountant under a coverslip (two forewings [1/3 of left wing and 1/2 right wing] and 1/3 of two hindwing; CJ482); a specimen mounted by placing two forewings and one leg without mountant under a coverslip (almost full left wing and apical portion and basal half of right wing and one hind leg; CJ491b). The head, antenna, thorax, and legs for all specimens were sacrificed for molecular analysis.

Additional material. 2 larvae (CJ-445/AHE_44) entirely sacrificed for molecular analysis (Johns *et al*. 2018: fig. 2): 2 larvae, same locality and data as holotype, 26.vi.2015 (stored), CJ445, in FLMNH.

Diagnosis. Very similar to *Philodoria* that feed on Myrtaceae and *P. lama* **sp. n.**, but differs from them in having a valva with a dorsal process with a thick inner margin (Fig. 41M, N).

Description: Adult (Fig. 9D). Forewing length 3.4–3.5 mm in holotype. Head, antenna and thorax unknown. Forewing dark shiny, pale leaden gray with brownish ocherous patches enclosing gray fascia: **bp** from base to dorsum 1/3, contact to basal **tf**; **tf** from costal 1/3 to dorsal 1/2, **tp** after the middle to apical portion, distinctly narrowing in the dorsum, extending to dorsal 2/3, containing two short, shiny, steel gray costal spots; apical portion with black **as** and a large jet-black terminal patch from tornus to apex, containing two upright steel-gray spots near its opposite extremities; a single bright white spot in its middle; a very narrow ocherous line along the base of tornus; cilia shining, leaden gray with a blackish fringe line; two white costal streaks, long one extend apex; terminal cilia often blackish. Hindwing coppery brown; cilia tawny. Abdomen tawny brown, white below. Legs unknown.

Male genitalia (Figs. 41M, N, 42L, 43L) (n=2). Capsule 600 µm. Tegumen 0.7–0.8 x length of valva; valva 450–460 µm long, similar to *P. basalis* and *P. lama* except inner margin of dorsal process thicken (Fig. 41M, N). Phallus 550 µm long (Fig. 43L).

Female genitalia Unknown.

Distribution. Kauai.

Host plants. Ebanaceae: *D. hillebrandii* (A.DC.) Fosberg and/or *Diospyros sandwicensis* (A.DC.) Fosberg. We could not distinguish the two *Diospyros* species, *D. hillebrandii* and the closely related *D. sandwicensis. Diospyros sandwicensis* is found on all of the main Hawaiian islands. It often occurs as a dominant plant in dry to moist forests and occasionally in wet forests. It grows at elevations ranging from close to sea level to 1200 m (4000ft) (Wagner 1990).

Biology. Unknown, but it is presumably similar to those of *P. basalis*, *P. lama* and *P. splendida*, whose larvae pupate in a "taco" like cocoon.

Philodoria lama Kobayashi, Johns & Kawahara, sp. n.

Figs. 9C, 41L, 42K, 43K, 56L, 73E, F, 83.

Philodoria sp. 9; Johns *et al*. 2018: fig. 2.

Type locality. Kanepuu (Lanai).

Etymology. The specific epithet, *lama* (pronounced 'La-mah') is a noun in apposition taken from the Hawaiian name of the host plant, *Diospyros*.

Type material. Holotype ♂, Kanepuu, Lanai, 24.viii.2014 (stored), K. Bustamente leg., host: *Diospyros sandwicensis*, 5.viii. 2014, CJ382, SK744♂ in BPBM. Paratype 4 (3♂, 1♀), All types were preserved in BPBM. 3♂, 1♀, Lualailua, Maui, 24.v.2016 (stored), K. Bustamente leg., host: *D. sandwicensis*, Spring. 2016, CJ540, SK813♀, SK814♂. The holotype was mounted by placing four wings without mountant under a coverslip (2/3 of two forewings and apical half of two hindwings); four paratypes: a female specimen mounted as a dry pinned specimen with the nearly entire right forewing without mountant under a coverslip; CJ540 / SK813); two male specimens mounted as dry pinned specimens with its near complete forewing without mountant under a coverslip; a male specimen mounted by placing two forewings without mountant under a coverslip (two near complete forewings slightly

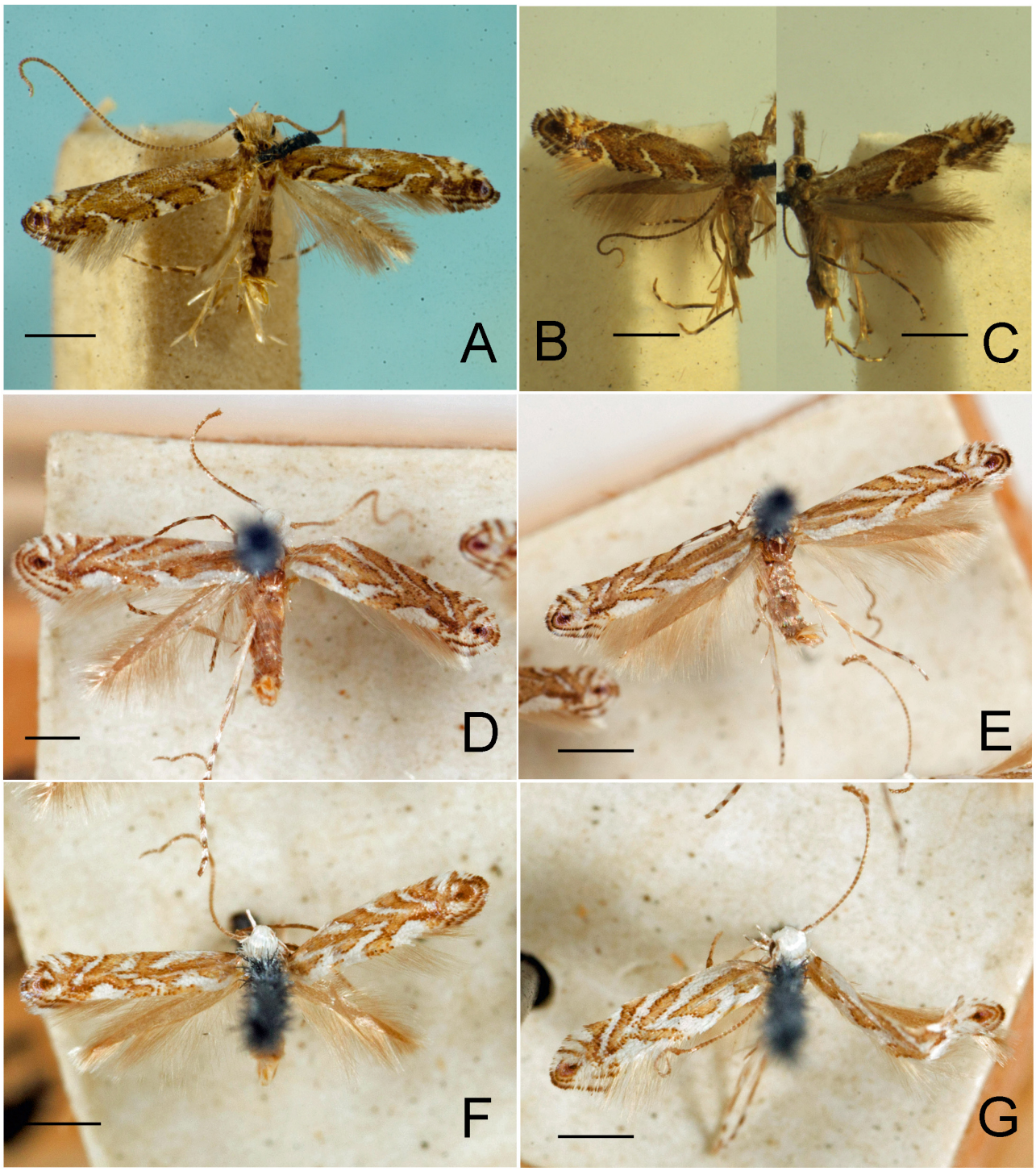

FIGURE 23. Adults of *Philodoria* species. **A** *P. marginestrigata* (Walsingham, 1907) paralectotype male (BPBM 34197), **B** *P. marginestrigata* (Walsingham, 1907) Lectotype female, left wings, **C** Same specimen, right wings, **D** *P. lipochaetaella* (Swezey, 1940) paralectotype male, one of four cotypes on the same mount (upper left specimen on mount), **E** Lectotype male (upper right specimen on mount), **F** Paralectotype female (lower left specimen on mount), **G** Paralectotype (sex unknown, lower right specimen on mount). Scale bar 1 mm.

damaged at base; CJ540 / SK814). The head, antenna, thorax, and legs for all specimens were sacrificed for molecular analysis.

Additional material. 1♂, Lualailua, Maui, 30.xii.2013 (stored), C.A. Johns leg., host: *D. sandwicensis*, 24.xii.2013, CJ161, PHIL0037♂ (abdomen only) in BPBM.

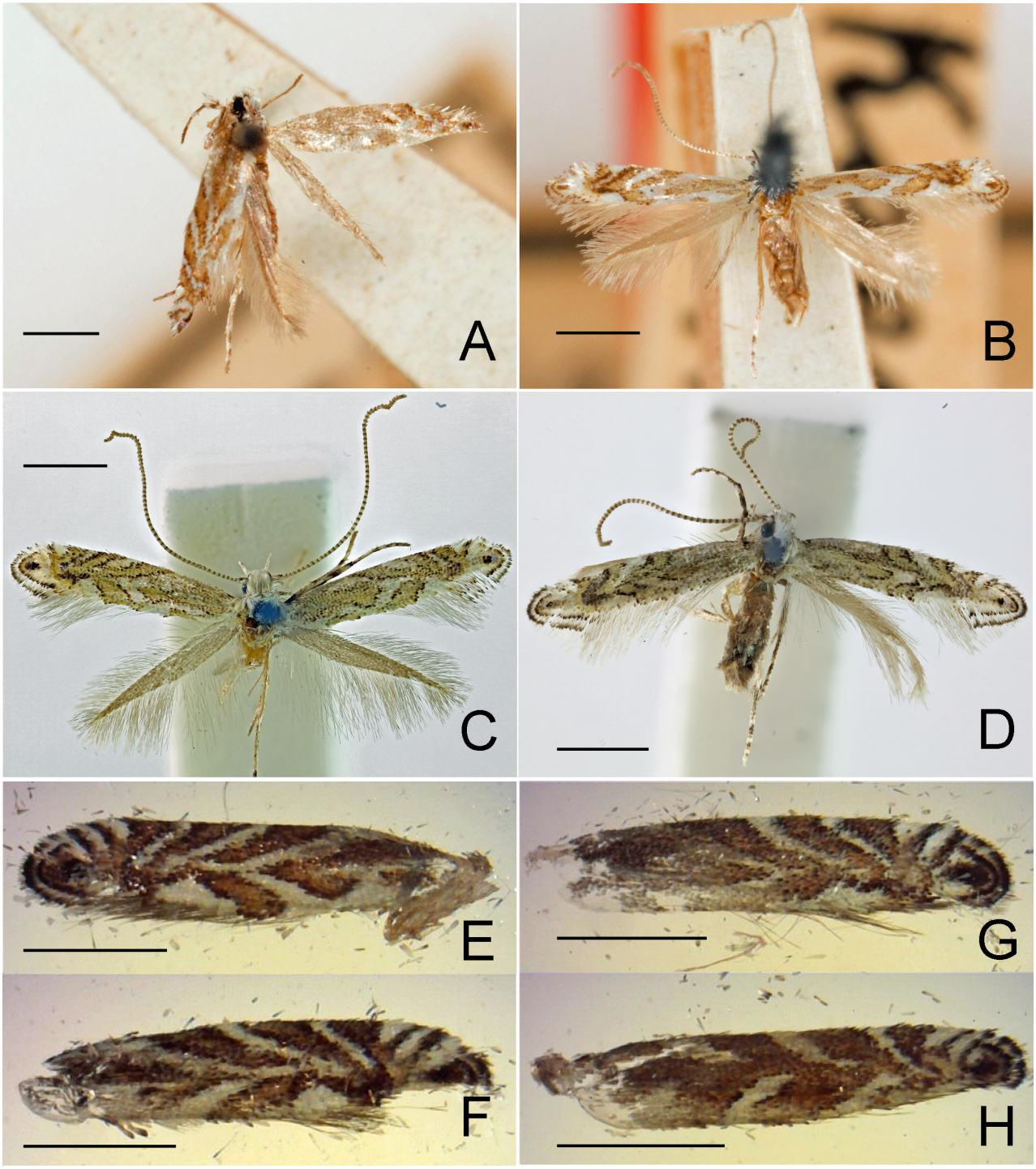

FIGURE 24. Adults of *Philodoria* species. **A** *P. lipochaetaella,* specimens originally described as *Parectopa lipochaetae* Swezey, 1946, syntype male **B** *P . sciallactis* (Meyrick, 1928) lectotype male **C** Paralectotype male **D** Paralectotype female **E** Male left forewing of specimen CJ164, host: *Melanthera kamolensis*, Maui **F** Same specimen, right forewing **G** Male right forewing of specimen CJ189, host: *Melanthera kamolensis*, Maui **H** *Philodoria* sp. B nr. *P. sciallactis* (specimen CJ483, sex unknown) right forewing, host: *Lipochaeta acris*, Kauai. Scale bar 1 mm.

Diagnosis. The forewing pattern, genital structure and larval habit are very similar to those of *P. splendida* Walsingham and *P. basalis* Walsingham, but are distinguished from them because of the basal oblique fascia of the forewing, slender saccus and longer coecum in male genitalia, and coecum which is about 1/4 length of phallus in *P. lama*, but about 1/6~1/5 length in *P. splendida* (Figs. 9C, 42I, 43I, 73E, F).

Description: Adult (Figs. 9C, 73E, F). Forewing length 3.4, 3.5 mm in two paratypes. Head and frons brown;

maxillary palpus reduced; labial palpus ocherous to brown with dark brown scales at apex. Antenna grayish fuscous, about 4.2 mm long in paratype. Thorax gray. Forewing dark shiny, pale leaden gray with brownish ocherous patches enclosing gray fascia: **bp** sometimes absent in Lanai specimens, from base along to dorsum 1/4, sometimes from near base of costal fold to near dorsum 1/4 in Maui specimens; **tf** from costal 1/3 to dorsal 1/2, **tp** after the middle to apical portion, distinctly narrowing in the dorsum, extending to dorsal 2/3, containing two short, shiny, steel gray costal spots; apical portion with black **as** and a large jet-black terminal patch from tornus to apex, containing two upright steel-gray spots near its opposite extremities; a single bright white spot in its middle; a very narrow ocherous line along the base of tornus; cilia shining, leaden gray with a blackish fringe line; two white costal streaks, long one extend apex; terminal cilia often blackish. Hindwing coppery brown; cilia tawny. Abdomen tawny brown, white below. Legs grayish fuscous, with white spots on the tarsal joints; spurs white with fuscous scales.

Male genitalia (Figs. 41L, 42K, 43K) (n=3). Capsule 810 µm. Tegumen slightly shorter than length of valva; valva 460 µm long, similar to *P. splendida* except minute spines on dorsal process covered from apically to basally and on inner margin (Fig. 41L). Phallus 560 µm long (Fig. 43K).

Female genitalia (Fig. 56L) (n=1). 1240 µm long. Lamella antevaginalis 160 µm in length. Corpus bursae 770 µm long. Similar to *P. basalis* and *P. splendida*.

Distribution. Oahu, Lanai, and Maui.

Host plants. Ebenaceae: *Diospyros sandwicensis* (A.DC.) Fosberg and/or *D. hillebrandii* (A.DC.) Fosberg. We could not separate the two *Diospyros* species, *D. sandwicensis* and the closely related *D. hillebrandii*.

Biology. (Fig. 83). Biology unknown, but it is presumably similar to that of *P. basalis* and *P. splendida*. Larvae form an elongate blotch mine on the adaxial leaf surface (Fig. 83A–C). One mine per leaf (Fig. 83A). Most of the "Taco" cocoons were still attached to the leaf and leaves with cocoons were both on ground and on tree, based on observations at Lualailua, Maui.

Remarks. We have observed *Philodoria* leaf mines on *Diospyros* on Oahu, but we were unable to find any mines with larvae in them (Fig. 83D). Swezey (1910a) described the *Diospyros* leaf-miner, *Gracilaria* [sic] (= *Caloptilia*) *mabaella* from Oahu and did not mention the unnamed *Philodoria* leaf miner on *Diospyros*. Zimmerman (1978a) noted that *Caloptilia mabaella* might be an introduced species from Japan or North America. We observed the *P. lama* and *Caloptilia mabaella* (CJ333) (Fig. 73D), occurring sympatrically at Kanepuu, Lanai. The mine of *Caloptilia* is distinguished from that of *P. lama* by the brown in coloration and oval cocoon which is situated at the end of the mine.

***Philodoria costalis* Swezey, 1934**

Figs. 10A, 57A, B, 61I–N.

Philodoria costalis Swezey, 1934: 524–525; Zimmerman 1978a: 708, figs. 462, 469, 476.

Type locality. Makaha ridge, 3000 ft, west side of Mount Kaala (Oahu).

Type material. Lectotype ♂, Makaha ridge, 3000 ft, west side of Mount Kaala, Waianae Mountains, Oahu, 15.iv.1934, O.H. Swezey Collecter, [host:] *Pipturus*, |Holotype|*Philodoria costalis* Sewezey Det. by O. H. Swezey| Type no. 4269 in BPBM (here designated). Paralectotypes 2♂, 2♀, same locality and data as lectotype, |Paratype| 34153/Z-XII-20-60-2♂, SK652♀|♂ paratype to ECZ 7-17-61[= 17.vii.1961]| BPBM34154, SK683♂|BPBM34155, SK653♀|BPBM34156. Described from presumably six specimens that Swezey (1934) examined, reared from numerous mines on *Pipturus*. One specimen was labeled 'holotype' and five others as 'paratypes'. Given the manner in which the descriptions were written, Swezey likely considered these specimens to be the holotype and paratypes. But as a holotype was not specified in the description, the so-labeled holotype and paratypes are all to be considered syntypes under Article 73.2 of the Code (ICZN 1999), and any one is thus eligible for designation as lectotype under Article 74 of the Code (ICZN 1999). The 'Holotype, type no. 4269', which Swezey indicated as holotype in the specimen label, is here designated as lectotype (Fig. 10A). The remaining syntypes are paralectotypes.

Diagnosis. Swezey (1934) noted that this species is very similar to *Philodoria micropetala* Walsingham, but it is distinguishable by the white costal line and the lack of fuscous scales along middle of apical orange area (Fig. 10A). The forewing pattern and genitalia are similar to that of *P. pipturiella* Swezey, but distinguished by the rather oblong forewing with a small white spot at middle (Fig. 10A); the straight base of valva; and a rather short ductus bursae.

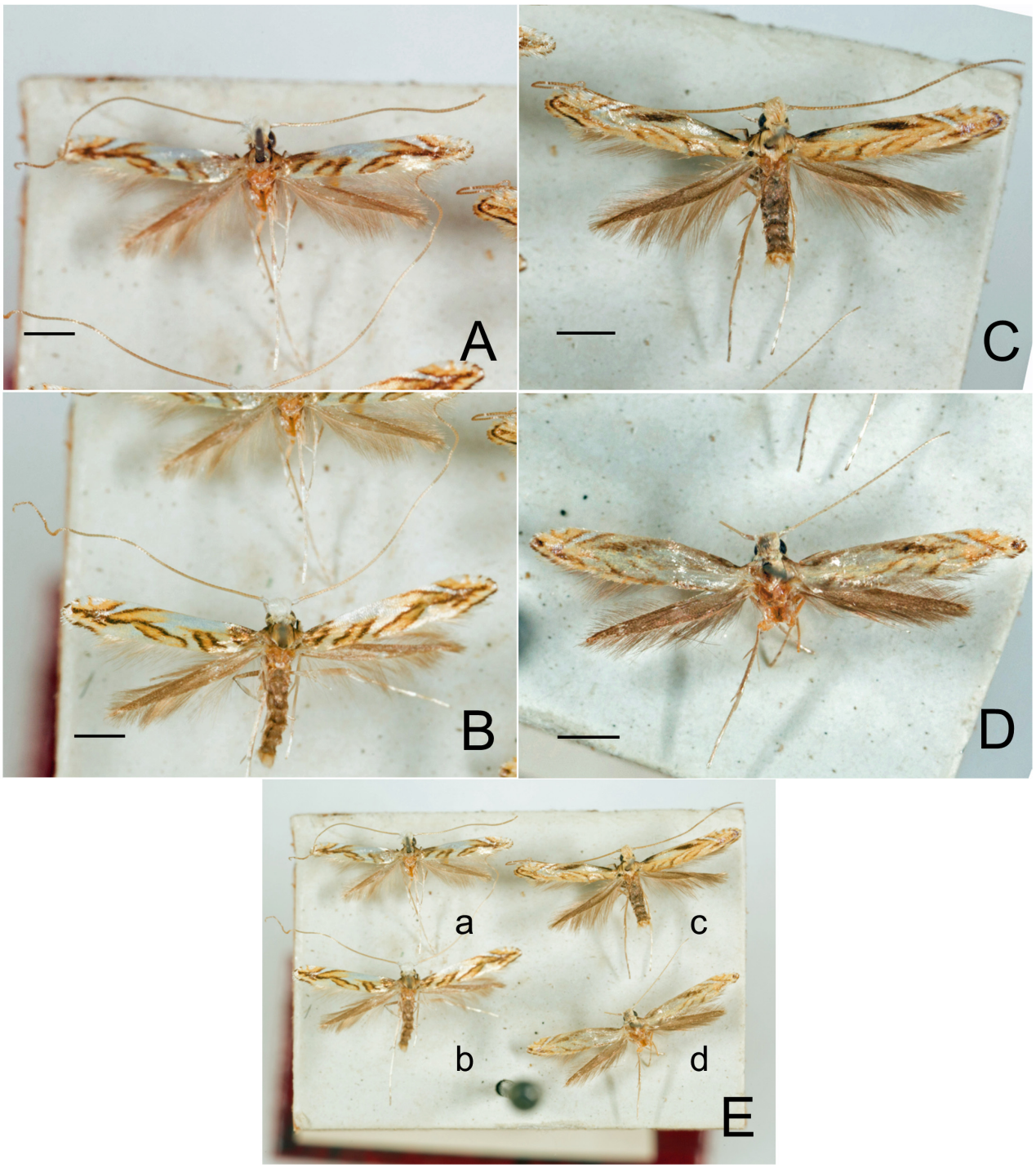

FIGURE 25. Adults of *Philodoria ureraella* (Swezey, 1915) and *P. opuhe* **sp. n. A** *P. ureraella* paralectotype (sex unknown) one of four cotypes on the same mount (upper left specimen on mount), **B** lectotype male (lower left specimen on mount), **C** *P. opuhe* holotype male (upper right specimen on mount), **D** *P. opuhe* paratype (sex unknown, lower right specimen on mount), **E** Types of *P. ureraella* and *P. opihe* on type mount 213 (BPBM) (= four cotypes of '*P. ureraella*' by Swezey). Scale bar 1 mm.

Redescription: Adult (Fig. 10A). Wingspan 7–8 mm; forewing length 3.5 mm in lectotype, 2.4–3.0 mm in paralectotypes. Head tawny brown; frons white; maxillary palpus reduced; labial palpus white shaded with brownish externally on apex of median joint and most of the terminal joint. Antenna uniformly light brown, about 1.25 x length of forewing. Thorax and abdomen tawny brown, white beneath. Forewing tawny brown, suffused with orange patches at apical portion; a broadly oval to nearly circular white spot (**ws**) about middle or just beyond middle of fold, not reaching dorsum; a narrow white line (**cl**) on costa from base to about 2/3; white costal spot (**cs**) at 2/3,

this line enclosing fuscous scales; two white bands on both extremities of shiny pale blue color band (**bb$_3$**): **w$_1$** at costal 1/4, bent **w$_2$** near opposite at dorsal 1/4; another blue apical spot (**as**) extending into apical cilia; costal cilia with two white spots (**a, b**), rest of apical and the terminal cilia brown. Hindwing and cilia brownish fuscous. Legs light brown, white beneath.

Male genitalia (Fig. 61J–N). See Zimmerman (1978a: fig. 469). Tegumen 0.8–0.9 x length of valva; valva rather short, tapering along costal margin from 1/2 to apex with short spines at basal region; apical half digitiform, near straight; along the inner side of valva, a series of small spines (Fig. 61J, L). Saccus short and tapering toward the point (Fig. 61K). Phallus rather short and thick with two series of minute cornuti in vesica (Fig. 61M).

Female genitalia (Fig. 57A, B) (n=2). 900 µm long. Ostium bursae large; antrum cup-shaped with a pair of slender lateral lobes; lamella antevaginalis 160 µm, weakly sclerotized, widening toward anterior margin of A7. Ductus bursae 300–350 µm; terminus of ductus bursae biforked; corpus bursae oblong, 520 µm; paired rows of wrinkles running longitudinally, some sclerotized.

Distribution. Oahu (Swezey 1934).

Host plants. Urticaceae: *Pipturus* sp. (Swezey 1934).

Biology. Unknown, other than that an oval brown cocoon has been reported to be situated on the surface of a leaf (Swezey 1934).

Philodoria pipturiella Swezey, 1923

Figs. 10B, C, 26I, J, 44A, B, 45A, 46A, 57C, 64E, F.

Philodoria pipturiella Swezey, 1923: 294–295; Zimmerman 1978a: 715, figs. 464, 480.

Type locality. Palolo (Oahu).

Type material. Lectotype ♂, Palolo, Oahu, 11.xii.1923?, Swezey Coll., [host:] *Pipturus*, top one of two types on the same mount, |Holotype|*Philodoria pipturiella* Swezey|, Type no. 4273, in BPBM (Here disginated). Paralectotype 31 (6♂, 5♀, 20 sex unknown). 1♂, bottom one of two types on the same mount of lectotype; Oahu Is., O.H. Swezey, [host:] *Pipturus*: 4♂, 2♀, 9 (sex unknown), Tantalus, |Paratype|SK720♀|BPBM34269 (1♀, 2 sex unknown on the same mount), |Paratype|SK719♂|BPBM34274 (1♂, 1 sex unknown), 3 mount |Paratype| (3♂, 1♀, 6 sex unknown) in USNM; 1♀, 6 (sex unknown), Kaumuahona, 12.i.1919, BPBM34273 (1♀, 3 sex unknown), BPBM34275, BPBM 34276, BPBM34277; 1♂, 2♀, 1 (sex unknown), Kaumuahona, 12.i.1919, '*Philodoria micropetala*, aB/1915', 54, SK727♂, SK728♀ in USNM; 1♂, Manoa, BPBM34278. 1 (sex unknown), Pacific Heights, BPBM34271; 2 (sex unknown), W. Sida Mt. Kaala 1.vi.1919, BPBM34279; 1 (sex unknown), W. Sida Mt. Kaala 1.vi.1919 in USNM. Described from three specimens, one specimen labeled 'Holotype' and one 'type' each from Palolo, and Tantalus, Oahu. Given the manner in which the descriptions were written, Swezey likely considered these specimens as the holotype and two paratypes, as indicated on their specimen labels. But because a holotype was not specified in the description, the so-labeled types and paratypes are all to be considered syntypes under Article 73.2 of the Code (ICZN 1999), and therefore a new formal lectotype can be designated under Article 74 of the Code (ICZN 1999). The syntype 'Holotype' (top specimen on mount) which was figured as holotype by Zimmerman (1978a, fig. 464), is here designated as lectotype (Fig. 10B). The remaining syntypes, which were collected from Palolo, Kaumuahona, Tantalus, Pacific Heights and Mt. Kaala, are paralectotypes.

Additional material. (4 ♂, 4 ♀, 2 sex unknown). 2♂, 1♀, 2 (sex unknown), Palikea, Waianae Mt., Oahu, 3.ii.1935, Z-XII-1962-22♀, SK721♂ (top specimen), SK722♀ (right middle specimen), BPBM34268; 2♂, 3♀, near Nanakuli Forest Reserve, Oahu, 28.iii.2016 (stored), K. Bustamente leg., host: *Pipturus* sp., Keahi Accession Spring 2016: '20151110 KMB02', CJ529, SK846♂ in BPBM.

Diagnosis. Differs from other *Pipturus* miners by having a large oval white spot in middle and a large white band in the dorsal 3/4 of the forewing (Fig. 10B, C); male genitalia with rather short valva, 400 µm in length, others 500 µm. Female genitalia very similar to that of *P. costalis*, but *P. pipturiella* is distinguished by forewing characters.

Redescription: Adult (Fig. 10B, C, 26I, J). Wingspan 5–6 mm in type series; forewing length 2.3 mm in lectotype, 2.3–2.5 mm in paralectotypes. Head grayish brown; frons white; maxillary palpus reduced; labial palpus white inwardly, externally brown at apical portion of median and terminal joints. Antenna brown. Thorax grayish

brown. Forewing bronze, narrowly white line (**cl**) from costal fold to about 2/3, apicaly curved inward, pointing obliquely outward; a large nearly circular **ws** in middle of wing at about 1/3; an orange patch (**op**) at costal 3/4; two white bands on both extremities of bronze color band (**bb$_3$**) at 3/4, **w$_2$** widening toward the wing margin; a large **op** at apical portion of the wing, with a black **as**; cilia otherwise brown, with two white costal spots (**a, b**). Hindwing brown, cilia paler brown. Abdomen bronze, white beneath. Legs pale brown, white beneath.

Male genitalia (Figs. 44A, B, 45A, 46A) (n=2). Capsule 570 µm. Tegumen 0.9 x length of valva; valva 400 µm long, rather short, tapering along costal margin from basal 1/3 to apex with short spines at basal portion; dorsal margin of valva rounded; along the inner side of valva, a series of small spines arranged (Fig. 44A, B). Saccus very short and tapering toward the point (Fig. 45A). Phallus 380 µm long with two series of minute cornuti in vesica (Fig. 46A).

Female genitalia (Figs. 57C, 64E) (n=2). 870 µm long. Ostium bursae large; antrum cup-shaped with a pair of slender lateral lobes; lamella antevaginalis 180–190 µm, weakly sclerotized, widening toward anterior margin of A7. Ductus bursae 300–350 µm; terminus of ductus bursae biforked; Corpus bursae oblong 520 µm; paired rows of wrinkles running longitudinally, some sclerotized.

Distribution. Oahu (Swezey 1923).

Host plants. Urticaceae: *Pipturus* sp. (Swezey 1923).

Biology. Swezey (1923: 295) reared this species numerous times from mines in *Pipturus* leaves collected at various places in the southeastern Koolau Mountains and Mount Kaala and Makaleha, in the Waianae Range. He stated: "The large leaves of *Pipturus* often contain great numbers of the mines, even up to a hundred, but usually the larvae in most of them die or are parasitized so that but few of them reach their full growth and spin cocoons. The cocoons are made on the under side of the leaf along side a prominent vein, white and not very conspicuous." Swezey (1923) noted that this species can be found anywhere on Oahu, wherever *Pipturus* grows. We found *Philodoria* leaf mines in West Oahu (Fig. 86A).

Parasitoids. Eulophidae: *Euderus metallicus* (Ashmead, 1901), *Neochrysocharis formosus* (Westwood, 1833), *Sympiesis vagans* (Timberlake, 1926) (Zimmerman 1978a).

Philodoria pipturicola Swezey, 1915

Figs. 11A–D, 44C, D, 45B, 46B, 57D, E.

Philodoria pipturicola Swezey, 1915: 96–97; Zimmerman 1978a: 709, figs. 464.

Type locality. Punaluu (Oahu).

Type material. Lectotype ♂, Punaluu, Oahu, 13.ix.1914, O.H. Swezey, ex *Pipturus*, |215 TYPE OF *Philodoria pipturicola* Swezey| right top species on a mount with three others is the lectotype, Type no. 215 in BPBM designated by Zimmerman (1978a). Paralectotype 9 (4♂, 4♀, 1 sex unknown): 1♂, 2♀, same mount of lectotype in BPBM; 1♂, 1♀, same data as locality as lectotype, |*Philodoria pipturicola* Paratypes Swezey| SK715♂ (right specimen), SK716♀ (left specimen), BPBM34257; 2♂, 1♀, 1 (sex unknown), same data and locality as lectotype, |*Philodoria pipturicola* Swezey|, SK717♀ (top right one), SK829♂ (top left specimen), SK830♂ (bottom left specimen) in USNM. This species was described from ten specimens: four specimens on type mount no. 215 and six 'paratypes' reared from mines in the leaves of *Pipturus*. Given the manner in which the descriptions were written, Swezey likely considered these specimens as the holotype and paratypes, as indicated on their specimen labels. Zimmerman (1978a, fig. 464) designated a lectotype selected from the series of four syntypes on the type mount in the BPBM.

Diagnosis. The forewing pattern is similar to *P. pipturiella* Swezey, but distinguished by an oblique white patch at near middle and two small white bands in the forewing (Fig. 11A–D).

Redescription: Adult (Fig. 11A–D). Wingspan 6–7 mm in type series; forewing length 3 mm in lectotype. Head grayish fuscous; frons white; maxillary palpus reduced; labial palpus white, median joint slightly fuscous externally. Antenna dark fuscous. Thorax slate grey fuscous. Forewing fuscous suffused with orange patches at apical portion, with white spots: a **cl** from near base to about 2/3, apical potion bends inward; two white bands (**w$_{1, 2}$**) on both extremities of pale blue color band (**bb$_3$**) at 3/4, widest in the the middle; an oblique **ws** near middle of the wing, narrowly toward dorsum and not reaching dorsal margin; cilia fuscous with two white spots in costal cilia, **a** at the end of **w$_1$**, **b** smaller and a little nearer the apex; a large pale-bluish patch (**as**) in terminal cilia; Hindwing and cilia dark fuscous. Abdomen dark fuscous, white beneath. Legs fuscous, white beneath.

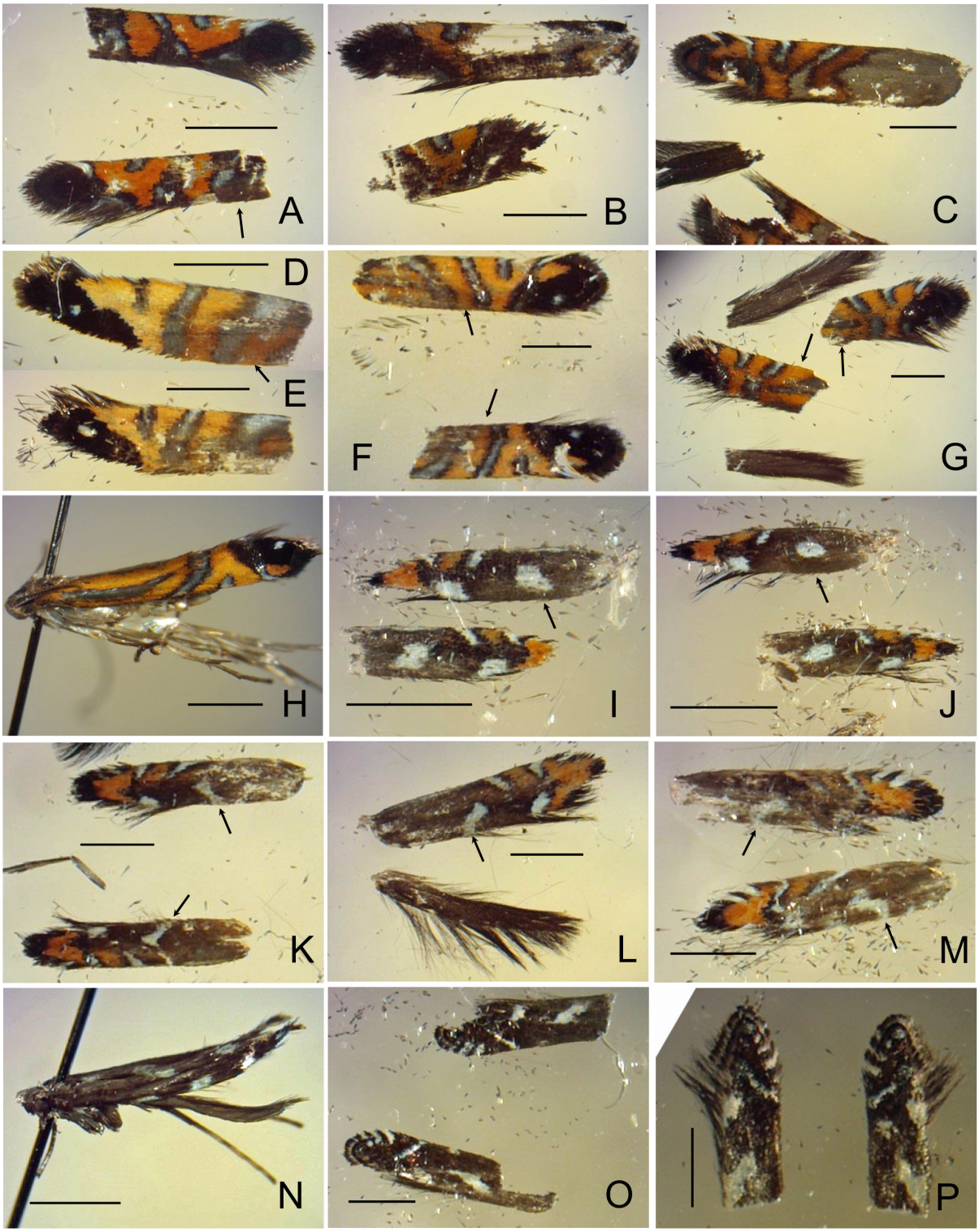

FIGURE 26. Forewing pattern variation in *Philodoria*. Specimens from recent collection efforts that were preserved in ethanol or RNA stabilization reagent, originally for molecular studies. Wings were placed without mountant under a coverslip. **A** *P. succedanea* (sex unknown, CJ419)**, B** *P. auromagnifica*, male (CJ148/SK689), **C** *P. basalis*, female (CJ410), **D** *P. splendida*, female (CJ488a), host: *Syzygium* sp., **E** *P. splendida* (sex unknown, CJ488b), host: *Syzygium* sp., **F** *P. molokaiensis*, male (CJ509b/SK667), **G** *P.* sp. A nr. *P. lysimachiella*, female (CJ346a/SK753), **H** *P. lysimachiella*, female (CJ530), lateral view, **I** *P. pipturiella*, female (CJ529), **J** Same species, male (CJ529), **K** *P. haelaauensis*, female (CJ209), **L** Same species, female (CJ216), **M** *P. floscula*, female (CJ426/SK845), **N** *P. wilkesiella*, male (CJ009/SK649), **O** *P. epibathra*, male (CJ506a/SK678), **P** Same species, female (CJ506b/SK681). Arrows point to diagnostic characters of species: black patch at base (A), basal fascia (D), transverse fasciae (tf) (F, G), white spot (ws) (I, J), white patch (K–M). Scale bar 1 mm.

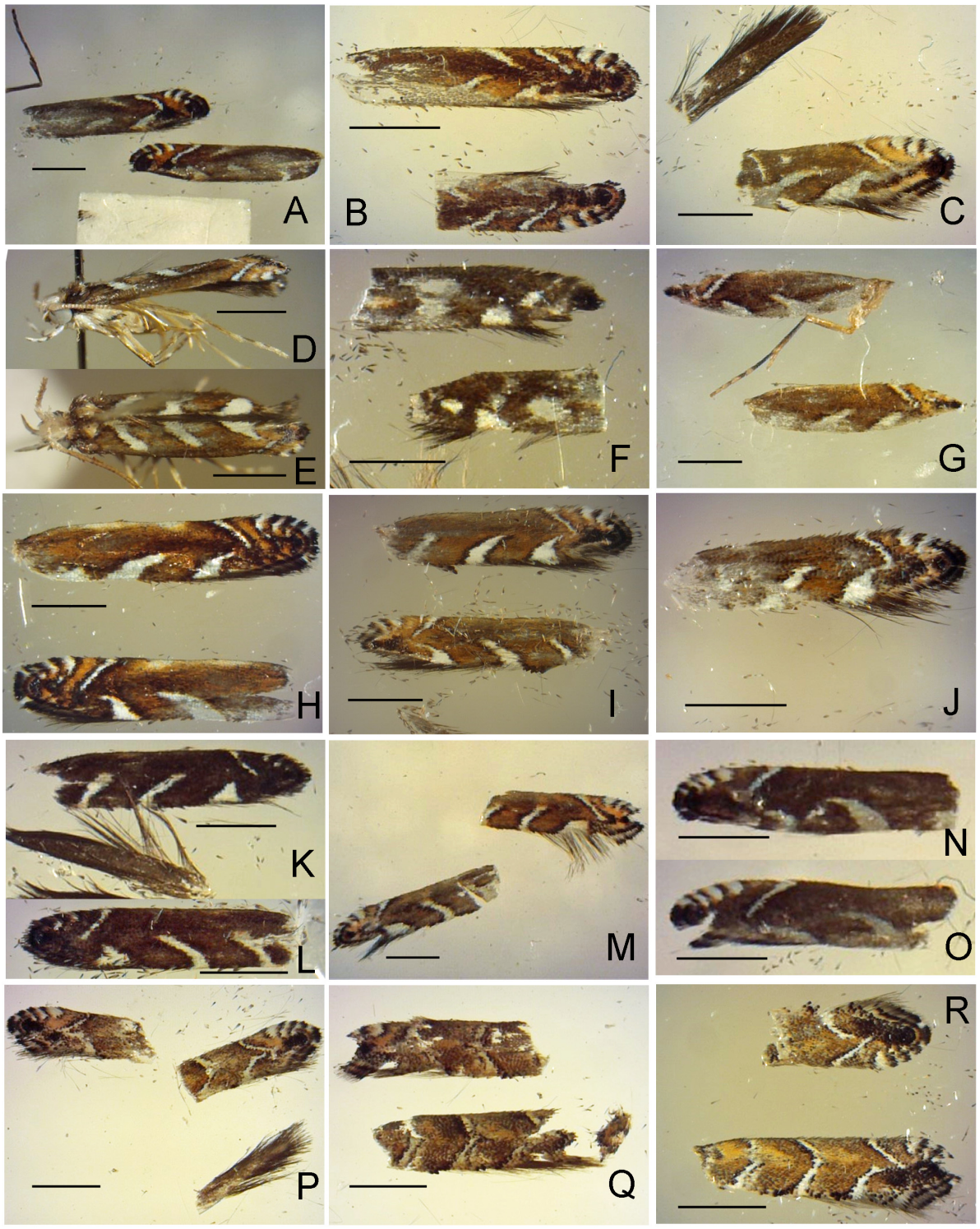

FIGURE 27. Forewing pattern variation in *Philodoria*. Specimens from recent collection efforts that were preserved in ethanol or RNA stabilization reagent, originally for molecular studies. **A** *P. dubauticola*, male (CJ402/SK812), **B** *P. dubautiella*, male CJ524a/SK686), **C** *P. hibiscella*, female (CJ399/SK723), **D** Same species, male (CJ089/SK724), lateral view, **E** Same species, dorsal view, **F** *Philodoria* sp., male, host: *Dubautia plantaginea*, Maui (CJ352c/SK770), **G** *Philodoria* sp., female (CJ500), host: *Dubautia plantaginea*, Oahu, **H** *P. naenaeiella* (CJ188), abdomen missing, **I** *P. neraudicola*, female (CJ336/SK838), host: *Pipturus albidus*, **J** Same species, female (CJ369), host: *Pipturus* sp., **K** *P. obamaorum,* female (CJ423/SK844), **L** Same species, left forewing, **M** Same species, female (CJ403a/SK735), **N** *P. touchardiella*, female (CJ401a/SK764), **O** Same species, male (CJ401b/SK765), **P** *P. marginestrigata*, male (CJ165/SK760), host: *Lipochaeta rockii*, **Q** Same species, male (CJ187/SK771), host: *Abutilon menziesii*, **R** Same species, male (CJ379c), host: *Sida fallax*. Scale bar 1 mm.

FIGURE 28. Labels and pupal exuvia of *Philodoria* type specimens. **A** *P. succedanea* Walsingham, 1907, lectotype female, **B** *P. auromagnifica* Walsingham, 1907, holotype male, **C** *P. basalis* Walsingham, 1907, lectotype male, **D** Paralectotype male, **E** *P. splendida* Walsingham, 1907, lectotype male, **F** *P. lysimachiella* Swezey, 1928 lectotype male, **G** *P. molokaiensis* Swezey, 1928 lectotype male, **H** Same as G, additional label, **I** *P. costalis* Swezey, 1934 lectotype male, **J** *P. pipturiella* Swezey, 1923 lectotype male, two types on the same mount, **K** Pupal exuvia of *P. pipturiella* lectotype, **L** *P. pipturicola* Swezey, 1915 lectotype male, four cotypes on the same mount, **M** *P. floscula* Walsingham, 1907, lectotype female, **N** Paralectotype male, **O** *P. micropetala* Walsingham, 1907 holotype female, **P** *P. pipturiana* Swezey, 1923 holotype male, left lateral view, **Q** *P. wilkesiella* Swezey, 1940 lectotype male, **R** *P. epibathra* (Walsingham, 1907) holotype female, **S** *P. nigrella* (Walsingham, 1907) lectotype male.

FIGURE 29. Labels of *Philodoria* type specimens. **A** *P. nigrella* (Walsingham, 1907), paralectotype male, **B** *P. dubauticola* Swezey, 1940, lectotype female, **C** *P. dubautiella* (Swezey, 1913), lectotype male (two cotypes on the same mount), **D** *P. hibiscella* (Swezey, 1913), lectotype male (two cotypes on the same mount), **E** *P. naenaeiella* (Swezey, 1940) lectotype male (two cotypes on the same mount), **F** *P. neraudicola* (Swezey, 1920), lectotype male, **G** *P. urerana* (Swezey, 1915) lectotype female, two cotypes on the same mount (this one is the upper specimen), **H** *P. hauicola* (Swezey, 1910), lectotype male, **I** *P. pittosporella* (Swezey, 1928), holotype male, **J** *P. touchardiella* (Swezey, 1928), lectotype female, **K** *P. nigrelloides* (Swezey, 1946), holotype female, **L** *P. marginestrigata* (Walsingham, 1907), lectotype, **M** Same species, paratype female, **N** *P. lipochaetaella* (Swezey, 1940), lectotype male (one of four cotypes on the same mount, this one is the upper left specimen on mount), **O** *Parectopa lipochaetae* Swezey, 1946 (= synonym of *P. lipochaetaella*), syntype male, **P** *P. sciallactis* (Meyrick, 1928), lectotype male.

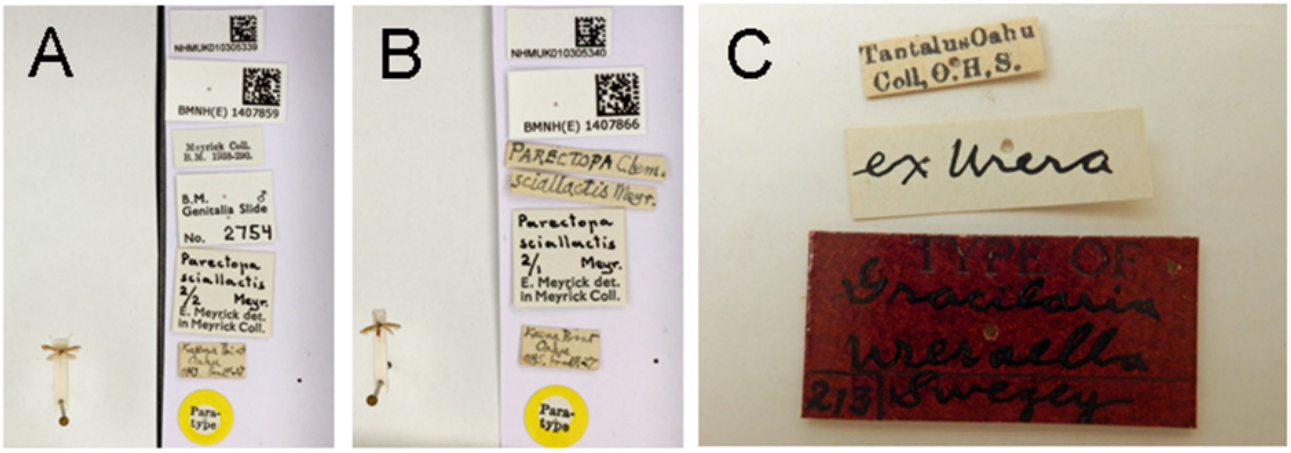

FIGURE 30. Labels of *Philodoria* type specimens. **A** *P. sciallactis* (Meyrick, 1928), paralectotype male, **B** Same species, paralectotype female, **C** *P. ureraella* (Swezey, 1915), paralectotype (sex unknown), one of four cotypes on the same mount (these are the labels of the upper left specimen on mount).

Male genitalia (Figs. 44C, D, 45B, 46B) (n=3). Capsule 700 µm. Tegumen 0.8–0.9 x length of valva; valva 510–530 µm long, slender and tapering toward the apex; dorsal margin of valva slightly angled with short spines; a series of small spines arranged along the inner margin of valva (Fig. 44C, D). Phallus 500 µm long, straight in lateral view with two series of minute cornuti in vesica (Fig. 46B).

Female genitalia (Fig. 57D, E) (n=2). 1050 µm long. Ostium bursae large; antrum cup-shaped with a slender pair of lateral lobes; lamella antevaginalis 160 µm, weakly sclerotized, widening toward anterior margin of A7. Ductus bursae 270–300 µm; terminus of ductus bursae biforked; corpus bursae oblong, 640 µm; paired rows of wrinkles running longitudinally, some sclerotized, indistinct at middle.

Distribution. Oahu (Swezey 1915).

Host plants. Urticaceae: *Pipturus* sp. (Swezey 1915).

Biology. Swezey (1915: 97) reported the mine form as "at first serpentine, later a blotch. The larva emerges to spin a light brownish cocoon on some convenient surface." Immature stages reported by Swezey (1915: 96): "*Mature larva*. 7 mm. Pale yellowish in colouration; head with a dark brown or blackish spot in each lobe; deeply bilobed and mostly retracted into segment 2, which is wider than the rest, other segments gradually tapering backwards; distinct constrictions between segments; cervical shield somewhat roughened, two pale brownish longitudinal streaks; thoracic legs feeble; abdominal prolegs on segments 7-9. *Pupa*. 3 mm. very pale brownish, abdomen yellowish in colouration; wing-sheaths pointed, extending to 5th abdominal segment; posterior leg-sheaths extend to apex of abdomen; antenna-sheaths extend beyond apex of abdomen and curve over dorsally and forward about two segments."

Parasitoids. Eulophidae: *Euderus metallicus* (Ashmead, 1901), *Pnigalio externa* (Timberlake, 1927) (Zimmerman1978a).

Remarks. Maui records were misidentified, see description of *P. haelaauensis*. Johns *et al*. (2016) recorded this species from Palikea, Oahu (Coll ID CJ-101 / GenBank accession no. ID KT982409). CJ101 was sacrificed entirely for molecular analysis and CJ093 which is in the same series as CJ101, only has its genitalia and abdomen remaining. Female genitalia of CJ093 / PHIL0020 lacks signa on its corpus bursae and is similar to that of *P. costalis*, *P. pipturiella*, *P. pipturicola*. Because we do not have sufficient data, we here do not assign a formal new name to this species.

***Philodoria haelaauensis* Kobayashi, Johns & Kawahara, sp. n.**

Figs. 11E, F, 26K, L, 39C, 44E–H, 45C, D, 46C, D, 57F, 63H, 64A–D, 74, 84.

Philodoria pipturicola Swezey, 1915; Zimmerman 1978a: 709, figs. 471, 476, 479 (Misidentification).
Philodoria sp. 10; Johns *et al*. 2018: fig. 2.

Type locality. Haelaau (Maui).

Etymology. The specific epithet is derived from the type locality, Haela`au (pronounced 'Haye-La-ahoo').

Type material. (6♂, 1♀, 7 sex unknown). Holotype ♂, Haelaau, Maui Is., 18.xii.1928, O.H. Swezey Collector, *Pipturus*, SK718, BPBM34265. Paratype 19 (6♂, 1♀, 12 sex unknown): 1♂, 7 sex unknown, same data and locality as holotype, BPBM34260, 34261, |*Philodoria pipturicola* Det. By O.H. Swezey| BPBM34262, BPBM34263, BPBM34264, |1♂ Same date ex to Tribert, 1993|BPBM34265, BPBM34266, BPBM34267. 1♂, 1♀, 2 sex unknown,Wailuku, 2000ft, Maui, 9.xii.1922, O.H. Swezey, *Pipturus*, Z-XII-19-62-23♂, Z-XII-19-62-24♀, BPBM34253; 4♂, 5 sex unknown (missing abdomen), Same data and locality, '♂ + ♀ genitalia on slide 99, aB Oct 15 1940', SK822♂(middle), SK827♂(top middle), SK828♂(top right), BPBM34254.

Additional material. 14 (5 ♂, 6 ♀, 3 sex unknown). **Molokai**: 1♀, Kamiloloa, 19.xii.1925, 3200ft, O.H. Swezey Collector, *Pipturus*, |*Philodoria floscula* Det by O.H. Swezey|, SK705♀, BPBM34170; 1♂, Kaibalu, 2000–3000ft, 28.vii.1928, O.H. Swezey Collector, on *Pipturus*, |*Philodoria floscula* Det by O.H. Swezey|, SK704♂, BPBM34171; 1♂, 1♀, 3 sex unknown, Kamiloloa, Mol., 19.xii.1925, 3200ft, O.H. Swezey Collector, *Pipturus*, BPBM 34172–34176.

Maui: 1♂2♀, Makawao Forest Reserve, 11&15.i.2014 (stored), W. Haines leg., host: *Pipturus rockii*, 28.xii.2013, CJ209 / PHIL0016♀, CJ216 / SK821♀, CJ227 / PHIL0019♂ (Fig. 74) in BPBM. 2♂, 2♀, Honokohau, 9.viii.2014 (stored), K. Bustamente leg., host: *Pipturus albidus*, Summer. 2014., CJ348b / SK789♂, CJ348c / SK790♂, CJ348d / SK791♀, CJ348e / SK792♀ in BPBM.

Diagnosis. The forewing pattern is similar to *P. pipturicola* Swezey but distinguished by an oblique white patch in the middle of the forewing, that reaches the dorsal margin (Fig. 11E, F); male valva same width at apical half; female with spiny pyriform signa and lacking sclerotized structure at the joint of the ductus bursae and corpus bursae. The new species and *P. alakaiensis* both have two pairs of coremata in the male 8th segment (Fig. 39C, D). Swezey (1923) misidentified specimens of *P. haelaauensis* from Wailuku, Maui as *P. pipturicola* and Zimmerman (1978a: figs. 471, 476, 479) described in error that the genitalia of *P. haelaauensis* as those of *P. pipturicola*.

Description: Adult (Figs. 11E, F, 26K, L). Wingspan 7.1 mm in holotype, 6.3–7.2 mm in paratypes; forewing length 3.3, 3.4 mm in holotype, 2.8–3.4 mm in paratypes. Head slate grey fuscous; frons white; maxillary palpus reduced; labial palpus white, median joint slightly fuscous externally. Antenna dark fuscous. Thorax slate grey fuscous. Forewing fuscous suffused with orange patches at apical portion: an obscure **cl** from near base to about 2/3, apical potion bends inward; two white bands ($\mathbf{w_{1, 2}}$) on both extremities of pale blue color band ($\mathbf{bb_3}$) at 3/4, widest in the the middle; a large oblique **ws** near middle of wing, reaching dorsal margin; a large pale-bluish patch (**as**) at apex; cilia fuscous with two white spots (**a, b**) in costal cilia; Hindwing and cilia dark fuscous. Abdomen dark fuscous, white beneath. Legs fuscous, white beneath.

Male genitalia (Figs. 44E–H, 45C, D, 46C, D, 64A, B) (n=5). Capsule about 750–800 µm. Tegumen 0.8–0.9 x length of valva; valva 530, 550 µm long, similar to *pipturicola* except apical half of valva not tapering at apex, almost same width in lateral view (Fig. 44E–H). Saccus triangular (Fig. 45C). Phallus 310 µm, straight in lateral view with two series of minute cornuti in vesica (Fig. 46C, D).

Female genitalia (Figs. 57F, 63H) (n=3). 1250–1300 µm long. Ostium bursae large; antrum wide with a slender pair of lateral lobes; lamella antevaginalis 220–230 µm, weakly sclerotized, widening toward anterior margin of A7. Ductus bursae 600–650 µm, posterior extremity widening and membranous, and median section narrowing weakly sclerotized and flattened; terminus of ductus bursae membranous. Corpus bursae pyriform, 540–550 µm; signum a conical plate with minutely spined surface.

Distribution. Maui (Swezey 1923a) and Molokai: new record.

Host plants. Urticaceae: *Pipturus* sp. (Swezey 1923a), *P. albidus* A.Gray ex H.Mann and *P. rockii* Skottsb.: new record.

Biology. (Fig. 84). Larvae form a tortuous linear to blotch mine (Fig. 84A–D) that expands as they feed and grow (Fig. 84E, G); the frass line is black. 1–5 mines per leaf. Pupation occurs in the cocoon outside of the mine, on the abaxial leaf surface; cocoon orangish brown (Fig. 84F).

Philodoria spilota (Walsingham, 1907)

Elachista spilota Walsingham, 1907: 513–514, pl. 15, fig. 18.
Philodoria spilota (Walsingham, 1907); Zimmerman 1978a: 718, figs. 434, 467, 480.

Type locality. Haleakala (Maui).

Type material. Holotype ♀ (=Type ♂ (28405) Mus. Wlsm.), Haleakala, 5000ft, Maui, v.1896, slide 2030 in NHMUK (specimen missing), described based on a single specimen from Maui. The type specimen, designated by Walsingham, but not formally stated as the holotype in the original descirption is here formally designated as the holotype following article 73.1.2 (ICZN 1999). Walsingham (1907) noted that the type was 'injured when being figured'.

Diagnosis. Very similar to *P. haelaauensis* **sp. n.**, but is distinguished by its dark brown forewing, white spot (**ws**) in the middle, not extending to the dorsal margin and lacking an orange patches at the wing apex. A white basal streak from forewing base to the costal fold was illustrated in original figure (Walsingham 1907: pl. 15, fig. 18) but not mentioned in the original description. Zimmerman (1978a: 702, 718, fig. 467) noted that "The unique holotype is a faded, damaged female and not a male as Walsingham stated in his original description. This [holotype] hardly resembles the Walsingham 1907, pl. 15, fig.18. The photograph does not reveal the basal white streak on the fold that is shown on the Walsingham figure." The holotype photograph showing the forewing base appears to lack brownish fuscous scales and basal white forewing color. Zimmerman also reported that the holotype has badly broken hindwings, a damaged body and is missing the left antenna. The holotype was not found where it should have been stored at the NHMUK (D.C. Lees, pers. comm.).

Description: Adult (Walsingham 1907: pl. 15, fig. 18; Zimmerman 1978a: 718, figs. 434, 467). Wingspan 7 mm; forewing length 3 mm. The following is from Walsingham (1907: 513–514): "Head brownish fuscous; maxillary palpus reduced; labial palpus white, the terminal joint speckled with fuscous beneath, the outer end of the median joint fuscous. Antenna pale brownish fuscous. Thorax brownish fuscous. Forewings bronze fuscous, with silvery white spots; one square, resting on the middle of the fold, another, also square, on the dorsum at the end of the fold; between these a short outwardly oblique costal streak, a small costal spot between this and the apex and a larger spot at the apex; cilia brownish fuscous. Hindwing and cilia brownish fuscous. Abdomen fuscous. Legs pale cinereous."

Male genitalia Unknown.

Female genitalia See Zimmerman (1978a: fig. 480). Similar to *P. haelaauensis*. Ostium bursae large; antrum wide with a pair of slender lateral lobes; lamella antevaginalis weakly sclerotized, widening toward anterior margin of A7. Ductus bursae slender, posterior extremity slightly widening and membranous, and middle section narrowing weakly sclerotized and flattened; terminus of ductus bursae membranous. Corpus bursae pyriform; signum a conical plate with minutely spined surface.

Distribution. Maui (Walsingham 1907).

Host plants and **Biology.** Unknown.

Philodoria floscula Walsingham, 1907

Figs. 10D, E, 26M, 44I, J, 45E, F, 46E, 57G.

Philodoria floscula Walsingham, 1907: 718–719, pl. 25, fig. 21; Zimmerman 1978a: 708, figs. 462, 477.

Type locality. Hilo (Big Island).

Type material. Lectotype ♀ [=Type "♂ (28597) Mus. Wlsm." in original description], Hilo, 2000ft, xii.1895, Perkins.28597, |PHILODORIA FLOSCULA, Wlsm Fn Hawaii I descry. fig^{d}| Walsingham Collection. 1910–427 .|NHMUK010305334|TYPE|TYPE ♂ BM ♀ Genitalia slide no. 3950| in NHMUK. **Paralectotype** ♂, Olaa, Hawaii, ix. 1896, Perkins.28063, |*Philodoria floscula* Wlsm PARATYPE 1/1| Walsingham Collection. 1910 427.|NHMUK010305335| PARATYPE| in NHMUK. Described from two specimens: 'Type ♂ (28597)' and one 'paratype'. Given the manner in which the descriptions were written, Walsingham likely considered these specimens as the holotype and paratype, as indicated on their specimen labels. But because as a holotype was not formally specified in the text of his study, the so-labeled type and paratype are all to be considered syntypes under Article 73.2 of the Code (ICZN 1999), and any one is thus eligible for designation as lectotype under Article 74 of the Code (ICZN 1999). The syntype 'Type ♂ [= ♀] (28597)', which Walsingham listed first and figured, is here designated as lectotype (Fig. 10D). The other syntype is the paralectotype.

Additional material. 2♂, 3♀, 1 (sex unknown), Upper Hamakua Ditch trail, Hawaii (Big Island), 29.x.&4.

xi.2014 (stored), C.A. Johns leg., host: *Pipturus albidus*, CJ394 / SK818♂, SK819♀, CJ395 / PHIL0001♂, 0002♂, 0003♀, SK734♀ in BPBM; 1♀, Same locality, 15.v.2016 em., C.L.-Vaamonde & C. Doorenweerd leg., host: *Pipturus* sp., 24.iv.2016 (cocoon), CLV0017, SK824♀ in BPBM. 1♀, Puu Makaala Natural Area Reserve, Hawaii (Big Island), 9.vi.2015 (stored), C.A. Johns leg., host: *Pipturus* sp., 25.v.2015, CJ426 in BPBM.

Philodoria* sp. near *P. floscula: 1♀, Hawaii (Big Island), Volcanoes National Park, Napau Crater area, 8.vi.1976, K. & E. Sattler, B.M. 1976-605BMNH(E)1621114, *Philodoria* sp. 6 (Hawaii), D. C. Lees Sep. 2016 in NHMUK.

Diagnosis. The forewing pattern is very similar to that of *P. haelaauensis* **sp. n.** and *P. micropetala* Walsingham but distinguished by its rather narrow two costal white bands (**cs** and $\mathbf{w_1}$) in the forewing (Figs. 10D, E, 26M); the female genitalia has a pair of sinuous line-shaped signa with series of minute spines (Fig. 56E). We treat the record from Molokai (Swezey & Bryan, 1929: 301) as incorrect, as the Molokai specimens of '*P. floscula*' identified by Swezey are *P. haelaauensis* **sp. n.** based on our examination of genitalia.

Redescription: Adult (Figs. 10D, E, 26M). Wingspan 8 mm in type series. Head brownish gray above; frons white; maxillary palpus reduced; labial palpus white, a dark spot at the end of the median joint, the terminal joint also shaded with fuscous. Antenna brownish. Thorax bronze. Forewing bronze, with four rather outwardly oblique, silver-white marginal band; dorsal **ws** before the middle crossing the fold; one **cs** about the middle; two white bands ($\mathbf{w_{1, 2}}$) on both extremities of shining, pale green $\mathbf{bb_3}$ at 3/4, beyond which the apical portion bright orange with a black **as** before the shiny, green cilia; tornal cilia tawny gray. Hindwing tawny brown; cilia tawny. Abdomen fuscous above, white beneath. Legs brown.

Male genitalia (Figs. 44I, J, 45E, 46E, F) (new record) (n=3). Capsule 740 µm. Tegumen 0.8 x length of valva; valva 410–570 µm long, similar to *P. pipturicola* and *P. haelaauensis*, except dorsal margin of basal portion rounded (Fig. 44I, J). Saccus rather slender and needle-shaped (Fig. 45E, F). Phallus 410–420 µm long, slightly curved toward dorsal side with two series of minute cornuti in vesica (Fig. 46E).

Female genitalia (Fig. 57G) (n=4). 1200 µm long. Ostium bursae large; antrum wide with a slender pair of lateral lobes; lamella antevaginalis 220–230 µm, weakly sclerotized, widening toward anterior margin of A7. Ductus bursae 450–500 µm and median section narrowing weakly sclerotized and flattened; terminus of ductus bursae broad and weakly sclerotized. Corpus bursae oblong 660–670 µm; paired signa as sinuous lines each with a series of minute spines.

Distribution. Maui (Zimmerman 1978a: 708) and Hawaii (Big Island) (Walsingham 1907).

Host plants. Urticaceae: *Pipturus* sp. (Swezey, 1923), *Pipturus albidus* A.Gray ex H.Mann: new record.

Biology. Unknown. See also biology of *P. obamaorum* **sp. n.**

Remarks. We observed several *Pipturus* miners, namely *P. floscula*, *P. obamaorum,* and nr. *P. haelaauensis* occurring together at Puu Makaala Natural Area Reserve, Hawaii (Big Island) (Fig. 70).

Philodoria micropetala Walsingham, 1907

Fig. 10F

Philodoria micropetala Walsingham, 1907: 719, pl. 25, fig. 22; Zimmerman 1978a: 709, figs. 463, 476.

Type locality. Halemanu (Kauai).

Type material. Holotype ♀, Halemanu, 4000ft, Kauai, v.1895., Perkins 27560, |PHILODORIA MICROPETALA, Wlsm Fn Hawaii I descry. fig[d]| Walsingham Collection. 1910–427.| NHMUK010305336|TYPE|BM ♀ Genitalia slide no. 3951| in NHMUK. Described based on a single specimen from Kauai. The 'type' specimen, designated by Walsingham is here thus the holotype following article 73.1.2 (ICZN 1999).

Diagnosis. The forewing pattern is similar to that of *P. floscula*, but distinguished by an erect dorsal **ws** in the forewing (Fig. 10F). The female genitalia were incompletely described by Zimmerman (1978a: fig. 476) who mentioned only the ostium and apophyses.

Description: Adult (Fig. 10F). The following is from Walsingham (1907: 719): "Antennae brownish. Palpi white, a dark spot at the end of the median joint, the terminal joint also shaded with fuscous. Head and Thorax bronze. Forewings bronze, with four white spots; the first on the outer half of the fold, not touching the dorsum; the second on the costa beyond the middle, pointing obliquely outward and dark-margined externally; the other two situated as in *floscula,* but dark-margined on their inner sides, the metallic spot between them being bright steel-

blue; beyond this an orange spot, with three white streaks in the costal cilia above it, alternate with brownish, a few fuscous scales scattered across the middle of this patch terminate in a blackish spot at its outer edge, followed by shining, steel-blue, which extends through the ternlinal and apical cilia. Exp. al. 8 mm. Hindwings tawny brown; cilia tawny. Abdomen fuscous above, whitish beneath. Legs brownish, spurs and a few tarsal spots whitish."

Male genitalia Unknown.

Female genitalia See Zimmerman (1978a: fig. 476). Ostium bursae large; antrum wide with a slender pair of lateral lobes; lamella antevaginalis weakly sclerotized, widening toward anterior margin of A7. Ductus bursae and corpus bursae not figured.

Distribution. Kauai (Walsingham 1907).

Host plants. Urticaceae: *Pipturus* sp. (Zimmerman 1978a).

Biology. Unknown.

Parasitods. Eulophidae: *Euderus metallicus* (Ashmead, 1901), *Neochrysocharis formosus* (Westwood, 1833) (Zimmerman 1978a).

Remarks. Zimmerman (1978a) noted that the records from outside Kauai, i.e. from the islands of Hawaii (Big Island), Maui, Molokai, and Oahu mentioned by Swezey (1913b: 222) were likely in error and attributable to other *Pipturus* miners; *P. micropetala* appears to be restricted to Kauai. We accept Zimmerman's suggestion in recognizing that only the specimens from Kauai are attributable to this species.

Philodoria pipturiana Swezey, 1923

Fig. 12A–C.

Philodoria pipturiana Swezey, 1923: 295; Zimmerman 1978a: 709, figs. 465, 466.

Type locality. Upper Hamakua Ditch Trail, Kohala Mts. (Big Island).

Type material. Lectotype ♂, Upper Hamakua Ditch Trail, [Kohala Mountains, Hawaii (Big Island)], 31.vii.1921, Swezey Coll., *Pipturus*, |*Philodoria pipturiana* Swezey |Holotype |♂ genitalia on slide Z-I-10-67-A |Type no. 4272 in BPBM. Described from two specimens: the holotype was originally in the collection of the Hawaiian Entomological Society and the paratype in the collection of the Hawaiian Sugar Planter's Association. The 'holotype' is now preserved in BPBM. Given the manner in which the description was written, Swezey considered these specimens as holotype and paratype, as indicated on their specimen labels. But because the holotype was not formally specified in the description, the so-labeled holotype and paratype are to be considered syntypes under Article 73.2 of the Code (ICZN 1999), and either is eligible for designation as lectotype under Article 74 of the Code (ICZN 1999). The 'Holotype, type no. 4272', which Swezey indicated as holotype in the specimen label, is here designated as lectotype (Fig. 12A–C). The other syntype is the paralectotype, but we could not locate that specimen.

Diagnosis. The forewing pattern is similar to *P. wilkesiella* Swezey, but is distinguished by its longitudinal basal streak and oval white spot in the middle in the forewing (Fig. 12A–C). The male genitalia are similar to those of the Asteraceae-feeding *Philodoria* species (e.g., *P. wilkesiella* and *P. hesperomaniniella* **sp. n.)** in having a broad dorsal margin of valva, but *P. pipturiana* differs from later two species by its slender saccus.

Redescription: Adult (Fig. 12A–C). Wingspan of specimens in the type series 8–9 mm; forewing length 4 mm in lectotype. Head dirty white; frons white; maxillary palpus reduced; labial palpus white, streaked with fuscous externally. Antenna pale fuscous, apical portion white. Thorax dark fuscous, white below. Forewing dark fuscous to nearly black, with several white patches: one outwardly oblique white costal spot at about 1/2, another at 2/3, recurves to the costa, terminating in a few white scales in the costal cilia; a curved transverse white streak at apical portion of wing, nearly interrupted in the middle, with a few white scales in the costal cilia (not present in the paratype); a longitudinal white streak from base to 1/3, followed by a large oval white spot about the middle of wing; a large oval white spot on dorsal 3/4; cilia fuscous except for the white scales previously noted in costal cilia and a few white scales at base of apical cilia. Hindwing and cilia dark fuscous. Abdomen fuscous. Legs pale fuscous, tarsi white spotted.

Male genitalia (Zimmerman 1978a: fig. 465). Tegumen oblong, 0.8 x length of valva; valva tapering along costal margin from base 2/5 to apex; dorsal margin of valva broad. Saccus slender. Phallus straight in lateral view with spiny cornuti in vesica.

Female genitalia Unknown.

Distribution. Hawaii (Big Island) (Swezey 1923).

Host plants and **Biology.** Unknown.

Remarks. Swezey (1923) described this species from two specimens collected on a *Pipturus* plant which had leaves containing leaf-miners, but according to Zimmerman (1978a) these specimens were not reared. Therefore, we have removed this plant genus as a possible host. Much of the type locality habitat has been destroyed due to non-native plant species, and few host plants remained in sections of the Upper Hamakua Ditch Trail that we surveyed.

Philodoria wilkesiella Swezey, 1940

Figs. 12D, 26N, 47A, 48A, 49A, 58A, 88A.

Philodoria wilkesiella Swezey, 1940: 464–465; Zimmerman 1978a: 718, figs. 467, 473, 480.

Type locality. Puu Kukui (Maui).

Type material. Lectotype ♂, Puu Kukui, Maui, 20.xii.1928, O.H. Swezey Collector, *Wilkesia grayana* (=*Argyroxiphium grayanum*), |Holotype *Philodoria wilkesiella* Sweszey|, Type no. 4274 in BPBM. Paralectotype missing. Described from nine specimens reared from mines in leaves of "*Wilkesia grayana*", Puu Kukui, Maui, December 20, 1928. Given the manner in which the description was written, Swezey considered these specimens as holotype and paratypes, as indicated on their specimen label. However, because a holotype was not formally specified in the description, the so-labeled holotype is to be considered syntype under Article 73.2 of the Code(ICZN 1999), and either is eligible for designation as the lectotype under Article 74 of the Code (ICZN 1999). We formally designate the specimen bearing the label 'Holotype' as the lectotype (Fig. 12D) and the remaining syntypes are paralectotypes. Zimmerman (1978a) illustrated the genital character with photographs: paratype male, slide no. Z-XII-19-62-18 8, fig. 473; paratype female, Z-XII-19-62-19, ostial plate (corpus bursae missing), fig. 480. We were unable to find the paratype specimens and genital slides in BPBM.

Additional material. 5 (3♂, 2♀) All specimens preserved in BPBM. 3♂, 2♀, Haelaau, Maui, 10.iv.2013 (stored), C.A. Johns leg., adult on *Argyroxiphium grayanum*, CJ007 / SK647♂, CJ009 / SK648♂, CJ010 / SK649, CJ012 / SK650, CJ013 / PHIL0007♂.

Diagnosis. Brownish fuscous ground color with a number of white spots on the forewing (Fig. 12D). *Philodoria pipturiana* Swezey is similar in color pattern of its forewing, but distinguished from *P. wilkesiella* by its dark fuscous ground color and a white longitudinal basal streak (Fig. 12A–C). Genital characters of *P. wilkesiella* resemble Asteraceae-feeding *Philodoria* species, e.g., *P. epibathra* Walsingham and *P. naenaeiella* (Swezey). However, it differs in having a valva with a broad apical half and a shorter male saccus. The female has a semicircular shaped lamella antevaginalis and shorter ductus bursae.

Redescription: Adult (Fig. 12D, 26N). Wingspan 7 mm in type series; forewing length 3.25 mm in lectotype. Head white; frons white with some brownish scales; maxillary palpus reduced; labial palpus white with a few brownish scales externally. Antenna grayish fuscous, 1.2–1.3x length of forewing. Thorax white with brownish scales at the sides, white beneath. Forewing brownish fuscous with a number of white spots: three dorsal ones, the smaller one near base, two outwardly oblique larger spots at 1/3 and 3/5; a narrow elongate spot at about middle of the costa, two or three white costal spots towards apex, a small transverse white spot at apex and sometimes two or three small spots preceding this in apical area of wing. Cilia gray, dark at base, with a few white scales in vicinity of white spots. Hindwing uniform gray. Abdomen gray. Legs gray, with tarsi banded with white.

Male genitalia (Figs. 47A, 48A, 49A) (n=3). Capsule 620 µm. Tegumen 0.7 x length of valva; valva tapering along costal margin from base 2/5 to apex; along the inner side of valva, a series of small spines arranged; apical half of valva straight in lateral view (Fig. 47A). Saccus short, stick-shaped (Fig. 48A). Phallus 570 µm long, slender with developed coecum (Fig. 49A).

Female genitalia (Fig. 58A) (n=3). 890–900 µm long. Ostium bursae large; antrum cup-shaped with wavy pair of lateral lobes; lamella antevaginalis 160–170 µm, weakly sclerotized, semicircular in ventral view, widening toward anterior margin of A7. Ductus bursae thick, 270–300 µm. Corpus bursae small 560 µm; paired rows of wrinkles, some sclerotized.

Distribution. Maui (Swezey 1940).

Host plants. Asteraceae: *Argyroxiphium grayanum* (Hillebr.) O.Deg. (Swezey 1940). The host plant is located on the windy and rainy bogs of the summit of West Maui.

Biology. (Fig. 88A). Similar to *Dubautia* miners, in that its first and second instar larvae mine along the length of the leaf, following leaf veins. Pupation occurs in the cocoon inside of the mine terminus, usually with one or both extremities of the white cocoon exposed (Fig. 88A). Three mines per leaf. Adults were observed on the host plant surface during sunny and less windy periods, and then they retreated to the substrate beneath the plant once these conditions subsided.

Remarks. Zimmerman (1978a: 718) mentioned that "one of the few moths known to attack the extraordinary endemic composite *Argroxiphium*". We surveyed other members of *Argyroxiphium* with glabrous leaves, investigated type locality of this moth, and a population of *A. grayanum* on east Maui, but leaf mines were not found. We also checked some herbarium plant specimens of this east Maui population, and specimens of the extinct species, *A. virescens*. No leaf mines were found on these herbarium specimens.

Philodoria epibathra (Walsingham, 1907)

Figs. 13A–C, 26O, P, 47B, 48B, 49B, 58B.

Gracilaria epibathra Walsingham, 1907: 722, fig. 27.
Parectopa epibathra (Walsingham, 1907); Swezey 1928: 190; Zimmerman 1978a: 679–680, fig. 459.
Parectopa epibathra (Walsingham, 1907) (=*Philodoria naenaeiella*); Swezey 1928: 190 (Misidentification).

Type locality. Molokai.

Type material. Holotype ♀ (= 'Type ♂ (26056)'), Molokai, '000ft.'[elevation blank], Hawaiian Is., 12.vi.1893, Perkins 26056, | B.M. Genitalia slide no. 2884| GRACILARIA EPIBATHRA, Wlsm. Fm. Hawaii I TYPE ♂ descr. fig[d].| Walsingham Collection, 1910—427.| BMNH(E) 1407695| NHMUK010305333| with capsulated left forewing in in NHMUK. Described based on a single specimen from Oahu. The 'type' specimen, labeled on the specimen by Walsingham is here formally designated as the holotype following article 73.1.2 (ICZN 1999).

Additional material. Molokai: 2♂, 2♀, Olokui, 26.vii.2015 (stored), KB Collection, host: *Dubautia laxa*, 28.i.2015, KMB19, CJ506a–CJ506d, SK678–681. 1♀, Waiehu, 21.vii.2015 (stored), C.A. Johns leg., host: *Dubautia* sp., 7.vii.2015, CJ492, SK837♀. All specimens preserved in BPBM.

Diagnosis. Similar to *P. nigrella* (Walsingham) and *P. touchardiella* (Swezey) in that forewing has $\mathbf{cs}_3$ and $\mathbf{ds}_{1–3}$, but differs from them by the wide $\mathbf{ds}_2$ and rather long ductus bursae and lack of spines on signa in the female (Figs. 13B, C, 58B). Male genitalia of this species differs from other congeneric species in having a very long saccus. We collected four adult moths reared from *Dubautia*; these adults have similar forewing pattern and female genitalia as the holotype except for the indistinct or lack of white $\mathbf{ds}_1$ at basal 1/3 (Figs. 13B, C, 26O, P).

Description: The following is from Walsingham (1907: 722): "Antennae brownish. Palpi white, a small spot on the outer side of the median joint at its apex. Head shining, dirty whtish, a few brownish scales posteriorly. Thorax olive-brow. Forewings olive-brown with three outwardly oblique broad pearly white dorsal streaks; the first near the base, somewhat rounded at its apex; the second at the middle, attenuate; the third near the tornus, quadrate; above the latter is an outwardly oblique slender white costal streak, followed by two smaller wllite streaks in the costal cilia before the apex; at the end of the oblique costal streak is a small patch of shining, blue scales, narrowly surrounded by pale ocherous; with a black spot at the apex, followed by shining blue at the base of the cilia; through these runs a curved metallic blue line, the space between which and an outer curved brownish line being whitish, tornal cilia smoky brownish. Exp. al. 7 mm. Hindwings brownish, with slightly paler cilia. Abdomen dark brown. Legs brownish, with whitish tarsal spots."

Male genitalia (Figs. 47B, 48B, 49B) (n=2). (new record). Capsule 910 µm. Tegumen 0.8 x length of valva; valva tapering along costal margin from base 2/5 to apex; basal portion humped along dorsal margin in lateral view (Fig. 47B). Saccus 230 µm, very long and wavy, slightly curved toward dorsal side (Fig. 48B). Phallus 690 µm long, straight in lateral view Fig. 49B).

Female genitalia. (Fig. 58B) (n=4). (Zimmerman 1978a: fig. 459). 1240 µm long. Ostium bursae large; antrum low-cup-shaped with a slender pair of lateral lobes; lamella antevaginalis 100–110 µm, weakly sclerotized, semicircular in ventral view, widening toward anterior margin of A7. Ductus bursae thick, posterior extremity widening

and membranous; terminus of ductus bursae biforked. Corpus bursae 540–550 μm, pyriform; paired rows consisting of wrinkles running longitudinally, some sclerotized.

Distribution. Molokai (Walsingham 1907).

Host plants. Asteraceae: *Dubautia laxa* Hook. & Arn.: new record and *Dubautia* sp.

Biology. Larvae mine leaves of *Dubautia* species, according to collecting data labels of adult specimens.

Remarks. "*P. epibathra*" had been frequently assigned to several *Dubautia*-feeding *Philodoria* species by Swezey. The Kauai record (Swezey 1928:190) is erroroneous (Swezey 1940; Zimmerman 1978a) and applies to *Philodoria knudseniiella* **sp. n.** The host plant records of *Dubautia* sp. (Swezey, 1910a: 89, footnote), *Dubautia laxa*, *Hesperomannia arborescens* (Swezey 1928: 190) are also in error and apply to host plants of *Philodoria naenaeiella* (Swezey, 1940: 463) and *P. hesperomanniella* **sp. n.** respectively. Some leaf mines were collected on *Dubautia* at Kamakou Boardwalk, Molokai. Some mines begin as spiral-shaped (Fig. 88L), but no adults were successfully reared from this plant.

Philodoria nigrella Walsingham, 1907

Figs. 13D, E.

Philodoria nigrella Walsingham, 1907: 721, pl. 25, fig. 25); Zimmerman 1978a: 690, figs. 444, 451.

Type locality. Mt. Kilauea, Hilo (Big Island).

Type material. Lectotype ♂, Mt. Kilauea, 2000ft, Hilo, Hawaii (Big Island), xii.1895, Perkins 28604, | B.M. ♂ Genitalia slide no. 4173| PHILODORIA NIGRELLA, ♂ Wlsm. Fn. Hawaii I. TYPE descr. fig^{d}.| Walsingham Collection, 1910—427| NHMUK010305337| in NHMUK (here designated). Paralectotype 1 ♂, Same locality, vii.1895, Perkins 27401| Philodoria nigrella, ♂ Wlsm. PARATYPE 1/1| Walsingham Collection, 1910—427| NHMUK010305338| in NHMUK. Described from two specimens, and Walsingham likely considered them as holotype and paratype, as indicated on their specimen labels. However, because a holotype was not specified in the description, the so-labeled types are syntypes under Article 73.2 of the Code (ICZN 1999), and any one of them is can be designated as lectotype under Article 74 of the Code (ICZN 1999). The syntype 'type (28604)', which Walsingham listed and figured, is here designated as lectotype (Fig. 13D) and the other syntype is the paralectotype.

Diagnosis. Blackish forewing with three white dorsal streaks and an outwardly white costal streak at 3/4. The forewing pattern is similar to *P. touchardiella*, but the latter has brownish forewing ground color and rather broad valva base.

Description: Adult (Fig. 13D, E). The following is from Walsingham (1907: 721): "Antennae fuscous, white at the apex. Palpi white, the median joint streaked with fuscous externally, the terrninal joint fuscous beneath. Head fuscous; face yellowish white. Thorax blackish. Forewings black, with a slight brownish gloss, a white spot at the extreme base below the middle and three short, outwardly oblique, white dorsal streaks, one near the base reaching to the fold, the second before the middle, crossing the fold, the third, shorter, at about the end of the fold; a little beyond the third dorsal is an oblique, narrow, spatulate leaden gray costal streak, which is succeeded by three white streaks in the costal cilia before the apex; at the apex is a black spot, separated beyond it by leaden gray and below it by chestnut-brown, from a black curved line around the base of the leaden gray cilia which blend with tawny fuscous about the tornus. Exp. al. 9 mm. Hindwing blackish; cilia tawny fuscous. Abdomen blackish, white beneath. Legs blackish, wllitish beneath; hind tarsi spotted with whitish."

Male genitalia (Zimmerman 1978a: fig. 451). Tegumen oblong, 0.8 x length of valva; valva oblong, dorsal margin indistinct and genitalia mounted in a poor condition. Saccus slender. Phallus straight in lateral view; cornuti in vesica indistinct.

Female genitalia Unknown.

Distribution. Hawaii (Big Island) (Walsingham 1907).

Host plants and Biology. Unknown.

Remarks. This species has not been collected since the original two male specimens in 1895 and we believe it may be extinct.

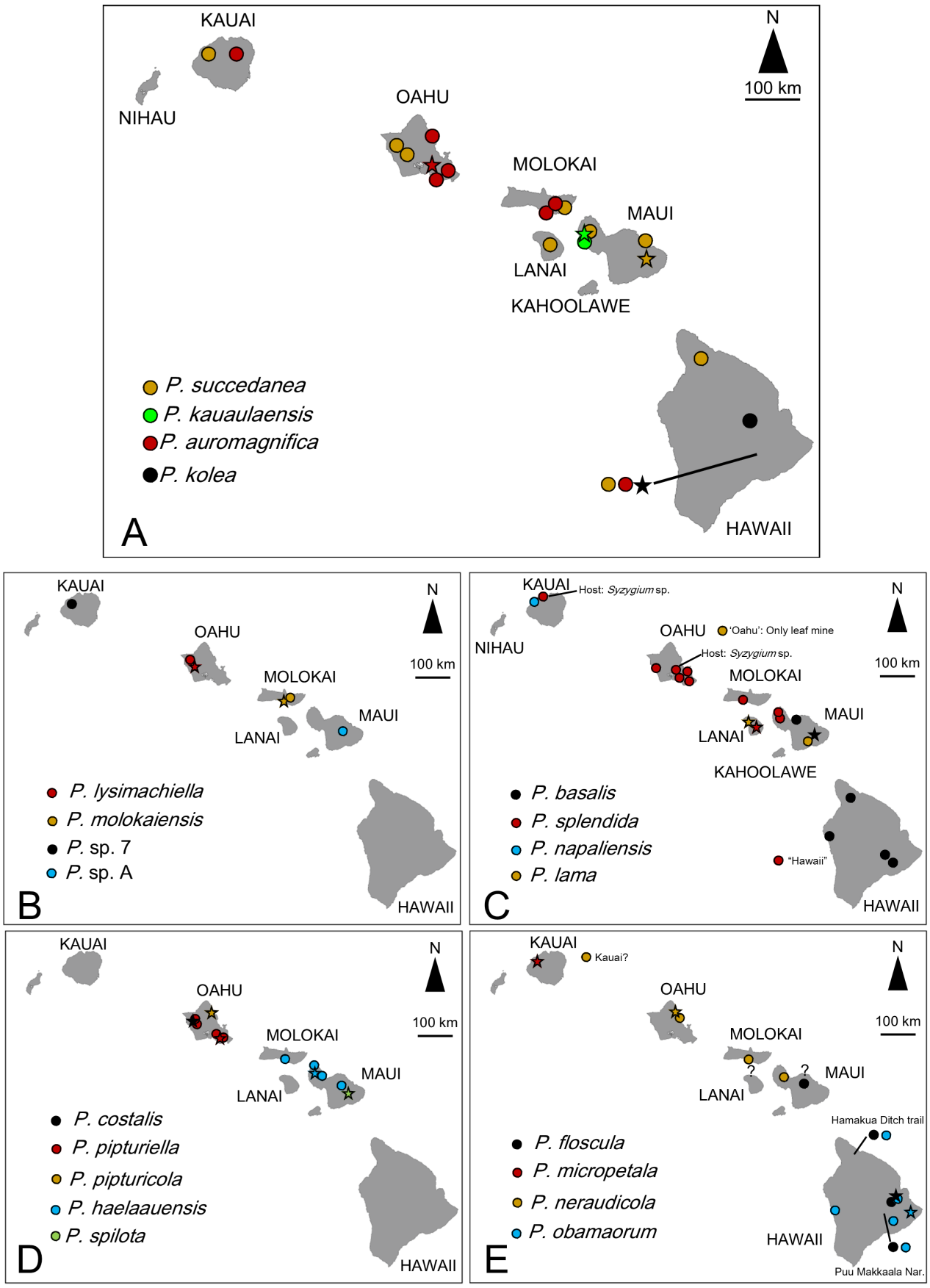

FIGURE 31. Distribution of *Philodoria* species that have a reduced maxillary palpus. **A** star indicates a species' type locality. Data based on recent fieldwork and historical museum specimen labels. Insert **A** is based on Kobayashi *et al*. (2018).

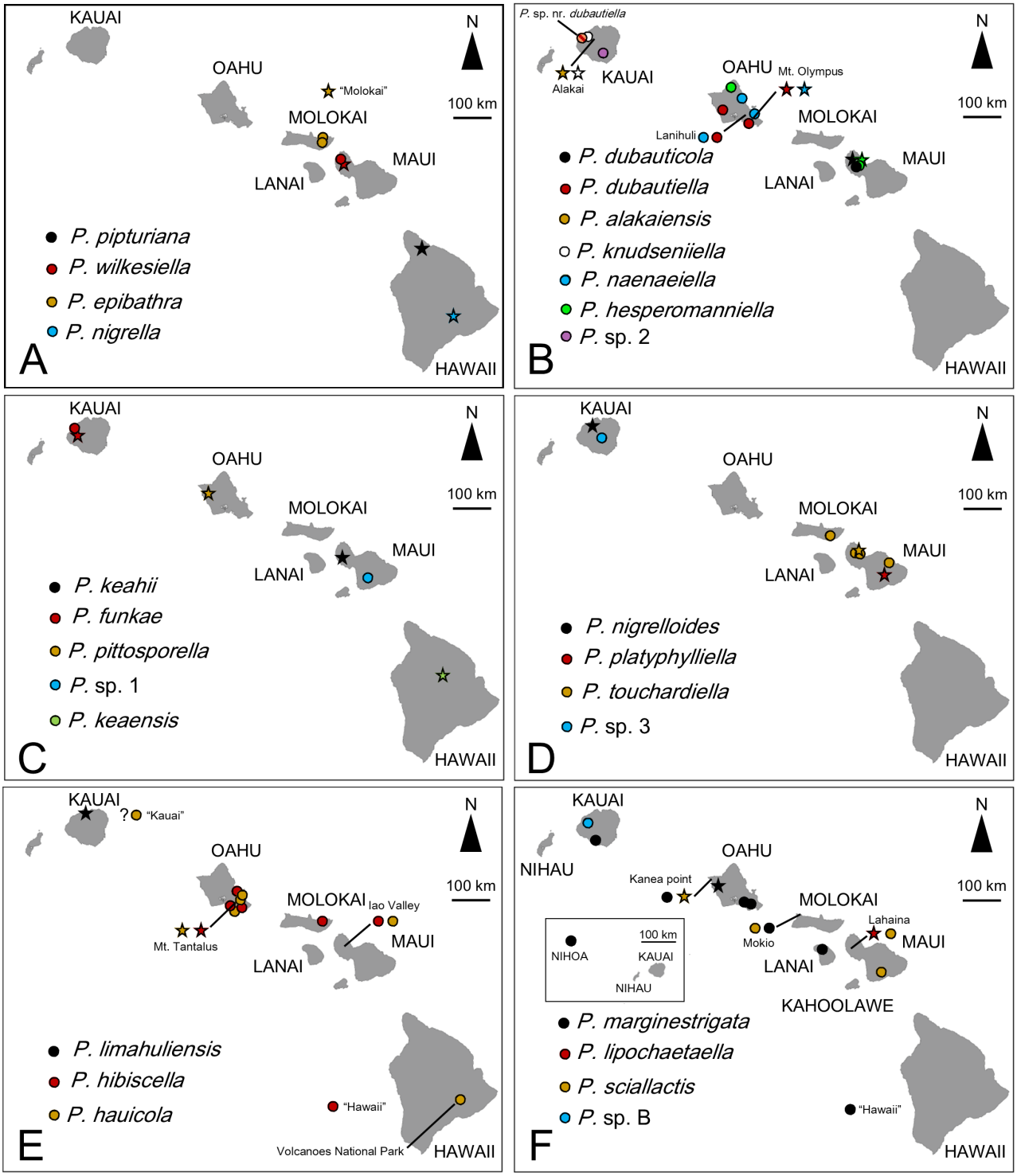

FIGURE 32. Distribution of *Philodoria* species. **A** star indicates a species' type locality. Data based on recent fieldwork and historical museum specimen labels.

***Philodoria dubauticola* (Swezey, 1940)**

Figs. 14A, 27A, 34E, 47C, 48C, 49C, 58C, D, 88B–F.

Parectopa dubauticola Swezey, 1940: 463–464.
Philodoria dubauticola Swezey, 1940; Zimmerman 1978a: 667, figs. 441, 447; Johns *et al*. (2016): 63, 64, fig. 1.

Type locality. Ridge above Haelaau (Maui).

Type material. Lectotype ♀, Ridge above Haelaau, Maui, 20.xii.1928, O.H. Swezey Collector, *Dubautia*, |Holotype *Parectopa dubauticola* Swezey | Type no. 4258 in BPBM (here designated). Described from three specimens reared from *Dubautia* leaf mines collected on the ridge above Haelaau, Maui. Swezey considered them as holotype and paratypes as indicated on their specimen labels. However, because a holotype was not specified in the original description, the so-labeled types can all be considered syntypes under Article 73.2 of the Code (ICZN 1999), and any of them is eligible for designation as lectotype under Article 74 of the Code (ICZN 1999). The syntype 'Holotype' is here designated as lectotype (Fig. 14A) and the remaining syntypes are paralectotypes, but we could not find them in BPBM.

Additional material. 7 (3♂, 3♀, 1 sex unknown): 2♂, 3♀, 1 (sex unknown), Haelaau, Maui, 29.iv.&7.v.2013 (stored), C.A. Johns leg., host: *Dubautia laxa*, 10.iv.2013, CJ077 / KT982408 (see Remarks), CJ083 / PHIL0023♂, CJ084, CJ094 / SK645♀, CJ111 / PHIL0008♀, CJ256 / SK646♂ in BPBM; 1♂, Helu, Maui, 14.iii.2015 (stored), K. Bustamente leg., host: *D. laxa*, 18.xii.2014, KMB01, CJ402, SK812♂ in BPBM.

***Philodoria* sp. nr *P. dubauticola*:** 3 (sex unknown), Nakula Natural Reserve, Maui, 1.viii.2014 (stored in RNAlater solution), C.A. Johns leg., host: *Dubautia platyphylla*, 26.vii.2014, CJ315 in FLMNH (Fig. 75A).

Diagnosis. Brownish fuscous forewing with a white longitudinal streak on the basal half of the wing. The species is similar in appearance to *P. dubautiella* (Swezey), but distinguishable from the latter by having two dorsal white streaks instead of three on the forewing, a rather broad saccus, and a large and well-sclerotized terminus of the ductus bursae.

Redescription: Adult (Fig. 14A, 34E). Wingspan 8 mm; forewing length 4 mm in holotype. Head dirty white; frons white; maxillary palpus white with few dark scales externally; labial palpus whitish, second segment broadly infuscated externally at apex, third segment with a few dark scales externally at apex and towards base (Fig. 34E). Antenna light fuscous, basal fourth white beneath, about 1.3–1.4x length of forewing. Thorax grayish brown, white beneath. Forewing brownish fuscous with white streaks margined with a few fuscous scales: a white longitudinal streak from base to about 2/5; two dorsal outwardly oblique ones (**$ds_{2, 3}$**) extending the middle of wing, the **ds_2** at 2/5, the **ds_3** at 3/5; white narrow costal line on basal 1/3; two outwardly oblique white costal streaks (**$cs_{2, 3}$**), **cs_2** at 1/2 and wider at costal side (not always distinct), the **cs_3** at 3/4, slender and of even width terminating in a patch of pale blue scales, a similar patch of blue scales at apex of wing (**as**); remainder of apical portion of wing suffused with ocherous; costal cilia with three white costal spots (**a, b, c**) before apex, separated by light fuscous scales. Cilia light fuscous with a distinct dark fuscous fascia at base. Hindwing uniform light fuscous, cilia paler. Legs light fuscous, tarsi banded with white. Abdomen grayish fuscous, white beneath.

Male genitalia (Figs. 47C, 48C, 49C) (n=3). Capsule 770 µm. Tegumen 0.8–0.9 x length of valva; valva tapering along costal margin from base 2/5 to apex; along the inner side of valva, a series of small spines arranged; apical half slender (Fig. 47C). Saccus short and thick (Fig. 48C). Phallus 500 µm long, slender and sinuous in lateral view with developed coecum; cornuti in vesica indistinct (Fig. 49C).

Female genitalia (Fig. 58C, D) (new record) (n=3). 1120 µm long. Ostium bursae large; antrum cup-shaped with a slender pair of lateral lobes; lamella antevaginalis 280 µm, large and weakly sclerotized, trapezoid in ventral view, slightly inflexed on the posterior margin, widening toward anterior margin of A7. Ductus bursae 400 µm; terminus of ductus bursae biforked. Corpus bursae 600 µm, pyriform; paired rows of wrinkles running longitudinally, some sclerotized.

Distribution. Maui (Swezey 1934).

Host plants. Asteraceae: *Dubautia plantaginea* Gaudich.? (Zimmerman 1978a) and *Dubautia laxa* Hook. & Arn. (Johns *et al*. 2016).

Biology. (Fig. 88B–F). Larvae form a slender linear mine on the adaxial leaf surface (Fig. 88B–D), that gradually expands as larvae feed and grow (Fig. 88E). One mine per leaf. Pupation occurs in the cocoon outside of the mine, on the adaxial surface of leaf (Fig. 88F).

Remarks. We identified one adult moth (Coll ID CJ-077 / GenBank accession no. ID KT982408) as *P. dubauticola*, based on the presence of a white longitudinal streak on forewing, and this specimen was sacrificed for molecular analysis (Johns *et al*. 2016).

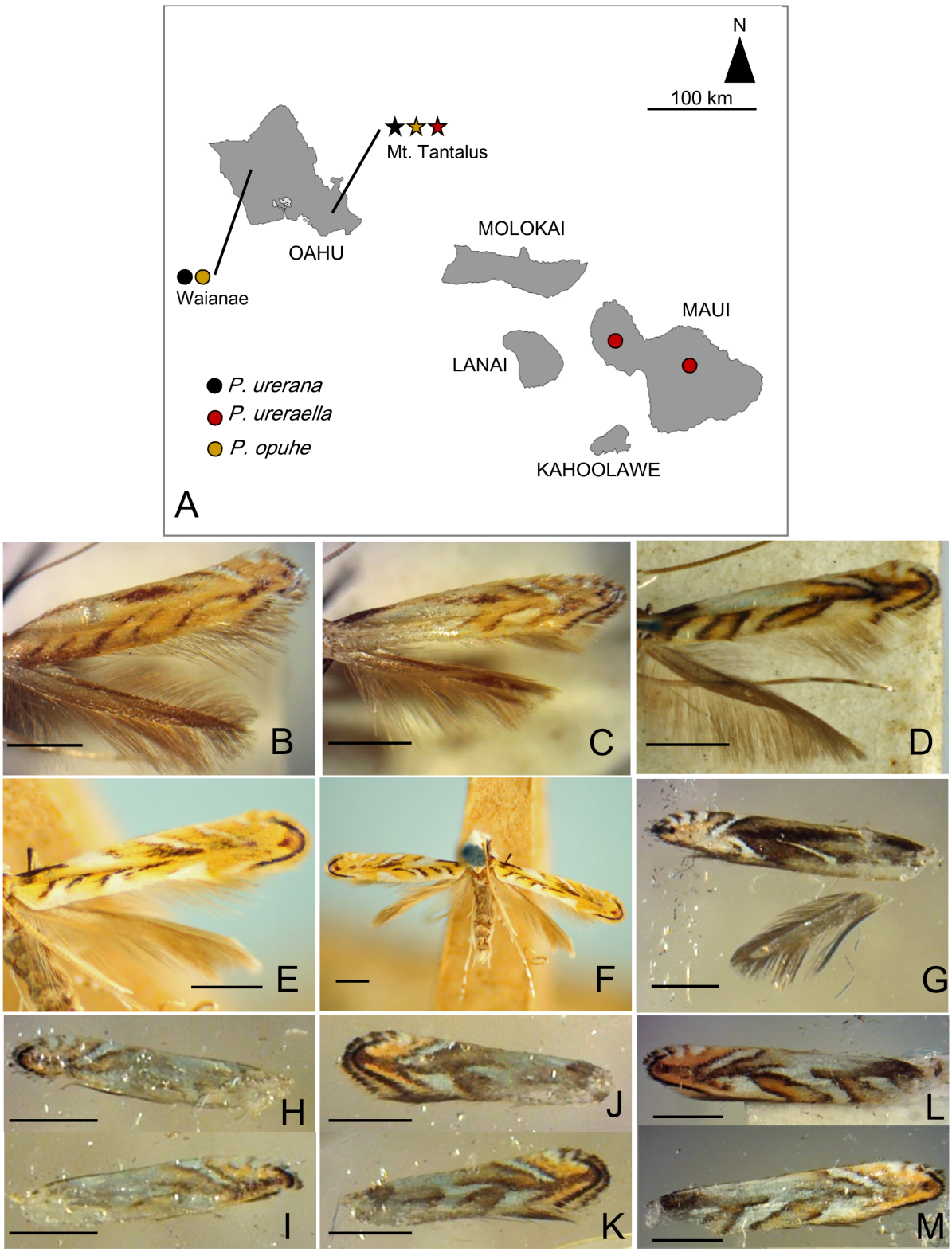

FIGURE 33. Distribution of *Urera*-mining *Philodoria* species and their forewing coloration and pattern. **A** Distribution of *Urera*-mining *Philodoria* species, stars indicate type localities, **B** *P. opuhe* paratype, female, right bottom specimen on mount, one of four types (including SK742), ex *Urera*, blotch mine, USNM, C Same species, paratype male, left bottom specimen on same mount as **B**, **D** *P. ureraella*, paralectotype male (SK742), **E**, **F** *P. opuhe*, male (SK682), ex blotch mine (USNM), **G** *P. urerana* male (SK670), **H**, **I** *P. ureraella* male (PHIL0005), Iao Valley, Maui, J, K Same species and locality, female (PHIL0006), **L**, **M** *P. ureraella* male (SK815), Waikamoi, Maui. Localities of **B–D** are Mt. Tantalus, **E–G** are Waianae Mts, Oahu. Data based on recent fieldwork and historical museum specimen labels. Scale bar 1 mm.

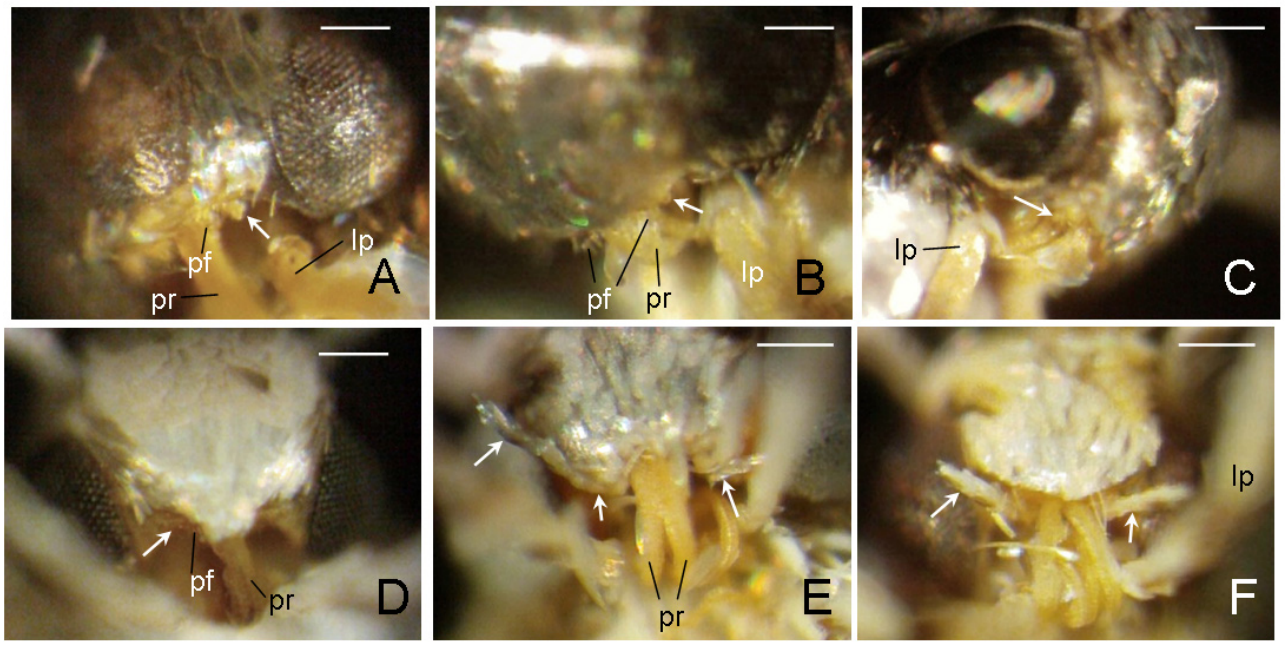

FIGURE 34. Adult female head of five species of *Philodoria*, showing their maxillary palpus. **A** *P. succedanea*, **B**, **C** *P. kolea*, paratype, **D** *P. basalis*, **E** *P. dubauticola*, **F** *P. hauicola*. lp: labial palpus, pf: pilifer, pr: proboscis. Arrows point to the maxillary palpus. Scale bar 0.1 mm.

Philodoria dubautiella **(Swezey, 1913)**

Figs. 14B–D, 27B, 47D, 48D, 49D, 58E.

Gracilaria dubautiella Swezey, 1913: 278–279 (first mentioned as "*Gracilaria dubautiella* Sw." in Swezey (1913b: 223) without any description).
Parectopa dubautiella (Swezey, 1913); Swezey 1928: 191.
Philodoria dubautiella (Swezey, 1913); Zimmerman 1978a: 667, figs. 441, 447, 454.

Type locality. Mt. Olympus (Oahu).

Type material. Lectotype ♂, Mt. Olympus, Oahu, i.1913, Coll. O.H.S (=O.H. Swezey), [ex *Dubautia plantaginea*], |TYPE OF 210 *Gracilaria dubautiella* Swezey| from top one of same mounted two syntypes in BPBM (here designated). Paralectotype 12 (7♂, 5♀). 1♀, same locality and data as holotype, bottom one of same mounted two syntypes in BPBM; 4♂, same locality and data as holotype, SK726♂, 733♂, BPBM34157, 2♂ in USNM; 3♂, 4♀, Pacific Heights Kidge, Oahu, O.H. Swezey Collector, ex *D. plantaginea* viii.–ix.1909 in USNM. Described from 'numerous' specimens collected from three localities on Oahu. The holotype was not specified in the original description, therefore the so-labeled types are all syntypes under Article 73.2 of the Code (ICZN 1999), and any specimen can be designated as a lectotype under Article 74 of the Code (ICZN 1999). The syntype labeled 'type' is here designated as the lectotype (Fig. 14B). The remaining syntypes are paralectotypes, but we could not find the series of 'syntypes' collected from Hillebrand's Glen, Oahu, xii.1912, in BPBM.

Additional material. 4 (2♂, 2♀): **Oahu**: 1♀, Kaumuahona, 12.i.1919, O.H. Swezey Collector, ex *Dubautia*, SK692, 34160 in BPBM; 1♀, Lanihuli, 24.xi.1918, O.H. Swezey Collector, ex *Dubautia*, SK693, 34161 in BPBM; 2♂, nr. Nanakuli Forest Reserve, Akupu, Oahu, 28.iii.2016 (stored), K. Bustamente leg., host: *D. laxa*, 10.xi.2015, 20151110 KMB01, CJ524ab, SK686♂, SK687♂ in BPBM; 1♀, Oahu 2400', Koolau Range, Poamoho Trail, 29.ix.1976, K. & E. Sattler, B.M.1976-605, *Philodoria* sp. 26 cf. *hibiscella* Sattler Coll., Color slide 140, D.C. Lees Sep. 2016, BMNH(E)1621252 in NHMUK.

Philodoria **sp. near** ***P. dubautiella***: 1♂, Kauai: Na Pali, Kona Forest Reserve, Pihea Trail, 4200', 11&26. ix.1973, K. & E. Sattler, B.M.1973-498, *Philodoria* sp. 29 & 23 (Kauai) Sattler Coll., D.C. Lees Sep. 2016, BMNH(E) 1621238, 1621684 in NHMUK (Fig. 14E).

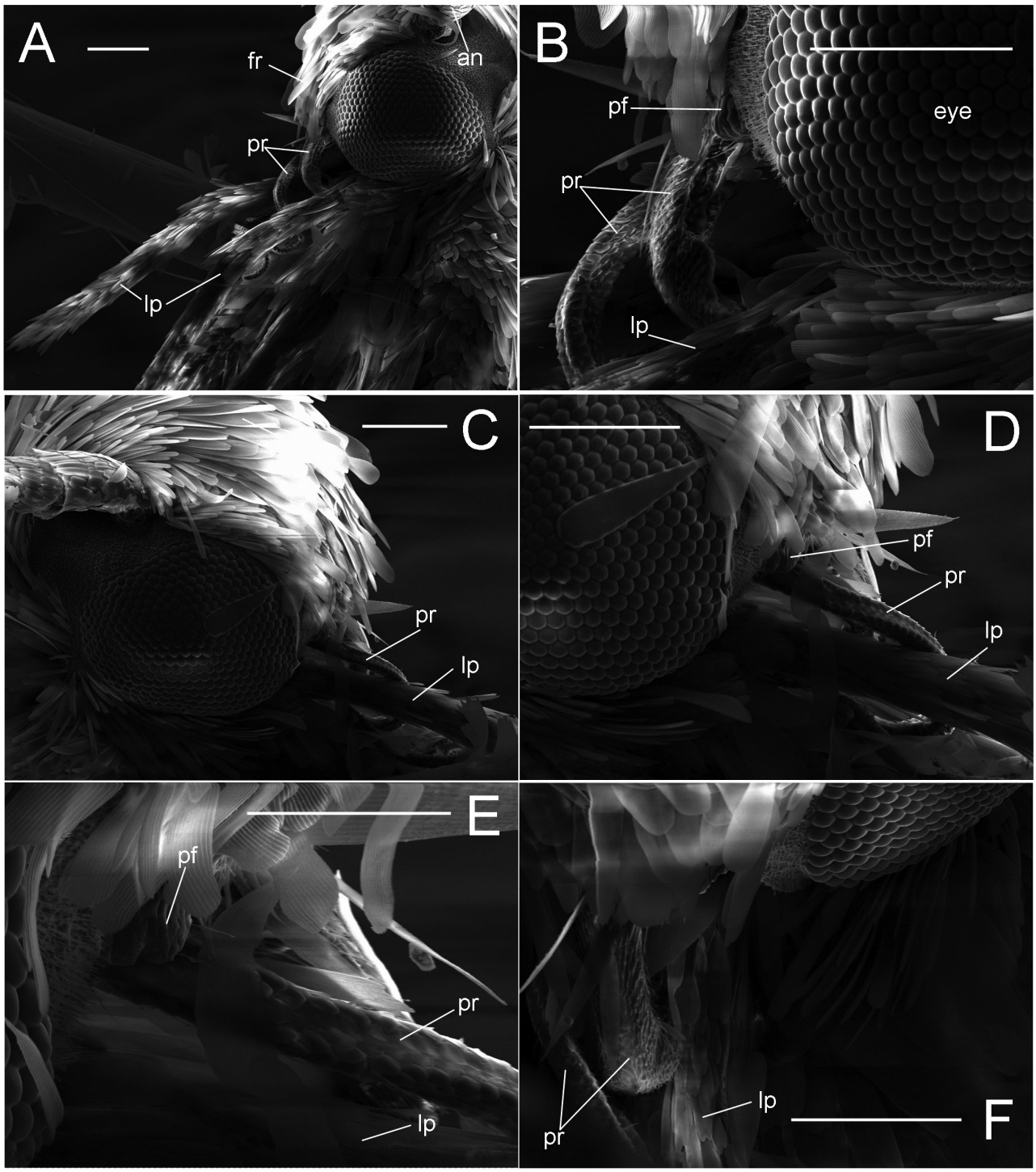

FIGURE 35. SEM scan of the head of *Philodoria kolea*, male (SK869). **A**, **B** Left lateral view, **C–E** Right lateral view, **F** Frontal view. an: antenna, ey: eye, fr: fron, lp: labial palpus, pf: pilifer, pr: proboscis. Scale bar 100 μm (A–D, F), 50 μm (E).

Diagnosis. Brownish forewing with five outwardly oblique white streaks: three dorsal ones (**ds**$_{1–3}$) and two slender costal ones (**cs**$_{2, 3}$) (Fig. 14B–D). Among the *Philodoria* species that have similar two costal streaks, *P. dubauticola* Swezey, *P. alakaiensis* **sp. n.** and *P. limahuliensis* **sp. n.**, *P. dubautiella* is most similar to *P. limahuliensis* , but is distinguishable by its valva having a slender apical region and shorter saccus. A Kauai specimen has similar forewing pattern to those of *P*. *dubautiella* and *P*. *alakaiensis* **sp. n.**, but has darker brown forewing and broad **ds**$_{1–3}$, and differs from *P. alakaiensis* in having **ds**$_{1}$ (Fig. 14E).

Redescription: Adult (Fig. 14B–D). Wingspan 7–9 mm; forewing length 3.5 mm in lectotype, 3.2–4.1 mm in paralectotypes. Head dirty white; frons white; maxillary palpus white with few dark scales at apex; labial palpus

white, a fuscous spot at apex of median segment and near middle of terminal segment. Antenna light fuscous, about 1.3–1.4x length of forewing. Thorax brownish ocherous. Forewing brown to ocherous with outwardly oblique white streaks: three dorsal ones (**ds**$_{1–3}$) and two slender costal ones (**cs**$_{2, 3}$) at the middle and 2/3 of costa respectively; all of these streaks margined with a few black or fuscous scales; three white costal spots (**a, b, c**) near apex; a spot of bluish scales at apex and a few bluish scales in a more or less fuscous streak between apex and end of third dorsal white streak; cilia white with terminally fuscous line at apex, fuscous fringe at tornus (**bl**$_1$). Hindwing and cilia grayish fuscous. Abdomen grayish-fuscous. Legs fuscous with white tarsal spots.

Male genitalia (Figs. 47D, 48D, 49D) (n=2). Capsule 800 μm. Tegumen 0.8 x length of valva; valva 580 μm long, tapering along costal margin from 2/5–1/2 to apex; a series of small spines arranged along the inner side of valva; apical half of valva rather slender and slightly pointed at apex compared to *P. dubauticola* (Fig. 47D). Saccus short and triangular in ventral view (Fig. 48D). Phallus 470 μm long, slender and nearly straight with developed coecum; cornuti in vesica indistinct (Fig. 49D).

Female genitalia (Fig. 58E) (n=2). 1120 μm long. Ostium bursae large; antrum cup-shaped with a slender pair of lateral lobes; lamella antevaginalis 280 μm, weakly sclerotized and large, trapezoid in ventral view, slightly indented near the posterior margin, widening toward anterior margin of A7. Ductus bursae 400 μm; terminus of ductus bursae biforked. Corpus bursae 600 μm, pyriform with paired rows of wrinkles running longitudinally, some sclerotized.

Distribution. Oahu (Swezey 1913c).

Host plants. Asteraceae: *Dubautia plantaginea* Gaudich. (Swezey1913b: 223; Swezey 1913c: 279) and *D. laxa* Hook. & Arn.: new record.

Biology. Immature stages were reported by Swezey (1913c: 279): *"Egg.* The eggs are deposited singly on the surface of the leaves; circular, about .5 mm. in diameter, broadly convex and with the surface reticulated and somewhat iridescent. The young larva on hatching, immediately eats into the leaf, at first producing a very slender mine length wise in the leaf and back and forth a few times, but eventually broadening to a blotch. A purplish discoloration is produced in the leaf by the mining larva, forming streaks following the course of the mines. Often several mines are begun in the same leaf. The cocoon is made within the mine, its position being indicated by a little of its silk being visible through a slit that was made in the epidermis for emergence. I have found this very abundant generally in the mountains back of Honolulu. I have found as many as 11, but not all of the larvae reach maturity, however, often 3 or 4 cocoons are found in the same leaf.*Mature larva*. The full-grown larva is 6–7 mm long; pale greenish-yellow, head pale brownish, eyes black; head very deeply notched and retracted into segment 2 which is widened and has a fuscous longitudinal dorsal streak each side of median line, darkest at posterior margin; ventrally there is a large squarish patch of fuscous which is minutely roughened, cervical shield also slightly roughened. Abdominal prolegs on segments 7–10. *Pupa*. 4mm long, pale greenish, a little browned on thorax, and middle of dorsum of abdomen, leg and antenna-sheaths; wingsheaths extend about to apex of fifth abdominal segment; antenna-sheaths extend beyond apex, curved up over abdomen to near middle. The pupa is formed in a cocoon within the mine, its position being indicated by a bit of white silk showing where the larva ate a slit through the epidermis for the emergence of the moth."

Parasitoids. Bethylidae: *Sierola planiceps* Fullaway, 1920; Eulophidae: *Euderus metallicus* (Ashmead, 1901), *Pnigalio externa* (Timberlake, 1927; Zimmerman 1978a).

Remarks. Larval leaf mines may be abundant (Zimmerman 1978a).

Philodoria alakaiensis Kobayashi, Johns & Kawahara sp. n.

Figs. 14F, 15A–E, 36, 39D, 47E, 48E, 49E, 58F, G.

Philodoria sp. 15; Johns *et al*. 2018: fig. 2.

Type locality. Alakai (Kauai).

Etymology. The specific epithet is derived from the type locality, Alaka'i (pronounced 'Ala-Kayee') Wilderness Preserve, also known as Alaka'i Swamp, an important wet forest area for Hawaiian endemic plants.

Type material. Holotype ♂, Alakai, Kauai Is., 9.vii.2015 (stored), C.A. Johns leg., host: *Dubautia laxa* or *D. paleata*,18.vi.2015, CJ473, SK836 in BPBM. Paratype 7 (3♂, 3♀, 1 sex unknown): 1♂, same data and locality as holotype, CJ468 in BPBM; 2♂, 2♀, 1 (sex unknown), same data and locality as holotype, 11.vii.2015 (stored),

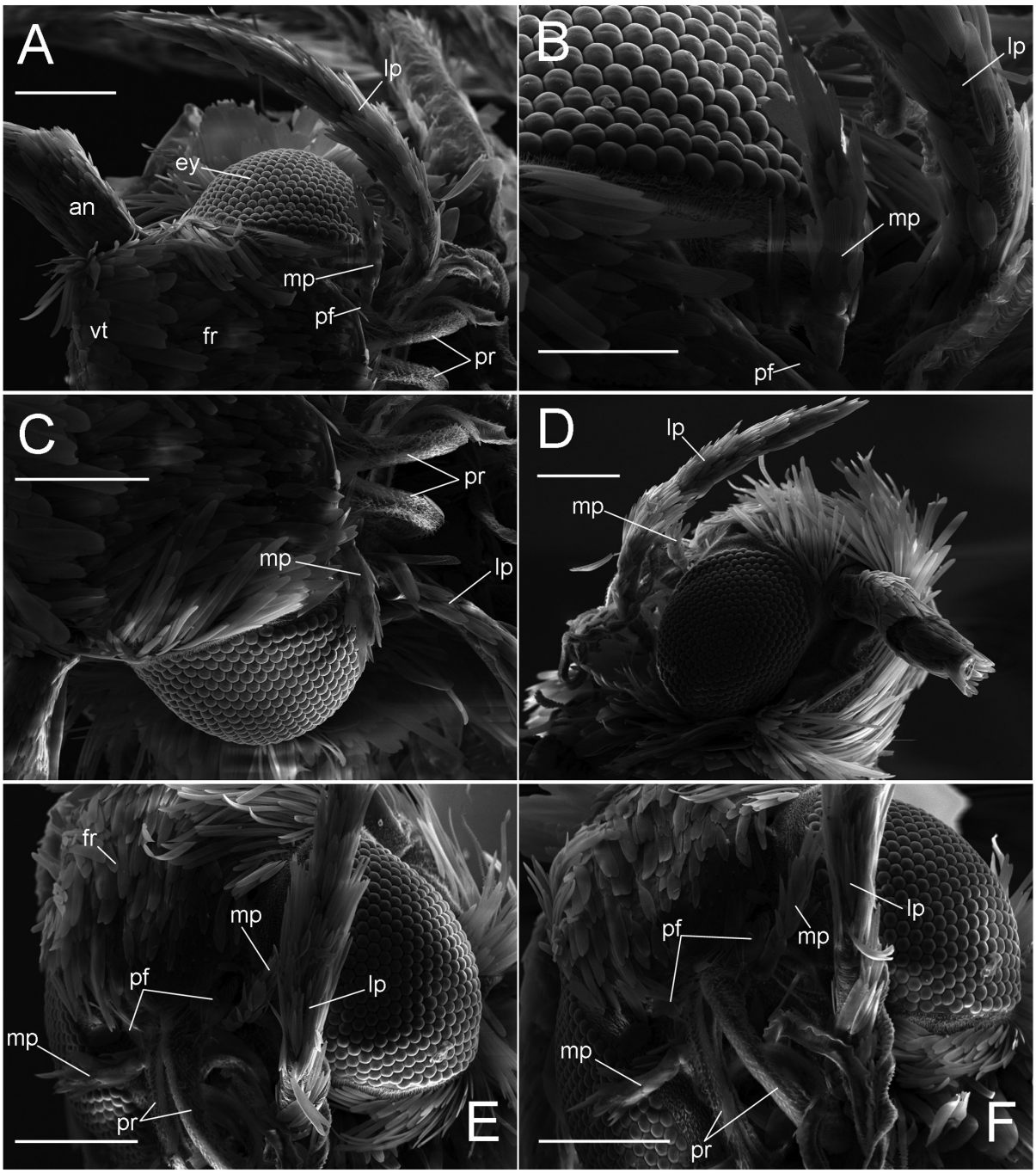

FIGURE 36. SEM scan of the head of *Philodoria alakaiensis*, paratype female (SK870). **A** Anterior view of head from front, **B** Left palpus, **C** Right side of head, frontal view, **D** Right side of head, lateral view, **E** Anterolateral view of head, **F** Ventral view. an: antenna, ey: eye, fr: fron, lp: labial palpus, mp: maxillary palpus, pf: pilifer, pr: proboscis, vt: vertex. Scale bar 100 µm (A, C–F), 50 µm (B).

CJ479/SK658♂, SK659♀, SK660♂, SK661♀ in BPBM; 1♀, same locality as holotype, 11.vii.2015 (stored), 18.vi.2015, host: *Dubautia laxa* or *D. paleata*, CJ481/SK864♀, SK870 (SEM) in BPBM; 1♂, Kauai, 4520', Alakai Swamp, Kelekua Hut, 13.ix.1973, K. & E. Sattler, B.M.1973-498, *Philodoria* sp. 30 cf nigrelloides, Colour slides 133-4, 139 Pl. 3 Fig. 5 Zimmerman 1978a Sattler Coll., D.C. Lees Sep. 2016, BMNH(E)1621107 in NHMUK; 1♀, Kauai, 4520', Alakai Swamp, Kelekua Hut, 5.vii.1973, K. & E. Sattler, B.M.1982-342, *Philodoria* sp. 28, Sattler Coll., D.C. Lees, Sep. 2016, BMNH(E)1621109 in NHMUK. The holotype was mounted as a dry pinned specimen with its four wings placed without mountant under a coverslip: forewings slightly damaged at base, basal 2/3 of hindwings broken.

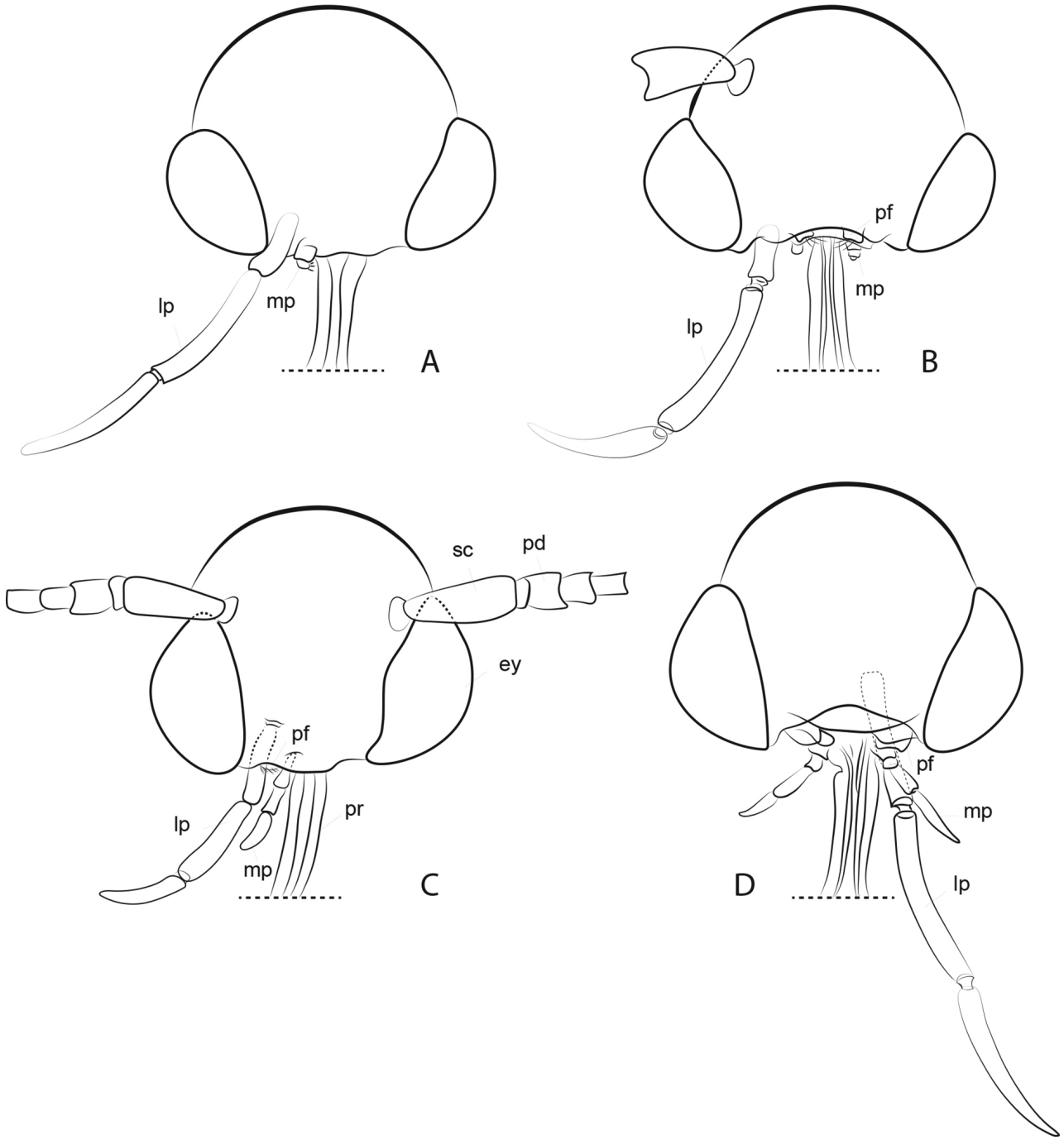

FIGURE 37. Illustrations of the head of *Philodoria*. **A** *P. basalis*, female, Hawaii (Big Island) (SKH09-1, SK615), host: *Metrosideros polymorpha*, **B** *P. lysimachiella*, male, Oahu (CJ530a/SK749), host: *Lysimachia hillebrandii*, **C** *P. marginestrigata* (sex unknown), Molokai (CJ186), host: *Abutilon grandiflorum*, **D** *P. hauicola*, female, Oahu (SKH08-9/SK750), host: *Hibiscus tiliaceus*. ey: eye, lp: labial palpus, mp: maxillary palpus, sc: scape, pd: pedicel, pf: pilifer, pr: proboscis.

Diagnosis. Dark brownish forewings with four outwardly oblique white streaks: two dorsal ones and two slender costal ones (Figs. 14F, 15A–E). Differs from other *Philodoria* species in having two costal streaks, but lacks a $\mathbf{ds}_1$ and a short $\mathbf{cs}_1$ in the forewing; valva slender and slightly rounded apically. An Alakai species, *P. nigrelloides* (Swezey) (male unknown, feeding on *Dubautia*) differs from the new species in lacking the $\mathbf{cs}_1$ and having a tubular antrum (Zimmerman 1978a: fig. 459).

Description: Adult (Figs. 14F, 15A–E, 36). Forewing length 3.8–3.9 mm in holotype, 3.3–3.9 mm in paratype. Head dark brown; frons white; maxillary palpus white; labial palpus white but with dark brown scales below at

apex (Fig. 36); antenna dark brown, white beneath, about 1.1x length of forewing. Thorax brown. Forewing brown to dark brown with outwardly oblique white streaks that are found at: **cs**$_2$ short one at about 1/2, **cs**$_3$ slender at 3/4; **ds**$_1$ very small at base along the dorsum; **ds**$_2$ large at 1/3; **ds**$_3$ at 3/4; some fuscous scales scattering from 1/2 to 3/4; apical portion orangish brown; three white costal spots (**a, b, c**) near apex; a spot of bluish scales at apex (**as**) and a few bluish scales in a more or less fuscous patch between apex and end of **ds**$_3$; cilia fuscous with two white spot at termen; **bl**$_1$ black from termen to tornus, fuscous fringe at tornus. Hindwing and cilia fuscous. Legs pale fuscous with dark brown scales.

Male genitalia (Fig. 39D, 47E, 48E, 49E) (n=2). Capsule 800 µm. Tegumen 0.7–0.8 x length of valva; valva 590 µm long, tapering along costal margin from base 2/5–1/2 to apex, slightly rounded at apex and narrowing once at middle; a series of small spines arranged, along the inner side of valva (Fig. 47E). Saccus triangular in ventral view (Fig. 48E). Phallus 550 µm long, rounded at phallobase with developed coecum; two series of spiny minute cornuti in vesica (Fig. 49E).

Female genitalia (Fig. 58F, G) (n=3). 1280 µm long. Ostium bursae large; antrum low, cup-shaped with a slender pair of lateral lobes; lamella antevaginalis 210 µm, weakly sclerotized, trapezoid in ventral view, slightly inflexed on the posterior margin, widening toward anterior margin of A7. Ductus bursae 400–450 µm; terminus of ductus bursae biforked. Corpus bursae 690–700 µm, oblong with paired rows of wrinkles running longitudinally, some sclerotized.

Distribution. Kauai.

Host plants. Asteraceae: *Dubautia* sp. (*D. laxa* or *D. paleata*). Several species of *Dubautia* co-occur in the Alakai swamp area and it is unclear whether the specimens found by N. Tangalin were on *Dubautia laxa* or *D. paleata*. These mines were very abundant during our surveys in the summer of 2015.

Biology. The larva mines fresh fuzzy leaves.

Parasitoids. Braconidae sp.? (Fig. 105A–L).

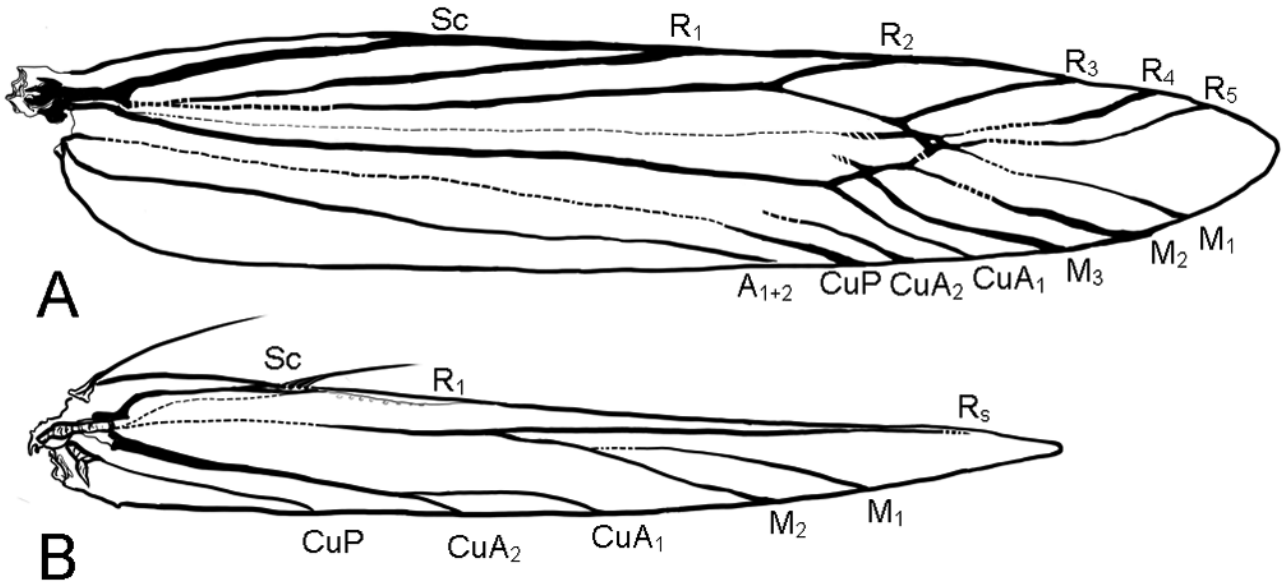

FIGURE 38. Schematic illustration of *Philodoria* wing veins, this image showing veins of *P. lysimachiella*, male, Oahu (CJ530a/SK751), host: *Lysimachia hillebrandii*. **A** forewing, **B** hindwing.

Philodoria limahuliensis Kobayashi, Johns & Kawahara sp. n.

Figs. 15F, G, 47F, 48F, 49F.

Philodoria sp. 8; Johns *et al*. 2018: fig. 2.

Type locality. Limahuli (Kauai).

Etymology. The specific epithet is derived from the type locality, Limahuli (pronounced 'Lee-Mah-Hoo-Lee') Garden and Preserve, northern coast of Kauai.

Type material. Holotype ♂ Limahuli, Kauai Is., 9.vii.2015 (stored), C.A. Johns leg., host: *Hibiscus waimeae* subsp. *hannerae*, 21.vi.2015, CJ472b/SK731♂ in BPBM. Paratype 2♂, same locality and data as holotype, 9&21.vii.2015 (stored), CJ472a / SK730♂, CJ490 / SK732♂ in BPBM. Three specimens are incomplete but they have features that are distinctive enough to allow this species to be described. What remains of three specimens is: holotype mounted by placing four wings without mountant under a coverslip: two forewings (9/10 of left wing and 2/3 right wing slightly damaged) and one full hindwing and another 4/5 hindwing; two paratypes: a specimen mounted by placing three wings without mountant under a coverslip (two forewings [4/5 of left wing and halves of right wing] and right hindwing missing at base; CJ472a); a specimen mounted by placing four wings and two legs without mountant under a coverslip (full forewings slightly damaged at base, full two hindwings and two hind or mid legs; CJ490).

Diagnosis. A dark brown forewing with five outwardly oblique white streaks (Fig. 15F, G). The male genitalia is similar to that of *P. hibiscella* (Swezey), from which it is distinguishable by its darker forewing with two costal streaks. See also diagnosis of *P. dubautiella*.

Description: Adult (Fig. 15F, G). Forewing length 3.9 mm in holotype, 3.5 mm in paratype. Head and frons ocherous; maxillary palpus and labial palpus white fuscous below; antenna missing; thoracic characters, other than the legs and wings, are unknown. Adult head, thorax were used for molecular analysis. Forewing dark brown with outwardly oblique white streaks: **ds**$_{1–3}$ and slender **cs**$_{1, 2}$ at the middle and 2/3 of costa respectively; all of these streaks margined with a few black or fuscous scales; apical portion orangish brown; three white costal spots (**a, b, c**) near apex; a spot of bluish scales at apex (**as**) and a few bluish scales in a more or less fuscous streak between apex and end of third dorsal white streak; cilia fuscous with a white spot at termen; **bl**$_1$ black from termen to tornus, fuscous fringe at tornus. Hindwing and cilia fuscous. Legs pale fuscous with dark brown scales.

Male genitalia (Figs. 47F, 48F, 49F) (n=3). Capsule 980 μm. Tegumen 0.9 x length of valva; valva 700 μm long, oblong, tapering along costal margin from base 2/5 to apex; apical half digitiform, same width in lateral view; a series of small spines along the inner side of valva (Fig. 47F). Saccus slender and digitiform in ventral view (Fig. 48F). Phallus 710 μm long, slender, straight and sinuous at phallobase with developed coecum; cornuti in vesica indistinct (Fig. 49F).

Female genitalia Unknown.

Distribution. Kauai.

Host plants. Malvaceae: *Hibiscus waimeae* A. Heller subsp. *hannerae*.

Biology. Unknown.

Parasitoids. Chalcidoidea sp. (Fig. 106M, N).

Remarks. We examined fewer than 10 larva and adults of *H. waimeae* in Upper Limahuli Preserve (many of those reared did not become adults). It is possible that *P. limahuliensis* mines other *Hibiscus* species on Kauai. Future field surveys should look for other individuals of this plant host and related plants around the type locality. There are several extremely rare, endemic Malvaceae known from Kauai (e.g., *Hibiscadelphus distans*, *Kokio kauaiensis*) that could serve as larval hosts to *Philodoria.*

Philodoria hibiscella (Swezey, 1913)

Figs. 16A, B, 27C–E, 47G, 48G, 49G, 58H, 77B–D, 93A, B, D, E.

Graclaria hibiscella Swezey, 1913: 279–280 (first mentioned as "*Gracilaria hibiscella* Sw." in Swezey (1913b: 224) without any description).
Parectopa hibiscella Swezey, 1913; Swezey 1928: 191.
Philodoria hibiscella (Swezey, 1913); Zimmerman 1978a: 680–681, figs. 437, 440, 442, 448, 455.

Type locality. Mt. Tantalus (Oahu).

Type material. Lectotype ♀, Mt. Tantalus, Oahu, x.1911, Coll. O.H.S., "from mines in leaes (=leaves) of native *Hibiscus*", Type no. 211, bottom one of two cotypes on the type mount in BPBM. Paralectotype ♂, top one of two cotypes on same mount of lectotype in BPBM.

Described from three specimens collected from type locality from mines in leaves of *Hibiscus*. We found the lectotype and a paralectotype on same type mount designated by Zimmerman (1978a) but could not find the second paralectotype (sex unknown) (Fig. 16A, B).

Additional material. 13 (5♂, 3♀ 5 sex unknown): **Oahu**: 1♂, 2 (sex unknown), Honolulu, 1.iii.1914 em., Coll. O.H.S., ex *Hibiscus*, 24.ii.1914 (Cocoon), SK684♂ BPBM34179, BPBM34180, BPBM34183; 1♀, Manoa, 26.v.1932, O.H. Swezey Collector, ex leaf of *Hibiscus*, BPBM34181; 1♂, Waiahole, 13.viii.1933, O.H. Swezey Collector, *Hibiscus*, genitalia slide no. Z-1-26-61(2), BPBM34176; 3♂, 2♀, 3 (sex unknown), Tantalus, Coll. O.H.S., ex native *Hibiscus*, BPBM34177, SK685♀|BPBM 34178, ♀|BPBM34182, J.F.G.C. #3753♂, 3754♀ and 1♂, 2 (sex unknown) in USNM. **Molokai**: 1♀, Waiehu Cliffs, 14.iii.2015 (stored), K. Bustamente leg., host: *H. arnottianus* subsp. *immaculatus*, 14.i.2012, 20141201KMB01, CJ399, SK723♀ in BPBM. **Maui**: 1♂, 1♀, Iao Valley, 29.iv.2013 (stored), C.A. Johns leg., host: *Hibiscus tiliaceus*, 14.iv.2013, CJ088 / SK725♀, CJ089 / SK724♂ in BPBM.

Diagnosis. Ocherous forewing with four outwardly oblique white streaks: slender **ds**$_{1-3}$ and one slender **cs**$_{3}$ (Fig. 16A, B). Among *Philodoria* species having similar **ds**$_{1-3}$ and **cs**$_{3}$, i.e. *P. naenaeiella* (Swezey), *P. hesperomanniella* **sp. n.**, *P. neraudicola* (Swezey), *P. obamaorum* **sp. n.** and *P. urerana* (Swezey), *P. hibiscella* is most similar to *P. urerana* (feeding on *Urera*), but is distinguishable by the ocherous forewing; males have a rather broad saccus and slender and sinuous phallobase; females signa as two short rows of minute spines in the central area of the corpus bursae.

Redescription: Adult (Fig. 16A, B). Wingspan 9–10 mm in type series; forewing length 4 mm in paralectotype, 3.8–4.5 mm in the additional material examined. Head pale brownish-ocherous; frons white; maxillary palpus brown with white scales; labial palpus pale ocherous-white, terminal segment somewhat fuscous on outer side. Antenna pale ocherous barred with dark fuscous, 1.3–1.4x length of forewing. Thorax pale brownish-ocherous. Forewing ocherous, outwardly-oblique **ds**$_{1-3}$, widened and black-margined at dorsum; A slender outwardly-oblique narrowly black-margined **cs**$_{3}$ at costal 3/4; 3 or 4 black costal line on apical cilia; a black wide subterminal streak with a few bluish scales; cilia at apex blacky on termen gray with a black line at base. Hindwing and cilia grayish-fuscous. Abdomen gray. Legs pale ocherous, anterior legs fuscous on outer side.

Male genitalia (Figs. 47G, 48G, 49G) (n=3). Capsule 920 µm. Tegumen 0.9–1.0 x length of valva; valva 630 µm long, similar to *P. limahuliensis* except basal portion of valva humped along dorsal margin (Fig. 47G). Saccus slender and digitiform in ventral view (Fig. 48G). Phallus 580 µm long, slender, straight and sinuous at phallobase with developed coecum; cornuti in vesica indistinct (Fig. 49G).

Female genitalia (Fig. 58H) (n=4). 1410 µm long. Ostium bursae large; antrum wide tubular with a slender pair of lateral lobes; lamella antevaginalis 220 µm, weakly sclerotized, trapezoid in ventral view, slightly inflexed on the posterior margin, widening toward anterior margin of A7. Ductus bursae slender, 400–450 µm; terminus of ductus bursae biforked. Corpus bursae 840 µm, pyriformwith paired rows of wrinkles running longitudinally, some sclerotized; two short linear signa with minute spines.

Distribution. Oahu (Swezey 1913c), Maui, Molokai: new record, Hawaii (Big Island) (Zimmerman 1978a: 680).

Host plants. Malvaceae: *Hibiscus arnottianus* A. Gray, *H. rosasinensis* L. (Swezey 1928), *Hibiscus* sp. (Swezey 1913b: 224, 1913c: 280), *H. arnottianus* subsp. *immaculatus* and *H. tiliaceus* L.: new record, endangered subspecies.

Biology. (Fig. 93A, B, D, E). Swezey (1913c: 280) reported its biology: "The mine usually begins towards base of leaf, proceeding upward irregularly and following the margin for a part of its course, it eventually reaches the apex, then follows down the opposite margin of the leaf rapidly widening until the larya, has finished its growth. It then breaks through the epidermic to form its white oval cocoon on the surface of the leaf. Pupal stage about a week." Zimmerman (1978a) noted that larvae occasionaly cause severe local damage to ornamental *Hibiscus*, and extensively mined leaves may drop from the plants and the white, oval cocoon is made on the surface of a leaf. We also observed larvae forming first a slender mine along the leaf margin on the adaxial surface that elongated into a blotch mine (Fig. 93B) and expanded as the larva grew (Fig. 93A, B). The frass is brownish green and is deposited in a spiral line. One mine per leaf. Leaves with old mines remained on the host plant and we did not find any indication that larvae cause mined leaves to fall to the ground as in other *Philodoria* species. The late instar larva is pale yellow to green (Fig. 93D) and pupation occurs in the white cocoon outside of the mine on the leaf adaxial surface (Fig. 93E).

Parasitoids. Eulophidae: *Diglyphus* sp., *Euderus metallicus* (Ashmead, 1901), *Neochrysocharis formosus* (Westwood, 1833), *Pauahiana maculatipennis* (Ashmead, 1901), *Pnigalio externa* (Timberlake, 1927) *Sympiesis vagans* (Timberlake, 1926) (Zimmerman 1978a).

Remarks. The mature larva and pupa described by Swezey (1913c: 280): "*Mature larva*. The full-grown larva is about 9 mm.; pale bluish-green; head with blackish mouth-parts, eyes, and 2 lines bordering the paraclypeus, much

retracted into segment 2 which is widened, and has a large black spot ventrally and 2 black spots near the anterior margin dorsally; thoracic legs minute; abdominal prolegs on segments 7–9. *Pupa*. 5 mm.; pale testaceous-greenish, with a few fuscous markings ventrally; wing-sheaths extend to apex of fifth abdominal segment, free beyond fourth segment, dark fuscous at tip; posterior leg-sheaths extend to apex of abdomen; antenna sheaths extend beyond apex of abdomen, recurved over the back forward to base of fourth abdominal segment."

***Philodoria naenaeiella* (Swezey, 1940)**

Figs. 16C, D, 27H, 47H, 48H, 49H, 58I, J, 88G, H

Parectopa naenaeiella Swezey, 1940: 462–463.
Philodoria naenaeiella (Swezey, 1940); Zimmerman 1978a: 685–686, figs. 443, 449, 457, 458.

Type locality. Mt. Olympus (Oahu).

Type material. Lectotype ♂, Mt. Olympus, Oahu, [21.i.1912 or 30.i.1913], O.H. Swezey, *Dubautia* [*laxa*], |Holotype *Parectopa naenaeiella* Swezey, Type no. 4261, top one of two cotypes on the same mount, in BPBM (here designated). Paralectotype 37 (16♂, 5♀, 16 sex unknown): Host *Dubautia laxa*, O.H. Swezey on Oahu: 1♀, on same mount as holotype, bottom one of two cotypes; 6♂, 1♀, 12 (sex unknown), same data and locality as holotype, BPBM34235–34239, SK701♂|BPBM34240, BPBM34165, SK690♂, 691♂|BPBM34166; 2♀, same data and locality as holotype of "*Gracilaria epibathra* = *Parectopa naenaeiella* Swezey" in USNM; 4♂, same data and locality as holotype of "*Gracilaria epibathra* Wlsm aB 1914" in USNM; 1♂, Konahuanui, 22.ii.1914, ex *Dubautia laxa* var. *hirsute*, SK729♂; 3♂, 1 (sex unknown), Mt. Lanihuli, 12.xi.1922, BPBM34232, BPBM34233, 1♂, 1 (sex unknown) in USNM; 2♂, 1♀ 3 (sex unknown), Kahana, 4.ix.1927, BPBM34227, SK703♀|BPBM34228, BPBM342329–34231, SK702♂|BPBM34234. Described from leaf mines and cocoons on leaves of *Dubautia laxa* from Oahu; leaf mines of *Hesperomannia swezeyi* from Maui; and leaf mines of an unknown plant (*Dubautia latifolia*) from Kauai. The holotype was not specified in the original description, therefore any of the so-labeled types can considered syntype under Article 73.2 of the Code (ICZN 1999) and eligible for designation as lectotype under Article 74 of the Code (ICZN 1999). The syntype 'type' is here designated as lectotype (Fig. 16C) and the remaining 37 syntypes are paralectotypes. We identifed the Oahu 'paratypes' as *P. naenaeiella,* Maui 'paratypes' as the new species *P. hesperomanniella*, and a Kauai 'paratype' as the new species, *P. knudseniiella*.

Additional material. 3 (1♂, 2 sex unknown): **Oahu**: 1 (sex unknown), Konahuanui, 4.i.2014 (stored), C.A. Johns leg., Adult on *Dubautia plantaginea*, CJ188 in BPBM; 1 (sex unknown), Poamoho, 25.v.2013 (stored), C.A. Johns leg., host: *Dubautia* sp., 16.iv.2013, CJ142, KT982413 in BPBM; 1♂, 2400', Koolau Range, Poamoho Trail, 29.ix.1976, K. & E. Sattler, B.M.1976-605, *Philodoria* sp. 27 cf. *hibiscella* Sattler Coll., D.C. Lees Sep. 2016, BMNH(E)1621244 in NHMUK.

Philodoria* sp. nr.** ***P. naenaeiella: 1♀, Poamoho, Oahu, 24.vii.2015 (stored), C.A. Johns leg., host: *D. plantaginea*, 30.vi.2015, CJ500 (Fig. 27G).

Diagnosis. Pale brown forewing with four outwardly oblique white streaks: $\mathbf{ds_{1-3}}$ and slender $\mathbf{cs_3}$ (Figs. 16C, D, 27H). Female genitalia similar to *P. hesperomanniella* and *P. knudesiiella*, but *P. naenaeiella* differs from these two species in having a small white dorsal patch near the base on the forewing instead of a triangular streak.

Redescription: Adult (Fig. 16C, D).Wingspan 8–9 mm in type series; forewing length 4 mm in holotype, 3.5–4.0 mm in paratype. Head white, with some ocherous scales posteriorly; frons white; maxillary palpus white near base, dark brown at apex; labial palpus white, second segment broadly infuscated apically, third segment with slight infuscation near base and near apex. Antenna pale brown, basal segment paler and white beneath, about 1.3x length of forewing. Thorax pale brown. Forewing pale brown, with white patches: a small white patch ($\mathbf{ds_1}$) at near base; outwardly oblique white $\mathbf{ds_{2, 3}}$, all wide at dorsum and narrowing to a point about midway across the wing, $\mathbf{ds_2}$ about at dorsal 2/5, $\mathbf{ds_3}$ at dorsal 2/3; a slender outwardly oblique white $\mathbf{cs_3}$ from 3/5 terminating a little distad from apex of $\mathbf{ds_3}$, sccatterd with pale blue scales from there to apex; all of the white streaks margined with a few fuscous scales; apical portion orange; three white costal spots (**a, b, c**) between costal streak and apex, separated by fuscous scales; costa sometimes narrowly white; cilia light fuscous with distinct darker fuscous $\mathbf{bl_1}$, with white spots, dorsal cilia pale gray, very long. Hindwing and cilia uniformly grayish fuscous. Abdomen grayish brown. Legs grayish brown, tarsi white banded.

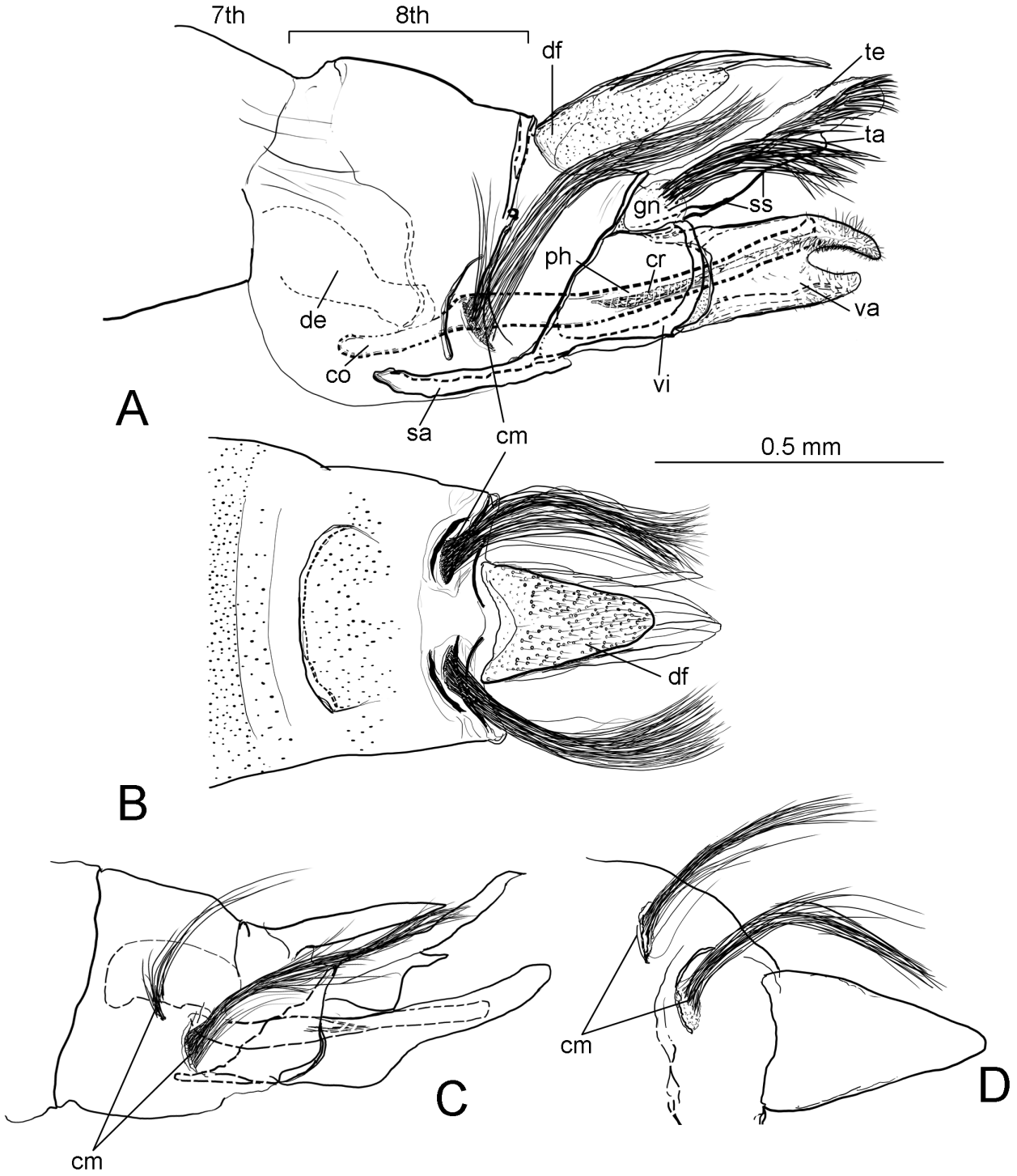

FIGURE 39. *Philodoria* male posterior end of abdomen. **A** *P. succedanea*, male, Hawaii (Big Island [SKH-13/SK633]), host: *Myrsine lessertiana*, **B** *P.* sp. 7 of Johns *et al*. (2018), male, Kauai (CJ451a/SK754), host: *Lysimachia kalalauensis*, **C** *P. haelaauensis*, male, Maui (34254/SK828), host *Pipturus* sp., **D** *P. alakaiensis*, holotype male, Kauai (CJ473/ SK836), host *Dubautia* sp. co: coecum, cm: coremata, cr: cornuti, df: dorsal flap, gn: gnathos, pb: phallobase, ph: phallus, sa: saccus, si: signum, ss: subscaphium, ta: tuba analis, te: tegumen, va: valva, vi: vinculum.

Male genitalia (Figs. 47H, 48H, 49H) (n=4). Capsule 840 µm. Tegumen 0.8 x length of valva; valva 580 µm long, tapering along costal margin from 2/5 to apex, becoming digitiform and straight in lateral view (Fig. 47H). Saccus slender and digitiform in ventral view (Fig. 48H). Phallus 600 µm long, pointed at apex, with developed coecum; two series of minute cornuti in vesica (Fig. 49H).

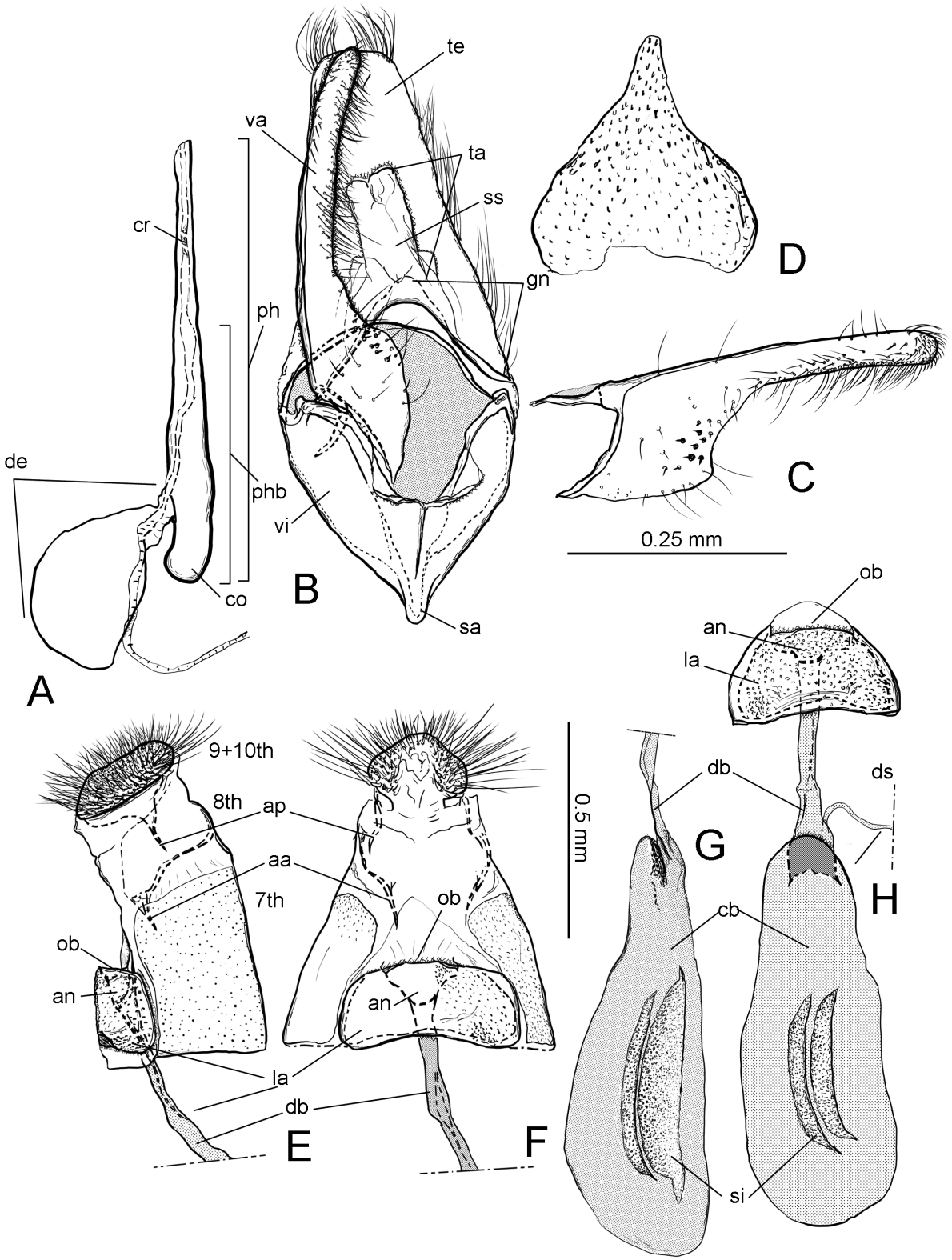

FIGURE 40. Genitalia of *Philodoria*. **A–D**: Male genitalia of *P. marginestrigata*, Kauai (CJ521/SK784), host: *Sida fallax*, **E–H**: Female genitalia of *P. basalis*, Hawaii (Big Island [SKH09-1]), host: *Metrosideros polymorpha*, **E–G**: SK617, **H**: SK616. A Phallus, lateral view, **B** Genitalia except right valva and phallus, ventral view, C Right valva, inside view, **D** Dorsal flap, inside view, **E, G** Female genitalia, lateral view, **F, H** Same, ventral view. aa: apophysis anterioris, an: antrum, ap: apophysis posterioris, cb: corpus bursae, co: coecum, cr: cornuti, db: ductus bursae, de: ductus ejaculatorius, ds: ductus seminalis, la: lamella antevaginalis, ob: ostium bursae, ph: phallus, phb: phallobase, sa: saccus, si: signum, ta: tuba analis, te: tegumen, va: valva, vi: vinculum.

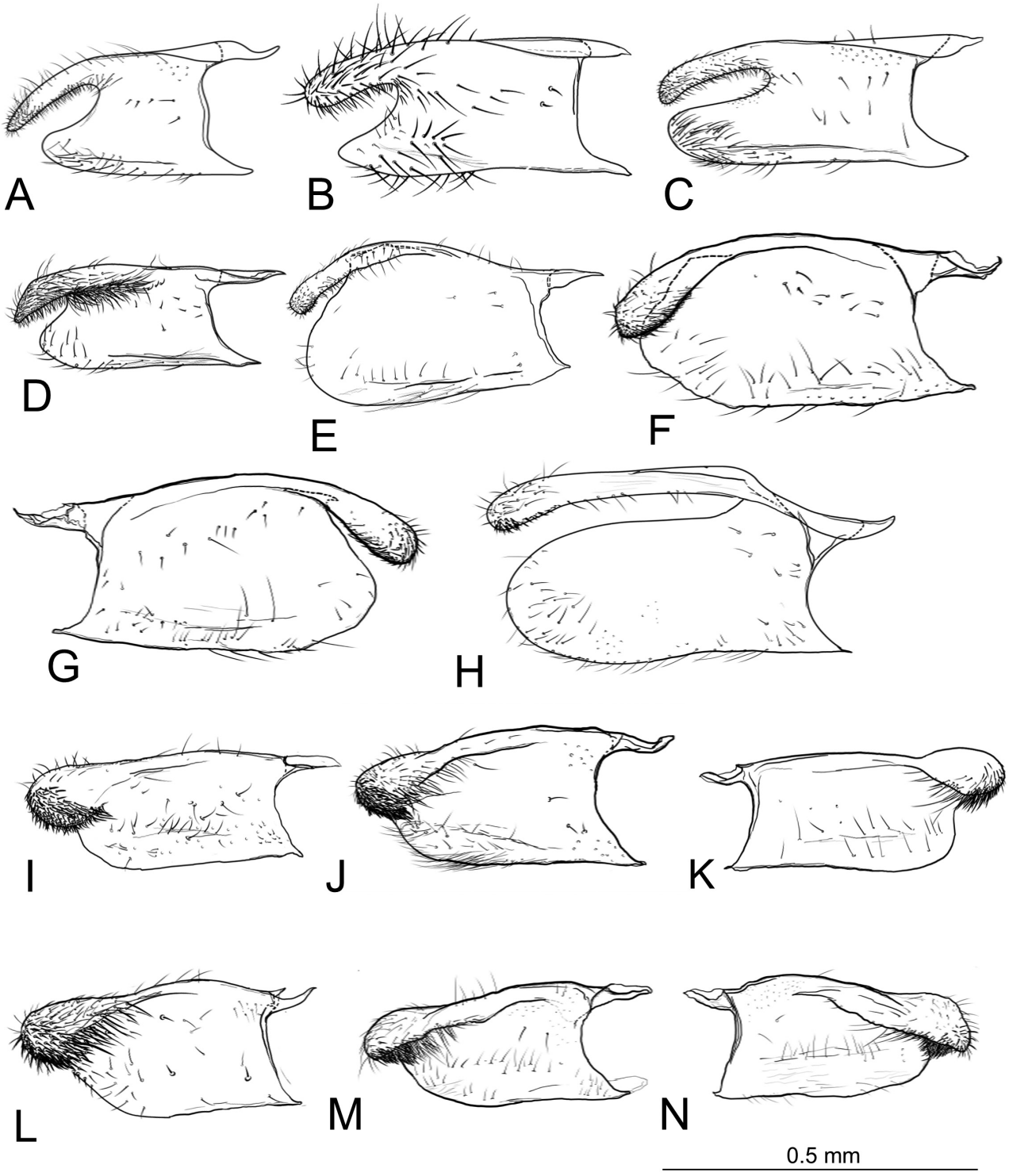

FIGURE 41. Male valva of *Philodoria*, inner view. **A–F**, **H–J**, **L**, **M**: Left valva, **G**, **K**, **N**: Right valva. **A** *P. succedanea*, Maui, SK641, **B** *P. auromagnifica*, Hawaii (Big Island), SK800, **C** *P. auromagnifica*, Kauai, SK689, **D** *P. kolea*, holotype, Hawaii (Big Island), SK851, **E** *P. lysimachiella*, Oahu, SK656, **F**, **G** *P.* sp. 7, Kauai, SK754, **H** *P. molokaiensis*, Molokai, SK666, **I** *P. basalis*, Hawaii (Big Island), SK614, **J** *P. splendida*, Maui, SK696, **K** Same species, Oahu, SK747, host *Syzygium* sp., **L** *P. lama*, holotype, Maui SK744, **M** *P. napaliensis*, paratype, Kauai, SK767, **N** Same as **L**, paratype, Kauai, SK745.

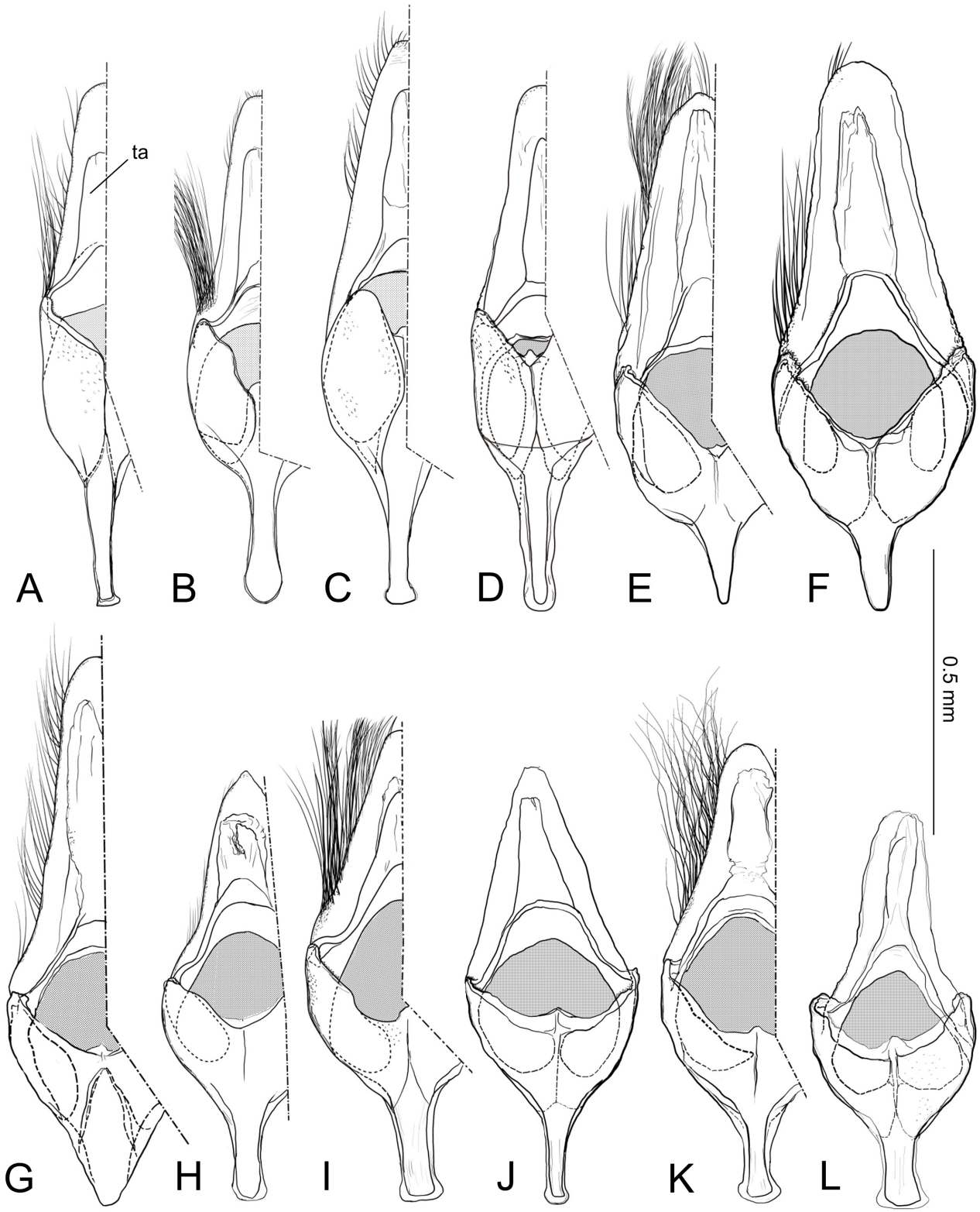

FIGURE 42. Genital capsule of *Philodoria*, excluding right portion of male genitalia, ventral view. **A** *P. succedanea*, Maui, SK641, **B** *P. auromagnifica*, Hawaii (Big Island), SK800, **C** *P. auromagnifica*, Kauai, SK689, **D** *P. kolea*, holotype, Hawaii (Big Island), SK851, **E** *P. lysimachiella*, Oahu, SK656, **F** *P*. sp. 7, Kauai, SK754, **G** *P. molokaiensis*, Molokai, SK666, **H** *P. basalis*, Hawaii (Big Island), SK614, **I** *P. splendida*, Maui, SK696, **J** Same species, Oahu, SK747, host *Syzygium* sp., **K** *P. lama*, holotype, Maui, SK744, **L** *P. napaliensis*, paratype, Kauai, SK745. Abbreviation: ta: tuba analis.

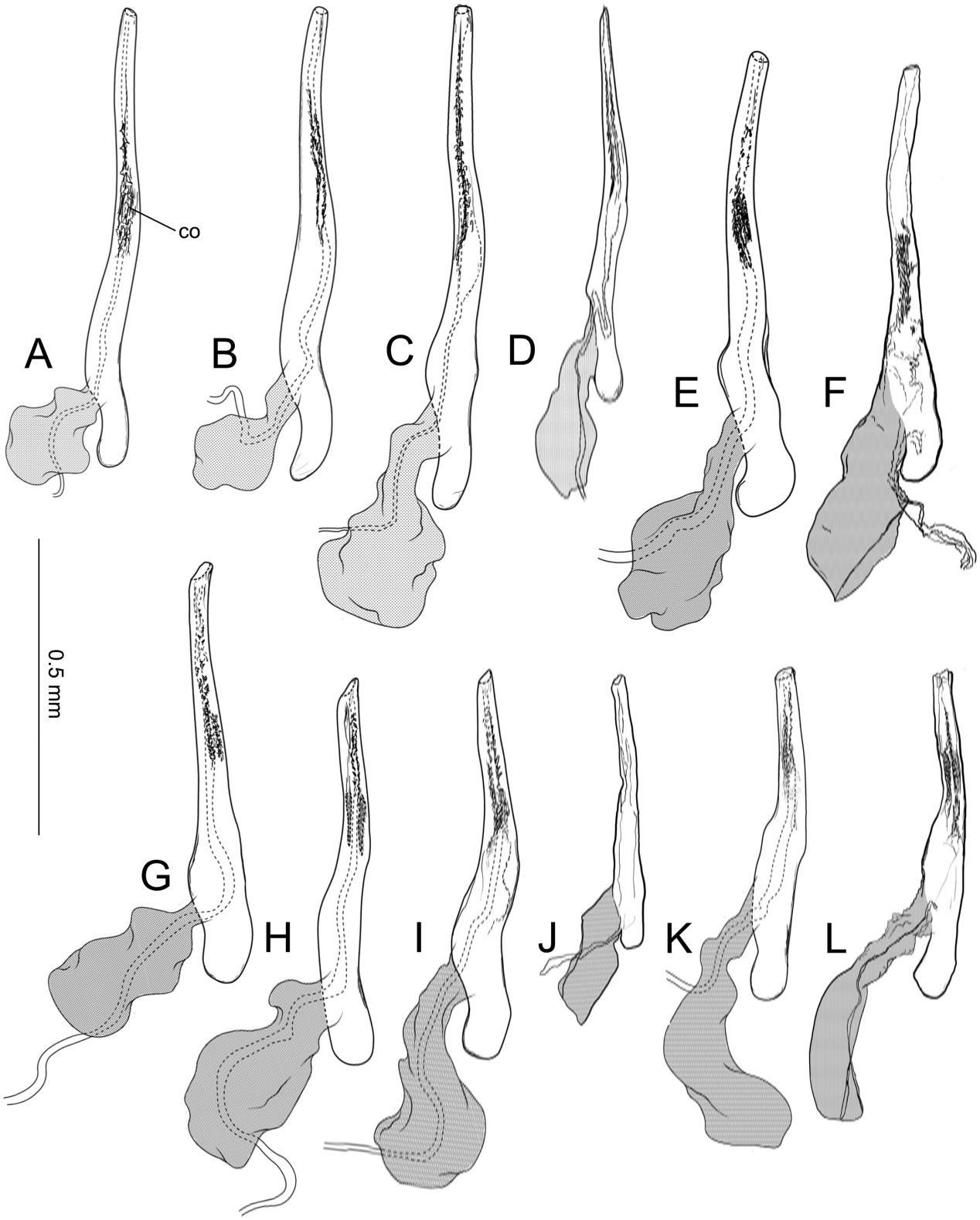

FIGURE 43. Phallus of *Philodoria*, lateral view. **A** *P. succedanea*, Maui, SK641, **B** *P. auromagnifica*, Hawaii (Big Island), SK800, **C** *P. auromagnifica*, Kauai, SK689, **D** *P. kolea*, holotype, Hawaii (Big Island), SK851, **E** *P. lysimachiella*, Oahu, SK656, **F** *P*. sp. 7, Kauai, SK755, **G** *P. molokaiensis*, Molokai, SK666, **H** *P. basalis*, Hawaii (Big Island), SK614, **I** *P. splendida*, Maui, SK696, **J** Same species, Oahu, SK747, host *Syzygium* sp., **K** *P. lama*, holotype, Maui, SK744, **L** *P. napaliensis*, paratype, Kauai, SK767.

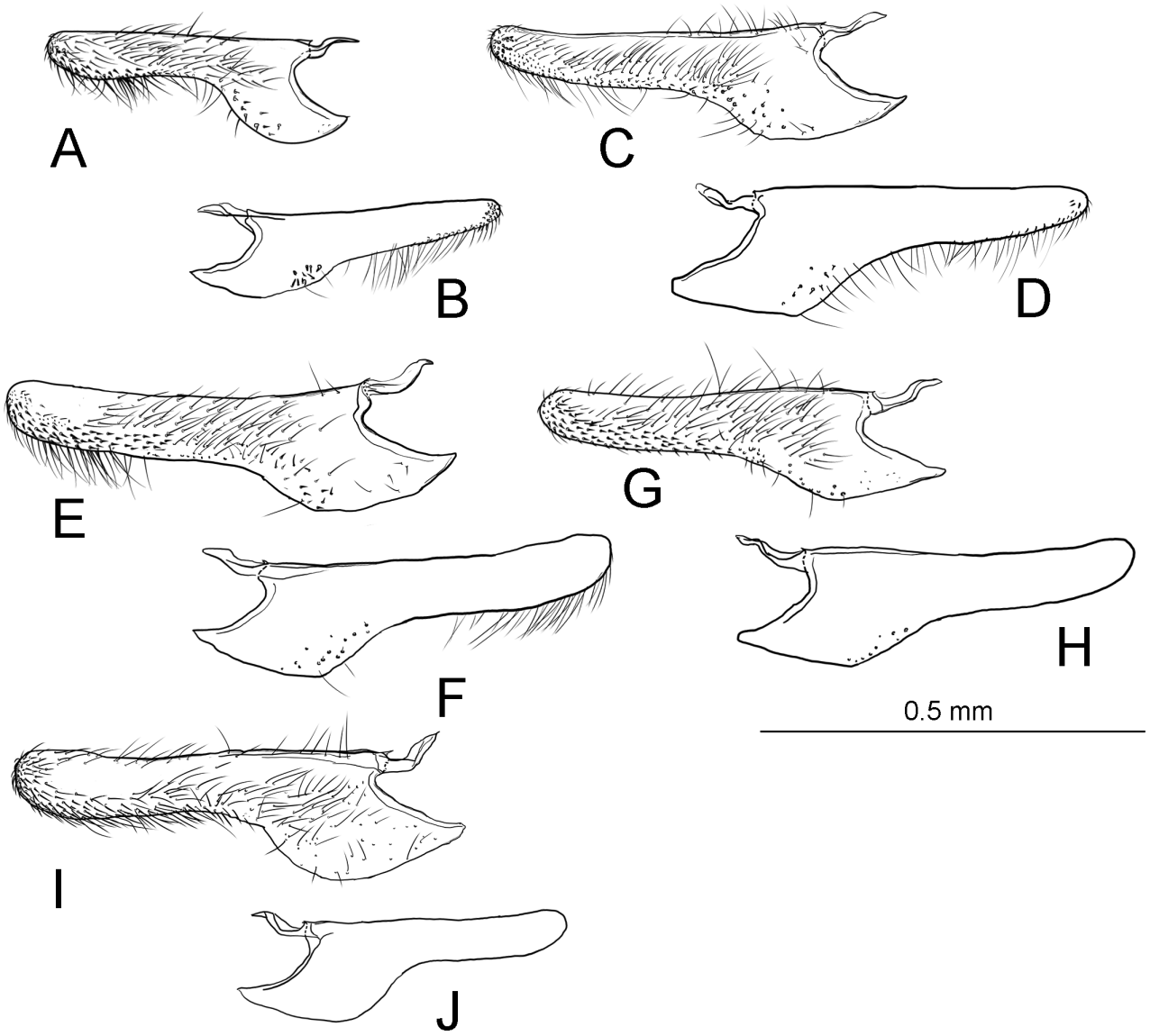

FIGURE 44. Valva of *Philodoria*, inner view. **A**, **C**, **E**, **G**, **I**: Left valva, **B**, **D**, **F**, **H**, **J**: Right valva. **A**, **B** *P. pipturiella*, paralectotype, Oahu, SK719, **C**, **D** *P. pipturicola*, paralectotype, Oahu, SK715, **E**, **F** *P. Haelaauensis*, holotype, Maui, SK718, **G**, **H** *P. haelaauensis*, Molokai, SK704 **I** *P. floscula*, Hawaii (Big Island), SK818, **J** *P. floscula*, Hawaii (Big Island), PHIL0001.

Female genitalia (Fig. 58I, J): new record (n=2). 1260 µm long. Ostium bursae large; antrum cup-shaped with a pair of lateral lobes; lamella antevaginalis 220–230 µm, weakly sclerotized, trapezoid in ventral view, inflexed on the posterior margin, widening toward anterior margin of A7. Ductus bursae short, terminus biforked. Corpus bursae 810 µm, oblong, signa a pair of longitudinal, partly sclerotized wrinkles.

Distribution. Oahu (Swezey, 1940).

Host plants. Asteraceae: *Dubautia laxa* Hook. & Arn. (Swezey, 1940) and *D. plantaginea* Gaudich.: new record.

Biology. (Fig. 88G, H). Swezey (1940: 463) reported its biology and compared it to *P. dubautiella*: "The present species is very close to *Parectopa dubautiella* (Swezey) which mines the leaves of *Dubautia plantaginea*, while our present species mines the leaves of *Dubautia laxa*, a pubescent leaved species, as well as some other species. The mines differ somewhat, possibly on account of the differently-shaped leaves in which they occur. The mine of *naenaeiella* is more irregular in its course and finally becomes a much larger blotch; whereas, the mine of *dubautiella* is narrower and extends nearly straight, following between the nearly parallel veins of the narrow elongate leaves for two or three loops almost the full length of the leaf. The larvae have slight differences, and the cocoon of *dubautiella* is made within the mine, whereas the larvae of *naenaeiella* often issue to form their white oval

cocoons on the surface of the leaf, sometimes on the leaves of adjoining plants. The adult of *naenaeiella* is larger than *dubautiella*, very similar in wing markings, except that it has only one oblique white costal streak, whereas *dubautiella* has two." We observed the larva mining *Dubautia* leaves, forming a linear to blotch mine. Leaf mines were common on *Dubautia laxa* in the southern Koolau mountains of Oahu, but we did not survey for this plant on the northern Koolau Mountains.

Parasitoids. Eulophidae: *Euderus metallicus* (Ashmead, 1901), *Sympiesis vagans* (Timberlake, 1926).

Remarks. We identified one adult moth (Coll ID CJ-142 / GenBank accession no. ID KT982413) as *P. naenaeiella*, based on the presence of a small white patch near the base on forewing, from which whole bodies were sacrificed for molecular analysis (Johns *et al*. 2016). *Philodoria naenaeiella* was treated as *Gracilaria epibathra* Walsingham (= *Philodoria epibathra*) before Swezey (1940). We apply the name *P. naenaeiella* to specimens on *Dubautia laxa* from Oahu.

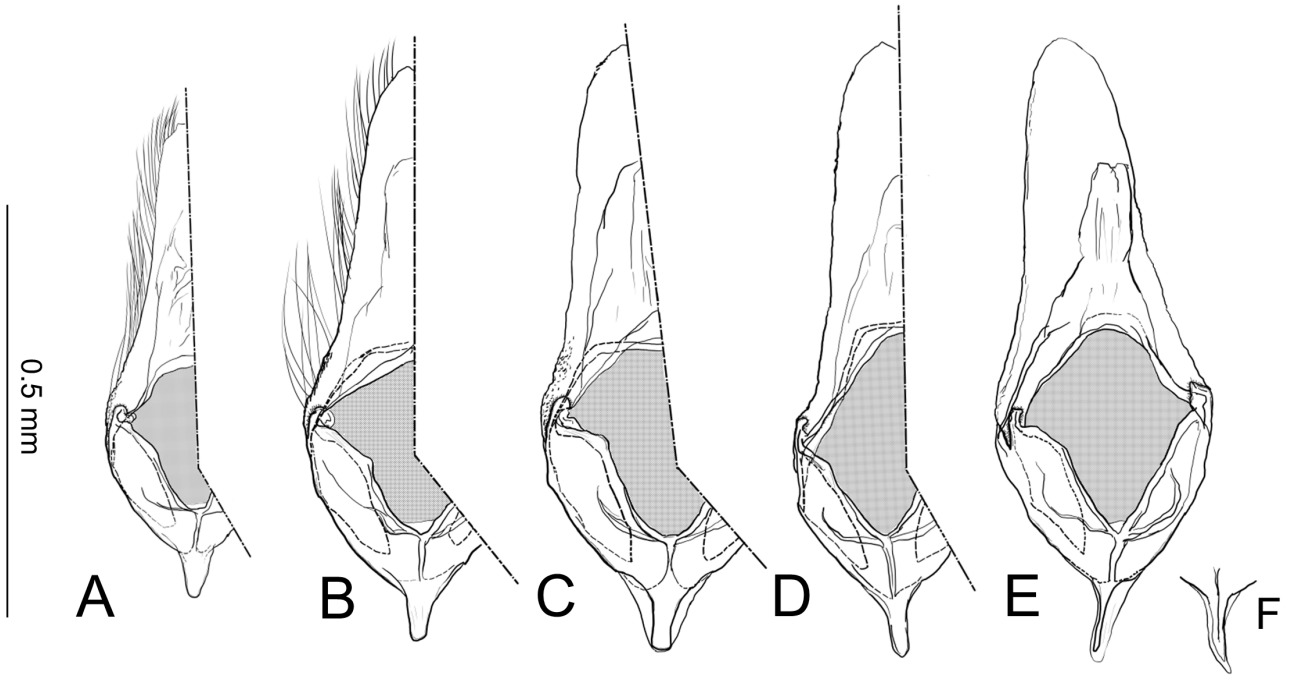

FIGURE 45. Genital capsule of *Philodoria*, excluding right portion of male genitalia, ventral view. **A** *P. pipturiella*, paralectotype, Oahu, SK719, **B** *P. pipturicola*, paralectotype, Oahu, SK715 **C** *P. haelaauensis*, holotype, Maui, SK718, **D** *P. haelaauensis*, Molokai, SK704, **E** *P. floscula*, Hawaii (Big Island), SK818, **F** Saccus, *P. floscula*, Hawaii (Big Island), PHIL0002.

Philodoria knudseniiella Kobayashi, Johns & Kawahara sp. n.

Figs. 17A–C, 47I, 48I, 49I, 58K, 62I, J.

Parectopa naenaeiella Swezey, 1940: 462–463.
Philodoria naenaeiella (Swezey, 1940); Zimmerman 1978a: 685–686, figs. 443, 449, 457, 458 (Misidentification).

Type locality. Alakai (Kauai).

Etymology. The specific epithet is derived from the host plant species name, *knudsenii*.

Type material. Holotype ♂, Alakai, Kauai, 11.vii.2015 (stored), C.A. Johns leg., 20.vi.2015, host: *Dubautia knudsenii* subsp. *nagate*, CJ480, SK862♂ in BPBM. Paratype 2♀: 1♀, same locality and data as holotype, CJ480, SK863 in BPBM. 1♀, Kumuwela, Kauai, 10.iii.1928, O.H. Swezey Collector ex Unknown Composite [*Dubautia latifolia* identified by Zimmerman (1978a)], 'syntype of *Parectopa* [= *Philodoria*] *naenaeiella*', Z-I-10-66-A, 34241 in BPBM. The holotype was preserved as a dry pinned specimen by placing four wings without mountant under a coverslip.

Diagnosis. Dark brown forewing with four outwardly oblique white streaks: wider $\mathbf{ds}_{1-3}$ and $\mathbf{cs}_{3}$ (Fig. 17A–C). Similar to *P. naenaeiella* (Swezey) and *P. hesperomanniella* **sp. n.**, but distinguished from *P. naenaeiella* by the $\mathbf{ds}_{1}$

reaching midway across the wing and from *P. hesperomanniella* by the wider **ds**$_{1–3}$ and indistinct fuscous patch from dorsal 3/4 to apex instead of bluish patch. Male genitalia differ from that of *P. hesperomanniella* by the digitiform saccus and rather slender valva; the apical region of the valva is slender and incurved. Female genitalia differ from those of *P. naenaeiella* and *P. hesperomanniella* by the rather semicircular lamella antevaginalis.

Description: Adult (Fig. 17A–C). Wingspan 9.3 mm in paratype; forewing length 4.1–4.3 mm in holotype, 4.1–4.4 mm in paratype. Head pure white, with brown scales posteriorly; frons white to ocherous; maxillary palpus white with dark brown scales; labial palpus white, second segment broadly infuscated apically, third segment with slight infuscation near base and near apex. Antenna pale brownish, basal segment paler and white beneath, about 1.3x length of forewing. Thorax dark brown anteriorly and white posteriorly colosed with dark brown scales. Forewing dark brownish with three outwardly oblique white dorsal streaks, to a point about midway across the wing: the wider **ds**$_1$ at near base, **ds**$_2$ about at dorsal 2/5, **ds**$_3$ at dorsal 2/3; a slender outwardly oblique white **cs**$_3$ from 3/5 terminating a little distad from apex of **ds**$_3$ with some fuscous scales; all of the white streaks margined with a few black scales; apical portion orange and three white costal spots (**a, b, c**) between **cs**$_3$ and apex, separated by fuscous scales; cilia fuscous with distinct darker fuscous basal line, with few white spots at apex, dorsal cilia blackish. Hindwing and cilia grayish fuscous. Abdomen grayish brown and white beneath. Legs brown, tarsi white banded.

Male genitalia (Figs. 47I, 48I, 49I) (n=1). Capsule 1020 µm. Tegumen 0.8 x length of valva; valva 780 µm long, widened at basal half and tapering along costal margin from 2/5 to apex, becoming very narrow and slightly curved inward (Fig. 47I). Saccus digitiform in ventral view (Fig. 48I). Phallus 780 µm long, straight with developed coecum; a series of fine cornuti on vesica (Fig. 49I).

Female genitalia (Figs. 58K, 62I) (n=3). Similar to *P. naenaeiella*. 1430 µm long. Ostium bursae large; antrum cup-shaped with a pair of lateral lobes; lamella antevaginalis 290 µm, weakly sclerotized, slightly inflexed on the posterior margin, widening toward anterior margin of A7. Ductus bursae short and middle region weakly sclerotized, round and flat; terminus of ductus bursae tubular, biforked. Corpus bursae 800 µm, oblong; signa a pair of longitudinal, partly sclerotized wrinkles.

Distribution. Kauai.

Host plants. Asteraceae: *Dubautia knudsenii* subsp. *nagate* (H. St. John) G. D. Carr and *D. latifolia* (A. Gray) D. D. Keck.

Biology. Unknown, but it is presumably similar to that of *P. naenaeiella*.

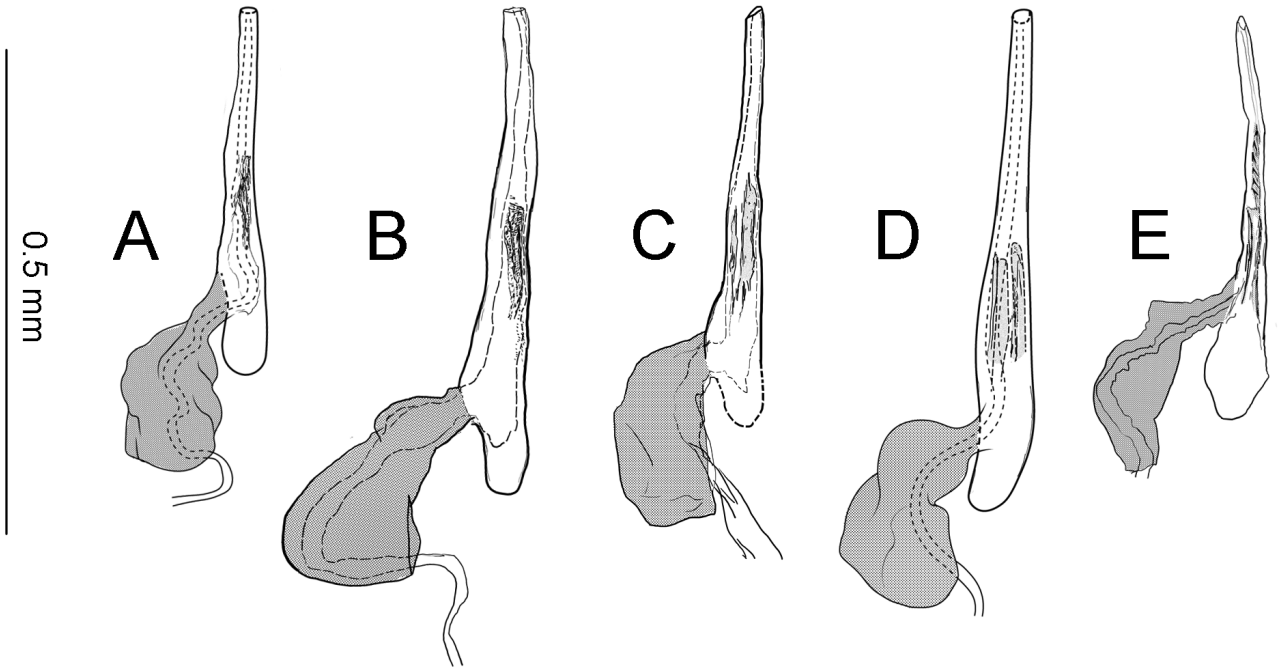

FIGURE 46. Phallus of *Philodoria*, lateral view. **A** *P. pipturiella*, paralectotype, Oahu, SK719, **B** *P. pipturicola*, paralectotype, Oahu, SK715, **C** *P. haelaauensis*, holotype, Maui, SK718, **D** *P. haelaauensis*, Molokai, SK704, **E** *P. floscula*, Hawaii (Big Island), SK818.

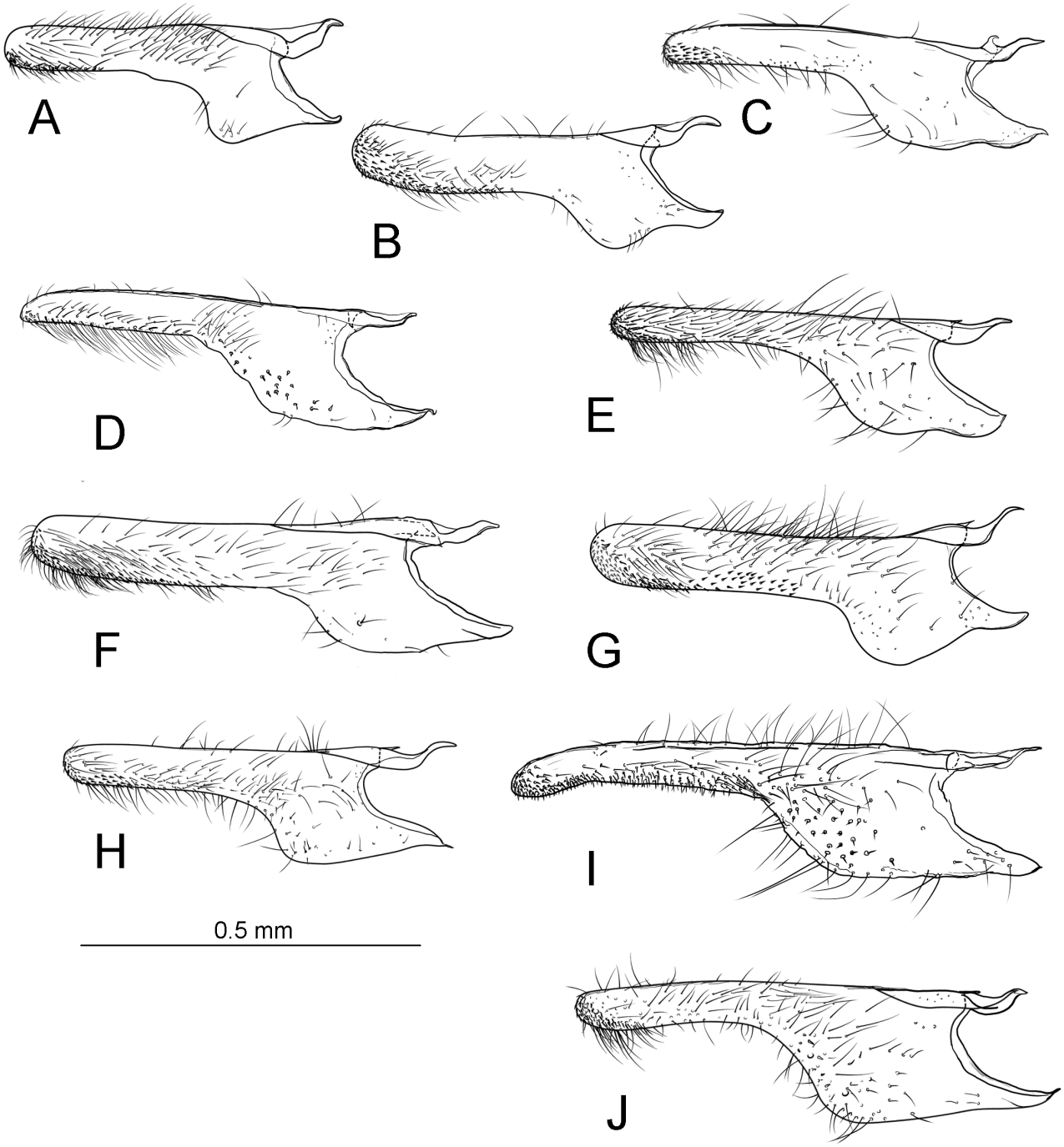

FIGURE 47. Left valva of *Philodoria*, inner view. **A** *P. wilkesiella*, Maui, PHIL0007, **B** *P. epibathra*, Molokai, SK678, **C** *P. dubauticola*, Maui, SK646, **D** *P. dubautiella*, paralectotype, Oahu SK726, **E** *P. alakaiensis*, paratype, Kauai, SK660, **F** *P. limahuliensis*, holotype, Kauai, SK731, **G** *P. hibiscella*, Oahu, SK684, **H** *P. naenaeiella*, paralectotype, Oahu, SK691, **I** *P. knudseniiella*, holotype Kauai, SK862, **J** *P. hesperomanniella*, holotype, Maui, SK831.

Philodoria hesperomanniella **Kobayashi, Johns & Kawahara sp. n.**
Figs. 18, 47J, 48J, 49J, 58L, M, 63A, B, 75B, C, 89.

Parectopa naenaeiella Swezey, 1940: 462–463.
Philodoria naenaeiella (Swezey, 1940); Zimmerman 1978a: 685–686, figs. 449, 457, 458.
Philodoria sp. 11; Johns *et al*. 2018: fig. 2.

Type locality. Waihee Valley (Maui)

Etymology. The specific epithet, *hesperomanniella* refers to the genus of the moth's host plant, *Hesperomannia*.

Type material. Holotype ♂, Waihee Valley, Maui, 12.viii.2014 (stored), C.A. Johns leg., 30.vii.2014, host: *Hesperomannia arborescens*, CJ367, SK831♂ in BPBM. Paratype 6 (3♀, 1 sex unknown). 1♀, Pupukea, Oahu, 17.xii.1933, O.H. Swezey Collector, *Hesperomannia swezeyi*, "paratype of *P. naenaeiella*", Z-V-17-61, BPBM 34224 (Fig. 18E); Host *H. swezeyi* in BPBM; 2♀, 1 (sex unknown), same locality and data as holotype, C.A. Johns leg., CJ367 / SK832♀, CJ372 / SK620♀. The holotype was mounted as a dry pinned specimen (Fig. 18B, C) by placing under a coverslip without mountant, two forewings and half of the two hindwings (Fig. 18A). The three paratypes were also mounted as partial dry pinned specimens: CJ367♀ comprises three wings without mountant under a coverslip, two complete forewings and 3/4 of one hindwing (Fig. 18D); CJ367 (sex unknown) hindwings missing; CJ372♀ left hindwing missing.

Additional material. 1♂, 1♀, Iao Valley, Maui, 11.viii.2014 (stored), C.A. Johns leg., 28.vii.2014, CJ362/ PHIL0035♂, 0036♀, only genitalia slides, deposited in BPBM. Two specimens have genitalia and abdomen intact.

Diagnosis. Described from a paratype of *P. naenaeiella* Swezey feeding on *Hesperomannia* and new specimens collected during fieldwork for the present study. Distinguished from *P. naenaeiella* by having an outwardly oblique white $\mathbf{ds_1}$ at near base and blue patch at apical potion in the forewing (Figs.18, 75B, C); the male genitalia have a valva widening from the base to the middle and a short and triangular saccus. Swezey (1940) described some paratypes of *P. naenaeiella* reared from leaves of *Hesperomannia swezeyi* collected along Pupukea-Kahuku Trail, April 5, 1925, and February 15, 1928. We could not find these specimens among the material in the BPBM.

Description: Adult (Figs.18, 75B, C). Wingspan 7–8 mm in paratype; forewing length 4.1–4.2 mm in holotype, 3.2–4.1 mm in paratype. Head pale ocherous, with some ocherous scales posteriorly; frons white; maxillary palpus white at basal part, mixed with dark brown scales at apex; labial palpus white, second segment broadly infuscated apically, third segment with slight infuscation near base and near apex. Antenna pale brown, basal segment paler and white beneath, about 1.3x length of forewing. Thorax pale brown. Forewing dark brown, with three outwardly oblique white dorsal streaks, all wide at dorsum and narrowing to a point about midway across the wing: $\mathbf{ds_1}$ at near base, $\mathbf{ds_2}$ about at dorsal 2/5, $\mathbf{ds_3}$ at dorsal 2/3; a slender outwardly oblique white $\mathbf{cs_3}$ from 3/5 terminating a little distad from apex of third dorsal streak, an interrupted blue patch from there to apex; all of the white streaks margined with a few black scales; three white costal spots (**a, b, c**) between $\mathbf{cs_3}$ and apex, separated by fuscous scales; cilia fuscous with distinct darker fuscous $\mathbf{bl_1}$, with white spots at the costal white spots, dorsal cilia pale gray, very long. Hindwing and cilia uniformly grayish fuscous. Abdomen grayish brown. Legs grayish brown, tarsi white banded.

Male genitalia (Figs. 47J, 48J, 49J) (n=2). Capsule 940 µm. Tegumen 0.9 x length of valva; valva 660 µm long, widened at basal half and tapering along costal margin from 2/5 to apex, becoming very narrow and slightly curved toward ventral side (Fig. 47J). Saccus short and triangular in ventral view (Fig. 48J). Phallus about 700 µm long and straight with developed coecum; cornuti in vesica indistinct (Fig. 49J).

Female genitalia (Figs. 58L, M, 63A) (n=4). Similar to *P. naenaeiella*. 1230 µm long. Ostium bursae large; antrum cup-shaped with a pair of lateral lobes; lamella antevaginalis 180 µm, weakly sclerotized, indented near the posterior margin, widening toward anterior margin of A7. Ductus bursae short, and middle region weakly sclerotized, round and flat; terminus of ductus bursae tubular, biforked. Corpus bursae 720 µm, nearly pyriform, signa a pair of longitudinal, partly sclerotized wrinkles.

Distribution. Oahu and Maui.

Host plants. Asteraceae: *Hesperomannia arborescens* A.Gray and *H. swezeyi* O.Deg. *H. arborescens* and *H. swezeyi* are two of Hawaii's most critically endangered plants (Morden & Harbin 2013).

Biology. (Fig. 89). Larvae at first form sinuous-linear mine along the leaf margin on the adaxial leaf surface (Fig. 89A), which expands as larvae grow (Fig. 89C, E). One or two mines per leaf. The late instar larva is pale yellow. The final instar larva folds the leaf tissue lined with silk threads and creates a cocoon on the adaxial leaf surface. The cocoon fold is white (Fig. 89F).

Remarks. We collected leaf mines from populations of *H. arborescens* in the Iao and Waihee valley (West Maui). We were unable to visit the Honokohau valley population of *H. arborescens*. We also visited the Molokai population of *H. arborescens* below Olokui summit at the Waiehu Sea Cliffs in July of 2015. No leaf mine activity was observed then. Herbarium specimens from the now extirpated population of *H. arborescens* on Lana'i (Morden & Harbin 2013) revealed leaf-miner damage from an undescribed, extinct *Philodoria* species (Johns *et al*. 2014).

We visited two populations of *H. swezeyi* in June/July of 2015. Neither population exhibited any signs of leaf mine damage. However, one collaborator (N. Tangalin) said she had seen leaf mines on these populations in previous years. Herbarium specimens of this plant species also show leaf miner activity. We have not surveyed *H. oahuensis* (Hillebr.) O.Deg for leaf mine damage. This should be a priority of future surveys of *Philodoria*, since *H. oahuensis* is a highly endangered plant (Morden & Harbin 2013).

Philodoria sp. 2 of Johns *et al*. (2018)

Fig. 90.

Philodoria sp. 2; Johns *et al*. 2018: fig. 2.

Material examined. 2 (sex unknown), Wahiawa Mts., Kauai, 18.vi.2013 (stored), host: *Hesperomannia lydgateyi*, CJ149. Two adults (CJ149/AHE_16) entirely sacrificed for molecular analysis (Johns *et al*. 2018, fig. 2).

Diagnosis. Genetically distinct from *P. hesperomanniella* **sp. n.** (Johns *et al*. 2018: fig. 2).

Adult. Unknown.

Distribution. Kauai. **Host plants.** Asteraceae: *Hesperomannia lydgateyi* C.N.Forbes.

Biology. (Fig. 90). Larvae form a sinuous linear mine along adaxial leaf margin that gradually expands as larvae feed and grow. One or two mines per leaf.

Remarks. Unfortunately, the two known specimens of this species were sacrificed for molecular analysis. DNA data suggest that this is a distinct species. Future surveys should survey the Wahiawa Mountains for this moth so that the morphology of this species can be studied and a formal species name can be assigned.

Philodoria neraudicola (Swezey, 1920)

Figs. 19A, B, 27I, J, 50A, B, 51A, 52A, 59A, B, 85E, 86C.

Gracilaria neraudicola Swezey, 1920b: 385–386.
Parectopa neraudicola (Swezey, 1920); Swezy 1928: 191.
Philodoria neraudicola (Swezey, 1920); Zimmerman 1978a: 689, fig. 444.

Type locality. Punaluu (Oahu).

Type material. Lectotype ♂, Punaluu, Oahu, 11.vi.1916, Coll. O.H.S. (= O.H. Swezey), ex *Neraudia* [*melastomifalia*], |*Gracilaria neraudicola* Swezey|Holotype| Type no. 4261 in BPBM (here designated). Paralectotype 5 (1♂, 1♀, 3 sex unknown): Host *N. melastomifalia*, |Paratype | O.H. Swezey: 1 (sex unknown), same data and locality as lectotype, missing abdomen, BPBM34243; 1♂, 1♀, 2 (sex unknown), Waiahole, Oahu, 13.viii.1916, SK708♀|BPBM34244, BPBM34245, BPBM34246, and 1♂, SK707♂ in USNM. Described from six specimens from Oahu. The holotype was not specified in the original description, therefore the so-labeled 'holotype' and 'paratypes' can be considered syntypes under Article 73.2 of the Code (ICZN 1999), and any of them is eligible for designation as lectotype under Article 74 of the Code (ICZN 1999). The syntype 'holotype' is here designated as lectotype (Fig. 19A) and the remaining syntypes are paralectotypes.

Additional material. 3 (sex unknown), Kamiloloa, Mol., 3200, 20.xii.1925, O.H. Swezey, *Pipturus*, BPBM34247, BPBM34249, BPBM34250; 4♀, Iao Valley, Maui, 9&10.viii.2014 (stored), C.A. Johns leg., host: *Pipturus albidus*, 28.vii.2014, CJ336, SK838♀ in BPBM; 1♀ 1 (sex unknown), Same locality, 10&12.viii.2014 (stored), C.A. Johns leg., host: *Pipturus* sp., CJ360, CJ369 in BPBM.

Diagnosis. The forewing pattern is similar to *P. hesperomanniella* **sp. n.** and *P. urerana* (Swezey), but *P. neraudicola* has an orangish ocherous apical region; the saccus is slender and pointed. Swezey (1920) noted that a series of five specimens reared from leaves of *Pipturus albidus* at Pahoa, Puna on the island of Hawaii (Big Island), September 20, 1918 seems to be the same species. However, the five syntypes from Swezey (1920) have distinguishable forewing pattern from that of *P. neraudicola*, and therefore we treat them here as new species, *P. obamaorum* **sp. n.** (See diagnosis of *P. obamaorum*).

Redescription: Adult (Fig. 19A, B). Wingspan 6.5–8.1 mm in type series; forewing length 3.75 mm in lectotype, 2.9–3.8 mm in paralectotype. Head creamy white; frons white; maxillary palpus white mixed with fuscous scales; labial palpus white, median joint fuscous at apex, terminal joint with fuscous band at middle and at apex.

Antenna brownish, basal segment pale. Thorax brownish fuscous, pale in middle and posteriorly. Forewing brownish fuscous, with three outwardly-oblique white dorsal streaks (**ds$_{1–3}$**) widened at base and margined with a few black scales, somewhat curved apically, the **ds$_3$** nearly connected with a white slender outwardly-oblique black-margined line (**cs$_1$**) at three-fourths of costa, beyond this white line, three or four white costal spots (**a, b, c**); a round black spot at apex with a few pale blue scales, a few pale blue scales between this spot and the **ds$_3$**, sometimes this area ocherous; apical and terminal cilia brown, paler near base and black **bl$_1$** at extreme base, tornal cilia- very pale brown. Hindwing and cilia pale brown. Abdomen pale brownish. Legs ocherous, anterior and middle tibiae and tarsi and posterior tarsi fuscous marked.

Male genitalia (Figs. 50A, B, 51A, 52A) (n=1). Capsule 780 µm. Tegumen 0.9 x length of valva; valva 540 µm long, tapering along costal margin from 2/5 to apex, slightly narrowing at middle with small spines at apex; a set of short spines arranged along inner side of basal region (Fig. 50A, B). Saccus slender and pointed at apex in ventral view (Fig. 51A). Phallus 570 µm long and thickened at phallobase with well-developed coecum; two series of minute cornuti in vesica (Fig. 52A).

Female genitalia (Fig. 59A, B) (n=2). 1100–1200 µm long. Ostium bursae large; antrum cup-shaped with a pair of lateral lobes; lamella antevaginalis 220 µm, weakly sclerotized, trapezoid in ventral view, widening toward anterior margin of A7. Ductus bursae slender, middle region weakly sclerotized, round and flat; terminus of ductus bursae tubular, biforked. Corpus bursae 670 µm, oblong; signa a pair of longitudinal, partly sclerotized wrinkles.

Distribution. Molokai (Zimmerman 1978a), Oahu (Swezey 1920), Maui: new record and possibly Kauai.

Host plants. Urticaceae: *Neraudia melastomifolia* Gaudich. (Swezey 1920), *Pipturus albidus* A.Gray ex H.Mann and *Pipturus* sp.

Biology. (Figs. 85E, 86C) Little is known about its biology. The larva on *Pipturus* form a blotch mine on the adaxial leaf surface that gathers the frass in the center (Fig. 85E); numerous mines and cocoons per leaf; pupation occurs in a brownish-white cocoon outside of the mine, which is usually on the adaxial leaf surface (Fig. 86C).

Parasitoids. Eulophidae: *Euderus metallicus* (Ashmead, 1901), *Pnigalio externa* (Timberlake, 1927); (Zimmerman 1978a).

Remarks. We could not locate the Kauai specimens and therefore the record from Kauai cannot be confirmed. Leaf mines on *Pipturus* in Iao Valley along Iao Stream were abundant during our survey in 2014. We also collected similar blotch mines (Fig. 86B) and tortuous linear to blotch mines (Fig. 85C, D) on West Maui and Hawaii (Big Island). Unfortunately, adults did not emerge, but these mines may be from larvae of *P. floscula* or *P. haelaauensis* **sp. n.** The host plant genus *Neraudia* has become exceedingly rare on the Hawaiian Islands with several species being listed as endangered. We were able to locate fewer than ten plants of *N. melastomifolia* throughout our surveys. None of these plants showed signs of leaf mine activity. However, surveys of *Neraudia* herbarium specimens (BPBM) revealed *Philodoria* leaf mines on several plants.

Philodoria obamaorum Kobayashi, Johns & Kawahara, sp. n.

Figs. 19C–E, 27K–M, 50C, D, 51B, 52B, 59C, D, 63C–G.

Gracilaria neraudicola Swezey, 1920: 385–386.
Parectopa neraudicola Swezey, 1920; Swezey 1928: 191.
Philodoria neraudicola (Swezey, 1920); Zimmerman 1978a: 689, figs. 449, 458.
Philodoria sp. 16; Johns *et al*. 2018, fig. 2.

Type locality. Pahoa (Big Island).

Etymology. The specific epithet, *obamaorum*, is named after Barack Hussein Obama II, the 44th president of the United States, born in Honolulu, Hawaii, and his wife, First Lady Michelle LaVaughn Robinson Obama. They have have continued to support nature conservation efforts in Hawaii. Following recommendation 31.1.2. of the International Code of Zoological nomenclature (ICZN, 1999) the specific name is treated as a noun in the genitive plural case.

Type material. Holotype ♂, Pahoa, Puna, Hawaii (Big Island), 20.ix.1918, O.H. Swezey, host: *Pipturus albidus* in USNM. Paratype 14 (4♂, 3♀, 7 sex unknown): 1♂, 1♀, same locality and data as holotype, SK710♀, in USNM; 3♂, 2♀, 2 (sex unknown), S. of Hilo, Hawaii, 25.vii.1921, Swezey coll., *Pipturus* 34248, SK709♂, BPBM34242, no. 4257 |Z-1-26-61(3) ♂, Z-V-18-61♀; 2 (sex unknown), Judd Trail, Hawaii, 13&14.viii.1919, OHS, *Pipturus*, BPBM 34251, BPBM34252.

Additional material. 4 (1♂, 3♀) 1♂, 2♀, Mauna Ulu Havo, Hawaii, 21.v.2015 (stored), C.A. Johns leg., host: *Pipturus* sp., 3.v.2015, CJ423 / SK844♀, 403M / SK736♂, 403O(b-2) / SK739♀ in BPBM; 1♀, Upper Hamakua Ditch trail, Hawaii, 15.v.2016 em., C.L.-Vaamonde & C. Doorenweerd leg., host: *Pipturus* sp., 24.iv.2016(cocoon), CLV0017, SK823♀ in BPBM; 2♀, Puu Makkaala Natural Reserve, Hawaii, 9.vi.2015 (stored), C.A. Johns leg., host: *Pipturus* sp. (B), 25.v.2015, CJ423 / SK844♀, CJ427 in BPBM. In NHMUK: 1♂, Hawaii 2800', Kau District, Ocean View, 23.vi.1976, K. & E. Sattler, B.M.1976-605, *Philodoria* sp. 25 cf *marginestrigata* (Hawaii) Sattler Coll., D.C. Lees Sep. 2016, BMNH(E)1621262; 1♀, Hawaii 1300', S. Hilo District, Upper Waiakea F. R., Stainback Highway, 12.vii.1976, K. & E. Sattler, B.M.1976-605, *Philodoria* sp. 21 (Hawaii) Sattler Coll., D.C. Lees Sep. 2016, BMNH(E)1621128.

Diagnosis. Distinguished from *P. neraudicola* by having a triangular white patch at 3/4 and two white dorsal streaks that are nearly the same width as in the forewing (Fig. 19C, D); saccus and coecum half the length of those of *P. neraudicola* (Figs. 51B, 52B).

Description: Adult (Fig. 19C–E). Wingspan 7.5 mm in holotype, 7.0–7.5 mm in paratype; forewing length 3.3, 3,4 mm in holotype, 3.0–3.5 mm in paratype. Head creamy white; frons white mixed with fuscous scales; maxillary palpus white mixed with fuscous scales; labial palpus white, median joint fuscous at apex, terminal joint with fuscous band at middle and at apex. Antenna brownish, basal segment white. Thorax brownish fuscous, pale in middle and posteriorly. Forewing brownish fuscous with white patches: two outwardly-curved white dorsal streaks: **ds**$_1$ at 1/4, slightly widened at base, **ds**$_2$ at 1/2, almost same width; a triangular white patch (**ds**$_3$) at 3/4, not reaching the middle of wing; a white slender outwardly-oblique **cs**$_3$ at 3/5; all streaks and patch margined with a few black scales; apical portion orangish ocherous; a round black **as** with a few pale blue scales, a few pale blue scales between this spot and **ds**$_3$; cilia brown with three white costal spots; apical and terminal cilia paler near base with black **dl**$_1$, tornal cilia very paler at apex. Hindwing and cilia pale brown. Abdomen pale brownish, white below. Legs ocherous, anterior and middle tibiae fuscous, and middle and posterior tarsi fuscous.

Male genitalia (Figs. 50C, D, 51B, 52B, 63E, F) (n=3). Capsule 700 µm. Tegumen 0.9 x length of valva; valva 480–500 µm long, tapering along costal margin from 2/5 to apex, similar to *P. neraudicola* (Fig. 50C, D). Saccus rather short and pointed at apex in ventral view (Fig. 51B). Phallus 520 µm long and nearly straight with developed coecum; two series of minute cornuti in vesica (Fig. 52B).

Female genitalia (Figs. 59C, D, 63C) (n=5). Similar to *P. neraudicola*. 890–1180 µm long. Lamella antevaginalis 200 µm. Corpus bursae 570 µm.

Distribution. Hawaii (Big Island).

Host plants. Urticaceae: *Pipturus albidus* A.Gray ex H.Mann (Swezey 1920), and *Pipturus* sp.

Biology. C.L.-Vaamonde and C. Doorenweerd collected larvae from leaves of *Pipturus* species in 2016. Larvae formed blotch mines and made six cocoons on the adaxial leaf surface; the orange oval cocoon is 6.0 mm in length and 2.5 mm in width. Two adults emerged from the cocoons, one was *P. obamaorum* and another *P. floscula* Walsingham.

Remarks. This species and other *Pipturus* miners occur together on Hawaii (Big Island). It is unclear which species of *Pipturus* these moths were on at Hawaii Volcanoes National Park, the site that was surveyed in 2016. Some *Philodoria* species may prefer certain species of *Pipturus*, but the determination of host preference is impeded by the unsettled taxonomy of this host plant genus. Future studies of these moths should focus on rearing different species of *Philodoria* from *Pipturus* to understand host plant specificity.

***Philodoria urerana* (Swezey, 1915)**

Figs. 20A, B, 33G, 50E, 51C, 52C, 59E, 78E, F, 95A–C.

Gracilaria urerana Swezey, 1915: 95–96.
Parectopa urerana (Swezey, 1915); Swezey 1928: 191.
Philodoria urerana (Swezey, 1915); Zimmerman 1978a: 691, figs. 446, 453, 460.

Type locality. Mt. Tantalus (Oahu).

Type material. Lectotype ♀, Mt. Tantalus, Oahu, 16.iii.1915, O.H. Swezey, ex *Urera* [*sandwicensis*], |TYPE OF 214 *Gracilaria urerana* Swezey | top one of two cotypes of the same type mount designated by Zimmerman (1978a, 691, fig. 446) in BPBM (Fig. 20A). Paralectotype 1 (sex unknown), bottom one of the same mount of lectotype (Fig.

20B). 17 including six 'syntypes' (2♂, 6♀, 9 sex unknown): 2♂, 4♀, 6 (sex unknown), same data and locality as lectotype, SK671♂, 672♂, 673♀|BPBM34363, BPBM34634 ("ex blotch mine"), BPBM34365–BPBM34369; 2♀, 3 (sex unknown), Same label, "ex serpentine mine" (3 sex unknown) in USNM. This species is described from eight specimens reared from *Urera sandvicensis* and from the same lot of leaves as those collected for *P*. '*ureraella*'. We examined the lectotype and 18 specimens in BPBM and USNM that bear the same data as the lectotype.

Additional material. Oahu: 1♂, Waianae, 28.iii.2016 (stored), K. Bustamente leg., host: *Urera glabra* 9.xi.2015, KMB02, CJ533, SK670♂ in BPBM; 1♂, 1♀, Kaau Crater, 27.vii.2014 (stored), C.A. Johns leg., 10.vii.2014, CJ307, PHIL0032♀, PHIL0033♂, in BPBM (only genitalia slides remain).

Diagnosis. Forewing brownish fuscous to brown with narrow oblique white $\mathbf{ds}_{1-3}$. Similar to *P. hibiscella* (Swezey), but distinguished by the darker forewing with pale lemon-yellow apex.

Redescription: Adult (Figs. 20A, B, 33G). Wingspan 9–11 mm in type series; forewing length 4.5 mm in lectotype, 3.5–4.6 mm in paralectotypes. Head dull ocherous; and frons ocherous; maxillary palpus ocherous, fuscous at apical portion; labial palpus white, terminal segment fuscous externally. Antenna fuscous, paler at the apex, 1.5x length of forewing. Thorax pale brownish ocherous. Forewing brownish fuscous to brown with narrow oblique white streaks: $\mathbf{ds}_1$ at 1/4, $\mathbf{ds}_2$ at 1/2, $\mathbf{ds}_3$ at 3/4, about equally spaced, wider at base, tapering to apex, bent outwards; $\mathbf{cs}_3$ at 2/3, meeting $\mathbf{ds}_3$ in the middle of wing; apical portion pale lemon-yellow with a pale blue spot, sometimes dorsal half with fuscous patch from the dorsum to termen. Cilia white, apical cilia with four fuscous costal lines, terminal cilia fuscous, yellowish at base. Hindwing and cilia light fuscous. Abdomen grayish fuscous. Legs ocherous, fore and mid tibiae fuscous above, tarsi barred with fuscous.

Male genitalia (Figs. 50E, 51C, 52C) (n=3). Capsule 1030 µm. Tegumen 0.8–0.9 x length of valva; valva 690 µm long, tapering along costal margin from 2/5 to apex, slightly rounded at apex and curvied toward dorsally (Fig. 50E). Saccus slender and needle-shaped in ventral view (Fig. 51C). Phallus 670 µm long and straight with developed coecum; cornuti in vesica indistinct (Fig. 52C).

Female genitalia (Fig. 59E) (n=1). 1450 µm long. Ostium bursae large; antrum deeply cup-shaped with a pair of thick lateral lobes; lamella antevaginalis 240 µm, weakly sclerotized, trapezoid in ventral view, widening toward anterior margin of A7. Ductus bursae slender and long, middle part weakly sclerotized, round and flat; terminus of ductus bursae tubular, biforked. Corpus bursae 740 µm, oblong, signa a pair of longitudinal, partly sclerotized wrinkles.

Distribution. Oahu (Swezey 1915).

Host plants. Urticaceae: *Urera sandvicensis* Wedd. (Swezey 1915) and *U. glabra* Wedd.: new record. *Urera* is now rare on the island of Hawaii (Big Island), but *U. glabra* can still be found in large numbers on Oahu.

Biology. (Fig. 95A–C) Swezey (1915: 96) reported the biology: "The mine is very slender where it starts from an egg placed on the under side of the leaf, it gradually widens as the larva grows, becomes serpentine and towards the last enlarges to a blotch. The larva emerges to spin its whitish cocoon on the surface of the leaf. The moths emerged from the cocoons in about ten days." We observed larvae mining leaves of *U. glabra* beginning with a slender, tortuous linear mine that became a blotch mine (Fig. 95A, B) that gradually expanded as larvae grew (Fig. 95A). Usually 2–3 mines per leaf. The final instar larva spun a reddish-brown cocoon at the leaf margin, the leaf margin was slightly curled upwards from the contraction of the cocoon silk (Fig. 95C). Mines were rarely observed during our field surveys, but nearly all mines that we did see were active or fresh.

Parasitoids. Eulophidae: *Sierola* sp., Bethylidae; *Euderus metallicus* (Ashmead, 1901) (Zimmerman 1978a).

Remarks. We discount the distribution records from the island of Hawaii (Big Island) determined by Swezey that were mentioned in Zimmerman (1978a). We could not identify the specimens from Kilauea, Hawaii (Big Island) stored in BPBM, USNM and NHMUK. We also investigated two populations of *Urera* plants on the island of Hawaii (Big Island), but these plants did not have any *Philodoria* mines. The type series was reared by Swezey from the same lot of leaves from which the type series of "*P. ureraella*" (*P. ureraella* and *P. opuhe* in the present study) was reared. In the present study, *P. urerana* was obtained from leaves of *Urera glabra* on Oahu.

Philodoria hauicola (Swezey, 1910)

Figs. 20C, 34F, 37D, 50F, 51D, 52D, 59L, 77A, 92, 93F.

Gracilaria hauicola Swezey, 1910: 106; pl. 3, fig. 5; Swezey 1913b: 224.
Parectopa hauicola (Swezey, 1910); Swezey 1928: 190.
Philodoria hauicola (Swezey, 1910); Zimmerman 1978a: 680, figs. 437, 438, 442, 448, 454.

Type locality. Mt. Tantalus (Oahu)

Type material. Lectotype ♂, Tantalus, Oahu, [summer.1909], Coll. O.H.S [O.H. Swezey], ex *Hibiscus* [*tiliaceus*], |TYPE OF 212 *Gracilaria hauicola* Swezey | in BPBM (here designated). Paralectotype 4♂, 4 (sex unknown); all specimens are same data and locality as lectotype; 2 (sex unknown), No. 34168, 34168 in BPBM; 4♂, ex "hau" (= *Hibiscus tiliaceus*) in USNM. Described from an unspecified number of specimens from Mt. Tantalus, Oahu. In the original description, Swezey mentioned that "My specimens were reared from cocoons collected this summer on Tantalus". We identified nine specimens, one labeled 'TYPE', and eight others. Given the manner in which the descriptions were written, Swezey likely considered the 'TYPE' specimen as the holotype and the remaining eight as paratypes, as noted in a caption by Zimmerman (1978a: 669). But because a holotype was not specified explicitly in the description, the so-labeled types and paratypes are can all be considered syntypes under Article 73.2 of the Code (ICZN 1999), and any of them can be designated as lectotype under Article 74 of the Code (ICZN 1999). The syntype specimen bearing the label 'TYPE' is here designated as lectotype (Fig. 20C) and the remaining syntypes are paralectotypes.

Additional material. 27 (9♂, 10♀, 8 sex unknown). **Oahu**: 4♂, 3♀, Waikiki, Coll. O.H.S, 'Hau tree' (= *Hibiscus tiliaceus*), 3♂, 2♀ in USNM, 1♂, 1♀, SK694♂|BPBM34167; 5♂, 4♀, 6 (sex unknown), Kaneohe T.H., 'ISS.' (= adult emrged) 27.vii.1915, Aug. Busck Collector, "Leaf mines on Hau", SK695♀ in USNM; 3♀, 1 (sex unknown), Nuuanu Pali, 16–21.v.2016 em., S. Kobayashi leg., host: *H. tiliaceus*, 3.v.2016(larva), SK618♀, SK619♀ / SK750(head) in BPBM; **Maui**: 1♀, 1 (sex unknown), Iao Valley, 26&29.iv.2013 (stored), C.A. Johns leg., host: *H. tiliaceus*, 14.iv.2013, CJ065 (sex unknown) / KT982405, CJ087♀ in BPBM. **Hawaii** (Big Island): 1♂, Hawaii, 0-50', Volcanoes Natn. [National] Park, Poupou Kauka, 20.vii.1976, K. & E. Sattler, B.M.1976-605, *Philodoria* sp. 17 (Hawaii), D. C. Lees Sep. 2016, BMNH(E)1621255 in NHMUK.

Diagnosis. Distinguished from other congeners by having a lemon-yellow streak from costal fold to 2/5, then obliquely, at 3/5 to middle the forewing (Fig. 20C); the male genitalia having a rather short and broad phallus (Fig. 52D); the female genitalia having two small pod-like signa with a series of minute spines (Fig. 59L).

Redescription: Adult (Figs. 20C, 34F, 37D). Wingspan 7–8 mm in type series; forewing length 3.25 mm in lectotype, 2.8–3.2 mm in paralectotypes. Head dirty white; frons white; maxillary palpus brown; labial palpus white ocherous, apex of median segment and apical half of terminal segment brown (Figs. 34F, 37D). Antenna white ringed with brown, basal segment white, a little longer than forewing. Thorax and abdomen pale brown above, white below. Forewing brown with a lemon-yellow streak from costal fold to 2/5, then obliquely, at 3/5 to middle to connect with oblique white $\mathbf{ds}_{1,2}$: $\mathbf{ds}_1$ at 2/5, $\mathbf{ds}_2$ at 1/4 almost reaches the yellow streak; a short outwardly oblique white $\mathbf{cs}_3$ at 3/5, almost meeting $\mathbf{ds}_3$; apical portion lemon yellow with two or three costal white lines (**a, b, c**); cilia pale brown. Hindwing and cilia dark fuscous. Legs brown, tarsi ringed with white.

Male genitalia (Figs. 50F, 51D, 52D) (n=1). Capsule 650 µm. Tegumen 0.8–0.9 x length of valva; valva 460 µm long, digitiform and slightly narrowing at middle and rounded at apex and slightly curved toward dorsal side (Fig. 50F). Saccus very slender and needle-shaped in ventral view (Fig. 51D). Phallus 430 µm long and straight with rather small coecum; two series of minute cornuti in vesica (Fig. 52D).

Female genitalia (Fig. 59L) (n=3). 1210 µm long. Ostium bursae large; antrum broad, cup-shaped with a pair of lateral lobes; lamella antevaginalis 180–190 µm, weakly sclerotized, widening toward anterior margin of A7. Ductus bursae broad, middle part weakly sclerotized, round and flat; terminal region of the ductus bursae tubular, biforked. Corpus bursae 680 µm, pyriform; anterior end of corpus bursae weakly sclerotized; paired rows of longitudinal, partly sclerotized wrinkles; two small podlike signa with a series of minute spines.

Distribution. Kauai, Oahu, Maui and Hawaii (Big island) (Swezey 1910b).

Host plants. Malvaceae: *Hibiscus tiliaceus* L. (Swezey 1910b).

Biology. (Figs. 92, 93F). Swezey (1913b: 224) reported that "this species very abundantly mines the leaves of the "hau" tree, *Partitium tiliaceum* (= *Hibiscus tiliaceus*), in the mountains, and the lowlands as well, of all the Islands. There are often many mines per leaf. The larvae emerge to pupate in white oval cocoons on the surface of leaves and other objects". We observed larvae forming a linear-blotch mine beginning with a very slender, linear shape (Fig. 92D, E) that gradually expanded as they fed and grew (Fig. 92H, I). In early instars, linear mine is 2.5–3.5 cm in length and 1–2 mm in width; frass is brown and 0.1–0.2 mm in width. Later blotch mine is 5–10 mm diameter (Fig. 92J). Usually 5–15 mines per leaf (Fig. 92A–C). Larva pale yellow, first to second instars are 1.5–2.5 mm long (Fig. 92G) and late instar is 4.0–6.0 mm long (Fig. 92I, J). Pupation in the white cocoon outside of mine,

on the adaxial leaf (Fig. 92K, L); 5.5 mm in length and 2.5–3.0 mm in width. At Iao Valley, Maui, we observed *P. hibiscella* and *P. hauicola* co-occuring on the same host plant, *H. tiliaceus*.

Parasitoids. (Fig. 106A–F). Eulophidae: *Pholetesor bedelliae* (Viereck, 1911), Braconidae; *Closterocerus* sp., *Euderus metallicus* (Ashmead, 1901), *Pnigalio externa* (Timberlake, 1927), *Sympiesis vagans* (Timberlake, 1926) (Zimmerman 1978a).

Remarks. Swezey (1910b: 106; 1954: 88) reported larval mines and similar mines on *Hibiscus*: "This moth I have named from the 'hau' tree (*Paritium tiliaceum*) whose leaves its larvae mine quite extensively. Some times one finds practically all of the leaves mined and often a dozen or more per leaf. It probably occurs on all the islands where the 'hau' tree occurs. I have observed it at Koloa, Kauai; Wailuku, Maui; Waikiki and Tantalus, Oahu. The white rounded-oval cocoons were found quite abundant on the surface of leaves, and also on fence-posts situated beneath 'hau' trees." Based on his records, these mines could be from a number of currently recognized different *Philodoria* species: Kauai: *P. limahuliensis* and/or undiscovered species, Oahu, Maui and Hawaii (Big island): *P. hauicola* and/or *P. hibiscella.* The host plant, *H. tiliaceus* was probably introduced by early Polynesians, about a thousand years ago (Zimmerman 1960; 1978a). Interestingly, larvae of *P. hauicola* have not been observed on Hawaiian endemic *Hibiscus* plants.

Philodoria sp. 1 of Johns *et al.* (2018)

Fig. 59F, G, 76, 87E, F.

Philodoria sp. 1; Johns *et al*. (2018): fig. 2.

Material examined. 3♀, 2 (sex unknown), Ulupalakua Ranch, Maui, 6–11.viii.2014 (stored), C.A. Johns leg., host: *Dubautia menzesii*, 23.vii.2014, CJ328 / SK835♀, CJ334 (1♀, 2 sex unknown, only photos), CJ364 /PHIL0021♀, in BPBM. The five specimens are all partial and none we felt were eligible as a type specimen, but we consider it distinctive enough and worth describing. What remains of the specimens, CJ328 was mounted as a dry pinned specimen with unspread wings, which has poor condition (stored originally in RNAlater solution); CJ364 only has the genitalia and abdomen remaining. CJ344 was entirely sacrificed for the molecular analysis of Johns *et al*. (2018).

Diagnosis. Among *Philodoria* species having similar $\mathbf{ds_2}$ at middle connecting basal patch i.e., *P. keahii*, **sp. n.**, *P. funkae* **sp. n.**, *P. pittosporella* (Swezey), *Philodoria* sp. 1 is distinguished by the narrowing and straight basal patch and pale orange or brown apical portion of the forewing (Fig. 76).

Description: Adult (Fig. 76). Forewing length < 2.0 mm, specimen examined was very damaged. Descriptions of the forewing was based on photographs of adult moths (CJ344). Head and frons white; maxillary palpus present; labial palpus white, basal half with ocherous scales. Antenna dark fuscous and same length as forewing. Thorax white and dark brown at lateral side. Forewing dark brown with three outwardly oblique white streaks: $\mathbf{cs_3}$ at 4/5; $\mathbf{ds_2}$ at about 1/2, $\mathbf{ds_3}$ at 2/3; a narrowing white band from base to 1/2 along dorsal margin, connecting a $\mathbf{ds_2}$; all streaks bordered with black scales; apical portion orangish brown and white at center with three costal white lines (**a, b, c**) at apical cilia; a fuscous spot at apex (**as**); a fuscous patch at dorsal 3/4; cilia fuscous, $\mathbf{bl_1}$ of terminal cilia orangish brown, tornal cilia interruputed with two white lines. Hindwing and cilia fuscous. Abdomen fuscous, yellow ground color, tuft white.

Male genitalia. Unknown.

Female genitalia. (Fig. 59F, G) (n=2). 1050 µm long. Ostium bursae large; antrum cup-shaped with a pair of lateral lobes,; lamella antevaginalis 180–190 µm, weakly sclerotized, indented near the posterior margin, widening toward anterior margin of A7. Ductus bursae rather broad, middle part weakly sclerotized, round and flat; terminus of ductus bursae tubular, biforked. Corpus bursae 530 µm, oblong; paired rows of longitudinal, partly sclerotized wrinkles.

Distribution. Maui.

Host plants. Asteraceae: *Dubautia menzesii* (A. Gray) D.D. Keck

Biology. (Fig. 87E, F). Larvae form a linear mine along the leaf margin making a near complete oval shape. As the larva grows, the mine turns into a blotch.

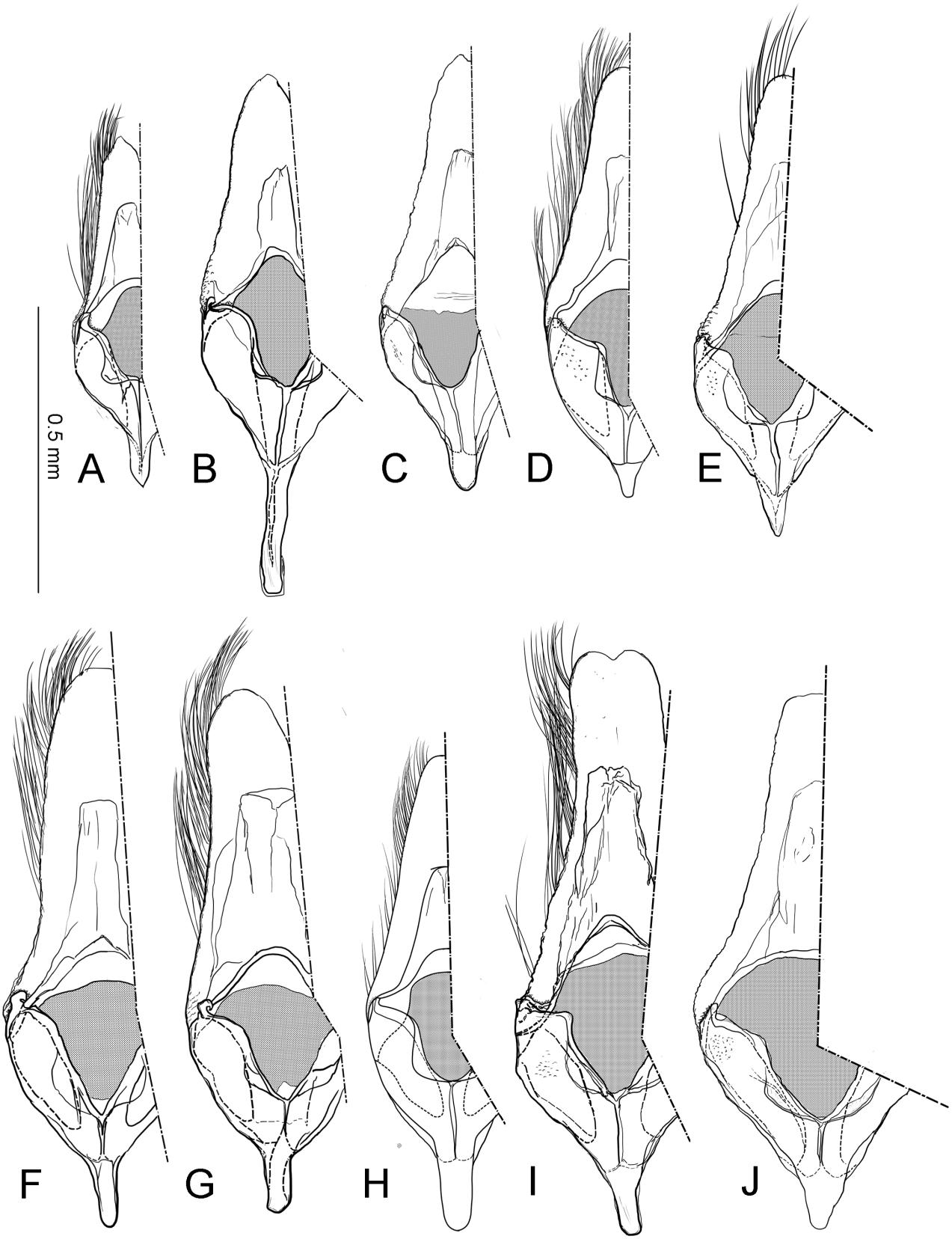

FIGURE 48. Genital capsule of *Philodoria*, excluding right portion of male genitalia, ventral view. **A** *P. wilkesiella*, Maui, PHIL0007, **B** *P. epibathra*, Molokai, SK678, **C** *P. dubauticola*, Maui SK646, **D** *P. dubautiella*, paralectotype, Oahu, SK733, **E** *P. alakaiensis*, paratype, Kauai, SK660, **F** *P. limahuliensis*, holotype, Kauai, SK731, **G** *P. hibiscella* Oahu SK684, **H** *P. naenaeiella* paralectotype, Oahu, SK691, **I** *P. knudseniiella*, holotype, Kauai, SK862, **J** *P. hesperomanniella*, holotype, Maui, SK831.

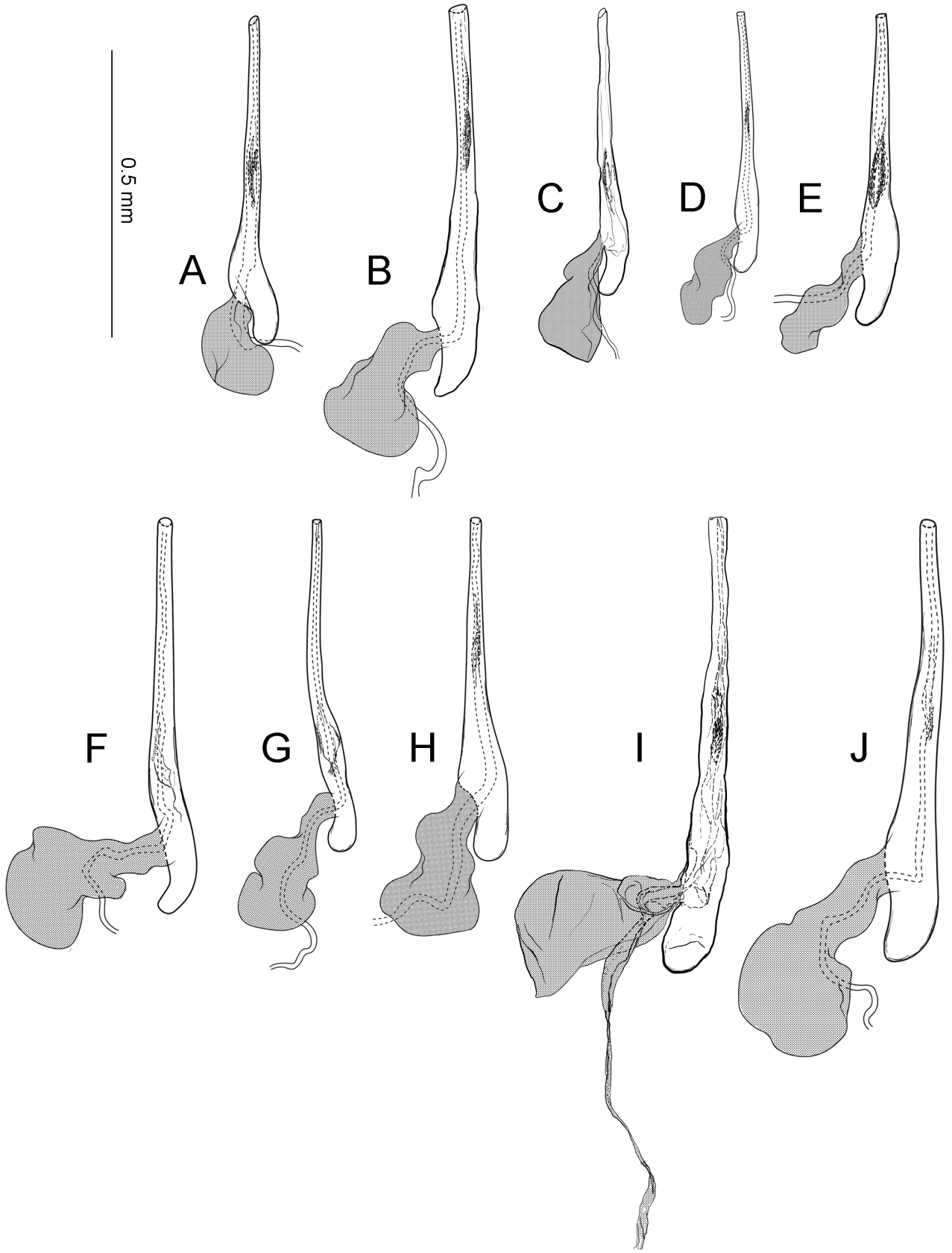

FIGURE 49. Phallus of *Philodoria*, lateral view. **A** *P. wilkesiella,* Maui, PHIL0007, **B** *P. epibathra,* Molokai, SK678, **C** *P. dubauticola*, Maui, SK812, **D** *P. dubautiella*, paralectotype, Oahu, SK733 **E** *P. alakaiensis*, paratype, Kauai, SK660, **F** *P. limahuliensis*, holotype, Kauai, SK731, **G** *P. hibiscella*, Oahu, SK684, **H** *P. naenaeiella*, paralectotype, Oahu, SK691, **I** *P. knudseniiella*, holotype, Kauai, SK862, **J** *P. hesperomanniella*, holotype, Maui, SK831.

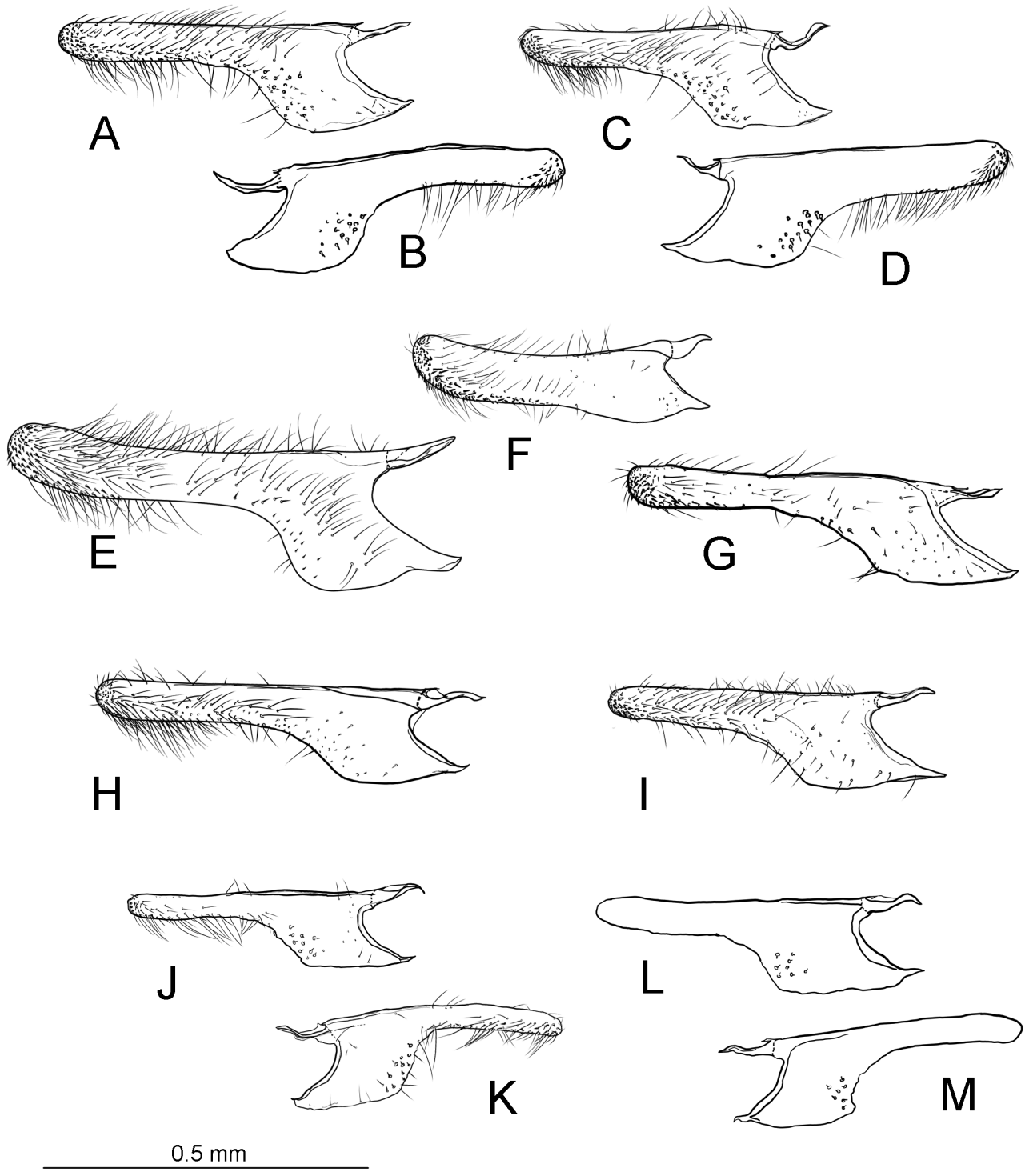

FIGURE 50. Valva of *Philodoria*, inner view. **A**, **C**, **E–J**, **L**: Left valva, **B**, **D**, **K**, **M**: Right valva. **A**, **B** *P. neraudicola,* paralectotype, Oahu, SK707, **C**, **D** *P. obamaorum*, paratype, Hawaii (Big Island), SK709, E *P. urerana*, Oahu, paralectotype, SK671, **F** *P. hauicola*, Oahu, SK694, **G** *P. keahii*, holotype, Oahu, SK758, **H** *P. touchardiella* Maui, SK643, **I** *P. platyphylliella*, holotype, Maui, SK833, **J**, **K** *P. marginestrigata*, Oahu, SK662, host: unknown, **L** Same species, Molokai, SK771, host: *Abutilon menziesii*, **M** Same species, Kauai, SK784, host: *Sida, fallax*.

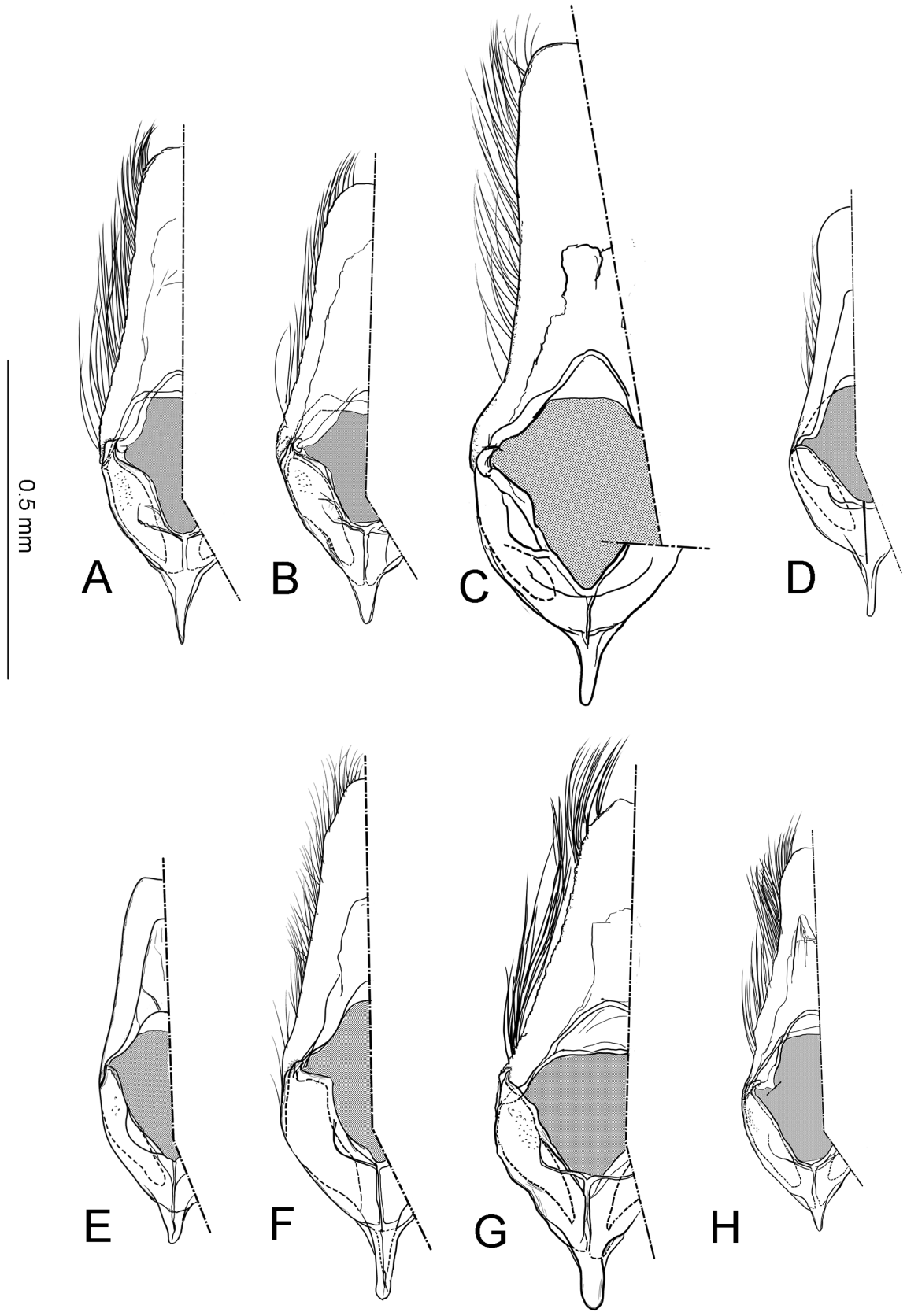

FIGURE 51. Genital capsule of *Philodoria*, excluding right portion of male genitalia, ventral view. **A** *P. neraudicola,* paralectotype, Oahu, SK707, **B** *P. obamaorum*, paratype, Hawaii (Big Island), SK709, **C** *P. urerana*, paralectotype, Oahu, SK671, **D** *P. hauicola*, Oahu, SK694, **E** *P. keahii*, holotype, Oahu, SK758, **F** *P. touchardiella* Maui, SK643, **G** *P. platyphylliella*, holotype, Maui, SK833, **H** *P. marginestrigata*, Oahu, SK662 host: unknown.

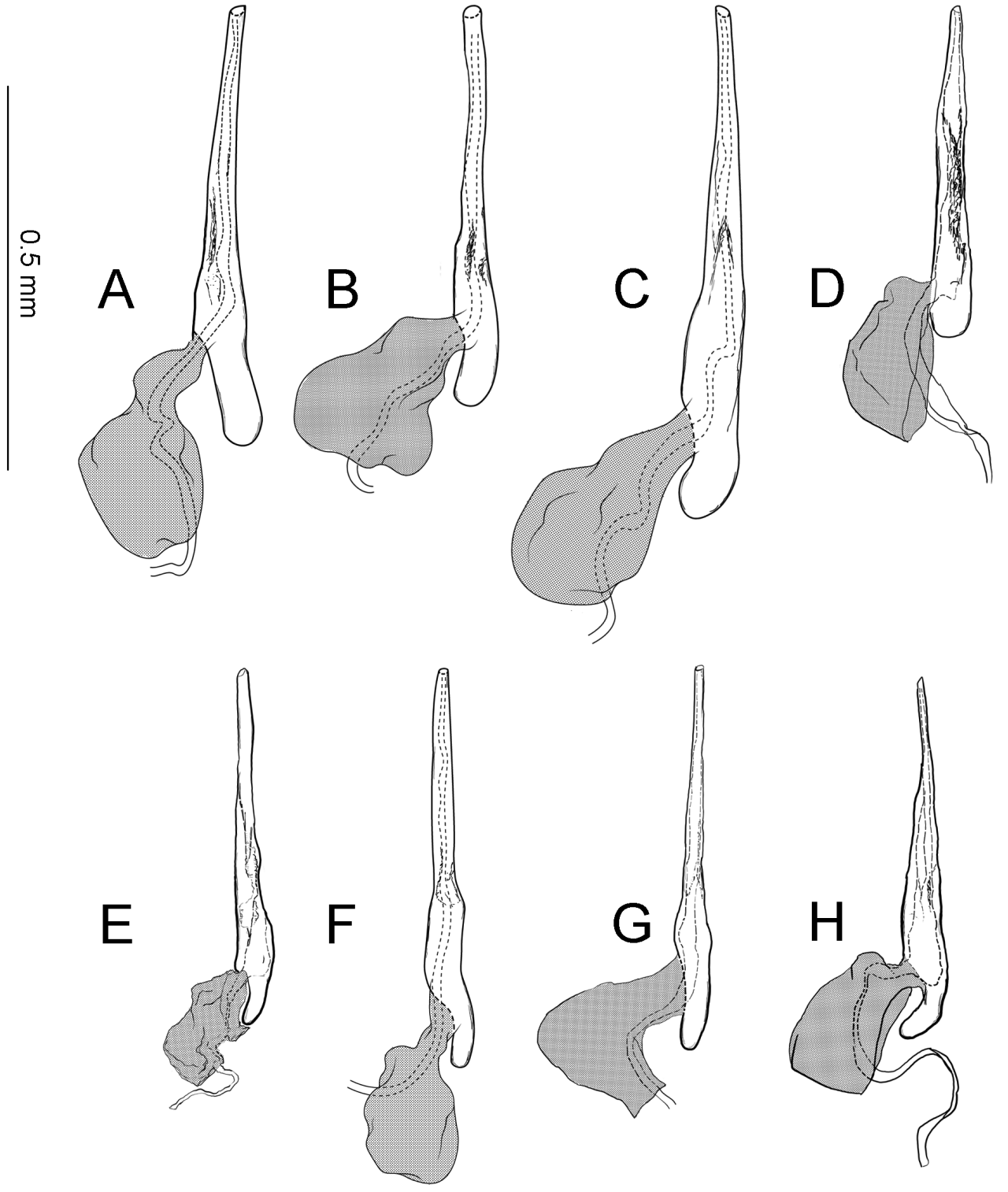

FIGURE 52. Phallus of *Philodoria*, lateral view. **A** *P. neraudicola*, paralectotype, Oahu, SK707, **B** *P. obamaorum*, paratype, Hawaii (Big Island), SK709, **C** *P. urerana*, paralectotype, Oahu, SK671, **D** *P. hauicola*, Oahu, SK695, **E** *P. keahii*, holotype, Oahu, SK758, **F** *P. touchardiella* Maui, SK643, **G** *P. platyphylliella*, holotype, Maui, SK833, **H** *P. marginestrigata*, Oahu, PHIL0029 host: *Abutilon incanum*.

***Philodoria keahii* Kobayashi, Johns & Kawahara, sp. n.**
Figs. 20D–F, 50G, 51E, 52E, 59H, 91H, I.

Philodoria sp. 13; Johns *et al*. 2018: fig. 2.

Type locality. Kauaula (Maui).

Etymology. The specific epithet, *keahii* is named after Keahi Bustamente, a native Hawaiian and plant and invertebrate conservation biologist that discovered a larva of this moth feeding on its host plant.

Type material. Holotype ♂, Kauaula, Maui, 17.viii.2014 (stored), C.A. Johns leg., host: *Remya mauiensis*, 31.vii.2014, CJ380 / SK758♂ in BPBM. Paratype 2♀, same locality and data as holotype, 9&16.viii.2014 (stored), CJ332 / SK756♀, CJ377 / SK757♀ in BPBM. The holotype mounted as a dry pinned specimen with three wings placed under a coverslip without mountant (1/2 of right forewing and 2/3 of two hindwings).

Diagnosis. The forewing pattern is similar to that of *P. pittosporella* (Swezey), but it is distinguished by its forewing which has a fuscous patch at 3/4 and rather narrowing dorsal streaks (Fig. 20F). Genitalia similar to that of *P. touchardiella* (Swezey), but it is distinguished from the latter by its short tegumen and saccus.

Description: Adult (Fig. 20D–F). Forewing length 2.4 mm in holotype, 2.7, 3.0 mm in two paratypes. Head and frons white; maxillary palpus white with dark brown scales at apex; labial palpus white with dark brown scales at apx. Antenna dark brown, bellow white about 3.0 mm long in holotype, 4.0 mm in paratype (SK757). Thorax brown. Forewing ocherous with three outwardly oblique white streaks: $\mathbf{ds_2}$ at about 1/2, $\mathbf{ds_3}$ at 2/3; a white band from base to 1/2 along dorsal margin, connecting $\mathbf{ds_2}$; $\mathbf{cs_3}$ at 4/5; apical portion pale orangish brown with three costal white lines **(a, b, c)** at apical cilia; a fuscous spot at apex (**as**); a fuscous patch at 3/4; cilia fuscous, $\mathbf{bl_1}$ of terminal cilia orangish brown, tornal cilia interruputed with a white line. Hindwing and cilia grayish fuscous.

Male genitalia (Figs. 50G, 51E, 52E) (n=1). Capsule 570 µm. Tegumen 0.7–0.8 x length of valva; valva 430 µm long, tapering along costal margin from basal 2/5 to apex, slightly narrowing at 2/3 and rounded at apex (Fig. 50G). Saccus short and triangular in ventral view (Fig. 51E). Phallus 460 µm long and nearly straight, slightly widening at phallobase with small coecum; cornuti in vesica indistinct (Fig. 52E).

Female genitalia (Fig. 59H) (n=2). 1200 µm long. Ostium bursae large; antrum cup-shaped with a pair of broad lateral lobes; lamella antevaginalis 130–140 µm, weakly sclerotized, slightly indented near the posterior margin, widening toward anterior margin of A7. Ductus bursae slender and long, middle part weakly sclerotized, round and flat; terminus of ductus bursae tubular, biforked. Corpus bursae 610 µm, pyriform; anterior end of corpus bursae weakly sclerotized; paired rows of longitudinal, partly sclerotized wrinkles.

Distribution. Maui.

Host plants. Asteraceae: *Remya mauiensis* Hillebr, a plant species known only from Maui (Fig. 69A, B).

Biology. (Fig. 91H, I). Larvae at first form a very slender linear mine (Fig. 91I), that gradually becomes an elongate blotch mine (Fig. 91H). One mine per leaf. Pupation occurs in the white cocoon outside of the mine on the abaxial leaf surface (Fig. 91H). Mines are very difficult to find and appear rare. When we visited the plant population in Ulupalakua Ranch in July 2014, we found less than 10 mines that were active or inactive after searching more than 50 plants.

Remarks. There is another population of *Remya* further east of Kauaula, but we did not investigate these plants. We also investigated outplanted individuals of *R. montgomeryi* and wild individuals of *R. kauaiensis* on Kauai Island (both species are endangered), but did not find any signs of *Philodoria* mines.

***Philodoria funkae* Kobayashi, Johns & Kawahara, sp. n.**
Figs. 21A–C, 59I.

Philodoria sp. 12; Johns *et al*. 2018: fig. 2.

Type locality. Kokee (Kauai).

Etymology. The specific epithet, *funkae*, is dedicated to the late Dr. Vicki Ann Funk, a Hawaiian aster systematist that contributed significantly to research on Hawaiian plants and island biogeography.

Type material. Holotype ♀, Kokee, Kauai Is., 9.vii.2015 (stored), C.A. Johns leg., host: *Wilkesia gymnoxiphium*, 26.vi.2015, CJ470 / SK761♀ in BPBM. Paratype 2♀: 1♀, same locality and data as holotype, 21.vii.2015

(stored), CJ489, SK762♀; 1♀, Kauai Is., N. Tangalin leg., host: *W. gymnoxiphium*, Summer.2015, AYK-13-0075, CJ523 / SK763♀ in BPBM. The type material does not include a complete specimen, but the specimens retained enough characteristics to describe as a separate species. What remains of the types were mounted on a cover slip (wings) or preserved as a gentialia slide mount. The holotype is represented by two forewings and two hindwings (completed right wing and 3/4 of left wing) (Fig. 21A, B); a paratype (CJ489) has four halves of wings; the paratype (CJ523) is two forewings with 1/4 of the wing missing, and two hindwing halves (Fig. 21C). The head, antenna, thorax, and legs were sacrificed for molecular analysis.

Diagnosis. The forewing pattern is similar to that of other Asteraceae feeders, namely *P. keahii* **sp. n.**, *P. naenaeiella* (Swezey) and *P. pittosporella* (Swezey), but *P. funkae* is distinguished from them by the broader $\mathbf{ds}_{2,3}$ and $\mathbf{ds}_{2}$ connecting basal patch of the forewing (Fig. 21A–C); in the female, the narrowed posterior region of lamella antevaginalis and corpus bursae bear several weakly sclerotized wrinkles (Fig. 59I).

Description: Adult (Fig. 21A–C). Forewing length 3.8 mm in holotype (Fig. 21B). Head and thorax characters are unknown. Forewing bronze with white patches: $\mathbf{cs}_{3}$ at 4/5; $\mathbf{ds}_{2}$ large and base broad from 1/4 to the middle, connecting with a basal patch ($\mathbf{ds}_{1}$); outwardly oblique large $\mathbf{ds}_{3}$ from 1/2 to 3/4; apical potion fuscous, costal area orangish brown with a blue **as**; cilia fuscous with three to four white apical spots (**a, b, c**); terminal cilia with orange $\mathbf{bl}_{1}$ and two white spots; tornal cilia two black fringe lines with an orange $\mathbf{bl}_{1}$. Hindwing and cilia gray.

Male genitalia Unknown.

Female genitalia (Fig. 59I) (n=3). 970 µm long. Ostium bursae large; antrum deeply cup-shaped with a pair of lateral lobes; lamella antevaginalis 160 µm, weakly sclerotized, posterior part narrowing and slightly inflexed on the posterior margin, widening toward anterior margin of A7. Ductus bursae short, middle part weakly sclerotized, round and flat; terminus of ductus bursae tubular and broad, biforked. Corpus bursae 530 µm, pyriform; anterior end of corpus bursae weakly sclerotized; paired rows longitudinal, partly sclerotized of wrinkles.

Distribution. Kauai.

Host plants. Asteraceae: *Wilkesia gymnoxiphium* A.Gray.

Biology. Leaf mines begin as slender mines near leaf apex and usually enlarge into a blotch in later larval stages. Blotch mines are typically situated at the leaf tips. Many older leaves of *Wilkesia gymnoxiphium* naturally brown at the tips, which can make it difficult to find active mines of this moth species.

Parasitoids. Bethylidae sp. (Fig. 105M–O).

Remarks. *Wilkesia* comprises of only two species, *W. gymnoxiphium* and *W. hobdyi*. Both are only known from Kauai. *Wilkesia hobdyi* is critically endangered (IUCN). We were unable to visit natural populations of *W. hobdyi* and survey for *Philodoria* because the remaining populations of this plant are located on a steep, dangerous cliff area.

Philodoria pittosporella (Swezey, 1928)

Fig. 21D.

Parectopa pittosporella Swezey, 1928: 189–190.
Philodoria pittosporella (Swezey, 1928); Zimmerman 1978a: 690, figs. 445, 452.

Type locality. Mt. Kaala, above 3000ft (Oahu).

Type material. Holotype ♂, Mt. Kaala, Waianae range, [above 3000 ft.], Oahu, 1.iii.1925, Swezey Coll., ex cocoon on leaf of *Pittosporum*, |Holotype |*Parectopa pittosporella* Swezey Det. by O.H. Swezey | ♂ holotype abdomen sent E.C.Z 11-8-60,| [Type] no. 4264 in BPBM.

Described based on a single specimen from Oahu.

Diagnosis. The forewing pattern is similar to that of *P. funkae* **sp. n.**, but it is distinguished by its light ocherous brown forewing and orange to light brown apex (Fig. 21D). See also the diagnosis of *P. keahii* **sp. n.**

Redescription: Adult (Fig. 21D). Wingspan 8.5 mm in holotype; forewing length 4 mm in holotype. Head and frons white; maxillary palpus white; labial palpus white, a little brownish externally. Antenna light ocherous brown, whitie at base, about 1.2–1.3x length of forewing. Thorax white. Forewing light ocherous brown with white patches: a large white $\mathbf{ds}_{2}$ at 1/2, connecting $\mathbf{ds}_{1}$ at 1/5, distad portion widened to fold, then with an oblique pointed extension continuing 2/3 across wing, another from 3/5 nearly to apex, an extension obliquely towards the end of white costal streak, not reaching it, with a few brown scales at 3/4; an outwardly oblique white $\mathbf{cs}_{3}$ at 4/5, margined with fuscous

scales; a few blue scales at apex; apical portion damaged, cilia gray with three white costal spots (**a, b, c**). Hindwing and cilia grayish fuscous. Legs grayish fuscous, somewhat banded with white. Abdomen grayish fuscous.

Male genitalia See Zimmerman (1978a: fig. 452). Tegumen oblong, 0.7–0.8 x length of valva; valva tapering along costal margin from basal 1/2 to apex; apical half slender and slightly curved toward inner margin. Saccus short and pointed at apex in ventral view. Phallus straight with small coecum; vesica with well-developed minute cornuti.

Female genitalia Unknown.

Distribution. Oahu (Swezey 1928).

Host plants. and **Biology.** Unknown.

Remarks. Zimmerman (1978a) incorrectly reported *Pittosporum* as the host plant and noted that the larva emerges from its mine to spin a cocoon on the leaf surface. Swezey (1928) noted that the holotype was reared from a cocoon found on a leaf of *Pittosporum* without mines on the leaves and pointed that *Pittosporum* was not the actual host plant. We observed leaf mines on *Pittosporum* on Kauai and Oahu, but it is unclear what insect makes these leaf mines as we have not been successful in finding a mine with a larva. It is likely that this mine is not made by *Philodoria*, but by another insect.

Philodoria touchardiella (Swezey, 1928)

Figs. 21E, 27N, O, 50H, 51F, 52F, 59J, 94.

Parectopa touchardiella Swezey, 1928: 189.
Philodoria touchardiella (Swezey, 1928); Zimmerman 1978a: 690, figs. 445, 452, 460.

Type locality. Black Gorge, north side of the Iao Valley (Maui).

Type material. Lectotype ♀, North side of Iao Valley, Black Gorge, 1800 ft., Maui, 15.i.1926 O.H. Swezey Collector, host: *Tonchardia latifolia*, Type no. 4265 in BPBM (here designated). Described from two specimens from Maui. Swezey noted that 'holotype and paratype in the collection of the Hawaiian Entomological Society'. However, because a holotype was not specified in the original description, the so-labeled holotype and paratype can be treated as syntypes under Article 73.2 of the Code (ICZN 1999), and any specimen can designated as lectotype under Article 74 of the Code (ICZN 1999). The syntype labeled 'holotype', which Zimmerman (1978a) treated as the holotype, is here formally designated as lectotype (Fig. 21E). The other syntype is the paralectotype, but we could not find 'Paratype' and its genital slide no. Z-VII-14-61 (Zimmerman 1978a, fig. 452) in BPBM, we only found a slip of paper in the specimen's box that read, 'paratype ♂ sent E.C.Z 6-5-61'.

Additional material. (3♂, 2♀, 1 sex unknown). **Adult**: 1♂, 1♀, Kaluaaha, Molokai, 14.iii.2015 (stored), K. Bustamente leg., host: *Tonchardia latifolia*, 5.xii.2014, KMB04|CJ401a / SK764♀, CJ401b / SK765♂ in BPBM; Maui Is: 2♂, Iao Valley, 11.viii.2014 (stored), host: *Tonchardia latifolia*, CJ365 / SK642♂, 643♂ in BPBM; 1♀, East Wailuaiki Stream, 26.vii.2015 (stored), K. Bustamente leg., host: *Tonchardia latifolia*, 26.vi.2015, KMB01|CJ507b / SK766♀ in BPBM. **Pupa**: 1 (sex unknown), same locality and data as holotype, BPBM34326.

Diagnosis. The forewing pattern and male genitalia are very similar to that of *P. nigrella* (Walsingham), but is distinguishable by its rather brown forewing with $\mathbf{ds}_1$ that does not reach the middle of the wing and slightly broad white $\mathbf{ds}_2$ (Fig. 21E). The female genitalia differ from other congeners in having a larger corpus bursae and a pair of small linear signa in the middle with a series of minute spines (Fig. 59J).

Redescription: Adult (Fig. 21E). Wingspan 6 mm in type series; forewing length 3.25 mm in holotype. Head light buff; frons white; maxillary palpus white; labial palpus white, median joint slightly infuscated externally at apex, terminal joint infuscated in front. Antenna light buff, infuscated on apical half, a little longer than forewing. Thorax, abdomen and legs olive brown, pale beneath. Forewing olive brown with white patches: three large triangular white dorsal streak ($\mathbf{ds}_{1-3}$) extending obliquely outward: $\mathbf{ds}_1$ at near base, $\mathbf{ds}_2$ at about middle, longer and narrower reaching to middle of wing, and $\mathbf{ds}_3$ near tornus; an outwardly oblique white $\mathbf{cs}_3$ at 3/4, with a few blue scales at its terminus; apical portion beyond the $\mathbf{cs}_3$ with a few yellow scales, and a few blue scales at extreme apex; cilia olive brown, with three white spots (**a, b, c**) in costal cilia alternating with black spots, terminal cilia with $\mathbf{bl}_1$ at base. Hindwing and cilia nearly uniform olive brown.

Male genitalia (Figs. 50H, 51F, 52F) (n=3). Capsule 820 µm. Tegumen 0.8–0.9 x length of valva; valva 570 µm long, tapering along costal margin and slightly sinuous from basal 2/5 to apex (Fig. 50H). Saccus rather long

and stick-shaped in ventral view (Fig. 51F). Phallus 520 μm long and straight, widening at phallobase with small coecum; cornuti in vesica indistinct (Fig. 52F).

Female genitalia (Fig. 59J) (n=2). 1280 μm long. Ostium bursae large; antrum cup-shaped with a pair of lateral lobes; lamella antevaginalis 210 μm, weakly sclerotized, semicircular in ventral view. Ductus bursae rather wide, middle part weakly sclerotized, round and flat; terminus of ductus bursae tubular, biforked. Corpus bursae 720 μm, pyriform; anterior end of corpus bursae weakly sclerotized with some minute wrinkles; two short linear signa with a series of minute spines.

Distribution. Molokai: new record, and Maui (Swezey 1928).

Host plants. Urticaceae: *Touchardia latifolia* Gaudich. (Swezey 1928).

Biology. (Fig. 94). Larvae form a broad linear mine (Fig. 94). Usually two or more mines per leaf. Pupation occurs in the cocoon outside of the mine on the leaf surface. The leaf mine quickly becomes discolored, turning black or dark gray, and can be mistaken for other forms of leaf damage. When *Touchardia* is present, leaf mines tend to be abundant.

Remarks. It is possible that this moth occurs on other Hawaiian Islands, but we were unable to survey *Touchardia* on the islands of Hawaii (Big Island), Lanai, and Oahu.

Philodoria sp. 3 of Johns *et al.* (2018)

Philodoria sp. 3; Johns *et al*. (2018): fig. 2.

Material examined. 3 pupae, Blue Hole, Kauai, 24.vii.2015 (stored in RNAlater solution), C.A. Johns leg., host: *Tonchardia latifolia*, 10.vi.2015, CJ494a–c, specimens in FLMNH.

Adult. Unknown.

Distribution. Kauai.

Host plants. Urticaceae: *Touchardia latifolia* Gaudich.

Biology. Unknown.

Parasitoids. Scelionidae? (Fig. 107).

Remarks. We have observed *Philodoria* leaf mines on *Touchardia* on Kauai at Blue Hole, but were unable to rear any adults. However, five pupae that failed to eclose were sequenced in the molecular analyses of Johns *et al*. (2018) and genetically distinct from Maui *P. touchardiella*. Therefore, we recognize "*Philodoria* sp. 3" of Johns *et al*. (2018) as a unique species but do not assign a name here because a morphological adult specimen does not exist. Future studies should revisit the Blue Hole on Kauai and rear an adult from a mine on *Touchardia latifolia* and compare its pupae to the eight pupae that were studied here.

Philodoria keaensis Kobayashi, Johns & Kawahara, sp. n.

Figs. 22A, B, 59K.

Type locality. Mauna Kea (Big Island).

Etymology. The specific epithet is derived from the type locality, Kea (pronounced 'Keh-ah').

Type material. Holotype♀, Mauna Kea, Hale Pohaku, 9,970ft (~3,038 m), Hawaii Is. [Big Island], 9.viii.2014 (stored), J. Eiben leg., adult on *Tetramolopium humile*, 27.vi.2012, CJ355 / SK777♀ in BPBM. The holotype was mounted as a dry pinned specimen by placing two forewings without mountant under a coverslip.

Diagnosis. Distinguished from other species by having a broad white streak at its costal fold and a transverse streak at 3/4 on the forewing (Fig. 22A, B). *Philodoria wilkesiella* Swezey and *P. touchardiella* (Swezey) have female genitalia that are similar in shape to *P. keaensis* **sp. n.**, but the former two are separated from the latter by a rather broad or long antrum and distinct forewing pattern.

Description: Adult (Fig. 22A, B). Forewing length 2.5 mm in holotype. Head and frons dark brown with white scales on lateral side; maxillary palpus white; labial palpus white above, brownish beneath. Thorax dark brown. Forewing brown to pale redish brown with white patches: a costal broad one along costal fold from base to costal 1/2; a dorsal broad outwardly oblique $\mathbf{ds}_2$ at 1/2 enclosing fuscous lines, connecting white line extending dorsal base of wing along dorsal margin; a white transverse fascia at 3/4; a large black patch nearby transverse streak with

shiny blue scales at center; apical portion orangish brown with a costal white spot (**b**) at apex of cilia; an apical black patch (**as**) with shiny blue scales; apical and terminal cilia fuscous, tornal cilia brown. Hindwing and cilia fuscous. Abdomen white below. Legs dark brown, tarsi spotted with white.

Male genitalia Unknown.

Female genitalia (Fig. 59K) (n=1). 960 µm long. Ostium bursae large; antrum cup-shaped with a pair of lateral lobes; lamella antevaginalis 160 µm, weakly sclerotized, semicircular, widening toward anterior margin of A7. Ductus bursae short, middle part weakly sclerotized, round and flat; terminus of ductus bursae tubular, biforked. Corpus bursae 570 µm, pyriform; anterior end of corpus bursae weakly sclerotized; paired rows of longitudinal, partly sclerotized wrinkles; very small paired signa with a pair of slender minute spines.

Distribution. Hawaii (Big Island).

Host plants. and **Biology.** Unknown.

Remarks. Jesse Eiben collected the holotype from beating the plant, *Tetramolopium humile* (A. Gray) Hillebr. (Asteraceae) at Mauna Kea, 9,970ft (~3,038 m), Hawaii Island (Big Island). We returned to this location in October 2014 and searched *Tetramolopium humile*, *Argyroxiphium sandwicense* DC. subsp. *sandwicense*, *Dubautia ciliolata* (DC.) D. D. Keck, and *D. linearis* (Gaudich.) D. D. Keck but none of the plants we checked had visible leaf mines. We also set blacklight bucket trap lights for two nights within five feet of these plants, but were unable to collect any *Philodoria* adults. Some leaves of *A. sandwicense* subsp. *sandwicense* had its layers of leaf tissue separated, roughly resembling the pockets that form within mined leaves, but we were unable to find any frass. We therefore do not consider these separations as damage created by *Philodoria* larvae. Jesse Eiben has been conducting arthropod surveys in this area for nearly a decade. Given the rarity of this *Philodoria* species despite years of comprehensive arthropod sampling in the area, it is possible that this insect does not belong here, but instead was windblown from elsewhere as is often seen with arthropods on Mauna Kea. Future surveys focused specifically on this insect would benefit from sampling known *Philodoria* host plants and where they are more abundant, at a lower elevation.

Philodoria nigrelloides (Swezey, 1946)

Fig. 22C.

Parectopa nigrelloides Swezey, 1946: 628.
Philodoria nigrelloides (Swezey, 1946); Zimmerman 1978a: 690, figs. 444, 459, 466.

Type locality. Alakai (Kauai).

Type material. Holotype ♀, Alakai Swamp, [4000 ft.], Kauai, 22.viii.1921, Swezey Coll., [ex] *Dubautia*, | Holotype *Parectopa nigrelloides* Swezey| ♀ genitalia on slide Z-I-10-67| Type no. 4262 in BPBM. Described by Swezey based on a single specimen from Kauai. This specimen, designated by Swezey is here thus the holotype following article 73.1.2 (ICZN 1999). Holotype was remounted by Zimmerman (1978a: figs. 444, 466) (Fig. 22C).

Diagnosis. The forewing pattern is similar to that of *P. nigrella* (Walsingham) and *P. touchardiella* (Swezey), but differs from either of them in having a very small dorsal patch at the base of its forewing (Fig. 22C).

Redescription: Adult (Fig. 22C). Wingspan 8 mm in holotype. Head brownish fuscous; frons white; maxillary palpus white; labial palpus white above, black beneath. Antenna black. Thorax brownish fuscous, white below. Forewing bronzed brown with outwardly oblique white streaks: **cs**$_3$ from 3/4, extending about 2/3 across wing; one very small dorsal white patch (**ds**$_1$) at base (Zimmerman 1978a: fig. 466); **ds**$_2$ at 2/5, extends to about middle of wing, wider at base and tapering to a point; a smaller **ds**$_3$ at 2/3. A few white scales on dorsum near base; apical portion with a blue spot (**as**) with black center; near apex of costa three spots (**a, b, c**), the **a** larger, separated by black spots; cilia concolorous with the white and black spots; terminal cilia fuscous, pale at base where they join a line of black scales marking the terminal border, tornal cilia fuscous. Abdomen white below. Legs pale brown, tarsi spotted with white.

Male genitalia Unknown.

Female genitalia (Zimmerman 1978a: fig. 459). Similar to *P. funkae*, but differs in having rather indistinct wrinkles on the corpus bursae.

Distribution. Kauai (Swezey 1946).

Host plants. Asteraceae: *Dubautia* sp. (Swezey 1946).

Biology. Swezey (1940) noted that the single specimen was reared from a leaf mine of *Dubautia*.

***Philodoria platyphylliella* Kobayashi, Johns & Kawahara sp. n.**
Figs. 22D, 50I, 51G, 52G, 75D–G, 87G–I.

Philodoria sp. 14; Johns *et al*. 2018: figs. 1A, 2.

Type locality. Nakula Natural Area Reserve (Maui).

Etymology. The specific epithet, *platyphylliella*, refers to the species epithet of *Dubautia platyphylla*, its host plant.

Type material. Holotype ♂, Nakula Nar, Maui Is., 11.viii.2014 (stored), C.A. Johns leg., host: *Dubautia platyphylla*, 26.vii.2014, CJ363, SK833♂ in BPBM. Paratype ♂, same locality and data as holotype, 10.viii.2014 (stored), CJ358, PHIL0026 (only abdomen) in BPBM. The holotype was mounted as a dry pinned specimen by placing two forewings without mountant under a coverslip. The head, antenna, thorax, and legs of paratype were sacrificed for molecular analysis.

Additional material. 1♀, same locality and data as holotype, 12.viii.2014 (stored), CJ368, PHIL0025 genitalia missing in BPBM.

Diagnosis. The forewing pattern similar to that of *P. nigrelloides* (Swezey) and *P. touchardiella* (Swezey), but is differs from them by having a darker brown forewing with a blue to fuscous patch at its apex (Fig. 22D). The male genitalia is similar to that of *P. touchardiella*, but is distinguished by its rather thick saccus.

Description: Adult (Fig. 22D, 75D–G). Forewing length 3.4, 3.6 mm in holotype. Head bronze; frons white; maxillary palpus pale bronze; labial palpus white basal half, bronze at apex; Antenna bronze, about 1.1–1.2 x length of forewing. Thorax dark brown. Forewing dun to bronze with three oblique white streaks: **ds$_2$** at about 2/5, extends to about middle of wing; a smaller **ds$_3$** at 2/3. a small costal spot at near base; **cs$_3$** from 3/4, extending about 2/3 across wing; apical portion dark orangish brown with a large **as** of blue scales; a blue to fuscous patch at 4/5; few shiny gray spot at the middle of apical portion; cilia fuscous mixed dark brown scales with three white costal spots (**a, b, c**) at apex; black **bl$_1$** at terminal cilia. Hindwing and cilia fuscous. Abdomen bronze, white beneath. Legs fuscous.

Male genitalia (Figs. 50I, 51G, 52G) (n=2). Capsule 800 µm. Tegumen 0.9 x length of valva; valva 590 µm long, tapering along costal margin from basal 1/2 to apex (Fig. 50I). Saccus digitiform in ventral view (Fig. 51G). Phallus 500 µm long and straight, slightly widening at phallobase with developed coecum; cornuti in vesica indistinct (Fig. 52G).

Female genitalia Unknown.

Distribution. Maui.

Host plants. Asteraceae: *Dubautia platyphylla* (A.Gray) D.D.Keck. *Dubautia platyphylla* is rare and restricted to Maui. We surveyed a small population of this plant species within Nakula Natural Area Reserve, Maui, in July 2014 (Fig. 69C, D). This plant population was located on a steep drainage and was out of reach of ungulates, goat, pig, and deer.

Biology. (Fig. 87G–I). Larvae form an oblong blotch mine (Fig. 87G–I). Pupation occurs in the white cocoon on the adaxial leaf surface (Fig. 87I).

***Philodoria marginestrigata* (Walsingham, 1907)**
Figs. 23A–C, 27P–R, 37C, 40A–D, 50J–M, 51H, 52H, 60A–C, 77E, F, 93C.

Gracilaria marginestrigata Walsingham, 1907: 721–722, pl. 25, fig. 26; Swezey 1913b: 223.
Parectopa marginiestrigata (Walsingham, 1907); Meyrick 1912b: 48. (mistake in the character)
Parectopa marginestrigata (Walsingham, 1907); Swezey 1928: 190.
Philodoria marginestrigata (Walsingham, 1907); Zimmerman 1978a: 681, 685, figs. 432, 443, 450, 455.

Type locality. Waianae Mts. (Oahu).

Type material. Lectotype ♀, Waianae Mts., 1400ft., OAHU, Hawaiian Is., iv.1892, Perkins. 25990 |Gracilaria marginestrigata Wlsm. ♀ PARATYPE 3/15| Walsingham Collection, 1910-427.| BMNH(E)1407669 in NHMUK. (here designated). Paralectotype 5 (1♂, 4♀; BPBM ones are all from above Walsingham accession and 'PARATYPE' below is short for 'Gracilaria marginestrigata Wlsm. PARATYPE' as printed on large black-margined labels,

with the 5-digit Walsingham specimen numbers whose first digit is '2' written on locality label): 1♂, Waianae Mts., 1400ft., OAHU, Hawaiian Is., iv.1892, Perkins. 25989| Gracilaria marginestrigata Wlsm. ♂ PARATYPE 2/15| Fauna Hawaiiensis Collection|BPBM 34197|; 1♀, Waianae Mts., 1400ft., OAHU, Hawaiian Is., iv.1892, Perkins. 25991| Gracilaria marginestrigata Wlsm. ♀ PARATYPE 4/15| Fauna Hawaiiensis Collection|BPBM 34195|; 1♀, Waianae Mts., 1400ft., OAHU, Hawaiian Is., iv.1892, Perkins. 25996| Gracilaria marginestrigata Wlsm. ♀ PARATYPE 8/15| Fauna Hawaiiensis Collection|BPBM 34198|; 1♀, Malaweli (sea level), KAUAI, Hawaiian Is., ex V. 1895 Perkins. 27969| Gracilaria marginestrigata Wlsm. ♀ PARATYPE 14/15| Fauna Hawaiiensis Collection|BPBM 34194|; 1♀, Mts. 3–4000 ft, KAUAI, Hawaiian Is., VI. 1895 Perkins. 27096| Gracilaria marginestrigata Wlsm. ♀ PARATYPE 12/15| Fauna Hawaiiensis Collection|BPBM 34196|. Described from 17 specimens: 'type ♀ (25992); ♂ (25991)' and 15 'paratypes' from Kauai, Oahu, Molokai. Given the way the description was written and the labels on the specimens, Walsingham likely considered them as holotype, allotype and paratypes. However, because a holotype was not formally specified in the original description, the so-labeled types should all be considered syntypes under Article 73.2 of the Code (ICZN 1999), and any of them can be designated as lectotype under Article 74 of the Code (ICZN 1999). Zimmerman (1978a, 701, fig. 443) provided the last known photograph for the 'type ♀ (25992)', which he treated as holotype in the NHMUK. The present curator of the NHMUK, D.C. Lees informed the authors that syntypes, 'type ♀ (25992); ♂ (25991)' and 11 'paratypes' are not stored where they should and are missing. The syntype (25990) is here designated as lectotype (Fig. 23A) and the remaining syntypes are paralectotypes.

Type material in original description. 'Type ♀ (25992); ♂ (25991) *Oahu*, Mus. Wlsm. HAB. Makaweli, sea-level, Kauai, larva mining various plants (2) excl. v.1895. Makaweli, Mts, 3000–4000ft., Kauai, larva mining various plants (2) excl. vi.1894. Waianae Mts., 1400ft., Oahu, on the leaves of a berry-bearing plant called "Kikania" [*Xanthium strumarium* ?](11) iv.1892. Sea-level, Molokai, (1) v.1893; above 3000ft, (1) 5.vi.1893.' (Walsingham 1907: 722).

Additional material. 75 (23♂, 16♀, 36 sex unknown). **Nihoa**, in BPBM: 12 (sex unknown), Nihoa I., 13.vi.1923, E.H. Bryan Jr. Collector, [host:] *Sida*, 34199–34210; 2 (sex unknown), Nihoa Island, 10.vi.1962, J.W. Beardsley, ex *Sida*, BPBM 34122| *Parectopa marginestrigata* Walsingham det by J.W. Beardsley| 34123; 3 (sex unknown), Hawaiian Is, Nihoa I: Miller Val. above campsite, 25.vi.1990 at UV light, J. Suazanac coll., 36525–36527; 1 (sex unknown), Nihoa I, 15.vi.1980 at light, Aoc. No. 1980.301, S. Conant Coll., BPBM 36528. **Oahu**: 1♂, 2♀, 2 (sex unknown), Koko Hd. [Koko head?, Oahu], 22.ii.1927, O.H. Swezey Collector, ex *Abutilon incanum*, BPBM34211–34215; 2 (sex unknown), Kaimuki, Oahu, Coll. O.H.S., BPBM34216, 34217; 2♂, 2♀, Kaimuki, Oahu, Coll. O.H.S., SK662♂, SK663♂, SK664♀, SK665♀, BPBM34220; 5 (sex unknown), Kaimuki, Oahu, Coll. O.H.S., BPBM34221; 3♂, 1 (sex unknown), Kaimuki, Oahu, Coll. O.H.S. ex *Sida* in USNM; 4♂, 2 (sex unknown), Kaimuki, Oahu, Coll. O.H.S., "♂ genitalia twice? on slide aB? Aug.22.1941" in USNM; 1 (sex unknown), Hawaiian Ids, Oahu, Honolulu, 9.iii.1917, J.C. Bridwell, BPBM34219; 4♂, 5♀, 5 (sex unknown), Punahou, Oahu, xi.1963, M. Chong Collector, ex. *Abutilon mlle* in USNM.1♂, Mokio, Molokai, 30.xii.2013 (stored), C.A. Johns leg., host *Lipochaeta rockii*16.xii.2013, CJ165, SK760♂ in BPBM. **Host:** ***Abutilon menziesii*:** 1♂, 1♀, Mokio, Molokai, 2&4.i.2014 (stored), C.A. Johns leg., 16.xii.2013, CJ175b / SK772♀, CJ187 / SK771♂ in BPBM. **Host:** ***Sida fallax***: C.A. Johns leg., all specimens were spreserved in BPBM: 1♂, Kokee, Kauai, 21.ix.2015 (stored), CJ521, SK784; 1♀ 1 (sex unknown), Kaena Point, Oahu, 17&21.v.2013 (stored), 19.iv.2013, CJ135(sex unknown) / KT982412, CJ138♀; 1♂, Same locality, 12.vii.2014 (stored), 1.vii.2014, CJ278b / SK785♂; 1♂1♀, Mokio, Molokai, 30.xii.2013 (stored), 16.xii.2013, CJ168 / SK782♂, CJ173 / SK783♀; 2♂, 2♀, Kanepuu, Lanai, 16.viii.2016 (stored), 5.viii.2014, CJ379a / SK786♂, CJ379b / SK787♀, CJ379c♂, CJ379d♀.

Diagnosis. The forewing pattern is similar to that of *P. lipochaetaella* (Swezey) and *P. sciallactis* (Meyrick), but distinguished by the narrowing $\mathbf{ds}_{1-3}$ and $\mathbf{cs}_{1-3}$. Genitalia are similar to that of *P. sciallactis*, but *P. marginestrigata* has a rather short and slender saccus.

Redescription: Adult (Fig. 23A–C, 37C). Wingspan 6.5 mm in 'Type ♀ (25992)', 6–7 mm for paralectotype; forewing length 2.4 mm in lectotype, 2.8 mm in paralectotype, 2.5–3.0 mm for the additional specimens examined. Head ocherous; frons white; maxillary palpus white with fuscous scales at the paex; labial palpus white, a dark spot at the end of the median joint and another before the apex of the terminal joint beneath (Fig. 37C). Antenna ocherous, faintly annulate with white. Thorax ocherous. Forewing ocherous, with six oblique white streaks, narrowing black-margined; three costal streaks ($\mathbf{cs}_{1-3}$): $\mathbf{cs}_1$ and $\mathbf{cs}_2$ small, nearly meeting the extremities of the larger $\mathbf{ds}_1$ and $\mathbf{ds}_2$ below them, which arise in each instance nearer to the base; $\mathbf{cs}_3$ at costal 3/4, slender, extending beyond the apex of the triangular, somewhat curved, $\mathbf{ds}_3$ below it; apical portion with shiny, steel-gray spot (**as**) with a patch of black

scales; an elongate patch shining blue-black scales from **ds$_3$** to the apex; cilia shiny, blue-gray, with three short costal spots (**a, b, c**) and a slender **bl$_1$** of black scales, bronze gray at the tornus. Hindwing and cilia bronze gray. Abdomen leaden gray. Legs gray with white spots at the extremities of the tibiae and tarsi.

Male genitalia (Figs. 40A–C, 50J–M, 51H, 52H) (n=7). Capsule 600 µm. Tegumen 0.8–0.9 x length of valva; valva 440–460 µm long, basal portion broad along dorsal margin, tapering along costal margin from basal 2/5–1/2 to apex; apical half slender and slightly curved toward inner margin with small spines at apex; a set of short spines arranged along inner side of basal region (Figs. 40C, 50J–M). Saccus short and triangular in ventral view (Figs. 40B, 51H). Phallus 460 µm long and nearly straight, slightly widening at phallobase with small coecum; cornuti in vesica indistinct (Figs. 40A, 52H).

Female genitalia (Fig. 60A–C) (n=4). 930 µm long. Ostium bursae large; antrum low cup-shaped with a pair of lateral lobes; lamella antevaginalis 110–160 µm, weakly sclerotized, sometimes slightly inflexed on the posterior margin, widening toward anterior margin of A7 (Fig. 60B, C). Ductus bursae short and broad, middle region weakly sclerotized, round and flat; terminus of ductus bursae tubular, biforked; middle region of ductus seminalis broad. Corpus bursae 570 µm, oblong with a very small spiny signa; anterior end of corpus bursae weakly sclerotized; paired rows of longitudinal, partly sclerotized wrinkles.

Distribution. Nihoa, Kauai, Oahu, Molokai, Hawaii (Big Island) (Zimmerman 1978a) and Lanai: new record.

Host plants. Asteraceae: *Dubautia* sp. and *Xanthium strumarium* (Swezey 1928: 190) (= *X. echinatum* (Zimmerman 1978a)), *Xanthium* sp. (Swezey 1913a: 223), and *Lipochaeta rockii* Sherff is new record; Malvaceae: *Abutilon grandifolium* (Willd.) Sweet [= *Abutilon molle* (Zimmerman 1978a: 681)], *A. incanum* (Link) Sweet (Swezey 1928: 190), *Abutilon* sp. (Swezey 1913a: 223), *Abutilon menziesii* Seem. (Endangered, IUCN) is new record, *Sida cordifolia* L., *S. fallax* Walp., *S. meyeniana* Walp., *S. rhombifolia* L. (Swezey 1928:190), *Sida* sp. (Swezey 1913a: 223).

Biology. (Fig. 93C). Swezey (1913b: 223) and Zimmerman (1978a: 685) reported its biology: "this species is a common leaf-miner in the lowlands and there may be as many as 12 mines in a single leaf, and the cocoon is made within the mine; the larvae feed introduced plants, as unusual for an endemic insect (Zimmerman 1978a: 685)". We collected larvae from three genera in two plant familes, Asteraceae (*Lipochaeta*) and Malvaceae (*Abutilon* and *Sida*). Larvae that mine leaves of *Sida fallax* formed a tortuous linear mine; 1–4 mines per leaf (Fig. 93C).

Parasitoids. (Figs. 108, 109). Braconidae: *Mirax* sp.; Eulophidae: *Cirrospilus* sp., *Diglyphus begini* (Ashmead, 1904), *Euderus metallicus* (Ashmead, 1901), *Neochrysocharis formosus* (Westwood, 1833), *Pnigalio externa* (Timberlake, 1927), *Sympiesis vagans* (Timberlake, 1926), *Zagrammosoma flavolineatum* (Crawford, 1913); Pteromalidae: *Lyrcus tortricidis* (Crawford, 1921) (Zimmerman 1978a).

Remarks. Walsingham (1907) presented an inaccurate and misleading figure of this moth (pl. 25, fig. 26), which does not show the distinct first white costal streak, which looks like a dorsal patch instead (after Zimmerman 1978a). Zimmerman (1978a) also noted that observations by Perkins and Walsingham are mixed and there may be more than one species involved in the literature records. We treat the first Nihoa record reported by Bryan (1926) from the 1923 Tanager Expedition as *P. marginestrigata*, but that specimen has three costal and three dorsal white streaks. There is some phenotypic variation in wing pattern and male genitalia (particularly in the shape of the valva (Figs. 27P–R, 50J–M)) between populations on different islands and those feeding on different host plants. DNA barcoding may help with the delimitation of this species.

Philodoria lipochaetaella (Swezey, 1940)

Figs. 23D–G, 24A.

Parectopa lipochaetaella Swezey, 1940: 464.
Philodoria lipochaetaella (Swezey, 1940); Zimmerman 1978a: 681, figs. 439, 442, 449, 455.

Type locality. A gulch above Lahaina (Maui).

Type material. Lectotype ♂, Gulch above Lahaina, Maui, 28.viii.1929, O.H. Swezey Collector, host: *Lipochaeta larvarum*, |Holotype *Parectopa lipochaetaella* Swezey|Type no. 4260 in BPBM. Paralectotype 7 (1♂, 2♀, 4 sex unknown): 1♂, 1♀, 1 (sex unknown), same mount of lectotype in BPBM, 1♀, 3 (sex unknown), same data and locality as lectotype, SK700♀|BPBM34187. Four paralectotypes missing. This species was described from 12 specimens from Maui. Zimmerman (1978a) designated Type no. 4260 (upper right of four syntypes) on a mount as lectotype (Fig. 23E), and the remaining syntypes are paralectotypes (Fig. 23D, F, G).

Diagnosis. Very similar to *P. sciallactis* (Meyrick), but can be distinguished by its round valva (Zimmerman 1978a: fig. 449).

Redescription: Adult (Figs. 23D–G, 24A). Wingspan 5–6 mm in type series; forewing length 3 mm in lectotype, 2.5–3.0 mm in paralectotype. Head and frons white; maxillary palpus white; labial palpus white with a black spot externally at apex of second, and third segments. Antenna white beneath, ringed with fuscous above. Thorax white. Forewing pale ocherous with white patches: a narrow white median line at basal half of fold; widely white basal patch (**ds**$_1$ + **ds**$_2$) extending inwardly and outwardly oblique to meet **cs**$_1$ at middle; a dorsal patch (**ds**$_3$) from 1/2 to 3/4, almost connecting with **cs**$_2$ and **cs**$_3$; three outwardly oblique costal ones (**cs**$_{1–3}$), **cs**$_1$ from base to 1/2, **cs**$_2$ at 3/4, **cs**$_3$ at 4/5; three white costal spots (**a, b, c**) near apex; apical portion white centered with a patch of pale blue scales (**as**); all white areas with a few marginal fuscous scales; cilia white with basal line of fuscous scales and a fuscous line near scale tips. Hindwing and cilia pale gray. Legs white, fore and middle legs and posterior tarsi with black spots. Abdomen white, anal tuft pale ocherous to white.

Male genitalia. See Zimmerman (1978a, fig. 449). Tegumen 0.7–0.8 x length of valva; valva digitiform and slightly narrowing at middle, rounded at apex, slightly curved toward dorsal side, similar to *P. hauicola*. Saccus slender and needle-shaped in ventral view. Phallus not examined.

Female genitalia. The female genitalia are very similar to that of *P. sciallactis*. See Zimmerman (1978a, fig. 455).

Distribution. Maui (Swezey 1940b).

Host plants. Asteraceae: *Lipochaeta lavarum* (Gaudich.) DC. (Swezey 1940b). *Lipochaeta* could not be found during our surveys of West Maui.

Biology. Unknown.

Remarks. We could not find the male specimen and male genitalia slide no. Z-I-27-61-3 of Zimmerman's figs. 449 and 451. Swezey (1940, 1946) described this species twice from two series, collected from the same locality and same host plant in 1928 and 1929. Zimmerman (1978a) placed *Parectopa lipochaetae* Swezey, 1946 (= the specimens series in 1928) in synonymy with P. lipochaetaella, but *P. lipochaetae* is synonymous with *P. sciallactis* based on the male genitalia. Zimmerman (1978a) also noted in his taxonomic key that *P. sciallactis* has a subbasal oblique white costal streak (**cs**$_1$) which continues along the costa to or close to the wing base and the second oblique white costal streak (**cs**$_2$) is discontinued distinctly across wing. However, the forewing alone cannot be used to distinguish the two species. We treat the type series from 1929 and the male specimens that have a rounded valva as *P. lipochaetaella.*

Philodoria sciallactis **(Meyrick, 1928)**

Figs. 24A–G, 53A, B, 54A, 55A, 60D, 78A–C, 91A–G.

Parectopa sciallactis Meyrick, 1928:104.

Parectopa lipochaetae Swezey, 1946: 627. A junior subjective synonym of *Parectopa lipochaetaella* Swezey, 1940, synonymized by Zimmerman (1978a: 681).

Philodoria sciallactis (Meyrick, 1928); Zimmerman 1978a: 690, figs. 445, 451, 458; Johns *et al*. 2016: 369, figs. 1, 2; Johns *et al*. 2018: fig. 2.

Philodoria sp. 6; Johns *et al*. 2018: fig. 2.

Type locality. Kaena Point (Oahu).

Type material. Lectotype ♂, Kaena Point, Oahu, 11.xi.1927, O.H. Swezey Collector, *Lipochaeta* [=*Melanthera integrifolia*], |Holotype |*Parectopa sciallactis* Mey. teste Meyr.| in BPBM. (here designated) Paralectotype 6 (3♂, 3♀). [Same data and locality as lectotype with following label: |Paratype |*Parectopa sciallactis* Mey. teste Meyr.|]: 2♂, 1♀, ♂|BPBM34280, SK713♀|BPBM34281, SK711♂|BPBM34282 ; 1♂, |B.M. Genitalia slide no. 2754|Meyrick Coll. B.M. 1938-290|BMNH(E) 1407859|NHMUK010305339|Paratype| in NHMUK; 1♀, |PARECTOPA Clem.|sciallactis Meyr.|BMNH(E)1407866|NHMUK010305340|Paratype| in NHMUK; 1♀, SK712♀ in USNM. Described from seven specimens reared from 'fleshy leaves of *Lipochaeta integrifolia* [=*Melanthera integrifolia*], growing in rocky places near the seashore' (Meyrick 1928). Specimen labels suggest that Meyrick considered one of these specimens to be the holotype and the remaining specimens as paratypes. However, because a holotype specimen was not formally designated in the original description, the so-labeled holotype and paratypes can be

considered syntypes under Article 73.2 of the Code (ICZN 1999), and any of them are eligible for designation as the lectotype under Article 74 of the Code (ICZN 1999). The syntype labeled 'Holotype' is here formally designated as lectotype (Fig. 24B) and the remaining syntypes are paralectotypes.

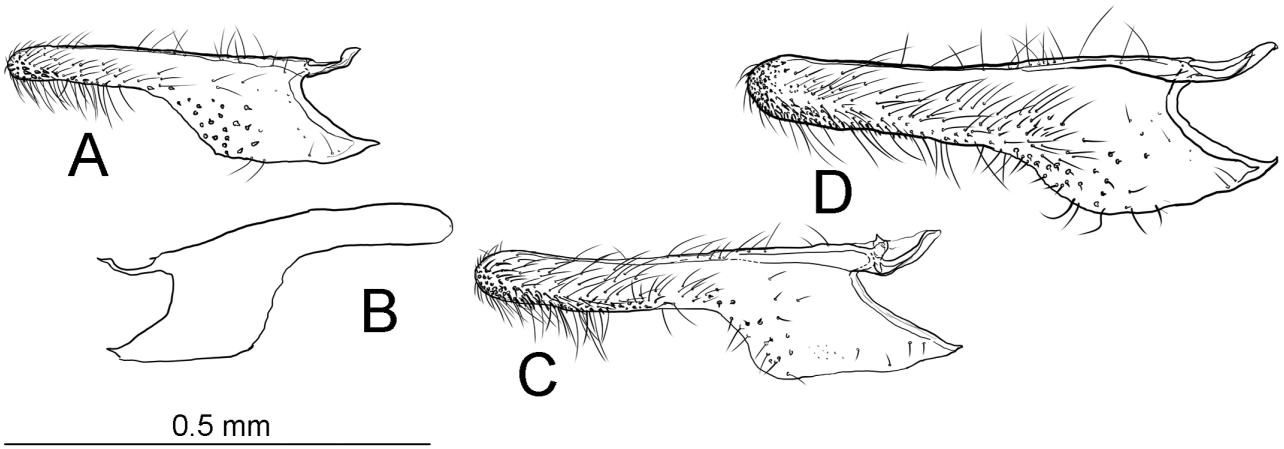

FIGURE 53. Valva of *Philodoria*. **A, C**, **D**: Left valva, **B**: Right valva. **A** *P. sciallactis* (syntype of *Parectopa lipochaetae*), Maui, SK699, **B** *P. sciallactis*, paralectotype, **C** *P. ureraella*, paralectotype, Oahu, SK676, **D** *P. opuhe*, paratype, Oahu, SK674.

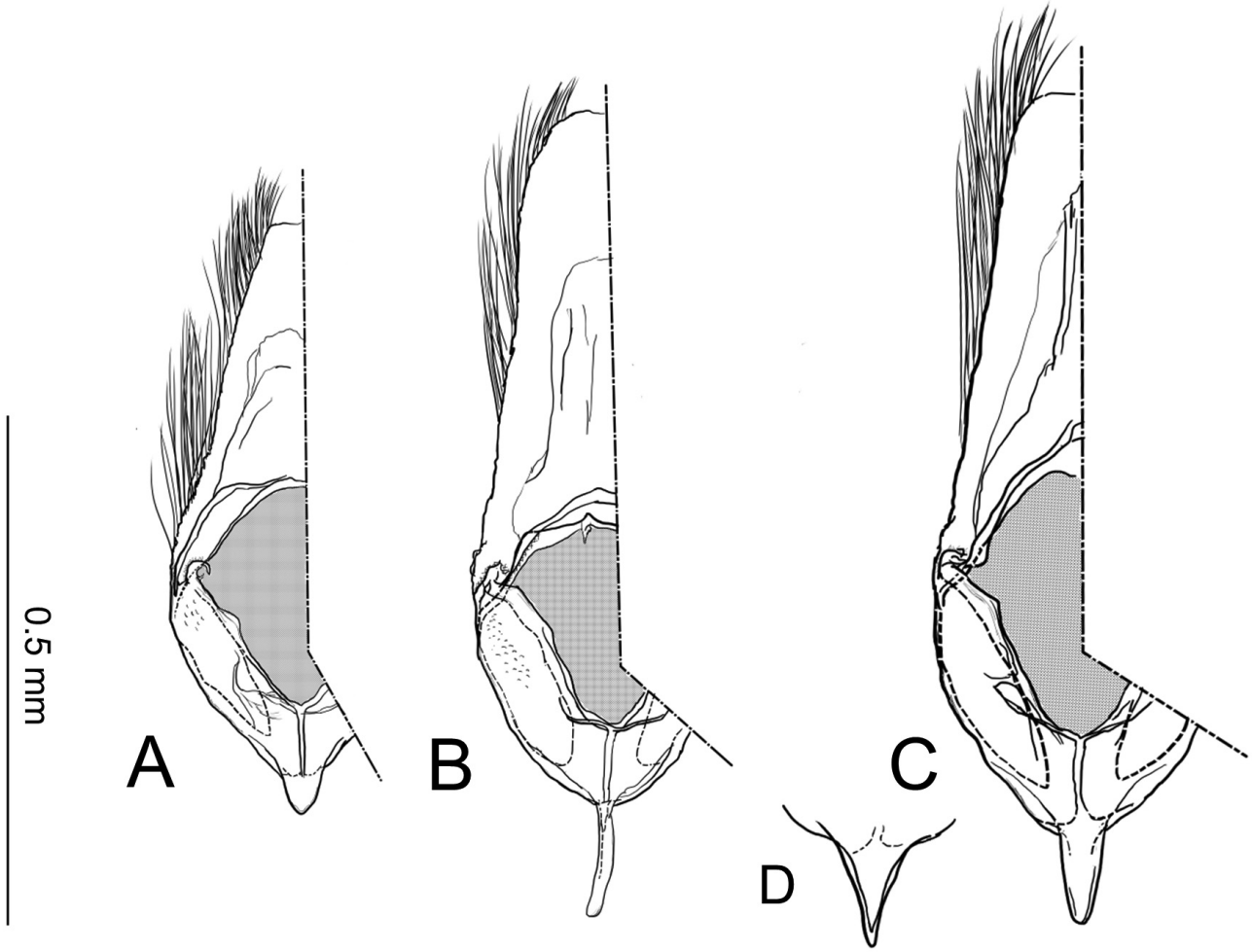

FIGURE 54. Genital capsule of *Philodoria*, excluding right portion of male genitalia, ventral view. **A** *P. sciallactis* (syntype of *Parectopa lipochaetae*), Maui, SK699, **B** *P. ureraella*, paralectotype, Oahu, SK676, **C** *P. opuhe*, paratype, Oahu, SK682, **D** Same as **C**, paratype, Oahu, SK674.

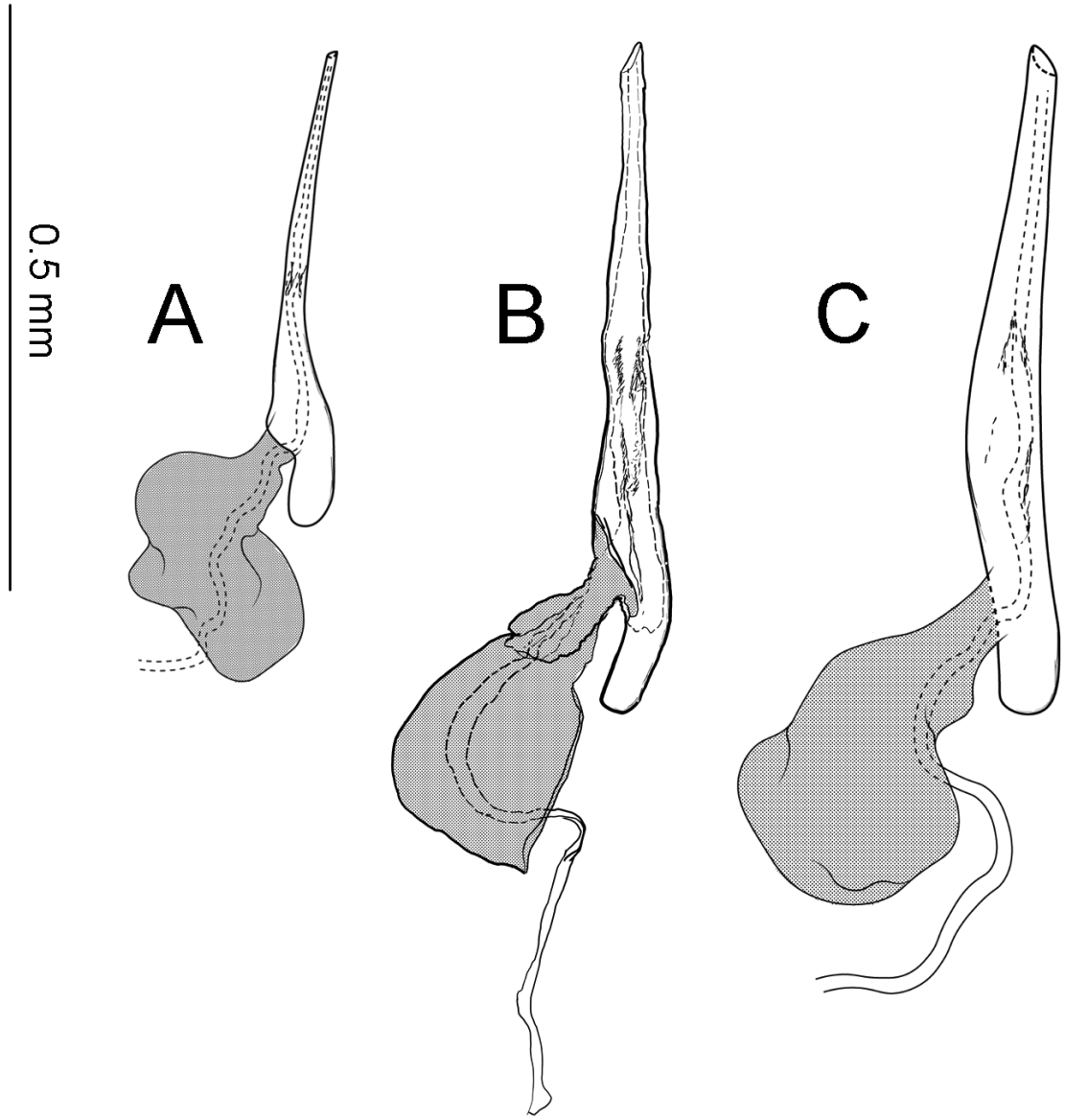

FIGURE 55. Phallus of *Philodoria*, lateral view. **A** *P. sciallactis* (syntype of *Parectopa lipochaetae*), Maui, SK699, **B** *P. ureraella*, paralectotype, Oahu, SK676, **C** *P. opuhe*, paratype, Oahu, SK674.

Additional material. (5♂, 1♀, 2 sex unknown) 1♂, Mokio, Molokai, 29.xii.2013 (stored), C.A. Johns leg., host: *Melanthera rockii* [= *Lipochaeta rockii*], 16.xii.2013, CJ159, SK759♂ in BPBM; Maui: 1♂, 1♀, 2 (sex unknown), Lahaina, 23.xii.1928, O.H. Swezey Collector, ex *Lipochaeta larvarum*, BPBM34184, SK699♂|BPBM34185, BPBM34186,|Holotype Parectopa lipochaetae Swezey|Type no. 4259|; 3♂, Lualailua, 30.xii.2013&4.i.2014 (stored), C.A. Johns leg., host: *Melanthera kamolensis*, 24.xii.2013, CJ163 / SK688♂, CJ164 / PHIL0024♂, CJ189 / SK689♂ in BPBM. 1♀, 2 (sex unknown), Kaena Point, Oahu, 6–11.vii.2014 (stored in RNAlater solution), C.A. Johns leg., host: *Melanthera integrifolia*, 1.vii.2014, AHE_56, CJ271 / PHIL0034♀, CJ273 (no abdomen), CJ274 (no abdomen), '*Philodoria* sp. 6 of Johns *et al*. (2018)', in FLMNH.

Diagnosis. The forewing pattern is similar to that of *P. marginestrigata* (Walsingham), but this specimen can be distinguished by its large white patches on the forewing (Fig. 24A–G). See also diagnosis of *P. lipochaetaella*.

Redescription: Adult (Fig. 24A–F). Wingspan 4.5–6 mm in paralectotype; forewing length 1.8–2.5 mm in paralectotype. Head and frons whitie; maxillary palpus white; labial palpus white, sometimes with fuscous rings at apex of second segment and in middle of terminal segment. Antenna white ringed fuscous. Thorax white to gray-white. Forewing white, sometimes partially suffused light gray with light ocherous to yellow patches, margined with fuscous scales: a median streak (**mp**) from base to 1/3, meeting apex of an oblique narrow line from base to 1/8 of

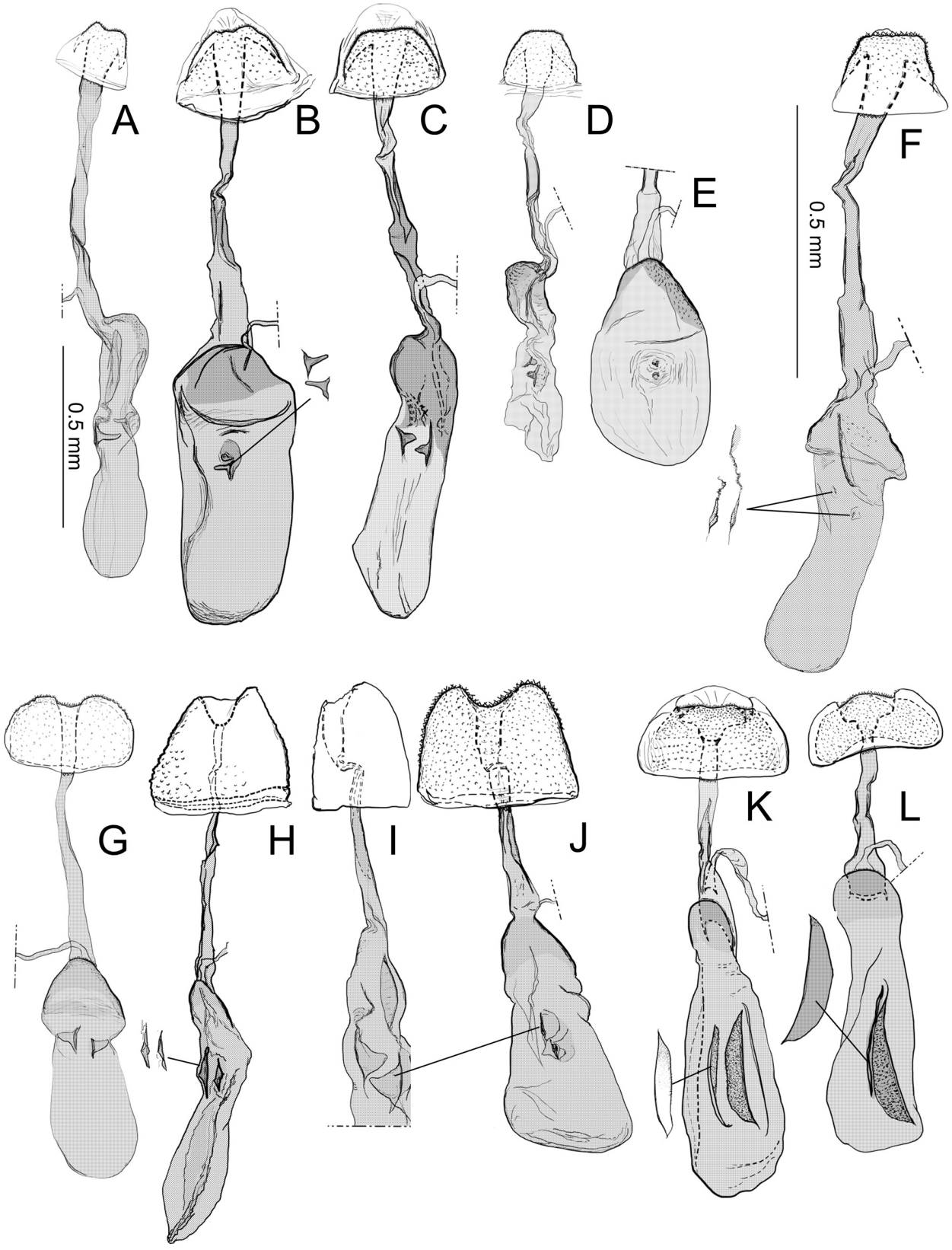

FIGURE 56. Female genitalia of *Philodoria*. **A** *P. succedanea*, paralectotype, Maui, SK714, **B** Same species, Hawaii (Big Island), SK624, **C** *P. auromagnifica*, Hawaii (Big Island), SK623, **D** *P. kauaulaensis*, holotype, SK690, **E** Same species, lateral view, **F** *P. kolea*, paratype, Hawaii (Big Island), SK634, **G** *P. lysimachiella*, SK654, **H** *P.* sp. A, SK753, **I** *P. molokaiensis*, SK668, lateral view, **J** Same ventral view, **K** *P. splendida*, SK621, **L** *P. lama*, paratype, SK813.

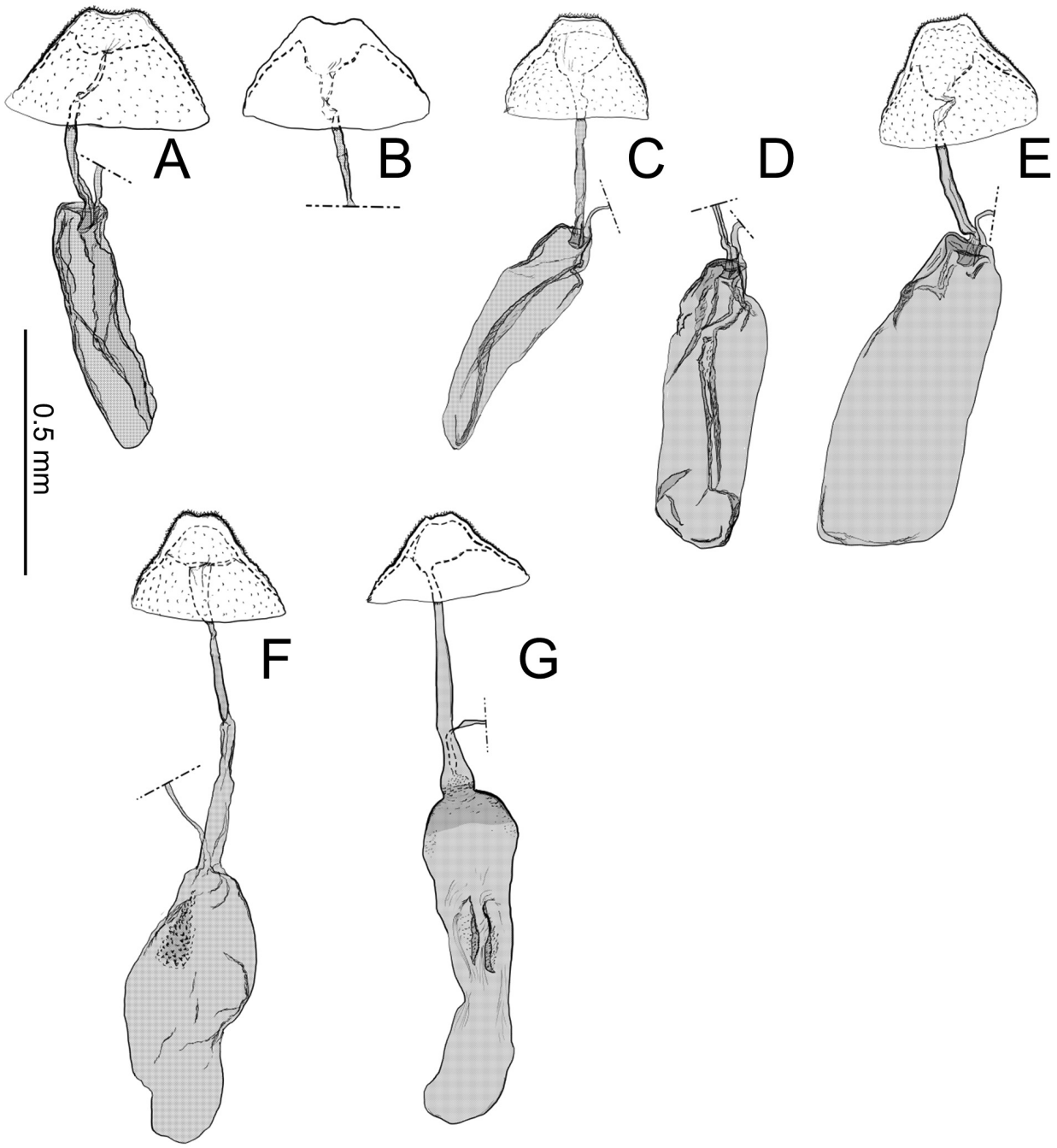

FIGURE 57. Female genitalia of *Pipturus*-mining *Philodoria*. **A** *P. costalis*, paralectotype, SK653 **B** Same species, paratype, SK652 **C** *P. pipturiella*, SK722 **D** *P. pipturicola*, paralectotype, lateral view, SK717 **E** Same species, paralectotype, SK716 **F** *P. haelaauensis*, SK792 **G** *P. floscula*, SK819.

near dorsum; a small spot at dorsal 1/7 (**dp**$_1$); three oblique costal patches (**cp**$_{1–3}$): **cp**$_1$ about 1/2, **cp**$_2$ at 3/4, reaching half across wing; **cp**$_3$ short, before apex; an oblique **dp**$_2$ at 1/2, meeting **cp**$_1$ and **cp**$_2$; apical portion white with light ocherous scales at middle, containing a black **as**; cilia white or white gray, with **bl**$_1$ and **bl**$_2$ from termen to tornus. Hindwing gray; cilia white. Abdomen ocherous. Legs white, tarsi with fuscous scales.

Male genitalia (Figs. 53A, B, 54A, 55A) (n=6). Capsule 590 µm. Tegumen 0.9 x length of valva; valva 420 µm long, tapering along costal margin from 1/2 to apex; apical half digitiform, slender and slightly curved toward inner margin with small spines at apex; a set of short spines arranged along inner side of basal region (Fig. 53A, B). Saccus short and triangular in ventral view (Fig. 54A). Phallus 400 µm long and slightly widening at phallobase with developed coecum; cornuti in vesica indistinct (Fig. 55A).

Female genitalia (Fig. 60D) (n=2). 1060 µm long. Ostium bursae large; antrum large, cup-shaped with a pair of lateral lobes; lamella antevaginalis 140 µm, weakly sclerotized, inflexed on the posterior margin, widening toward anterior margin of A7. Ductus bursae rather short, middle region weakly sclerotized, round and flat; terminus of the ductus bursae tubular, biforked. Corpus bursae 640 µm, pyriform; anterior end of corpus bursae weakly sclerotized; signa absent.

Distribution. Oahu (Meyrick, 1928), Molokai and Maui: new record.

Host plants. Asteraceae: *Melanthera integrifolia* (Nutt.) W.L.Wagner & H.Rob. (Meyrick 1928; Johns *et al*. 2016), *M. kamolensis* (O.Deg. & Sherff) W.L.Wagner & H.Rob. (Endangered, IUCN) and *Lipochaeta rockii* Sherff are new record.

Biology. (Fig. 91A–G) The larva mines the fresh leaves of *Melanthera integrifolia* forming a blotch mine which expands to cover the entire leaf as the larva grows (Fig. 91A, B). Pupation occurs in the cocoon outside of the mine; cocoon is white ellipsoid (Fig. 91C). Mines on *M. integrifolia* are very difficult to find. Larvae that feed on *Lipochaeta rockii* form a blotch mine and have a white, ellipsioid pupal cocoon (Fig. 91D, E). On a leaf of *M. kamolensis*, we observed a similar cocoon to that of *L. rockii*. Cocoons were often found on the adaxial leaf surface, centered on the midvein.

Remarks. We surveyed some *Melanthera* populations in the lowlands of Maui but did not find any *Philodoria* mines. The East Maui specimens feeding on *Melanthera kamolensis* have generally darker brown patches (Fig. 24E–G), similar to specimens from the type series of *P. lipochaetaella*, but these specimens are *P. sciallactis* based on male genitalia. The East Maui specimens are from the same series as *P. sciallactis* of Johns *et al*. (2018: fig. 2, AHE_4/CJ-145). *Pholodoria* sp. 6 of Johns *et al*. (2018) is here treated as *P. sciallactis* based on female genitalia: three specimens of *P*. sp. 6 (CJ271, 273 & 274) were collected from the type locality of *P. sciallactis* and female genitalia of CJ271 is poor condition, but similar to that of paralectotype of *P. sciallactis.* Two specimens (CJ273 & 274) were entirely sacrificed for molecular analysis (Johns *et al*. 2018), and no voucher remains. Among specimens from the populations on Oahu, Molokai and Maui, there is phenotypic wing pattern variation and a detailed DNA barcoding study in the future may prove beneficial to futher determine the species boundaries of *P. sciallactis* and *P. lipochaetaella*.

Philodoria sp. B near *P. sciallactis*

Fig 24H.

Material examined. 1 (sex unknown), Kokee, Kauai, 13.vii.2015 (stored), C.A. Johns leg., host: *Lipochaeta acris* [= *L. connata* var. *acris*], 15.vi.2015, CJ483 (abdomen missing) in BPBM. What remains of the specimens was mounted by placing two forewings without mountant under a coverslip and a 3/4 hindwing in capsule (Fig. 24H). The head, antenna, thorax, and legs were sacrificed for molecular analysis and the abdomen is missing.

Diagnosis. The forewing pattern is similar to *P. sciallactis* (Meyrick), but is distinguished by the round $\mathbf{ds_2}$ and brown $\mathbf{dp_1}$ and $\mathbf{dp_2}$ meeting at median line (Fig. 24H).

Male and female genitalia Unknown.

Distribution. Kauai.

Host plants. Asteraceae: *Lipochaeta connata* var. *acris* (Sherff) R.C.Gardner.

Biology. Unknown.

Remarks. Judging from forewing characters, we consider this species as a unique species. But because parts of its body are missing, we tentatively call it *Philodoria* sp. B near *P. sciallactis*. We hope that future studies will search *Lipochaeta acris* plants at Kokee, Kauai, so that additional specimens can be obtained.

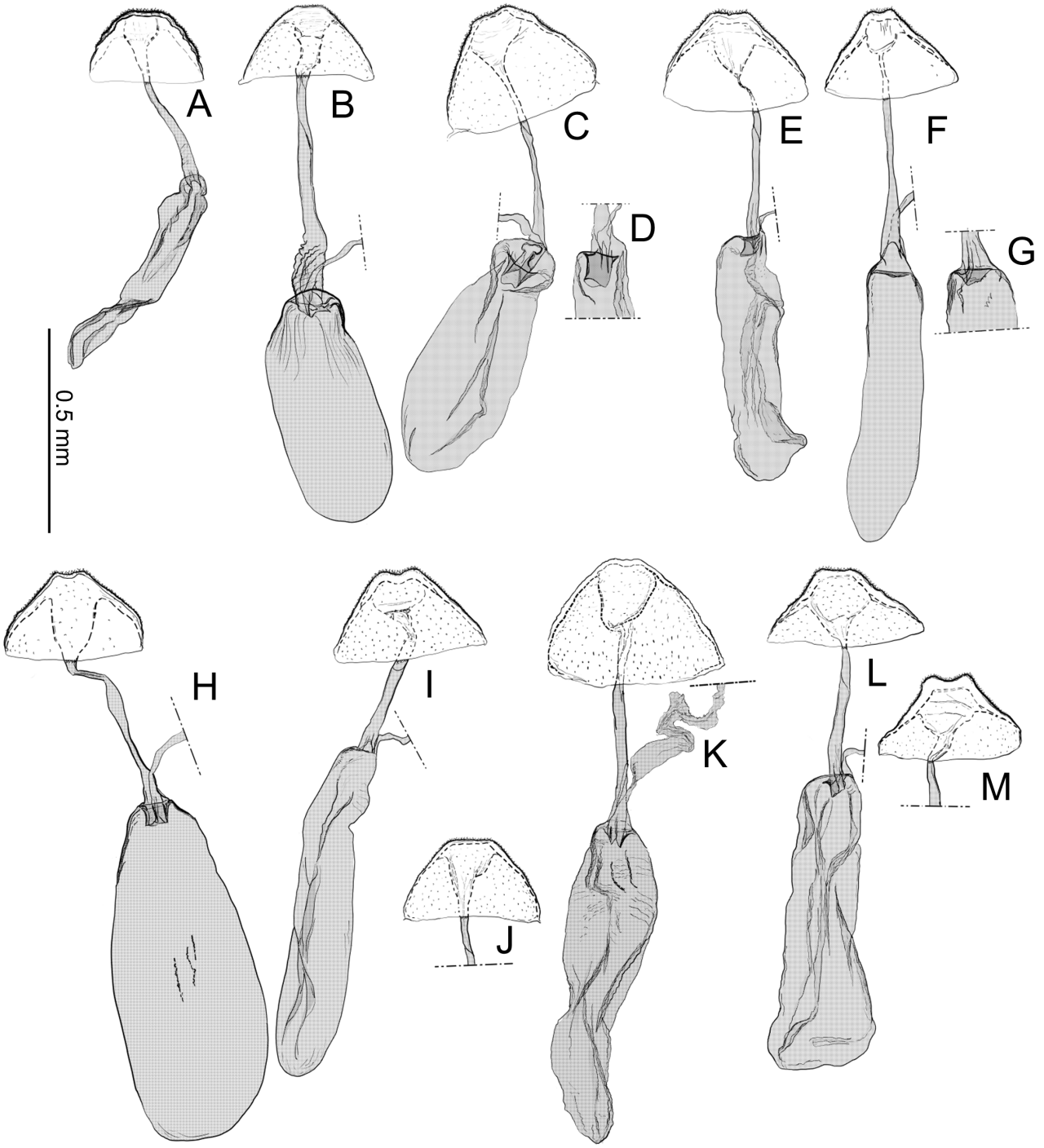

FIGURE 58. Female genitalia of *Philodoria*. **A** *P. wilkesiella,* SK761, **B** *P. epibathra*, SK679, **C** *P. dubauticola*, SK645, **D** Same species, PHIL0008, **E** *P. dubautiella*, SK692, **F** *P. alakaiensis*, paratype, SK659, **G** Same species, lateral view, **H** *P. hibiscella*, SK723, **I** *P. naenaeiella*, SK703, **J** Same species, SK834, **K** *P. knudseniiella*, paratype, SK863, **L** *P. hesperomanniella*, paratype, SK832, **M** Same species, SK620.

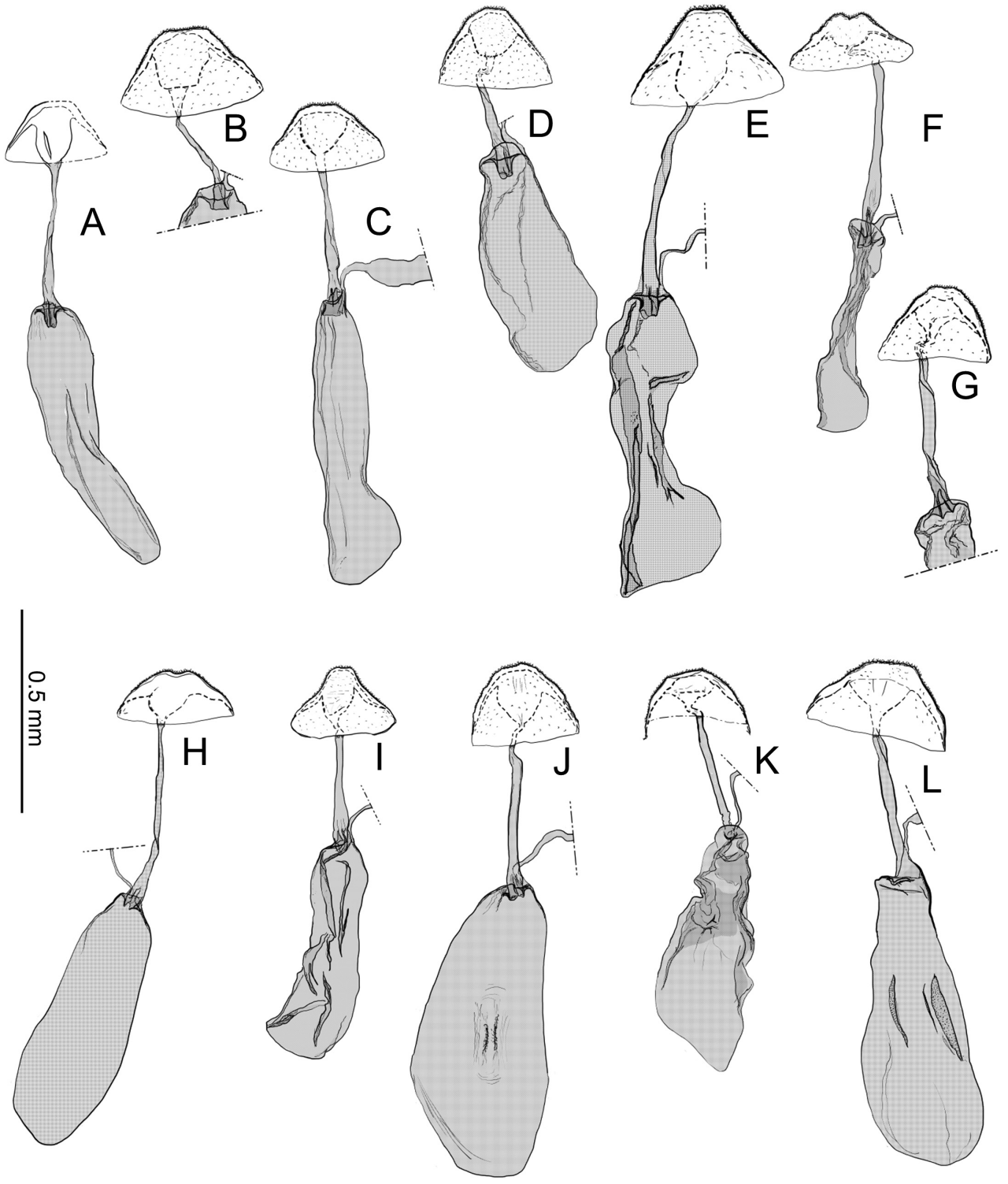

FIGURE 59. Female genitalia of *Philodoria*. **A** *P. neraudicola*, paralectotype, Oahu, SK708, host: *Neraudia melastomifalia*, **B** Same species, Maui, SK838, host: *Pipturus albidus*, **C** *P. obamaorum*, paratype, Hawaii (Big Island), SK710, host: *Pipturus albidus*, **D** Same species, Hawaii (Big Island), SK844 host: *Pipturus* sp., **E** *P. urerana*, paralectotype, SK672, **F** *Philodoria* sp. 1, SK835, **G** Same species, PHIL0021, **H** *P. keahii,* paratype, SK756, **I** *P. funkae*, holotype, SK761, **J** *P. touchardiella*, SK764, **K** *P. keaensis*, holotype, Hawaii (Big Island), SK777, **L** *P. hauicola*, Oahu, SK618.

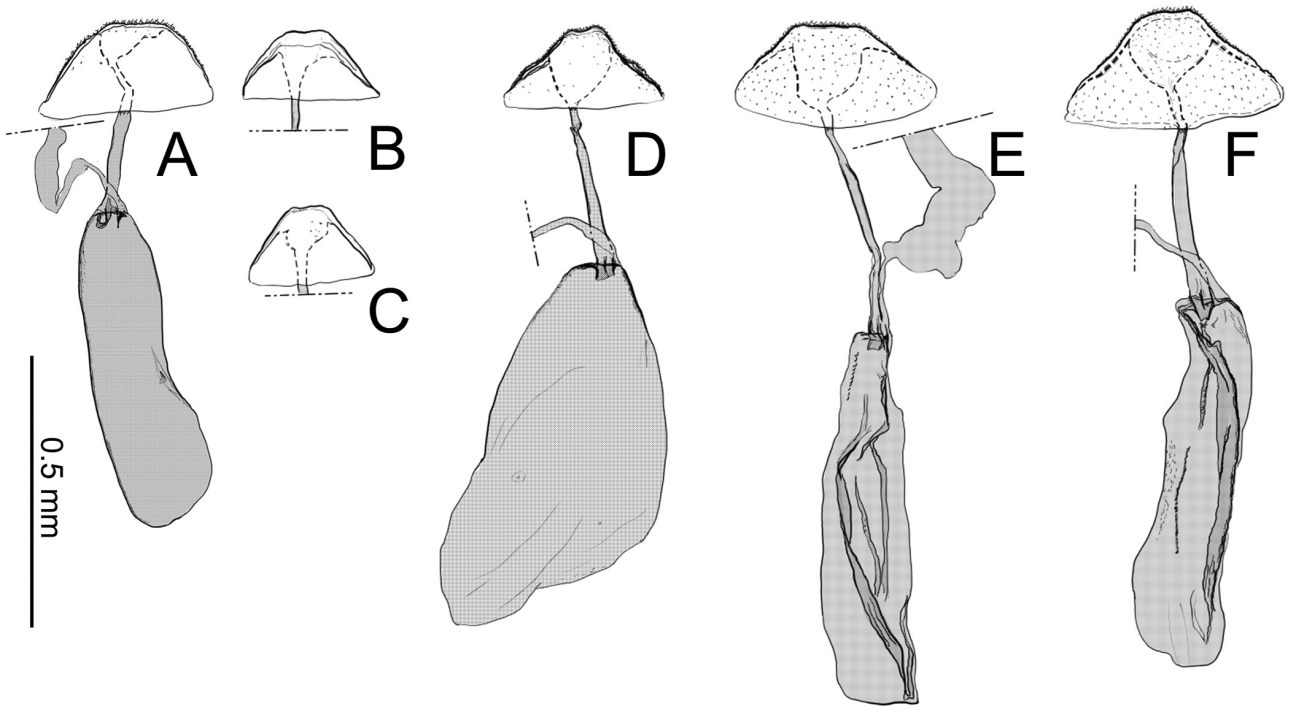

FIGURE 60. Female genitalia of *Philodoria*. **A** *P. marginestrigata*, SK665, **B** Same species, SK772, host: *Abutilon menziesi*, **C** Same species, SK787, host: *Sida fallax*, **D** *P. sciallactis*, paralectotype, SK713, **E** *P. ureraella*, paralectotype, SK677, **F** *P. opuhe*, paratype, SK675.

Philodoria ureraella (Swezey, 1915)

Figs. 25A, B, 33D, H–M, 53C, 54B, 55B, 60E, 78D, 95D–F.

Gracilaria ureraella Swezey, 1915: 94.
Parectopa ureraella (Swezey, 1915); Swezey 1928: 191.
Philodoria ureraella (Swezey, 1915); Zimmerman 1978a: 691, figs. 446, 453, 460.

Type locality. Mt. Tantalus (Oahu).

Type material. Lectotype ♂, Mt. Tantalus, Oahu, [15.iii.1914 or 16.iii.1915] O.H. Swezey, host: *Urera* [*sandwicensis*], |TYPE of *Gracilaria ureraella* Swezey [Type no.] 213| left bottom one of four types on the type mount, Type no. 213 in BPBM. [designated by Zimmerman (1978a)]. Paralectotype 10 (7♂, 1♀, 2 sex unknown). 6♂, 1♀, 1 (sex unknown), same data and locality as lectotype, SK676♂|BPBM34350, ♂|BPBM34351 (right bottom one of four types), BPBM34352 (3♂, 1 sex unknown) |ex. serpentine mine| 34355♂ (top one of two types), SK677♀|BPBM34360; 1♂, 1 (sex unknown), same data and locality as lectotype, bottom two of four types, SK742♂ in USNM. Described from 31 specimens: two series collected from leaf mines from *Urera sandwicensis* at Mt. Tantalus, Oahu: 13 specimens in March 15, 1914; and 20 more specimens from mined leaves of the same tree, on March 16, 1915 (Swezey, 1915). Swezey considered them as one species, '*ureraella*' and described 'wing pattern variation': '~sometimes the whitish markings are pure white' (= *ureraella*) (Fig. 25A, B) and 'sometimes they are ocherous concolorous with the other ocherous portions of the wing' (= new species, *opuhe* **sp. n.** in the present study) (Fig. 25C, D). Zimmerman (1978a: 673, fig. 446) designated the specimen that has whitish markings as the lectotype of *P. ureraella* from four syntypes on the single 'type' mount 213. We examined 70 paralectotypes designated by Zimmerman in BPBM and USNM of '*P. ureraella*' and we recognize 10 of them as paralectotypes of *P. ureraella*. The remaining 60 specimens from that series are here described as a new species, *P. opuhe* which has ocherous forewings and a distinct broad valva and saccus.

Additional material. 8 (4♂, 3♀, 1 sex unknown). Maui Is., C.A. Johns leg., host: *Urera glabra* in BPBM: 2♂, 1♀, 1 (sex unknown), Iao Valley, 1&9.viii.2014 (stored), 28.vii.2014, CJ316 / SK816♂, CJ337 / PHIL0005♂,

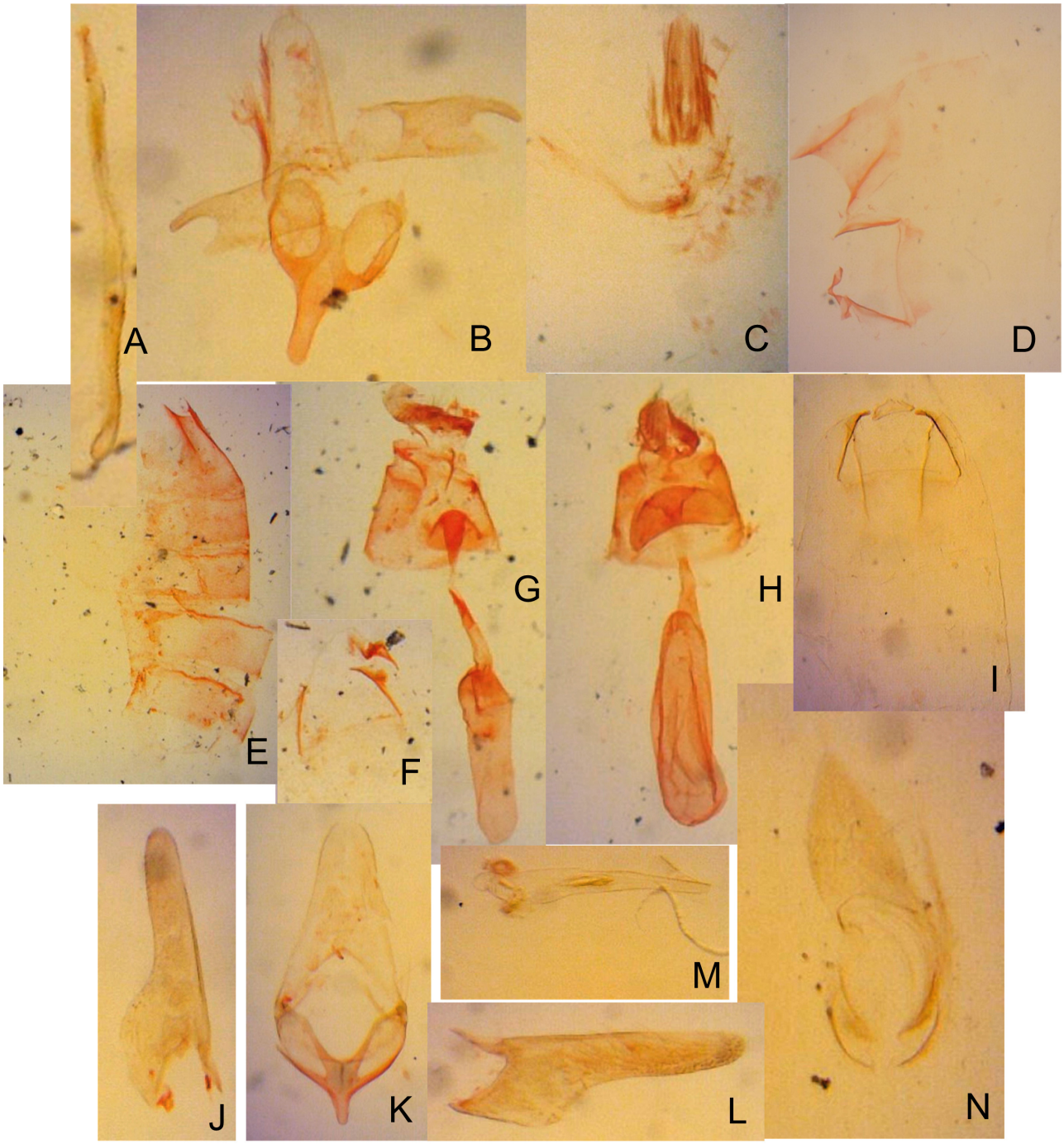

FIGURE 61. Images of genitalia slides prepared by E. C. Zimmerman. **A–D**: *P. auromagnifica*, male, Oahu, Z-XII-20-62-5, **E–G**: *P. auromagnifica*, female, Oahu, Z-XII-20-62-6, **H:** *P. basalis*, female, Hawaii (Big Island), Z-XII-20-62-4, **I–N**: *P. costalis*, paralectotype male, Oahu, Z-XII-20-62-2. **A**, **M** Phallus, lateral view, **B** Entire genitalia except phallus, ventral view, **C** Coremata, **D** Abdominal segments II–III, **E** Abdominal segments II–VI, **F** Tergum II, **G**, **H** Entire female genitalia, **I** Abdominal segments II–V, **J** Right valva, **K** Genital capsule, ventral view, **L** Left valva, **N** Abdominal segment VIII with dorsal flap and coremata.

0006♀; 1♂, 2♀, Waikamoi, 2.viii.2014 (stored), 21.vii.2014, CJ324/SK817♂; 1♂, Maile Trail lower Waikamoi, 24.v.2016 (stored), Spring.2016, CJ541/SK815♂.

Diagnosis. The forewing pattern is similar to that of *P. lipochaetaella* and *P. sciallactis*, but is distinguishable by the lack of a 2nd costal ocherous patch; the male genitalia have a very slender and needle-shaped saccus; the female genitalia have a corpus bursae with some wrinkles.

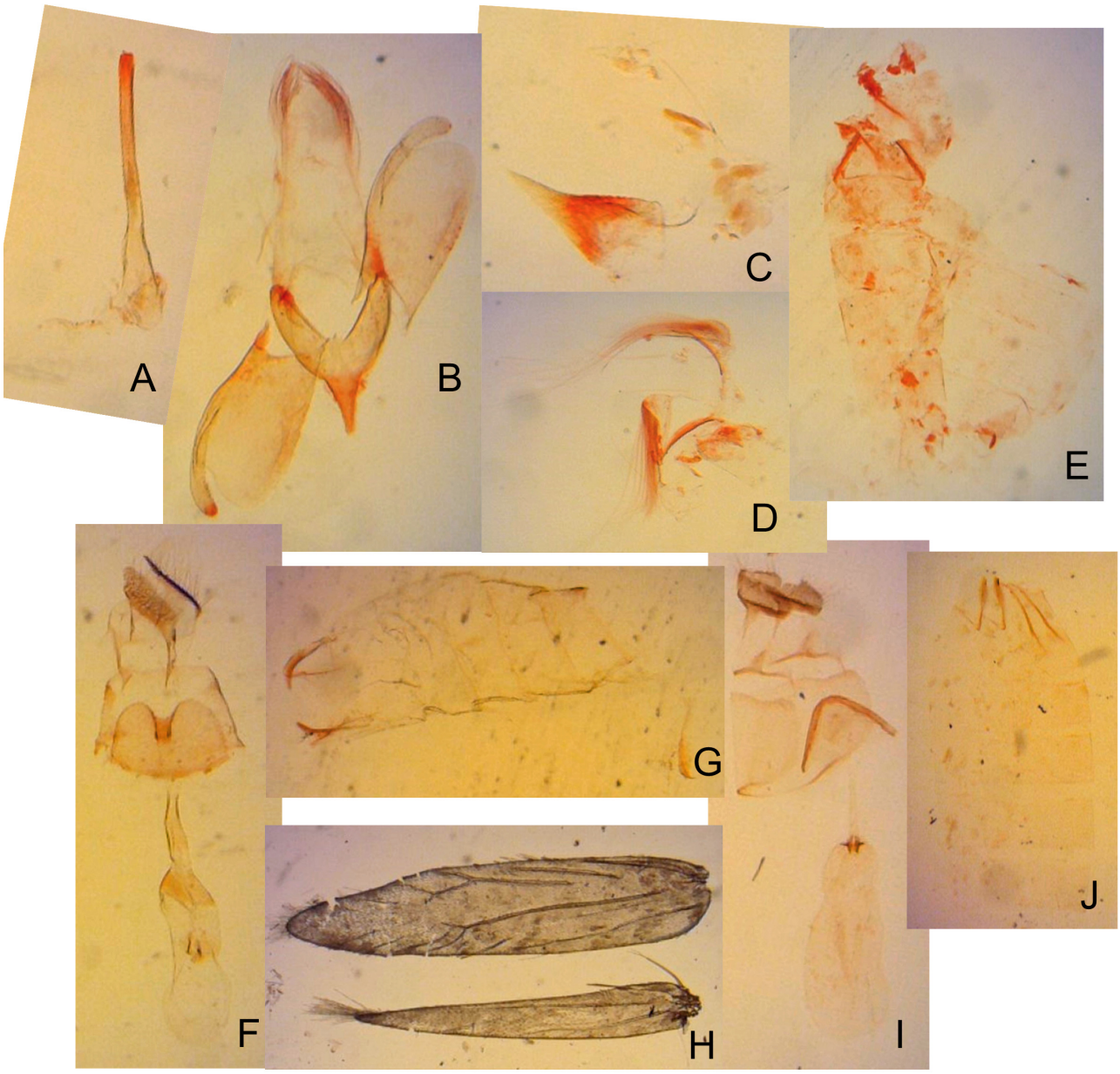

FIGURE 62. Images of genitalia and wing vein mounts prepared by E. C. Zimmerman. **A–E**: *P. lysimachiella*, male, Oahu, Z-XII-20-62-1, **F–H**: *P. molokaiensis*, paralectotype female, Molokai, **I**, **J**: *P. knudseniiella*, paratype female, Kauai, Z-I-10-66-A. **A** Phallus, lateral view, **B** Entire genitalia except phallus, ventral view, **C** Dorsal flap, **D** Pair of coremata, **E**, **G J** Abdominal segments, **F**, **G** Z-XII-19-62-26, **F**, **I** Female genitalia, ventral view, **H** Same species, left wing veins, Z-XII-20-65.

Redescription: Adult (Figs. 25A, B, 33D, H–M). Wingspan 7–9 mm in type series; forewing length 4 mm in lectotype (Fig. 25B), 3–4 mm in paralectotypes. Head and frons white; maxillary palpus white, dark brown beneath; labial palpus white, with fuscous externally. Antenna ocherous, fuscous on apical fourth, 1.3–1.4 x length of forewing. Thorax white to ocherous. Forewing pure white with orange ocherous patches enclosed fuscous scales: an obscure basal patch at 1/7 with slender orange line from 1/7 to near middle; a large $\mathbf{cp}_3$ from 3/4 to the middle, fuscous line of inside not reaching costa; one oblique $\mathbf{dp}_2$ at 1/4 connecting orange line of basal patch, $\mathbf{dp}_3$ about 1/2 reaching the middle of wing, connecting $\mathbf{cp}_3$; apical portion orange ocherous with costal and near dorsal black lines from 4/5 to black **as** of termen; cilia orange ocherous mixed with fuscous scales; three white spots (**a, b, c**) at apex and fuscous apical patch at termen and a dark fuscous $\mathbf{bl}_1$ from termen to tornus. Hindwing grayish fuscous, cilia paler. Abdomen grayish fuscous. Legs ocherous, fuscous above and tarsi barred with fuscous.

Male genitalia (Figs. 53C, 54B, 55B) (n=6). Capsule 780 µm. Tegumen 0.9–1.0 x length of valva; valva 540 µm long, tapering along costal margin from basal 2/5–1/2 to apex; apical half digitiform and slightly curved toward

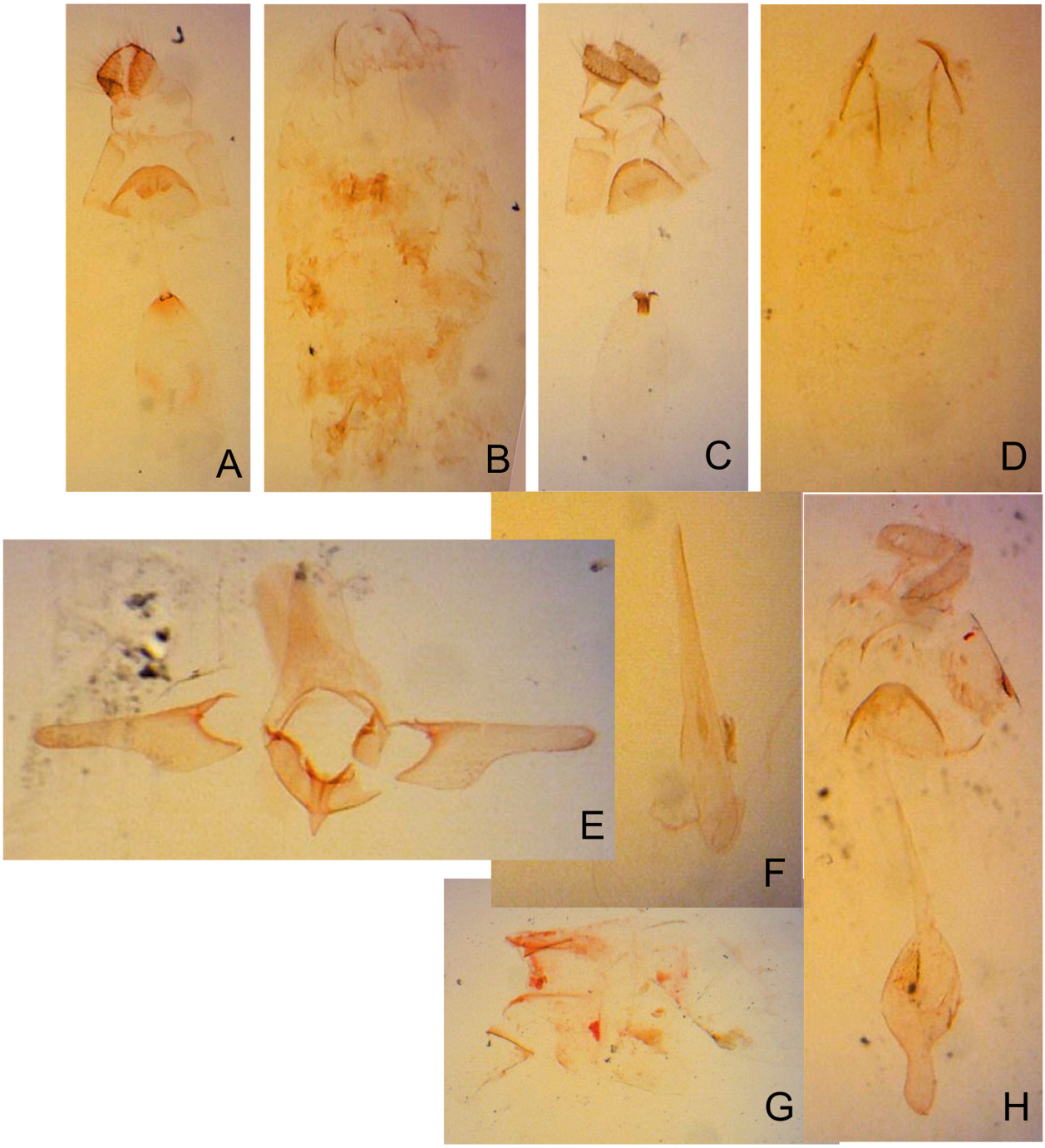

FIGURE 63. BPBM paratype, genitalia slides prepared by E. C. Zimmerman. **A**, **B**: *P. hesperomanniella* paratype female, Oahu, Z-V-17-61 **C**, **D**: *P. obamaorum* paratype female, Hawaii (Big Island), Z-V-18-61, **E–G**: *P. obamaorum* paratype male, Hawaii (Big Island), Z-1-26-61(3), **H**: *P. haelaauensis*, paratype female, Maui, Z-XII-19-62-24. **A**, **C**, **H** Female genitalia, ventral view, **B**, **D**, **G** Abdominal segments, **E** Male genitalia excluding phallus, ventral view, **F** Phallus, lateral view.

outer margin with small spines at apex; a set of short arranged spines along inner side of basal region (Fig. 53C). Saccus very slender and needle-shaped in ventral view (Fig. 54B). Phallus 570 µm long and nearly straight with developed coecum; cornuti in vesica indistinct (Fig. 55B).

Female genitalia (Fig. 60E) (n=2). 1230 µm long. Ostium bursae large; antrum large, cup-shaped with a pair of thick lateral lobes; lamella antevaginalis 180–190 µm, weakly sclerotized, trapezoid, widening toward anterior margin of A7. Ductus bursae slender and long, middle part weakly sclerotized, round and flat; terminus of ductus bursae tubular, biforked; middle part of ductus seminalis very broad. Corpus bursae 660 µm, oblong; anterior end of corpus bursae weakly sclerotized; paired rows of longitudinal, partly sclerotized wrinkles.

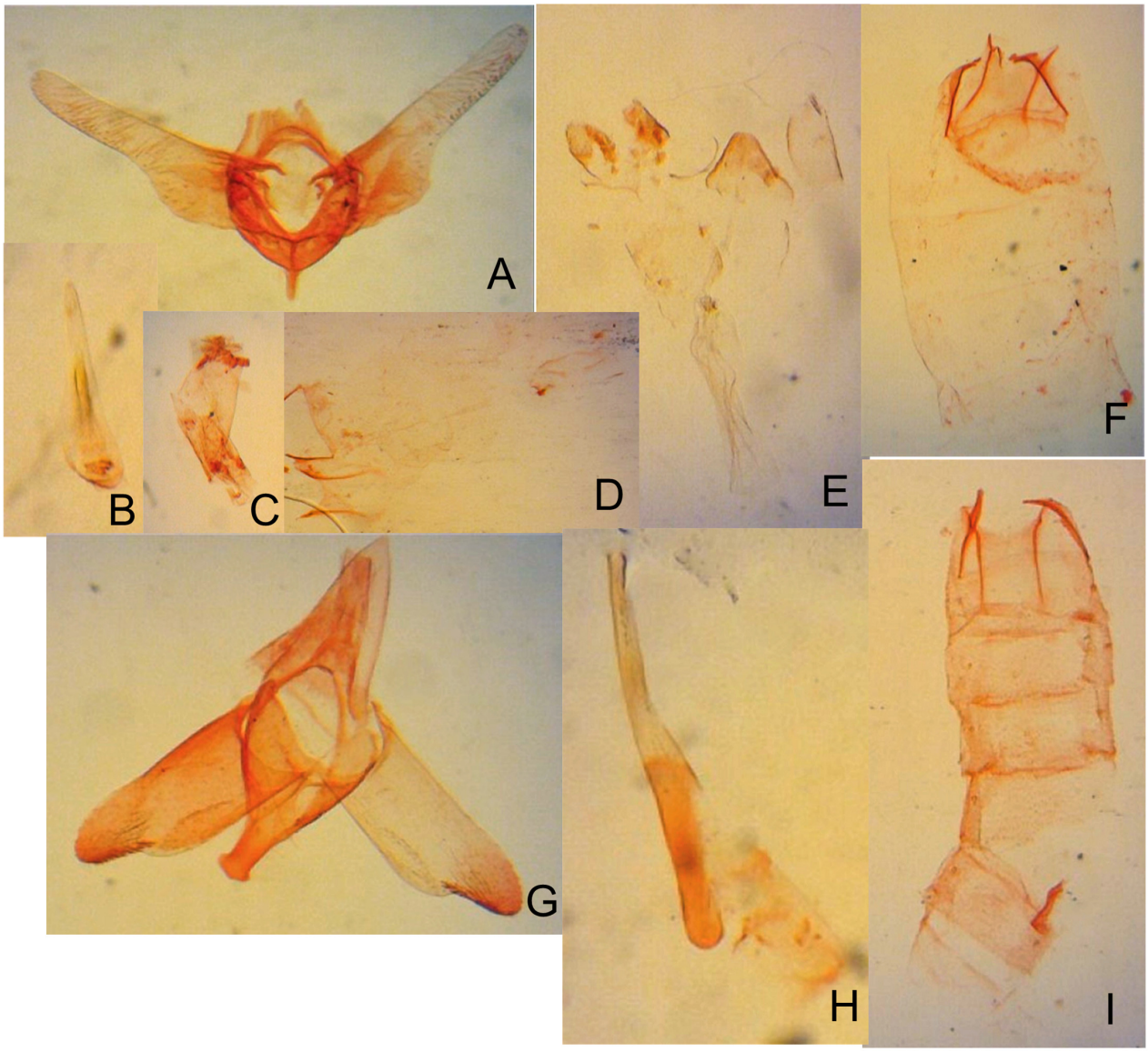

FIGURE 64. BPBM genitalia slides prepared by E. C. Zimmerman. **A–D**: *P. haelaauensis*, paratype male, Maui, Z-XII-19-62-23, **E**, **F**: *P. pipturiella* paratype female, Oahu, Z-XII-1962-22, **G–I**: *P. splendida*, male, Oahu, Z-XII-19-62-20. **A** Vinculum and valvae, tegumen broken, **B**, **H** Phallus, **C** Tegumen? **D**, **I** Abdominal segments, **E** Genitalia opened from left lateral side, **F** Abdominal segments II–VI, **G** Genitalia excluding phallus, ventral view.

Distribution. Oahu (Swezey 1915) and Maui: new record.

Host plants. Urticaceae: *Urera sandvicensis* Wedd. (Swezey 1915) and *U. glabra* Wedd. is new record. The record of *P. ureraella* from *U. kaalae* Wawra (Zimmerman 1978a; after Swezey 1933) is incorrect, and that host record should be attributed to *Philodoria opuhe*.

Biology. (Fig. 95D–F). Larvae of *P. ureraella* that feed on *Urera glabra* form a slender tortuous linear mine (Fig. 95D, E). Two mines per leaf. The pupal cocoon is situated outside of the mine, Pupation occurs in the cocoon outside of the mine; usually on the abaxial leaf surface; a pupal cocoon is white, near ellipsoid (Fig. 95F).

Remarks. We removed a female specimen from the paralectotypes of "*P. ureraella*", from the same mount of SK742♂ in USNM because this specimen is a *Chedra* sp. (Batrachedridae), not *Philodoria* (Fig. 96). Two *Chedra* species, *C. microstigma* (Walsingham, 1907) and *C. mimica* Zimmerman, 1978 were reported from Oahu and Hawaii (Big Island), and larvae of these species bore into Cyperaceae and Poaceae, respectively (Zimmerman 1978b). The unnamed *Chedra* species from type series of "*P. ureraella*" is distinguished from Hawaiian congeners in the having central fuscous patch and lacking three small fuscous dots in the forewing. It is possible that this mistake

took place because *Chedra* pupae can resemble the pupae of *Philodoria* (Zimmerman 1978b). Swezey (1915) recorded parasitoids of "*P. ureraella*", but these records cannot be attributed directly to what we treat currently as *P. ureraella* because they are reared from larvae and pupae of two species, *P. ureraella* and *P. opuhe*. Swezey (1915: 94) wrote: "From the lot of mined leaves collected March 15, 1914, 19 specimens of a new species of *Sierola* emerged; and from the lot collected March 16, 1915, two specimens, of *Omphale* [= *Euderus*] *metallicus* emerged, also 9 specimens of an undetermined Chalcid. Nearly as many parasites as there were moths." Zimmerman (1978a) reported three parasitoids of '*P. ureraella*'; these are Bethylidae: *Sierola pulchra* Fullaway, 1920; Eulophidae: *Euderus metallicus* (Ashmead, 1901), and *Pauahiana maculatipennis* (Ashmead, 1901).

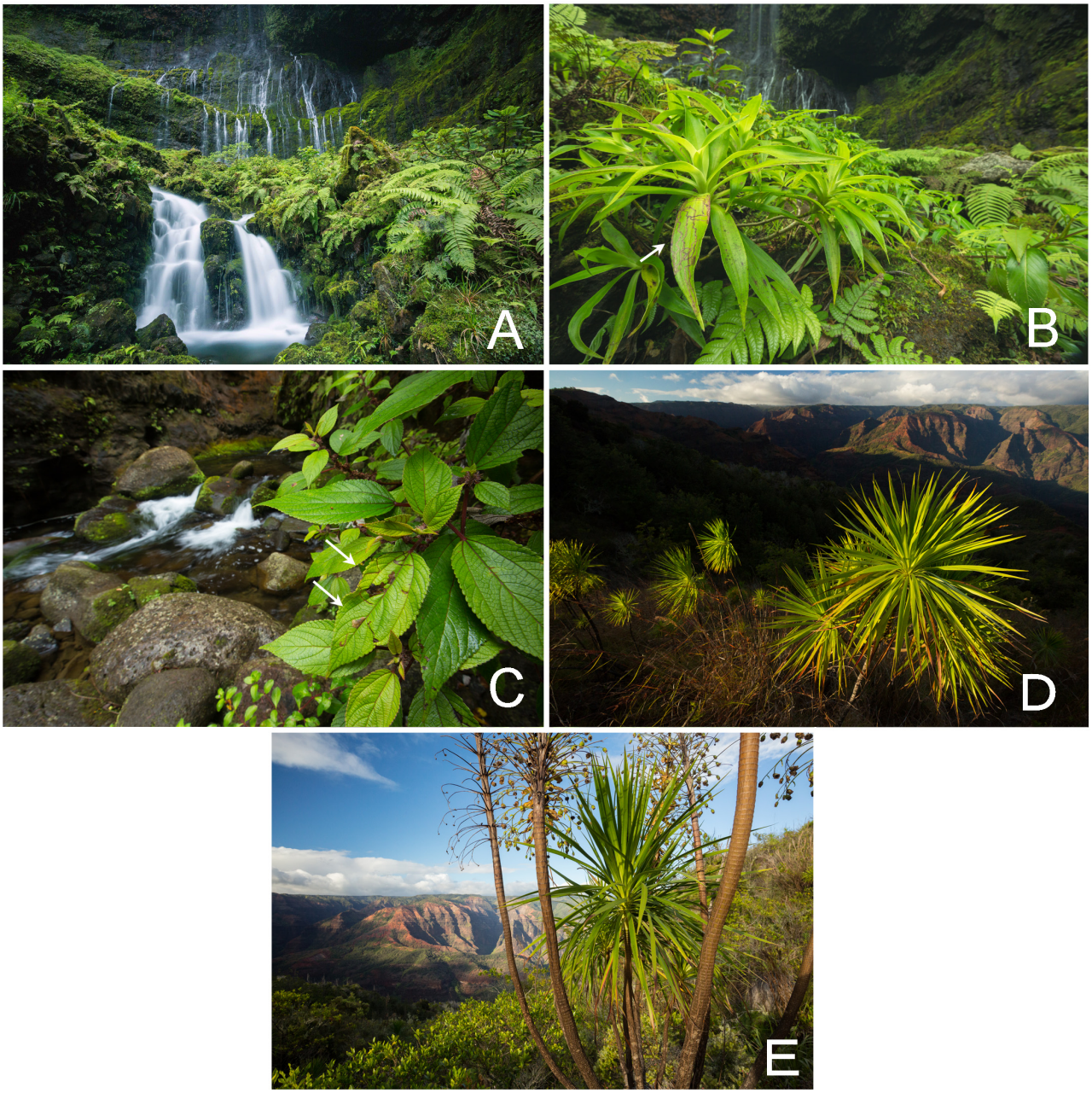

FIGURE 65. Habitats and host plants of *Philodoria* species on Kauai. **A–C**: Lihue-Koloa Forest Reserve, **D**, **E**: Waimea Canyon State Park. **A** Habitat, **B** *Philodoria* leaf mines on *Dubautia*, **C** *Philodoria* leaf mines on *Pipturus*, **D**, **E** *Wilkesia gymnoxiphium.* Arrows point to mines.

***Philodoria opuhe* Kobayashi Johns & Kawahara sp. n.**
Figs. 25C, D, 33B, C, E, F, 53D, 54C, D, 55C, 60F.

Gracilaria ureraella Swezey, 1915: 94.
Parectopa ureraella (Swezey, 1915); Swezey 1928: 191.
Philodoria ureraella (Swezey, 1915); Zimmerman 1978a: 691, figs. 446, 453, 460.

Type locality. Mt. Tantalus (Oahu).

Etymology. The specific epithet, *opuhe* is a noun in apposition taken from the Hawaiian name of the host plant, *Urera*.

Type material. Holotype ♂, Mt. Tantalus, Oahu, [15.iii.1914 or 16.iii.1915] O.H. Swezey, host: *Urera* [*sandwicensis*], |TYPE of *Gracilaria ureraella* Swezey [Type no.] 213| top right specimen is the designated specimen among four types on the same mount, Type no. 213 in BPBM (Fig. 25C). Paratypes: 59 (10♂, 7♀ 36 sex unknown, 6 pupae), Mt. Tantalus, Oahu, [15.iii.1914 or 16.iii.1915] O.H. Swezey, host: *Urera* [*sandwicensis*]: 1 (sex unknown), right bottom one of four types, same mount of holotype, 213 (Fig. 25D); 3♂, 3♀, 34 (sex unknown), BPBM34327–34348, SK674♂|BPBM34349, BPBM34351(1♂, 1♀, 1 sex unknown, three of four types, excluding the bottom right specimen), BPBM34353(four types), |ex blotch mine|BPBM34354, BPBM34355 (bottom ♀ of two types), SK746♂|BPBM34356, |ex blotch mine|BPBM34357 (four types), |ex blotch mine|BPBM34358, SK675♀|BPBM34361; 7♂, 4♀, 1 (sex unknown), same data and locality as holotype in USNM.

Pupa. 6 (sex unknown), same data and locality as holotype, BPBM 34354 (two types), BPBM 34359 (four types).

Additional material. 1♂, Puu Kaua (Peak of Waianae range 3127ft), Waianae Mts, Oahu, 6.xi.1932, O.H. Swezey, ex *Urera kaalae*, SK682|BPBM34362.

Diagnosis. Described based on paralectotypes of *P. ureraella* Swezey. *Philodoria opuhe* is distinguished from *P. ureraella* and similar species, e.g., *P. sciallactis* and *P. lipochaetaella*, by having a fuscous costal line from the base to about 1/2 in the forewing; the male genitalia have a rather oblong and straight valva and wide saccus; the female genitalia have a combination of rather small ostium and antrum, and sclerotized wrinkles on the corpus bursae. See also diagnosis of *P. ureraella*. A *Urera* mining species, *P. urerana* (Swezey), has female genitalia similar in shape to *P. opuhe* and *P. ureraella*, but *P. urerana* is distinct from the latter two species by having a fuscous to brown forewing (Figs. 20A, B, 33G).

Redescription: Adult (Figs. 25C, D, 33B, C, E, F). Wingspan 7–9 mm in type series; forewing length 3–4 mm in paralectotype. Head ocherous; frons white; maxillary palpus ocherous, dark brown below; labial palpus white to ocherous, with fuscous externally. Antenna ocherous, fuscous on apical fourth, 1.3–1.4 x length of forewing. Thorax ocherous. Forewing pure white to ocherous with ocherous patches enclosed fuscous scales: an obscure patch from base to 1/7; one large costal patch (**cp_2**) at 3/4 reaching near tornus, connecting a fuscous line from base of costal fold to beyond the middle, very narrow or interrupting from 1/7 to 1/3; obsure **dp_1** from 1/4 to 1/2, **dp_2** from about 1/2 reaching to the middleof wing; all fascia connect in the middle of wing forming ocherous obscure median line from base to 3/4; apical portion ocherous with costal and dorsal obscure black lines from 4/5 reaching black **as** of termen; cilia orange ocherous mixed with fuscous scales; three white spots (**a, b, c**) at apex and fuscous apical patch at termen and a dark fuscous **bl_1** from termen to tornus. Hindwing grayish fuscous, cilia paler. Abdomen grayish fuscous. Legs ocherous, fuscous above and tarsi barred with fuscous.

Male genitalia (Figs. 53D, 54C, D, 55C) (n=3). Capsule 820 µm. Tegumen 0.8 x length of valva; valva 620 µm long, rather gently tapering along costal margin from basal 2/5–1/2 to apex, apical half digitiform and slightly curved toward outer margin with small spines at apex, rather widening at middle compared to *P. ureraella*; a set of short spines arranged along inner side of basal region (Fig. 53D). Saccus digitiform (Fig. 54C) or triangular (Fig. 54D) in ventral view. Phallus about 600 µm long, rather thick, slightly sinuous in lateral view with developed coecum; cornuti in vesica indistinct (Fig. 55C).

Female genitalia (Fig. 60F) (n=1). Similar to *P. ureraella*, but differs in having a rather broad ductus bursae and slender ductus seminalis.

Distribution. Oahu (Swezey 1915).

Host plants. Urticaceae: *Urera kaalae* Wawra (Swezey 1933b; Zimmerman 1978a), *U. sandvicensis* Wedd. (Swezey 1915).

Biology. Swezey (1915: 94) reported the biology of '*P. ureraella*': "The mine at first is a small roundish blotch

becoming irregular as it becomes larger from the eating of the larva within. The larva emerges to spin its whitish cocoon on the surface of the leaf. The moths emerged from the cocoons in about ten days." We believe his report is for *P. opuhe* based on the specimen label "ex blotch mine". See also Biology and Remarks of *P. ureraella* and *P. urerana*.

Remarks. We were unable to survey for many *Urera* plants on Oahu but found a few *Philodoria* that are generally rare on Oahu. Swezey (1933) noted that specimens reared from *Urera kaalae* in the Waianae mountains differ slightly from the type series of '*P. ureraella*' from *U. sandwicensis* on Mt. Tantalus. We identified a *Philodoria* specimen from *U. kaalae* (Fig. 33E, F) as *P. opuhe* based on genitalia. *Urera kaalae* has become extremely rare and this plant should be considered for listing on the IUCN Red List. We observed two populations of *U. kaalae* in the Waianae mountains but found no signs of *Philodoria* mines.

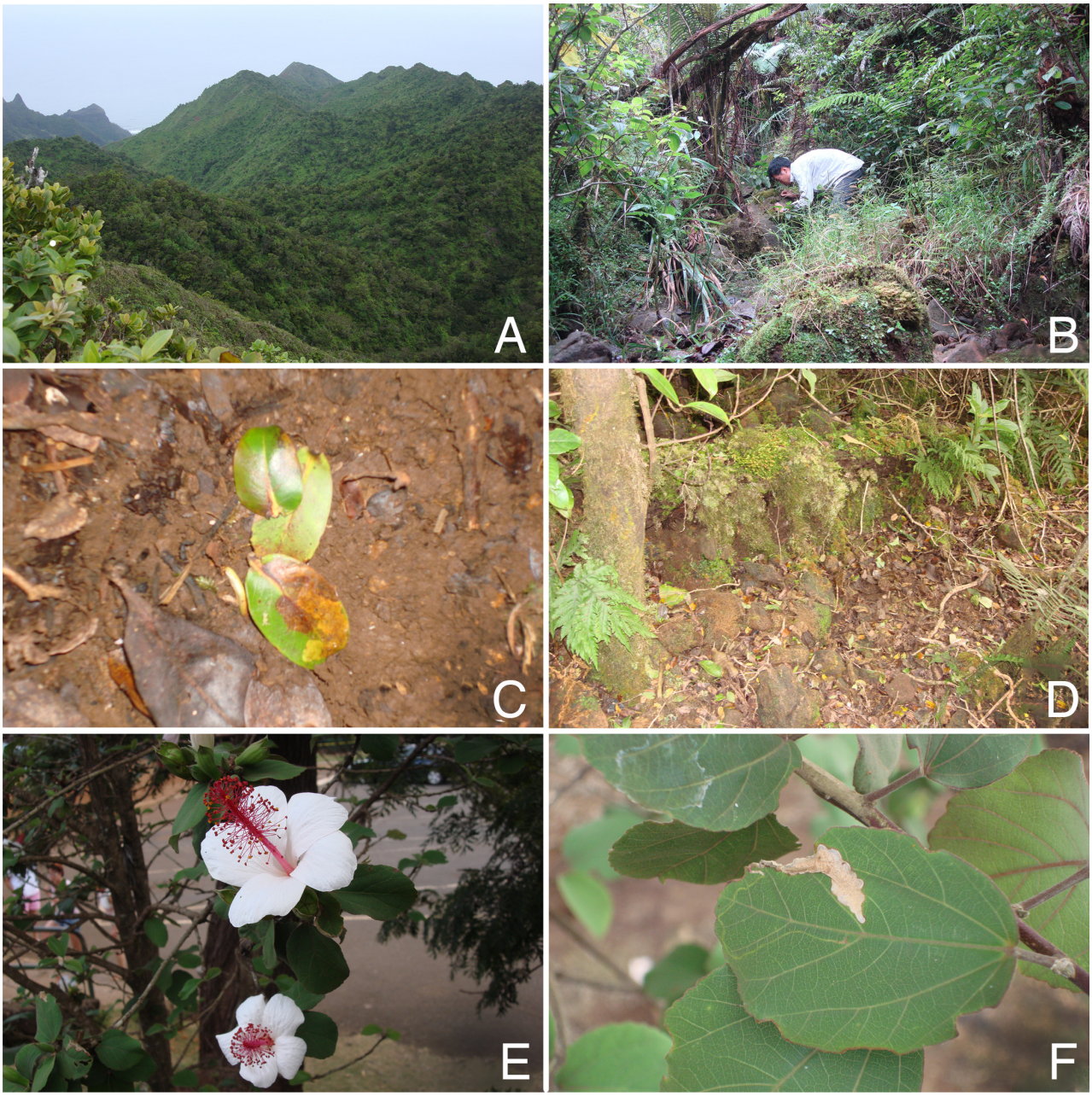

FIGURE 66. Habitats and host plants of *Philodoria* on Kauai. **A–D**: Upper Limahuli, **E**, **F**: Waimea Canyon. **A** Mountains of Limahuli, **B** Habitat with senior (last) author collecting specimens, **C** Same location as **B**, leaves with mines, **D** *Metrosideros polymorpha* leaves with mine on the ground with active larva, **E** *Hibiscus waimeae* subsp. *hannerae* flowers and leaf mines, **F** Leaf mine on same host plant as **E**. Arrows point to mines or larvae.

Discussion

Hawaii constitutes one of the most geographically isolated archipelagos and harbors thousands of unusual, highly threatened endemic plant and animal species. Baseline taxonomic research and natural history data for many of these endemics, especially diverse insect groups, is limited. Our study revised the taxonomy and provided new biological and distribution data for 51 species of *Philodoria*, which is thought to be one of the oldest extant arthropod lineages in the Hawaiian archipelago (Johns *et al.* 2018). Many new morphological characters and previously unknown host plant records were discovered through our present study, providing an opportunity to synthesize these results in an evolutionary context.

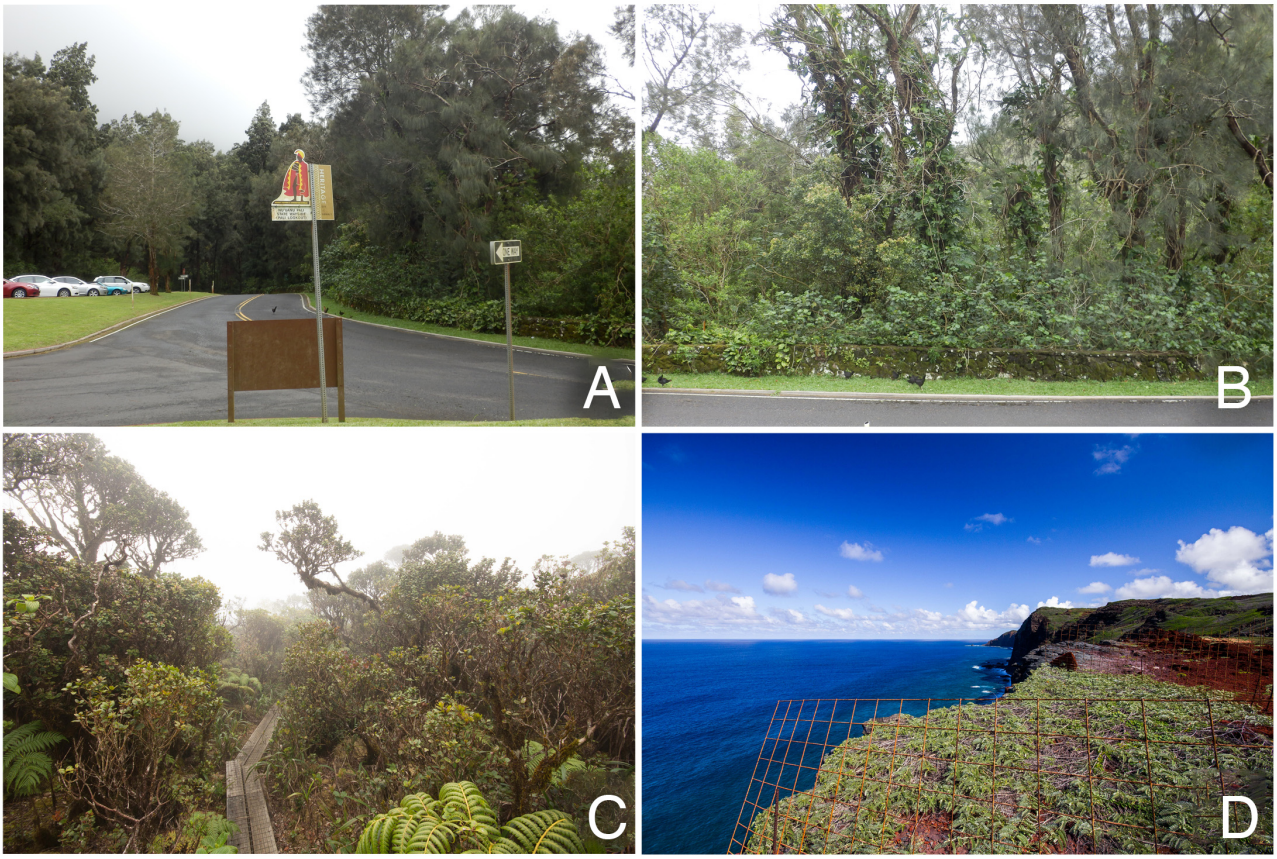

FIGURE 67. Habitats and host plants of *Philodoria* on Oahu and Molokai. **A**, **B**: Nuuanu Pali, Oahu, **C**: Mt. Kaala, Oahu, **D**: Mokio, Molokai **A**, **C**, **D** Habitat **B** *Hibiscus tiliaceus* trees, the host plant of *P. hauicola*.

The phylogenetic study of Johns *et al.* (2018) was based on 507 loci and 33 described and undescribed *Philodoria* species. Due to time constraints, the authors of that study were unable to formally describe species and left many species unnamed in their tree. Here, we assign names to 10 unnamed species in that study. We present a tree (Fig. 97) which is a revised version of Johns *et al.* (2018; fig. 2) showing the synthesis from our current work overlayed on the phylogeny published before. Using what we know now from morphology and host plant associations, we hypothesize the placement of species that could not be sequenced previously due to the lack molecular data (Fig. 97). Although *Philodoria* broadly splits into clades that are generally supported by morphological features and host plant associations, some inferences remain uncertain because the sister genus of *Philodoria* remains unknown. In the molecular phylogenetic analysis of Gracillariidae by Kawahara *et al.* (2017); a study that expanded the sampling of Kawahara et al. (2011), *Philodoria* was placed as a sister taxon to *Chileoptilia* Vargas & Landry, a monotypic genus from Chile. While outgroup sampling was limited, if the sister genus is *Chileoptilia,* this could imply that the ancestor of *Philodoria* originated in South America. Additional taxon sampling from closely-related genera of the Ornixolinae should be the focus of future biogeographic studies of *Philodoria*.

The evolution of host plant associations from what we have discovered here reveals that some plant genera are utilized by *Philodoria* as significant larval host plants, while others are not (Table 4). For example, Asteraceae is the most utilized larval host plant family for *Philodoria* with 18 associated species feeding on eight aster genera.

However, *Philodoria* is not known to mine two diverse Hawaiian aster genera, *Bidens* and *Tetramolopium*. It remains unknown why *Philodoria* does not mine these plant genera, but it may be due to plant chemical composition or plant physiological barriers. In another Hawaiian aster genus, *Argyroxiphium*, plant structural traits may prevent *Philodoria* from feeding. *Argyroxiphium* includes four extant species (Wagner *et al*. 1999) including *A. grayanum*, which is the only species that is host to *Philodoria,* perhaps because it is the only species in the genus that has glabrous leaves (Johns *et al*. 2016).

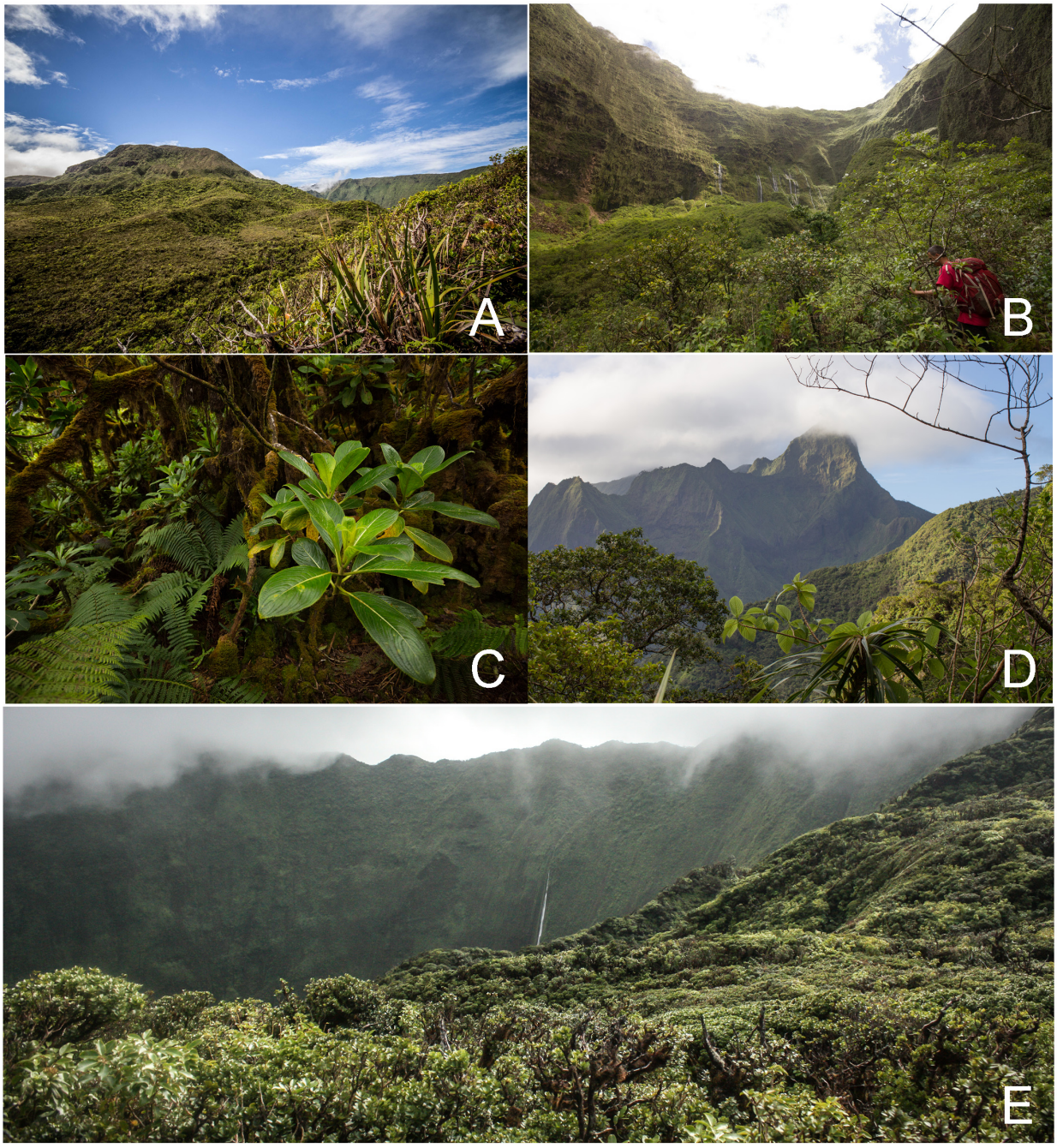

FIGURE 68. Habitats of *Philodoria* on Maui. **A** Eke, **B** Waihee Valley, **C** Hana Forest Reserve, **D** Iao Valley, E Haelaau.

Our study reveals that the second most utilized larval host plant family is Urticaceae. While *Philodoria* mines the plant genera *Neraudia*, *Pipturus*, *Touchardia*, and *Urera* in this family, it is surprising that the moth genus does not mine *Boehmeria*. This plant genus is the host to another leaf-mining moth, *Bedellia boehmeriella* Swezey, 1912 (Bedelliidae) on Oahu (Swezey 1912: 185–186). Thus it may be that the uneven pattern of host plant feeding is due to competition (competitive exclusion) among native Hawaiian micromoths on endemic plants. It is also possible that there is some aspect of *Boehmeria* that prevents *Philodoria* from mining the plant, or that we had missed

sampling *Philodoria* larvae mining *Boehmeria* during our surveys. A similar pattern exists in the Malvaceae, where *Hibiscus* is utilized as a host plant by *Philodoria hauicola, P. hibiscella* and *P. limahuliensis*. *Philodoria hauicola* is a relatively common species that is only known to feed on the non-native *Hibiscus tiliaceus*, which was introduced by early Polynesians about a thousand years ago (Zimmerman 1960, 1978a). Given that endemic *Hibiscus* species are relatively uncommon today, it is possible that we overlooked *Philodoria hauicola* on endemic *Hibiscus*. However, this may also be the result of competitive exclusion because two other *Philodoria* species (i.e. *P. hibiscella* and *P. limahuliensis*) feed on endemic Hawaiian *Hibiscus*.

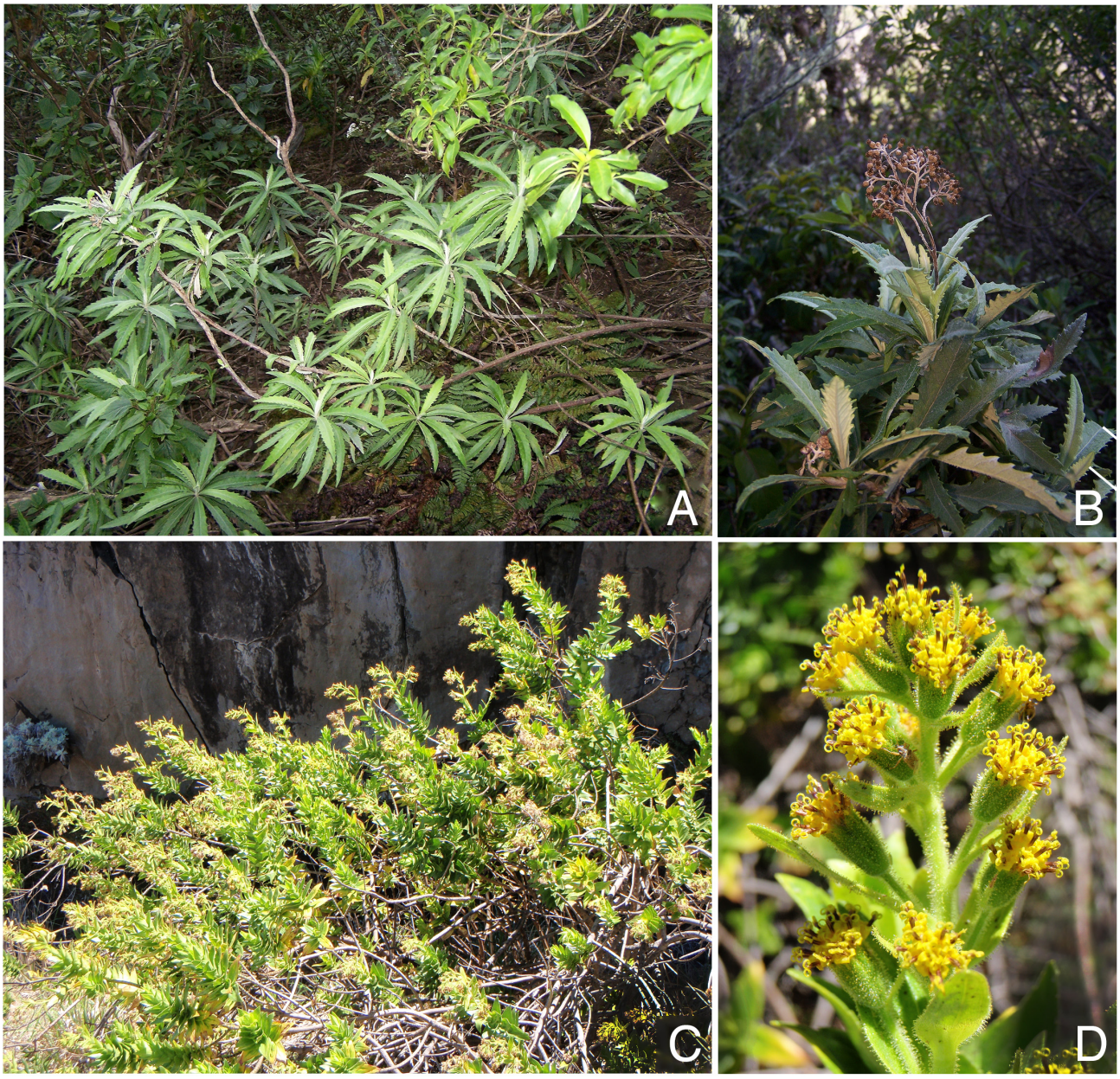

FIGURE 69. Habitats and host plants of *Philodoria* on Maui. **A** Kauaula, type locality of *P. keahii*, shown is its host plant *Remya mauiensis*, **B** Same as A, flowers, **C** Nakula Natural Area Reserve, type locality of *P. platyphylliella*, shown is its host plant *Dubautia platyphylla*, **D** Same as C, flowers.

In addition to uncovering new larval host records and patterns, our synthesis led to the discovery of unusual moth behavior. For example, we discovered that larvae of three species, *P. auromagnifica*, *P. basalis*, and *P. splendida* mine leaf petioles as they approach their final instar, causing the leaf to drop off the plant, allowing the moth larva to mine into the detached leaf after the leaf has fallen to the ground. This behavior may help avoid reception of plant toxins, or reduce parasitism. Many parasitoids primarily search the surface of host plant leaves (Hespenheide 1991), and by falling to the ground, the moth may reduce the chance of being detected by parasitoids. Because fallen

leaves are subject to dessication and browning, larvae of these three *Philodoria* species appear to prevent a fallen mined leaf from turning brown, and may delay plant aging, as reported in other gracillariid species, such as *Phyllonorycter blancardella* on *Malus* spp. (Rosaceae) in Europe (Kaiser *et al*. 2010) and *P. cavella* (Zeller) on *Betula platyphylla* (Betulaceae) in the Russian Far East (Kirichenko *et al*., 2019). These "green islands" may be the result of bacterial symbionts that cause cytokinin production in plant leaves (Giron *et al*. 2013). How larvae of leaf mining moths delay aging of leaves is an intriguing area of research (Walters *et al*. 2008).

FIGURE 70. Habitats and host plants of *Philodoria*, Puu Makaala Natural Area Reserve, Hawaii (Big Island). **A** Habitat, **B–D** *Pipturus* sp.

FIGURE 71. Habitat and host plant of *Philodoria*, Hawaii Volcanoes National Park, Hawaii (Big Island). **A**, **B** Habitat, **C**, **D** *Myrsine lessertiana* trees.

Historical records from Swezey's studies and museum specimens show that most *Philodoria* species have lost much of their original distributional range and are now restricted to small fragmented populations such as mountaintops. Many *Philodoria* species have historical records and type localities that are currently uninhabitable due to near complete incursion of invasive plant and animal species, as well as human activities (e.g., Mt. Tantalus, Palolo, Waikiki, etc.) (Gon *et al*. 2018). One of Hawaii's most critically endangered plant genera is the aster, *Hesperomannia,* comprised of four species, all of which are federally listed as endangered (Morden & Harbin 2013; U.S. Fish & Wildlife Service 2019). *Hesperomannia arborescens* is perhaps the most endangered among them, and leaves of this plant collected in 1929 on Lanai revealed that its leaves were mined by an unknown *Philodoria* species (Johns *et al*. 2014). However, the population of *Hesperomannia* on Lanai is now extirpated (Wagner *et al*. 1990; Morden & Harbin 2013). It remains unknown which *Philodoria* species fed on this plant on Lanai, but based on our research here, two species of *Philodoria, P. hesperomanniella* and *P.* sp. 2, still persist on small populations of this plant genus on Maui and Kauai, respectively. A summary of the distribution of *Philodoria* species by island is shown in Table 5.

Philodoria sciallactis is another example of a species that, today, has a highly restricted range. This species mines leaves of *M. integrifolia* at Kaena Point State Park on Oahu, a protected area that represents one of few remaining native coastal ecosystems on the island (Department of Land and Natural Resources, State of Hawai'i 2009). Based on surveys conducted during the present study and collection localities listed in Swezey (1954) and Zimmerman (1978a), it is likely that on Oahu, *P. sciallactis* persists only within the small confines of this conservation land. With such a narrow geographic range and specialized larval host plant repertoire, the monophagous *P.*

sciallactis is among the most threatened species of *Philodoria*, and we believe it requires urgent attention from the state of Hawaii, conservation organizations, and land managers.

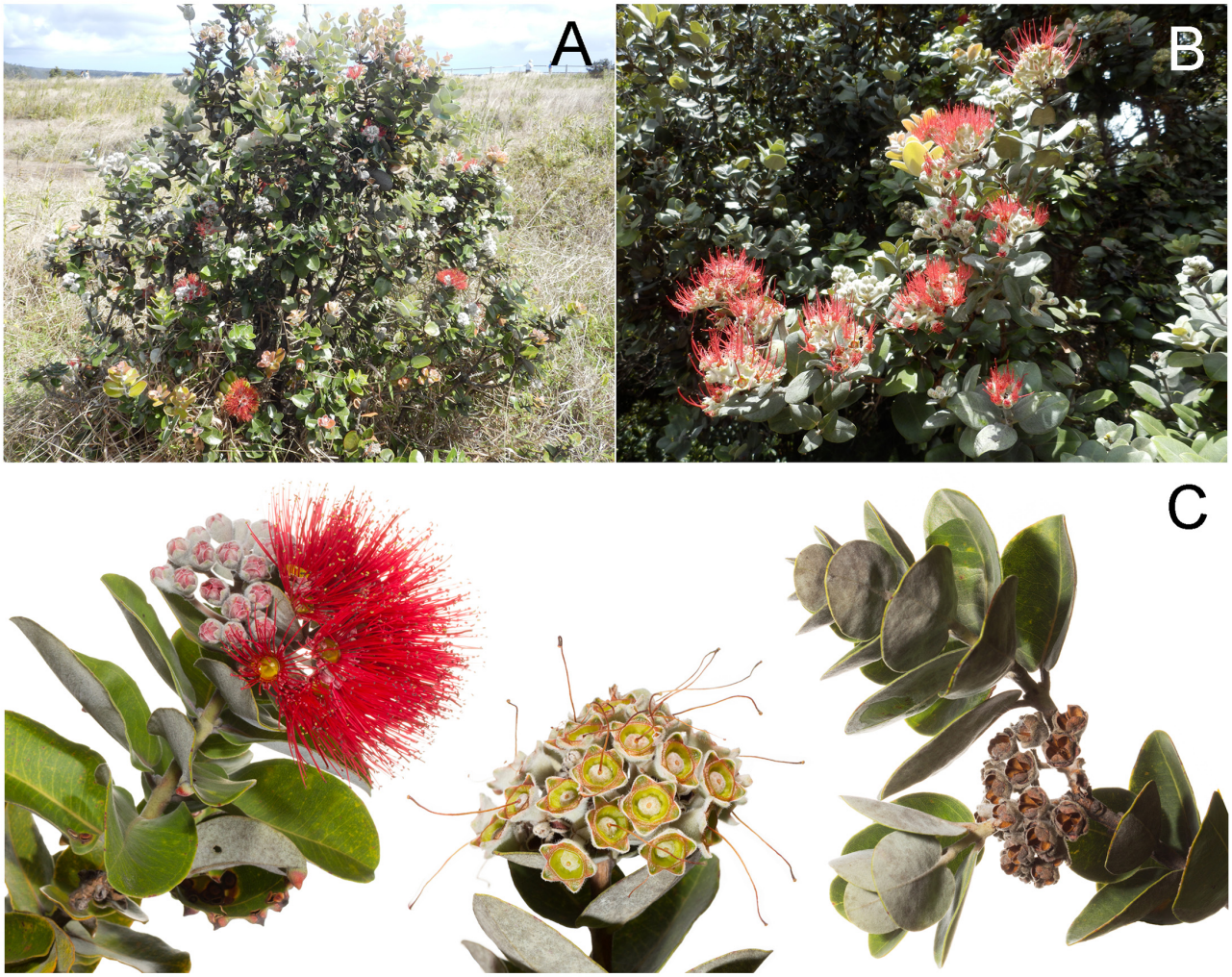

FIGURE 72. Habitat and host plant of *Philodoria basalis* on Hawaii (Big Island). **A** Pahoa Kilauea Cardera, **B** Napau Trail, **C** Flowers and leaves of host plant.

The Hawaiian Islands are just 0.02% of the size of the United States, but the state accounts for nearly 70% of the country's historically documented plant and animal extinctions (Wagner *et al*. 1999). In all, >360 Hawaiian animal and plant taxa are currently listed as either threatened or endangered under the federal and state Endangered Species Acts (U.S. Fish and Wildlife Service, 2019). More than 38% of native Hawaiian plants are threatened and 94% of Hawaiian insects are endemic (Evenhuis & Eldredge 1999). Given the extreme extinction risk that these insects face due to land use, invasive predators, and climate change (Howarth 1995) it is urgent that *Philodoria* be added to the IUCN Red List and incorporated into invertebrate conservation programs. Through our concerted efforts over the last decade to survey in or near their historical habitats, we were unable to confirm the existence of 10 *Philodoria* species (*P. costalis, P. lipochaetaella, P. micropetala, P. nigrella, P. nigrelloides, P. opuhe, P. pipturiana, P. pipturicola, P. pittosporella, P. spilota*), and propose that these 10 species be listed as critically endangered or possibly extinct. Twelve additional *Philodoria* species (*P. alakaiensis, P. haelaauensis, P. hespermanniella, P. funkae, P. kauaulaensis, P. keaensis, P. keahii, P. knudsniiella, P. limahuliensis, P. platyphylliella, P. sciallactis, P. wilkesiella*) are clearly threatened, and should be considered for listing on IUCN Red list, as they are very rare and some of them feed on plants that are nearly extinct.

While we conducted a fairly thorough survey of the Hawaiian Islands, there are some plants and regions that we were unable to access or search extensively. Future efforts should focus on leaf mines of asters, *Lysimachia,* and *Pipturus* from East Maui, *Hibiscus, Myrsine, Pipturus* from Kauai, *Diospyros, Myrsine, Pipturus* from Oahu, asters and *Pipturus* from Hawaii (Big Island), and plants on the North West Hawaiian Islands. Furthermore, *Hesperoman-*

nia arborescens, Hibiscadelphus distans and *Remya mauiensis* all belong to plant genera that have critically endangered species and these genera serve as *Philodoria* hosts. A published study (Johns *et al.* 2014) and our unpublished

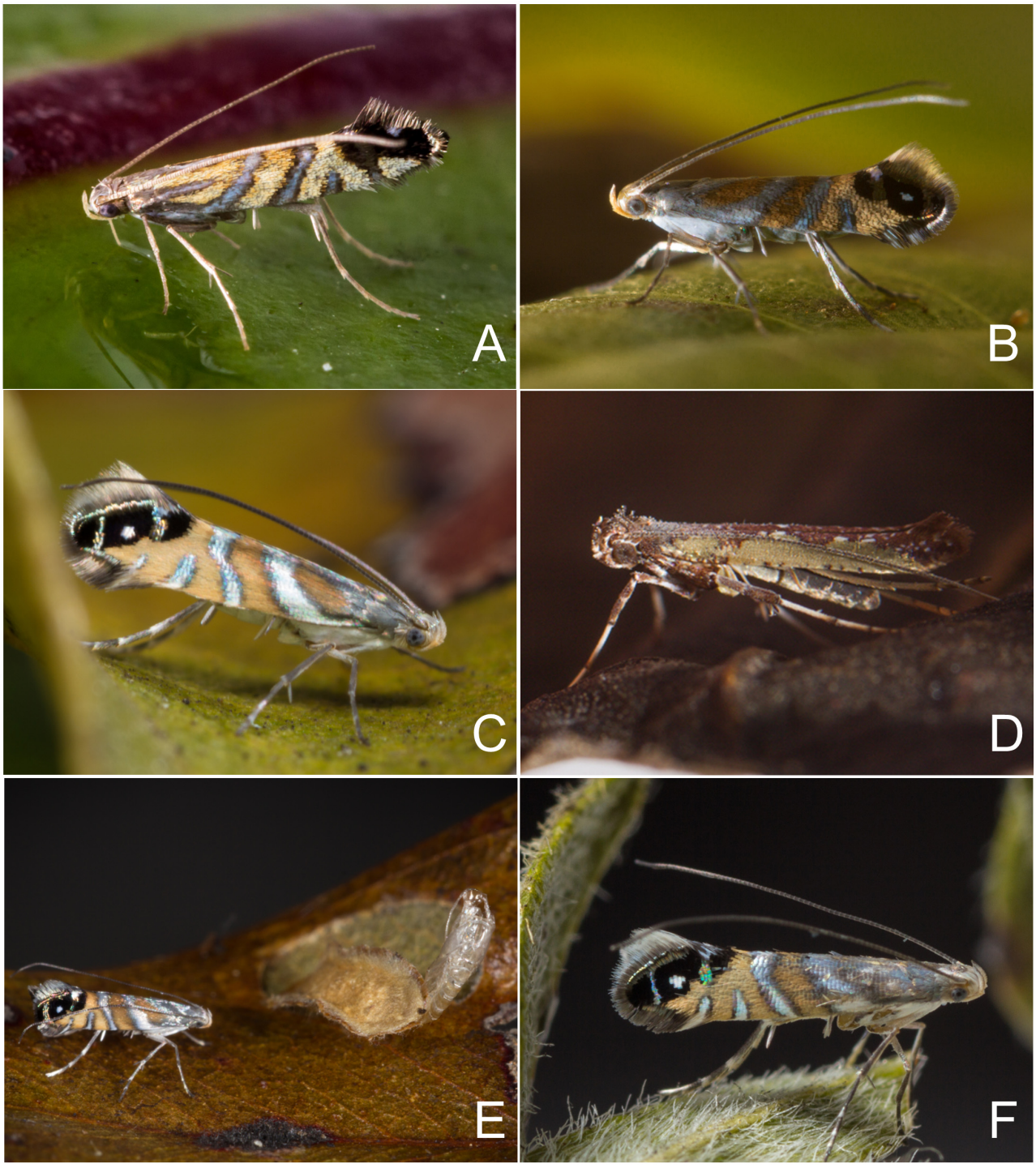

FIGURE 73. Resting posture of adult *Philodoria* and *Caloptilia*. **A** *P. molokaiensis*, Molokai, CJ229, host: *Lysimachia hillebrandii*, **B** *P. splendida*, Oahu, CJ319, host: *Metrosideros polymorpha*, **C** Same species, Oahu, **D** *Caloptilia mabaella*, Lanai, CJ333, host: *Diospyros sandwicensis*, **E** *P. lama*, Maui, CJ190, **F** Same species, Maui, CJ194.

investigations of herbarium leaves of these plants from the BPBM herbarium show signs of insect damage that resemble leaf-mining on these plants, but we were unable to find larvae. Future efforts should examine these plants for endemic leaf-miners when encountered. Because more than half of the 19 plant genera mined by *Philodoria* contain threatened or endangered species (Johns *et al*. 2016), it is essential that field surveys are continued regularly in Hawaii.

FIGURE 74. Resting posture of adult *P. haelaauensis*, male, Makawao Forest Reserve, Maui, CJ227/PHIL0019, host: *Pipturus rockii*. **A** lateral view, **B** dorsolateral view.

Finally, our work reveals that *Philodoria* serve as hosts to possibly more than 30 different species of parasitoid wasps. One endemic parasitoid wasp genus in particular, *Sierola* (Hymenoptera: Bethylidae) represents a major radiation on Hawaii with more than 170 described species (Magnacca 2019). At least five *Philodoria* species (*P. dubautiella*, *P. opuhe*, *P. splendida*, *P. ureraella*, *P. urerana*) are reported as hosts to these wasps based on our present study. Due to their very small size, there are likely many more undescribed species of *Sierola* in Hawaii (Magnacca 2019). Given that these wasps parasitize endemic leaf-mining moths that rely on many rare host plants, the impact of plant loss can have a negative multi-trophic cascading effect on the native Hawaiian ecosystem. There is a clear need to continue exploring the natural history of Hawaiian archipelago while taking urgent measures at the sate and individual level (Forister et al. 2019; Kawahara et al. 2021) to conserve endemic plants, animals and their native habitats.

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TABLE 3. Parasitoid wasps that emerged from *Philodoria* leaf mines or cocoons. "No." refers to the assigned parasitoid number. There were a few instances where the parasitoid did not emerge, and was thus that number was skipped in this table.

No.	Parasitoid wasp species	Number of specimens	Sample ID	Storage method	Host *Philodoria* species	Host plant of *Philodoria*	Collector
2	Chalcidoidea	2	CJ-062	Ethanol	*P. auromagnifica* or *P. succedanea*	*Myrsine lessertiana*	C.A. Johns
3	Chalcidoidea	1	CJ-133	Ethanol	*P. auromagnifica* or *P. kauaulaensis* or *P. succedanea*	*M. lessertiana*	C.A. Johns
4	Unidentified species	1	MYRISINAE (VNP)	Ethanol	*P. auromagnifica* or *P. kolea* or *P. succedanea*	*M. lessertiana*	A.Y. Kawahara
5	Unidentified species	1	SKH-10-A	Ethanol	*P. auromagnifica* or *P. kolea* or *P. succedanea*	*M. lessertiana*	A.Y. Kawahara
6	Unidentified species	1	SKH-10-B	Ethanol	*P. auromagnifica* or *P. kolea* or *P. succedanea*	*M. lessertiana*	A.Y. Kawahara
7	Unidentified species	1	SKH-10-C	Ethanol	*P. auromagnifica* or *P. kolea* or *P. succedanea*	*M. lessertiana*	A.Y. Kawahara
8	Unidentified species	1	SKH-10	Ethanol	*P. auromagnifica* or *P. kolea* or *P. succedanea*	*M. lessertiana*	A.Y. Kawahara
9	Unidentified species	1	SKH-13	Ethanol	*P. auromagnifica* or *P. kolea* or *P. succedanea*	*M. lessertiana*	A.Y. Kawahara
10	Unidentified species	1	SKH-15	Ethanol	*P. auromagnifica* or *P. kolea* or *P. succedanea*	*M. lessertiana*	A.Y. Kawahara
11	Unidentified species	6	CJ-511	RNAlater	*P. succedanea*?	*M. linearifolia*	C.A. Johns
12	Chalcidoidea	1	CJ-201	Ethanol	*P. molokaiensis*	*Lysimachia hillebrandii*	C.A. Johns
13	Chalcidoidea	3	CJ-203	Ethanol	*P. molokaiensis*	*L. hillebrandii*	C.A. Johns
14	Euplemidae	1	CJ-243	Dry (-80□)	*P. molokaiensis*	*L. hillebrandii*	C.A. Johns
16	Chalcidoidea	1	CJ-044	Ethanol	*P. basalis* or *P. splendida*	*Metrosideros polymorpha*	C.A. Johns
17	Chalcidoidea	1	CJ-113	Ethanol	*P. basalis* or *P. splendida*	*M. polymorpha*	C.A. Johns
18	Chalcidoidea	2	CJ-123	Ethanol	*P. basalis* or *P. splendida*	*M. polymorpha*	C.A. Johns

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TABLE 3. (Continued)

No.	Parasitoid wasp species	Number of specimens	Sample ID	Storage method	Host *Philodoria* species	Host plant of *Philodoria*	Collector
19	Chalcidoidea	1	CJ-290	Ethanol	*P. basalis* or *P. splendida*	*M. polymorpha*	C.A. Johns
20	Chalcidoidea	1	CJ-292	Ethanol	*P. basalis* or *P. splendida*	*M. polymorpha*	C.A. Johns
21	Chalcidoidea	1	CJ-298	RNAlater	*P. basalis* or *P. splendida*	*M. polymorpha*	C.A. Johns
22	Chalcidoidea	1	CJ-417	Ethanol	*P. basalis* or *P. splendida*	*M. polymorpha*	C.A. Johns
23	Unidentified species	1	CJ-515	RNAlater	*P. splendida*	*Syzygium* sp.	C.A. Johns
24	Chalcidoidea	1	CJ-206	Ethanol	Unidentified	*Pipturus rockii*	C.A. Johns
25	Chalcidoidea	2	CJ-224	Ethanol	Unidentified	*P. rockii*	C.A. Johns
26	Ichneumonids	1	CJ-235	Ethanol	Unidentified	*P. hawaiiensis*	C.A. Johns
27	Chalcidoidea	2	CJ-289	Ethanol	Unidentified	*Pipturus* sp.	C.A. Johns
28	Braconidae	1	CJ-295	RNAlater	Unidentified	*P. albidus*	C.A. Johns
29	Unidentified species	1	CJ-415	Ethanol	Unidentified	*Pipturus* sp.	C.A. Johns
30	Chalcidoidea	1	CJ-420	Ethanol	Unidentified	*Pipturus* sp.	C.A. Johns
31	Unidentified species	1	CLV017	Ethanol	*P. obamaorum* or *P. floscula*	*Pipturus* sp.	C.L.-Vaamonde & C. Doorenweerd
32	Unidentified species	1	CLV017	Ethanol	*P. obamaorum* or *P. floscula*	*Pipturus* sp.	C.L.-Vaamonde & C. Doorenweerd
34	Braconidae	1	CJ-208	Ethanol	*P. naenaeiella* or closely related species?	*Dubautia plantaginea*	C.A. Johns
35	Braconidae	1	CJ-242	Dry (-80□)	*P. naenaeiella* or closely related species?	*D. plantaginea*	C.A. Johns
36	Chalcidoidea	2	CJ-502	RNAlater	Unidentified	*D. plantaginea*	C.A. Johns
37	Braconidae	2	CJ-453	Ethanol	*P. alakaiensis*?	*D. laxa*	C.A. Johns
38	Braconidae	1	CJ-140	Ethanol	Unidentified	*Dubautia* sp.	C.A. Johns

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TABLE 3. (Continued)

No.	Parasitoid wasp species	Number of specimens	Sample ID	Storage method	Host *Philodoria* species	Host plant of *Philodoria*	Collector
39	Braconidae	2	CJ-248	Ethanol	*P. naenaeiella* or closely related species?	*Dubautia* sp.	C.A. Johns
40	Braconidae	1	CJ-313	RNAlater	Unidentified	*Dubautia* sp.	C.A. Johns
41	Braconidae	7	CJ-458	Ethanol	*P. alakaiensis*?	*Dubautia* sp.	C.A. Johns
43	Unidentified species	1	CJ-522	Ethanol	*P. funkae*	*Wilkesia gymnoxiphium*	N. Tangalin
44	Unidentified species	1	SKH8-3-A	Ethanol	*P. hauicola*	*Hibiscus tiliaceus*	S. Kobayashi
45	Unidentified species	1	SKH8-3-B	Ethanol	*P. hauicola*	*H. tiliaceus*	S. Kobayashi
46	Unidentified species	1	SKH8-3-C	Ethanol	*P. hauicola*	*H. tiliaceus*	S. Kobayashi
47	Braconidae	1	SKH-8-11-A	Ethanol	*P. hauicola*	*H. tiliaceus*	S. Kobayashi
48	Unidentified species	1	CJ-272	Ethanol	*P. hauicola* or *P. hibiscella*	*H. tiliaceus*	C.A. Johns
49	Chalcidoidea	3	CJ-236	Ethanol	*P. hibiscella*	*Hibiscus arnottianus*	C.A. Johns
50	Chalcidoidea	1	CJ-469	Ethanol	*P. limahuliensis*	*Hibiscus waimaeae* subsp. *haneri*	C.A. Johns
51	Unidentified species	8	CJ-449	Ethanol	*P. touchardiella*	*Touchardia latifolia*	C.A. Johns
52	Chalcidoidea	1	CJ-055	Ethanol	*P. marginestrigata*	*Sida fallax*	C.A. Johns
53	Eulophidae	1	CJ-056	Ethanol	*P. marginestrigata*	*S. fallax*	C.A. Johns
54	Chalcidoidea	11	CJ-137	Ethanol	*P. marginestrigata*	*S. fallax*	C.A. Johns
55	Eulophidae	1	CJ-193	Ethanol	*P. marginestrigata*	*S. fallax*	C.A. Johns
56	Eulophidae	1	CJ-205	Ethanol	*P. marginestrigata*	*S. fallax*	C.A. Johns
57	Eulophidae	1	CJ-378	Ethanol	*P. marginestrigata*	*S. fallax*	C.A. Johns
58	Eulophidae	2	CJ-407	Ethanol	*P. marginestrigata*	*S. fallax*	C.A. Johns
60	Chalcidoidea	2	CJ-180	Ethanol	*P. sciallactis* or *P. marginestrigata*	*Lipochaeta rockii*	C.A. Johns
61	Eulophidae	1	CJ-196	Ethanol	*P. sciallactis* or *P. marginestrigata*	*L. rockii*	C.A. Johns
62	Eulophidae	1	CJ-207	Ethanol	*P. sciallactis* or *P. marginestrigata*	*L. rockii*	C.A. Johns

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TABLE 3. (Continued)

No.	Parasitoid wasp species	Island	Location	Stored date	Collection date	Latitude	Longitude
2	Chalcidoidea	Oahu	Kaena point	26.iv.2013	19.iv.2013	21.57261	-158.2753
3	Chalcidoidea	Maui	Eke	15.v.2013	24.iv.2013	20.93787	-156.5801
4	Unidentified species	Hawaii	Hawaii Volcanoes National Park	27.iv.2016	29.iv.2016	19.41382	-155.238
5	Unidentified species	Hawaii	Hawaii Volcanoes National Park	17.v.2015	29.iv.2016	19.41382	-155.238
6	Unidentified species	Hawaii	Hawaii Volcanoes National Park	17.v.2015	29.iv.2016	19.41382	-155.238
7	Unidentified species	Hawaii	Hawaii Volcanoes National Park	17.v.2015	29.iv.2016	19.41382	-155.238
8	Unidentified species	Hawaii	Hawaii Volcanoes National Park	23.v.2016	29.iv.2016	19.41382	-155.238
9	Unidentified species	Hawaii	Hawaii Volcanoes National Park	11.v.2016	29.iv.2016	19.41382	-155.238
10	Unidentified species	Hawaii	Hawaii Volcanoes National Park	15.v.2016	22.iv.2016	19.41382	-155.238
11	Unidentified species	Kauai	Puu o kila	5.vii.2015	15.vi.2015	22.14759	-159.6323
12	Chalcidoidea	Molokai	Kamakou	6.i.2014	19.xii.2013	21.11847	-156.9245
13	Chalcidoidea	Molokai	Kamakou	7.i.2014	19.xii.2013	21.11847	-156.9245
14	Euplemidae	Molokai	Kamakou	30.i.2014	19.xii.2013	21.11847	-156.9245
16	Chalcidoidea	Oahu	Palikea	16.iv.2013	N/A, 15.iv.2013?	21.41245	-158.1001
17	Chalcidoidea	Oahu	Palikea	7.v.2013	15.iv.2013	21.40768	-158.0984
18	Chalcidoidea	Maui	Waihee ridge trail	8.v.2013	28.iv.2013	20.94806	-156.544
19	Chalcidoidea	Oahu	Waiaai trail	16.vii.2014	5.vii.2014	21.4207	-157.9082
20	Chalcidoidea	Oahu	Waiaai trail	16.vii.2014	5.vii.2014	21.4207	-157.9082
21	Chalcidoidea	Oahu	Waiaai trail	21.vii.2014	5.vii.2014	21.4207	-157.9082
22	Chalcidoidea	Hawaii	Kohala watershed partnership	4.vi.2015	18.v.2015	No data	No data
23	Unidentified species	Kauai	Limahuli	5.viii.2015	20.vi.2015	22.18667	-159.5865
24	Chalcidoidea	Maui	Makawao Forest Reserve	7.i.2014	28.xii.2013	20.80989	-156.25
25	Chalcidoidea	Maui	Kula Forest Reserve	15.i.2014	28.xii.2013	20.67238	-156.3402
26	Ichneumonids	Maui	Waikamoi	19.i.2014	30.xii.2013	20.80723	-156.2534
27	Chalcidoidea	Oahu	Kaau crater	16.vii.2014	10.vii.2014	21.33279	-157.7758
28	Braconidae	Oahu	Kaau crater	20.vii.2014	10.vii.2014	21.33279	-157.7758
29	Unidentified species	Hawaii	Puu Makaala NAR	2.vi.2015	25.v.2015	19.48133	-155.2794
30	Chalcidoidea	Hawaii	Puu Makaala NAR	9.vi.2015	25.v.2015	19.48133	-155.2794

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TABLE 3. (Continued)

No.	Parasitoid wasp species	Island	Location	Stored date	Collection date	Latitude	Longitude
31	Unidentified species	Hawaii	Upper Hamakua Ditch trail	10.v.2016	24.iv.2016	20.05231	-155.6398
32	Unidentified species	Hawaii	Upper Hamakua Ditch trail	16.v.2016	24.iv.2016	20.05231	-155.6398
34	Braconidae	Oahu	Konahuanui	11.i.2014	3.i.2014	21.35321	-157.7883
35	Braconidae	Oahu	Konahuanui	30.i.2014	3.i.2014	21.35321	-157.7883
36	Chalcidoidea	Oahu	Poamoho	24.vii.2015	30.vi.2015	21.53324	-157.9274
37	Braconidae	Kauai	Alakai	2.vii.2015	18.vi.2015	22.14729	-159.6088
38	Braconidae	Oahu	Poamoho	21.v.2013	16.iv.2013	21.53324	-157.9274
39	Braconidae	Oahu	Konahuanui	17.ii.2014	3.i.2014	21.35321	-157.7883
40	Braconidae	Oahu	Konahuanui	31.vii.2014	13.vii.2014	21.35339	-157.7887
41	Braconidae	Kauai	Alakai	6.vii.2015	18.vi.2015	22.14739	-159.6072
43	Unidentified species	Kauai	–	21.ix.2015	N/A	22.12231	-159.6941
44	Unidentified species	Oahu	Nuuanu Pali	10.v.2016	3.v.2016	21.36274	-157.7911
45	Unidentified species	Oahu	Nuuanu Pali	10.v.2016	3.v.2016	21.36274	-156.7911
46	Unidentified species	Oahu	Nuuanu Pali	10.v.2016	3.v.2016	21.36274	-155.7911
47	Braconidae	Oahu	Nuuanu Pali	21.v.2016	3.v.2016	21.36274	-155.7911
48	Unidentified species	Oahu	Tantalus	6.vii.2014	18.vi.2014	21.33942	-157.8108
49	Chalcidoidea	Oahu	Konahuanui	19.i.2014	3.i.2014	21.33928	-157.8112
50	Chalcidoidea	Kauai	Limahuli	9.vii.2015	21.vi.2015	22.18667	-159.5865
51	Unidentified species	Kauai	Blue hole	29.vi.2015	10.vi.2015	22.07158	-159.4953
52	Chalcidoidea	Maui	Waihee dunes mclt	23.iv.2013	14.iv.2013	20.9342	-156.5046
53	Eulophidae	Maui	Waihee dunes mclt	23.iv.2013	14.iv.2013	20.9342	-156.5046
54	Chalcidoidea	Oahu	Kaena point	17.v.2013	19.iv.2013	21.57261	-158.2753
55	Eulophidae	Maui	Kahikinui	4.i.2014	24.xii.2013	20.61585	-156.2953
56	Eulophidae	Maui	Waihee dunes mclt	7.i.2014	14.xii.2013	20.9342	-156.5046
57	Eulophidae	Lanai	Kanepuu	16.viii.2015	5.viii.2015	20.87427	-156.9753
58	Eulophidae	Hawaii	Punaluu beach	21.v.2015	2.v.2015	19.13359	-155.5062
60	Chalcidoidea	Molokai	Mokio	2.i.2014	16.xii.2013	21.21612	-157.2292
61	Eulophidae	Molokai	Mokio	6.i.2014	16.xii.2013	21.21612	-157.2292
62	Eulophidae	Molokai	Mokio	7.i.2014	16.xii.2013	21.21612	-157.2292

TABLE 4. Checklist of *Philodoria* species including their host plants and maxillary palpus morphology.

	Species	Host plant species[a,b]	Host plant family	Maxilary palpus	Study speciemen ID
1	*P. succedanea* Walsingham, 1907	*Myrsine knudsenii, M. lessertiana, M. linearifolia*, *M. sandwicensis*, *Myrsine* sp.	Primulaceae	Reduced	CJ-136, 419, 526, 531, 539; SKH-13
2	*P. kauaulaensis* Kobayashi, Johns & Kawahara, 2018	*Myrsine lanaiensis, M. lessertiana, M. sandwicensis*	Primulaceae	Unknown	CJ-381
3	*P. auromagnifica* Walsingham, 1907	*Myrsine lessertiana, M. sandwicensis*, *M. wawraea, Myrsine* sp.	Primulaceae	Reduced	CJ-148, 241; SKH-10, 13; HILO020, 053, 054, 059
4	*P. kolea* Kobayashi, Johns & Kawahara, 2018	*Myrsine lessertiana*	Primulaceae	Reduced	CJ-546; SKH-5-1, 15
5	*P.* sp. 7 of Johns *et al*. (2018)	*Lysimachia kalalauensis*	Primulaceae	Unknown	CJ-451
6	*P. lysimachiella* Swezey, 1928	*Lysimachia hillebrandii*	Primulaceae	Reduced	CJ-530
7	*P.* sp. A nr. *P. lysimachiella*	*Lysimachia* **sp. n.**	Primulaceae	Unknown	CJ-346
8	*P. molokaiensis* Swezey, 1928	*Lysimachia hillebrandii* var. and ***L. maxima***	Primulaceae	Reduced	CJ-229, 239, 509
9	*P. basalis* Walsingham, 1907	*Metrosideros polymorpha* and *Metrosideros* sp.	Myrtaceae	Reduced	CJ-112, 410, 416, 430, 431; SKH-09-1
10	*P. splendida* Walsingham, 1907	*Metrosideros polymorpha* and ***Syzygium* sp.**	Myrtaceae	Reduced	CJ-049, 105, 246, 247, 312, 488
11	*P. napaliensis* Kobayashi, Johns & Kawahara, **sp. n.**	*Diospyros sandwicensis* and/or *D. hillebrandii*	Ebanaceae	Unknown	CJ-445, 482, 491
12	*P. lama* Kobayashi, Johns & Kawahara, **sp. n.**	*Diospyros sandwicensis* and/or *D. hillebrandii*	Ebanaceae	Reduced	CJ-161, 382, 482, 491, 540
13	*P. costalis* Swezey, 1934	*Pipturus* sp.	Urticaceae	Reduced	Pinned specimen examined
14	*P. pipturiella* Swezey, 1923	*Pipturus* sp.	Urticaceae	Reduced	CJ-465, 527
15	*P. pipturicola* Swezey, 1915	*Pipturus* sp.	Urticaceae	Reduced	Pinned specimen examined
16	*P. haelaauensis* Kobayashi, Johns & Kawahara, **sp. n.**	*Pipturus* sp., *P. albidus* and *P. rockii*	Urticaceae	Reduced	CJ-209, 216, 227, 348
17	*P. spilota* (Walsingham, 1907)	Unknown	Unknown	Reduced	Not examined
18	*P. floscula* Walsingham, 1907	***Pipturus albidus*** and *Pipturus* sp.	Urticaceae	Reduced	CJ-394, 395, 426, CLV017
19	*P. micropetala* Walsingham, 1907	*Pipturus* sp.	Urticaceae	Reduced	Not examined
20	*P. pipturiana* Swezey, 1923	Unknown	Unknown	Reduced	Not examined
21	*P. wilkesiella* Swezey, 1940	*Argyroxiphium grayanum*	Asteraceae	Reduced	CJ-007, 009, 010, 012, 013

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TABLE 4. (Continued)

	Species	Host plant species[a,b]	Host plant family	Maxilary palpus	Study speciemen ID
22	*P. epibathra* (Walsingham, 1907)	***Dubautia laxa*** and *Dubautia* sp.	Asteraceae	Developed	CJ-492, 506
23	*P. nigrella* Walsingham, 1907	Unknown	Unknown	Developed	Not examined
24	*P. dubauticola* Swezey, 1940	*Dubautia plantaginea* and *D. laxa*	Asteraceae	Developed	CJ-077, 083, 084, 111, 256, 402
25	*P. dubautiella* (Swezey, 1913)	*Dubautia plantaginea* and ***D. laxa***	Asteraceae	Developed	CJ-524, 534
26	*P. alakaiensis* Kobayashi, Johns & Kawahara, **sp. n.**	*Dubautia* sp. (*D. laxa* or *D. paleata*)	Asteraceae	Developed	CJ-468, 473, 479, 481
27	*P. limahuliensis* Kobayashi, Johns & Kawahara, **sp. n.**	*Hibiscus waimeae* subsp. *hannerae*	Malvaceae	Unknown	CJ-472, 490
28	*P. hibiscella* (Swezey, 1913)	*Hibiscus arnottianus*, ***H. arnottianus* subsp. *immaculatus***, *H. rosasinensis*, ***H. tiliaceus*** and *Hibiscus* sp.	Malvaceae	Developed	CJ-088, 089, 238, 399
29	*P. naenaeiella* (Swezey, 1940)	*Dubautia laxa* and *D. plantaginea*	Asteraceae	Developed	CJ-142, 188
30	*P. knudseniiella* Kobayashi, Johns & Kawahara, **sp. n.**	*Dubautia knudsenii* subsp. *nagate* and *D. latifolia*	Asteraceae	Developed	CJ-480
31	*P. hesperomanniella* Kobayashi, Johns & Kawahara, **sp. n.**	*Hesperomannia arborescens* and *H. swezeyi*	Asteraceae	Developed	CJ-362, 367, 372
32	*P.* sp. 2 of Johns *et al*. (2018)	*Hesperomannia lydgateyi*	Asteraceae	Unknown	CJ-149
33	*P. neraudicola* (Swezey, 1920)	*Neraudia melastomifolia* and *Pipturus albidus*	Urticaceae	Developed	CJ-336, 360, 369
34	*P. obamaorum* Kobayashi, Johns & Kawahara, **sp. n.**	*Pipturus albidus* and *Pipturus* sp.	Urticaceae	Developed	CJ-403, 423, 427, CLV017
35	*P. urerana* (Swezey, 1915)	*Urera sandvicensis* and ***U. glabra***	Urticaceae	Developed	CJ-307, 533
36	*P. hauicola* (Swezey, 1910)	*Hibiscus tiliaceus*	Malvaceae	Developed	CJ-065, 087, 270; SKH-08
37	*P.* sp. 1 of Johns *et al*. (2018)	*Dubautia menzesii*	Asteraceae	Developed	CJ-320, 328, 334, 364, 376
38	*P. keahii* Kobayashi, Johns & Kawahara, **sp. n.**	*Remya mauiensis*	Asteraceae	Developed	CJ-332, 377, 380
39	*P. funkae* Kobayashi, Johns & Kawahara, **sp. n.**	*Wilkesia gymnoxiphium*	Asteraceae	Unknown	CJ-470, 489, 523
40	*P. pittosporella* (Swezey, 1928)	Unknown	Unknown	Developed	Pinned specimen examined
41	*P. touchardiella* (Swezey, 1928)	*Touchardia latifolia*	Urticaceae	Developed	CJ-365, 401, 507

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TABLE 4. (Continued)

	Species	Host plant species[a,b]	Host plant family	Maxilary palpus	Study speciemen ID
42	*P.* sp. 3 of Johns *et al*. (2018)	*Touchardia latifolia*	Urticaceae	Unknown	CJ-494
43	*P. keaensis* Kobayashi, Johns & Kawahara, **sp. n.**	Unknown	Unknown	Developed	CJ-355
44	*P. nigrelloides* (Swezey, 1946)	*Dubautia* sp.	Asteraceae	Developed	Not examined
45	*P. platyphylliella* Kobayashi, Johns & Kawahara, **sp. n.**	*Dubautia platyphylla*	Asteraceae	Developed	CJ-358, 363, 368
46	*P. marginestrigata* (Walsingham, 1907)	*Dubautia* sp., ***Lipochaeta rockii***, *Xanthium strumarium*, *Xanthium* sp., *Abutilon grandifolium*, *A. incanum*, *A. menzesii*, *Abutilon* sp., *Sida cordifolia*, *S. fallax, S. meyeniana*, *S. rhombifolia*, and *Sida* sp.	Asteraceae Malvaceae	Developed	CJ-138, 165, 168, 173, 175, 186, 187, 278, 379, 521
47	*P. lipochaetaella* (Swezey, 1940)	*Lipochaeta lavarum*	Asteraceae	Developed	Not examined
48	*P. sciallactis* (Meyrick, 1928)	*Lipochaeta rockii* and *Melanthera integrifolia,* ***M. kamolensis***	Asteraceae	Developed	CJ-159, 163, 164, 189, 195, 271, 273, 274
49	*P.* sp. B nr. *P. sciallactis*	*Lipochaeta connata* var. *acris*	Asteraceae	Unknown	CJ-483
50	*P. ureraella* (Swezey, 1915)	*U. sandvicensis* and ***U. glabra***	Urticaceae	Developed	CJ-316, 324, 337, 541
51	*P. opuhe* Kobayashi, Johns & Kawahara **sp. n.**	*Urera kaalae* and *U. sandvicensis*	Urticaceae	Developed	Pinned specimen examined

[a] Based on our new surveys and published records (e.g., Zimmerman 1978a; Johns *et al*. 2016; Johns *et al*. 2018; Kobayashi *et al*. 2018).

[b] Plant species names in **bold** indicate new records from the present study.

TABLE 5. Distribution of *Philodoria* species by island. A species name in bold indicates endemic species, i.e. collected only on that island (assigned "+" or "T"). Island accounts are from our new data or published data (e.g., Zimmerman 1978a; Johns *et al*. 2016; Johns *et al*. 2018; Kobayashi *et al*. 2018). +: recorded from island; –: not recorded from island; T: type-locality island; gray cells: new records from surveys conducted during the present study.

	Philodoria Species	Hawaiian island						
		Niohoa	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii
1	*P. succedanea* Walsingham, 1907	–	+	+	+	+	T	+
2	***P. kauaulaensis*** Kobayashi, Johns & Kawahara, 2018	–	–	–	–	–	T	–
3	*P. auromagnifica* Walsingham, 1907	–	+	T	+	–	–	+
4	***P. kolea*** Kobayashi, Johns & Kawahara, 2018	–	–	–	–	–	–	T
5	***P.* sp. 7** of Johns *et al*. (2018)	–	+	–	–	–	–	–
6	***P. lysimachiella*** Swezey, 1928	–	–	T	–	–	–	–
7	***P.* sp. A** nr. *P. lysimachiella*	–	–	–	–	–	+	–
8	***P. molokaiensis*** Swezey, 1928	–	–	–	T	–	–	–
9	*P. basalis* Walsingham, 1907	–	–	–	–	–	T	+
10	*P. splendida* Walsingham, 1907	–	+	+	+	T	+	+
11	***P. napaliensis*** Kobayashi, Johns & Kawahara, **sp. n.**	–	T	–	–	–	–	–
12	*P. lama* Kobayashi, Johns & Kawahara, **sp. n.**	–	–	+	–	T	+	–
13	***P. costalis*** Swezey, 1934	–	–	T	–	–	–	–
14	***P. pipturiella*** Swezey, 1923	–	–	T	–	–	–	–
15	***P. pipturicola*** Swezey, 1915	–	–	T	–	–	–	–
16	*P. haelaauensis* Kobayashi, Johns & Kawahara, **sp. n.**	–	–	–	+	–	T	–
17	***P. spilota*** (Walsingham, 1907)	–	–	–	–	–	T	–
18	*P. floscula* Walsingham, 1907	–	–	–	–	–	+	T
19	*P. micropetala* Walsingham, 1907	–	+	–	–	–	–	–
20	***P. pipturiana*** Swezey, 1923	–	–	–	–	–	–	T
21	***P. wilkesiella*** Swezey, 1940	–	–	–	–	–	T	–
22	***P. epibathra*** (Walsingham, 1907)	–	–	–	T	–	–	–
23	***P. nigrella*** Walsingham, 1907	–	–	–	–	–	–	T
24	***P. dubauticola*** Swezey, 1940	–	–	–	–	–	T	–
25	***P. dubautiella*** (Swezey, 1913)	–	–	T	–	–	–	–
26	***P. alakaiensis*** Kobayashi, Johns & Kawahara, **sp. n.**	–	T	–	–	–	–	–

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TABLE 5. (Continued)

	Philodoria Species	Hawaiian island						
		Niohoa	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii
27	***P. limahuliensis*** Kobayashi, Johns & Kawahara, **sp. n.**	–	T	–	–	–	–	–
28	*P. hibiscella* (Swezey, 1913)	–	–	T	+	–	+	+
29	***P. naenaeiella*** (Swezey, 1940)	–	–	T	–	–	–	–
30	***P. knudseniiella*** Kobayashi, Johns & Kawahara, **sp. n.**	–	T	–	–	–	–	–
31	*P. hesperomanniella* Kobayashi, Johns & Kawahara, **sp. n.**	–	–	+	–	–	T	–
32	***P.* sp. 2** of Johns *et al*. (2018)	–	+	–	–	–	–	–
33	*P. neraudicola* (Swezey, 1920)	–	+	T	+	–	+	–
34	***P. obamaorum*** Kobayashi, Johns & Kawahara, **sp. n.**	–	–	–	–	–	–	T
35	***P. urerana*** (Swezey, 1915)	–	–	T	–	–	–	–
36	*P. hauicola* (Swezey, 1910)	–	+	T	–	–	+	+
37	***P.* sp. 1** of Johns *et al*. (2018)	–	–	–	–	–	+	–
38	***P. keahii*** Kobayashi, Johns & Kawahara, **sp. n.**	–	–	–	–	–	T	–
39	***P. funkae*** Kobayashi, Johns & Kawahara, **sp. n.**	–	T	–	–	–	–	–
40	***P. pittosporella*** (Swezey, 1928)	–	–	T	–	–	–	–
41	*P. touchardiella* (Swezey, 1928)	–	–	–	+	–	T	–
42	***P.* sp. 3** of Johns *et al*. (2018)	–	+	–	–	–	–	–
43	***P. keaensis*** Kobayashi, Johns & Kawahara, **sp. n.**	–	–	–	–	–	–	T
44	***P. nigrelloides*** (Swezey, 1946)	–	T	–	–	–	–	–
45	***P. platyphylliella*** Kobayashi, Johns & Kawahara, **sp. n.**	–	–	–	–	–	T	–
46	*P. marginestrigata* (Walsingham, 1907)	+	+	T	+	+	–	+
47	***P. lipochaetaella*** (Swezey, 1940)	–	–	–	–	–	T	–
48	*P. sciallactis* (Meyrick, 1928)	–	–	T	+	–	+	–
49	***P.* sp. B** nr. *P sciallactis*	–	+	–	–	–	–	–
50	*P. ureraella* (Swezey, 1915)	–	–	T	–	–	+	–
51	***P. opuhe*** Kobayashi, Johns & Kawahara **sp. n.**	–	–	T	–	–	–	–
Total number of recorded species by island:		1	17	20	11	4	22	13

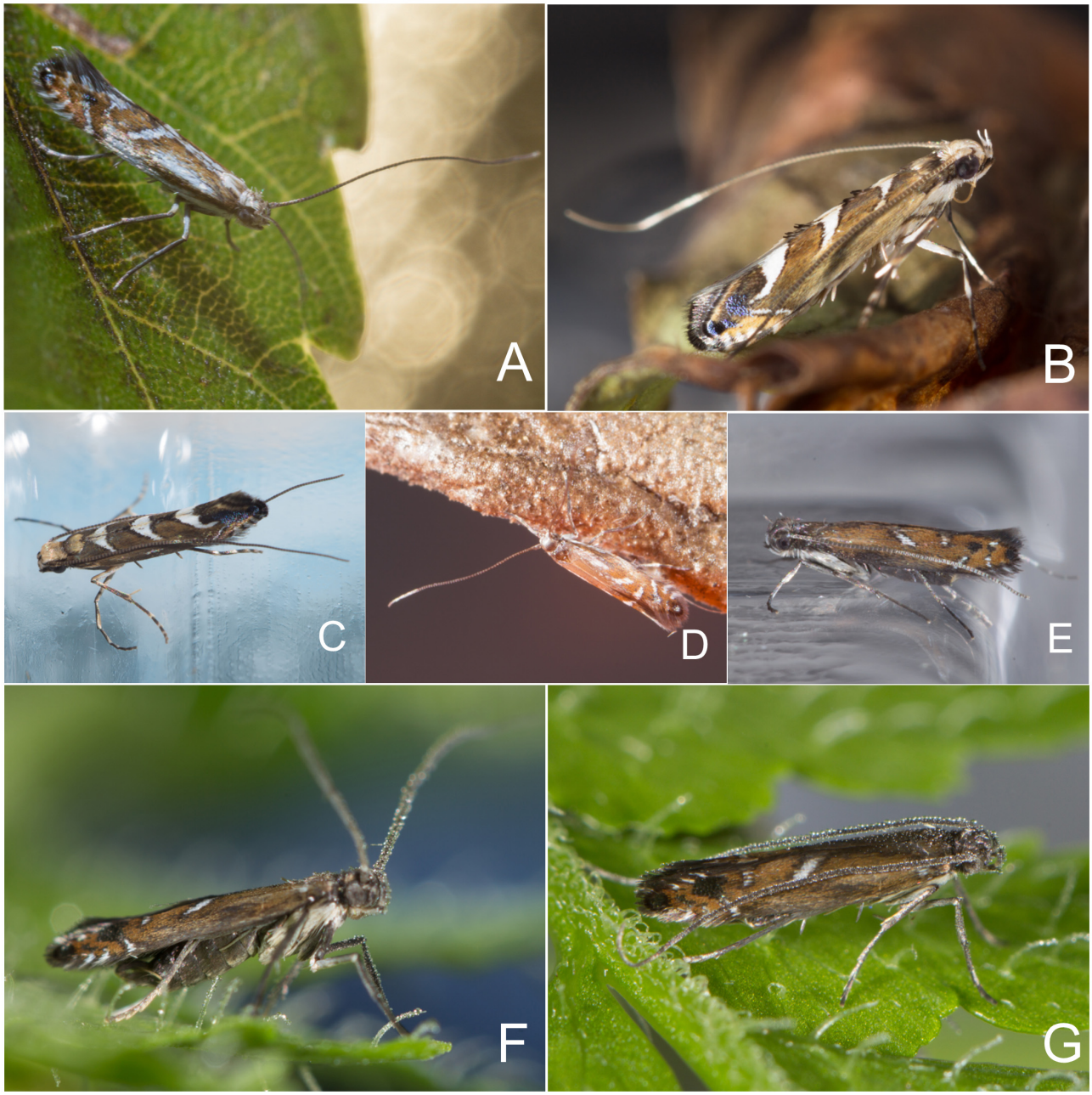

FIGURE 75. Resting posture of adult *Philodoria*. **A** *Philodoria* sp. nr. *P dubauticola*, Maui, CJ315, host: *Dubautia platyphylla*, **B** *P. hesperomanniella*, Maui, CJ367, host: *Hesperomannia arborescens*, **C** Same moth species and host plant, West Maui, CJ362, **D**, **E** *P. platyphylliella*, Maui, CJ368, host: *Dubautia platyphylla*, **F**, **G** Same moth species and host plant, male, Maui, CJ358.

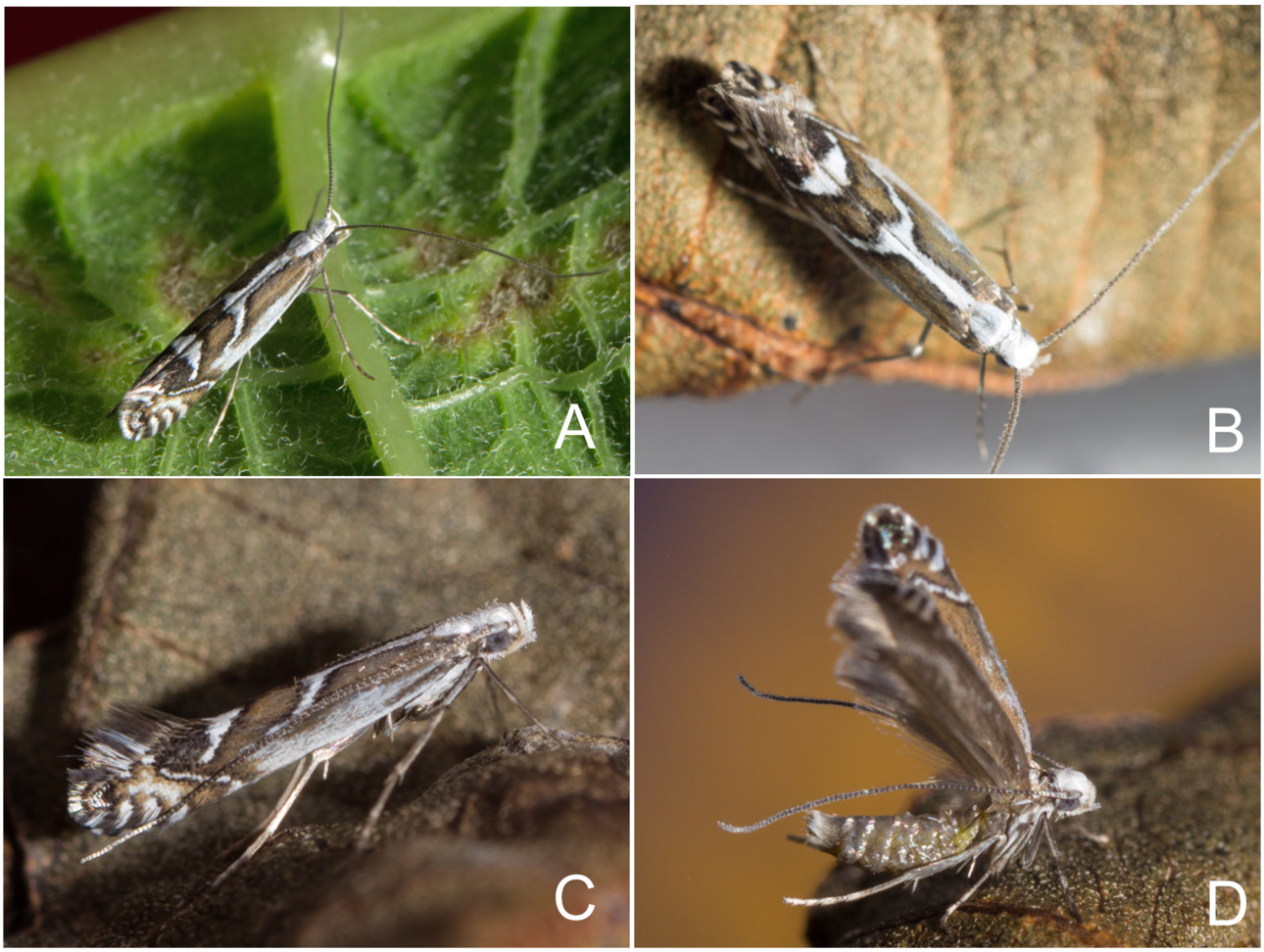

FIGURE 76. Resting posture of adult *Philodoria* sp. 1 on *Dubautia menzesii*, Maui (CJ334). **A** dorsolateral view, **B** dorsal view, **C** lateral view, **D** lateral view with wings held open.

FIGURE 77. Resting posture of adult *Philodoria*. **A** *P. hauicola*, Oahu, CJ270, host: *Hibiscus tilaceus*, **B–D** *P. hibiscella*, Oahu, CJ238, host: *Hibisucs arnottianus*, **E** *P. marginestrigata*, Molokai, CJ150, host: *Lipochaeta rockii*, **F** Same species, Molokai. CJ168/169, host: *Sida fallax*.

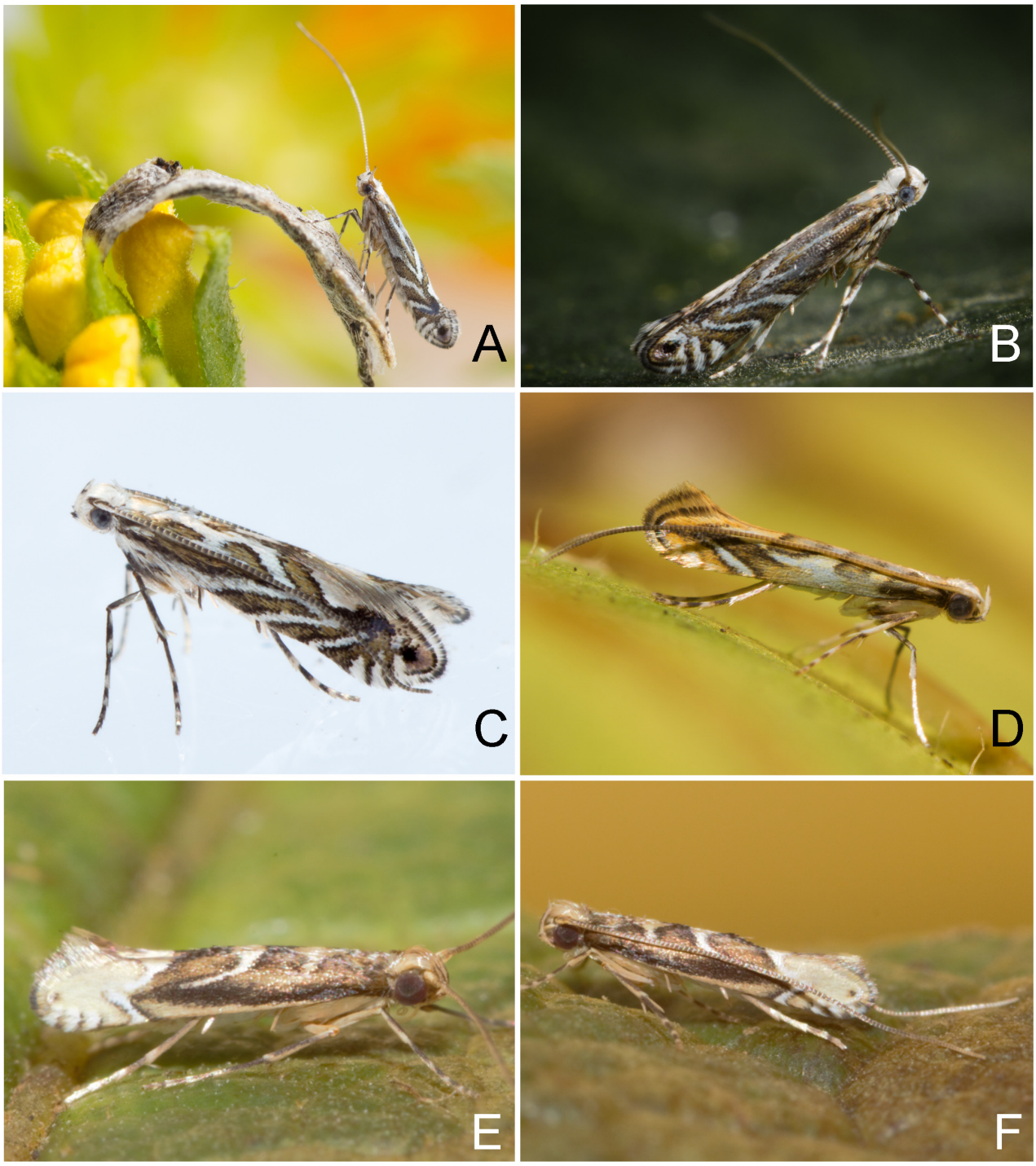

FIGURE 78. Resting posture of adult *Philodoria* on their larval host **A** *P. sciallactis*, Maui, CJ195, host: *Melanthera kamolensis*, **B**, **C** *P. sciallactis*, Maui, CJ164, 189, host: *M. kamolensis*, **D** *P. ureraella*, Maui, CJ316, host: *Urera glabra*, **E**, **F** *P. urerana*, Oahu, CJ307, host: *U. glabra*.

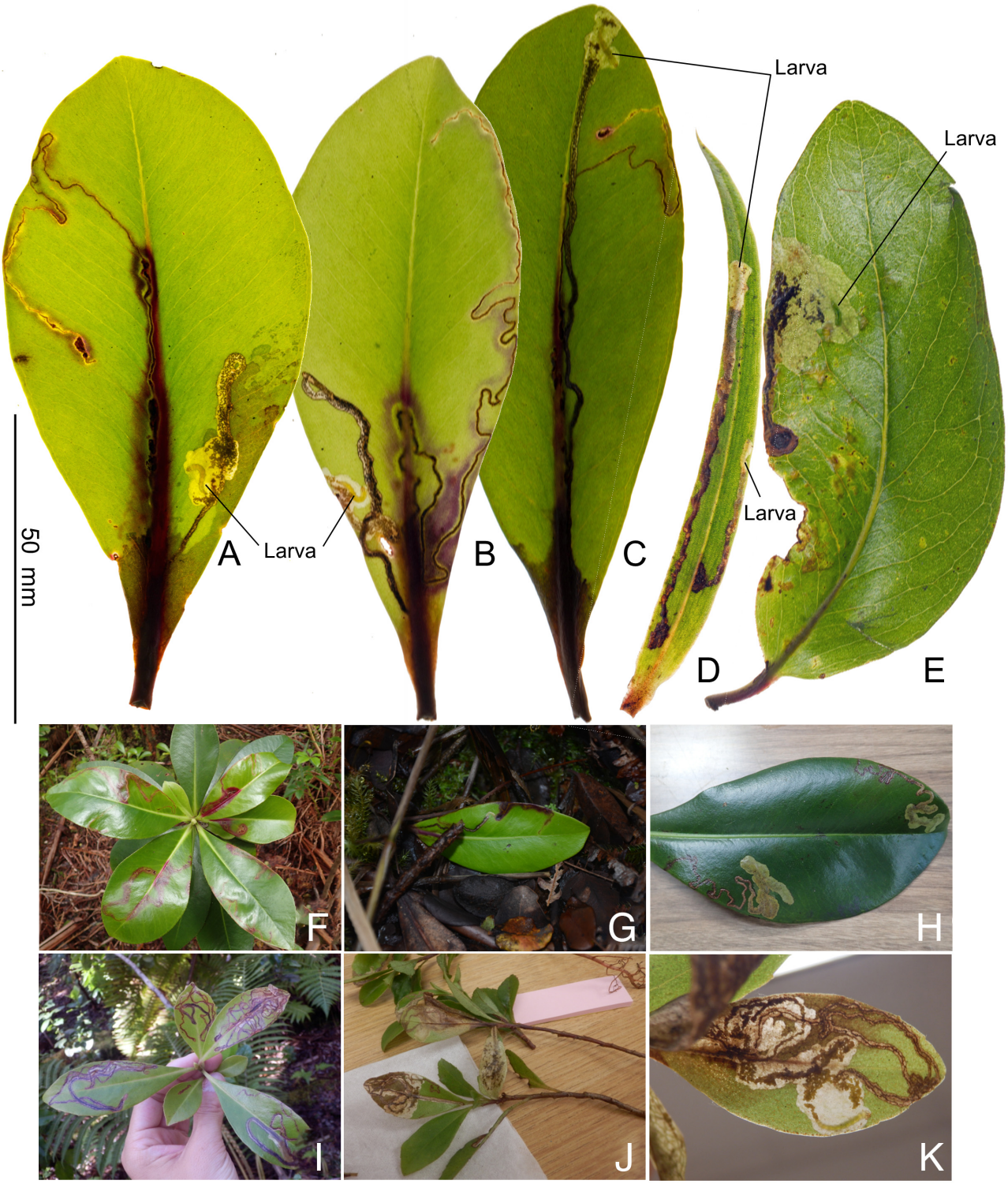

FIGURE 79. *Philodoria* species on the host plant, *Myrsine*. **A–D**, **F**, **G**: *P. succedanea*, **E**: *P. kauaulaensis*, **H**: *P. auromagnifica*. **A–C**, **F–K** host: *Myrsine lessertiana*, **D** *M. Linearifolia*, **E** *M. lanaiensis*. **A–C**: Molokai, **D**: Kauai, **E**: Maui, **A–E** Leaf mine and later larva **F–K**: Hawaii (Big Island). **F**, **I**, **J** Host plants and leaf mines, **G** Fallen leaf and leaf mine with larva, **H** Developing mine, **K** Near complete mine of late instar larva.

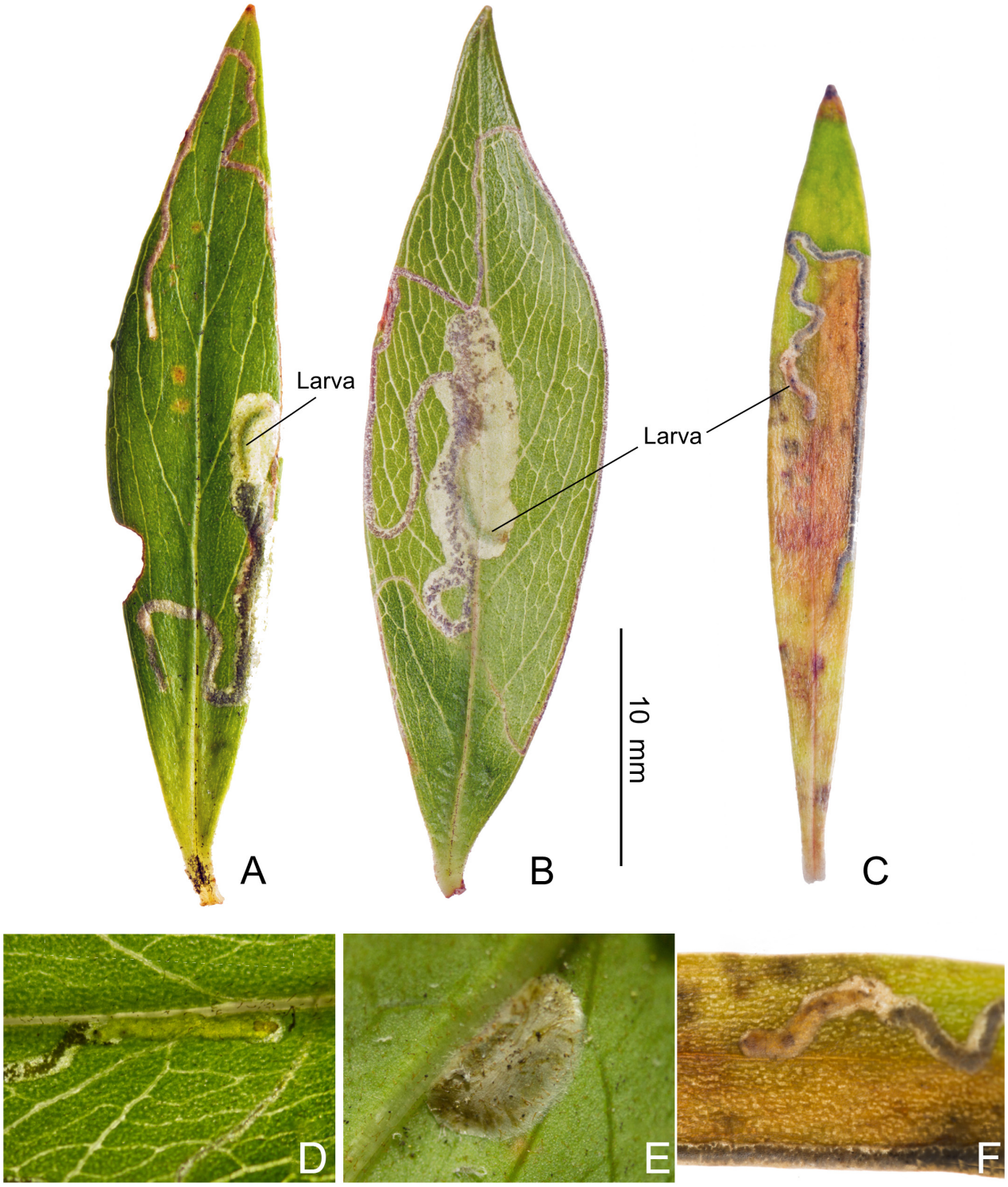

FIGURE 80. *Philodoria* species on the host plant, *Lysimachia*. **A**, **B**, **D**, **E**: *P. molokaiensis*, Molokai, host: *L. hillebrandii*, **C**, **F**: *Philodoria* sp., Maui, host: *L. remyi*. **A–C** Leaf mine, **D**, **F** Late instar larva, **E** Cocoon.

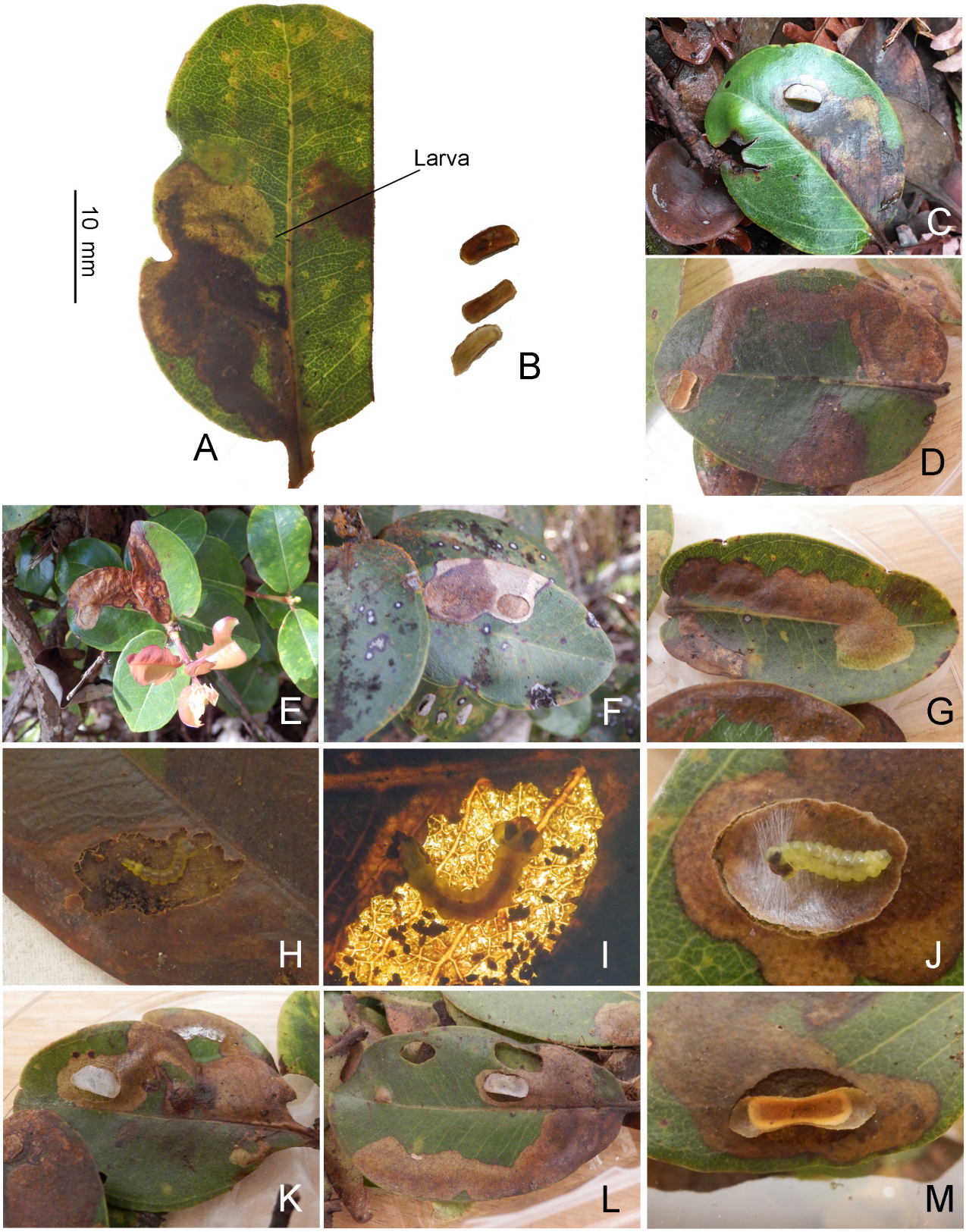

FIGURE 81. *Philodoria basalis* and its host plant, *Metrosideros polymorpha*. **A**, **B**, **D–M**: Hawaii (Big Island), **C**: Kauai. **A** Leaf mine of late instar larva, **B** Fallen cocoons in rolled leaf disc "tacos", **C** Fallen leaf and leaf mine with cocoon, **D** Cocoon and mine, **E**, **F** Old mine, **G** Mine made by late instar larva, **H**, **I** Late instar larva, **J** Final instar larva cutting out disc to create oval "taco" shelter with silk, **K**, **L** Cocoon and mine showing the "taco" cut out on the leaf, **M** Cocoon "taco", similar to **B**.

FIGURE 82. *Philodoria splendida* and its host plants. **A**, **D**, **E**: *Metrosideros polymorpha*, **B**, **C**, **F**: *Syzigium sandwicensis*. **A**: Maui, **B–F**: Oahu. **A**, **B** Leaf mine, **C** Cocoon and old mine, **D**, **E** Host plant with leaf mines, **F** Mine of late instar larva.

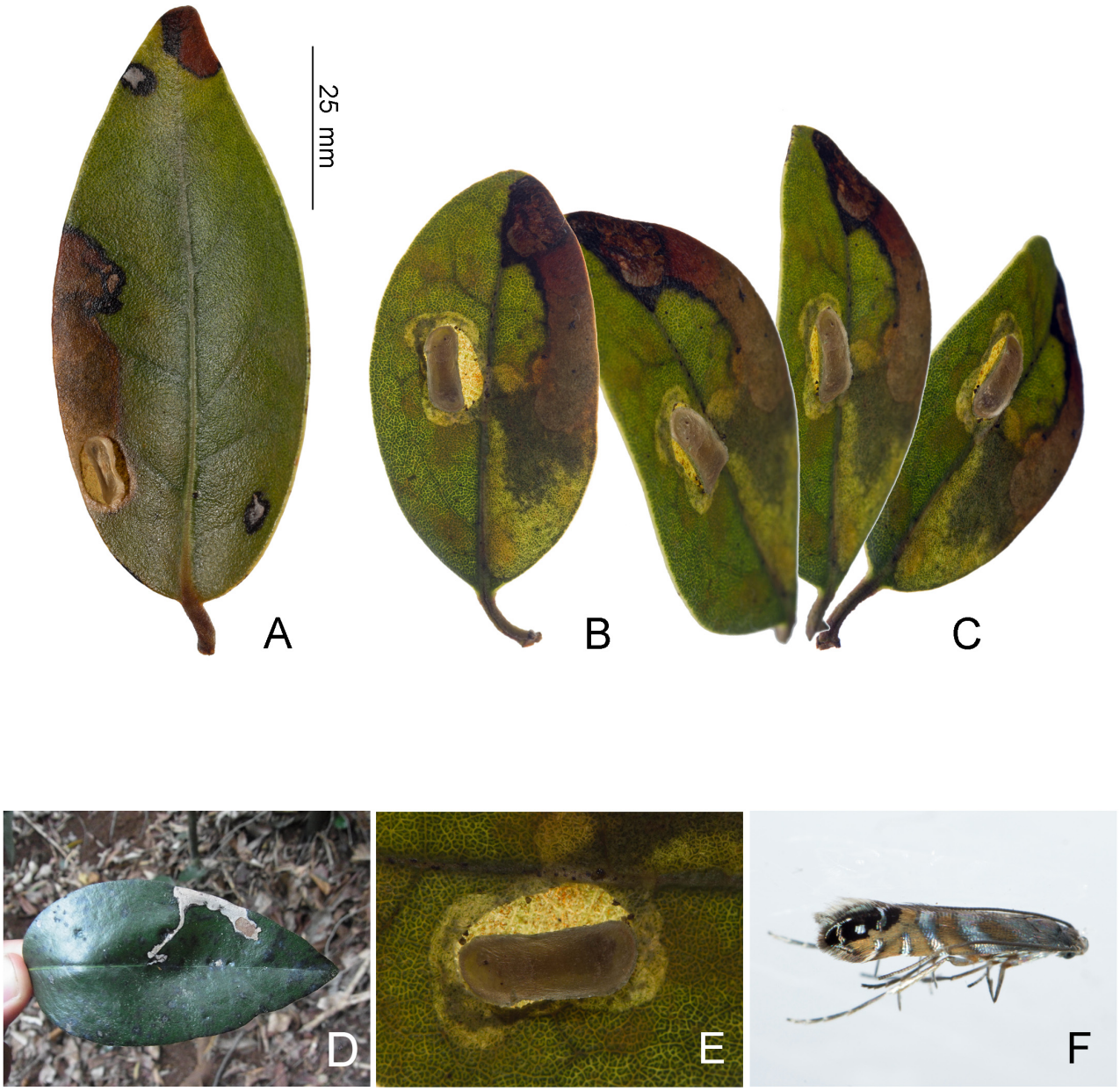

FIGURE 83. *Philodoria lama* with its host plant *Diospyros sandiwensis*. **A–C** Leaf mine with taco cocoon cut outs, **D** Old mine without taco, **E** Close-up view of "taco" cocoon, **F** Dead adult, lateral view (CJ161). **A**, **F**: East Maui, **B**, **C**, **E**: Lanai, **D**: Oahu.

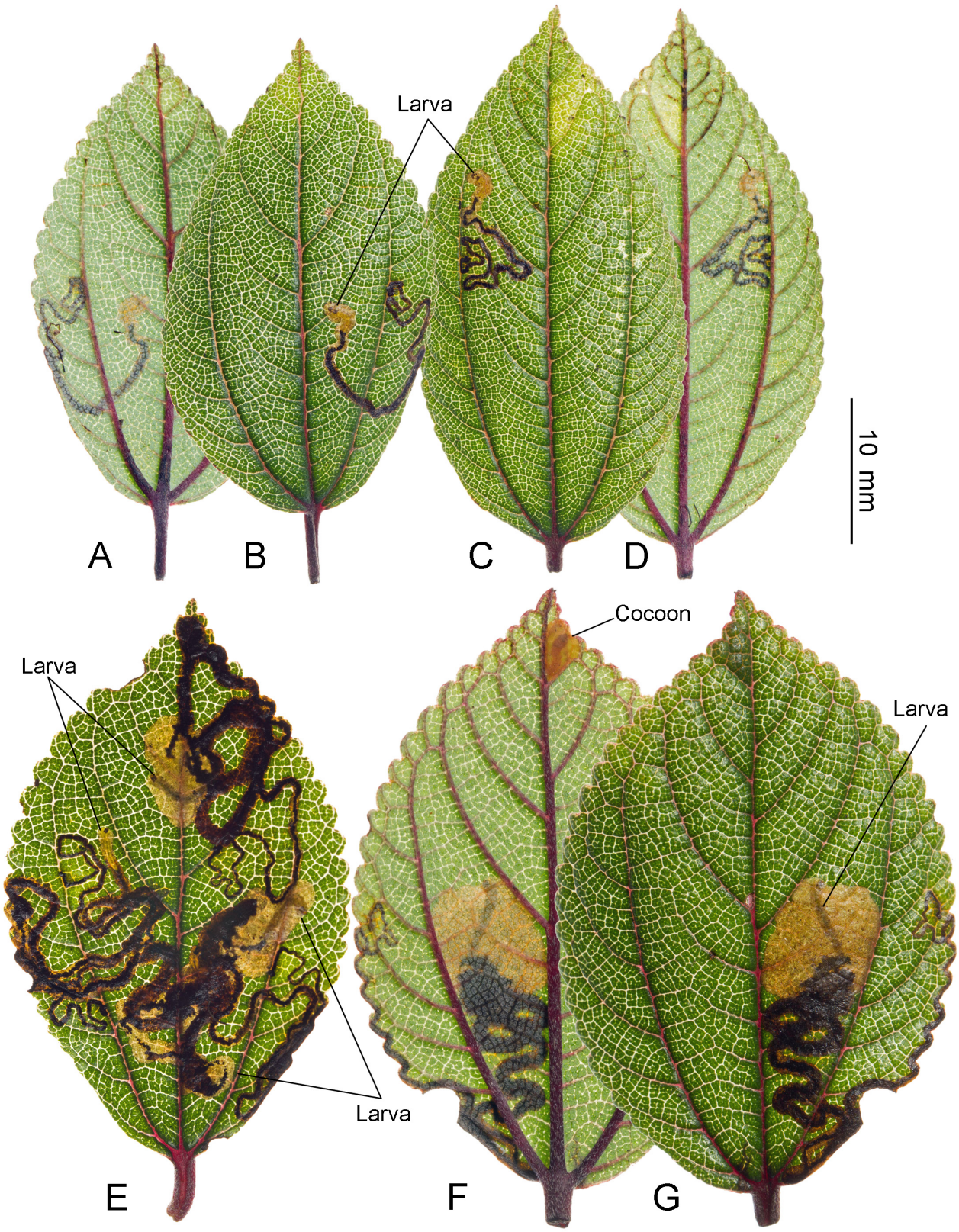

FIGURE 84. Mines of *P. haelaauensis* on leaves of its host plant, *Pipturus rockii*, Makawao Forest Reserve, East Maui, same series as CJ209, 216. **A**, **D**, **F**: Abaxial side of leaf, **B**, **C**, **E**, **G**: Adaxial side of leaf.

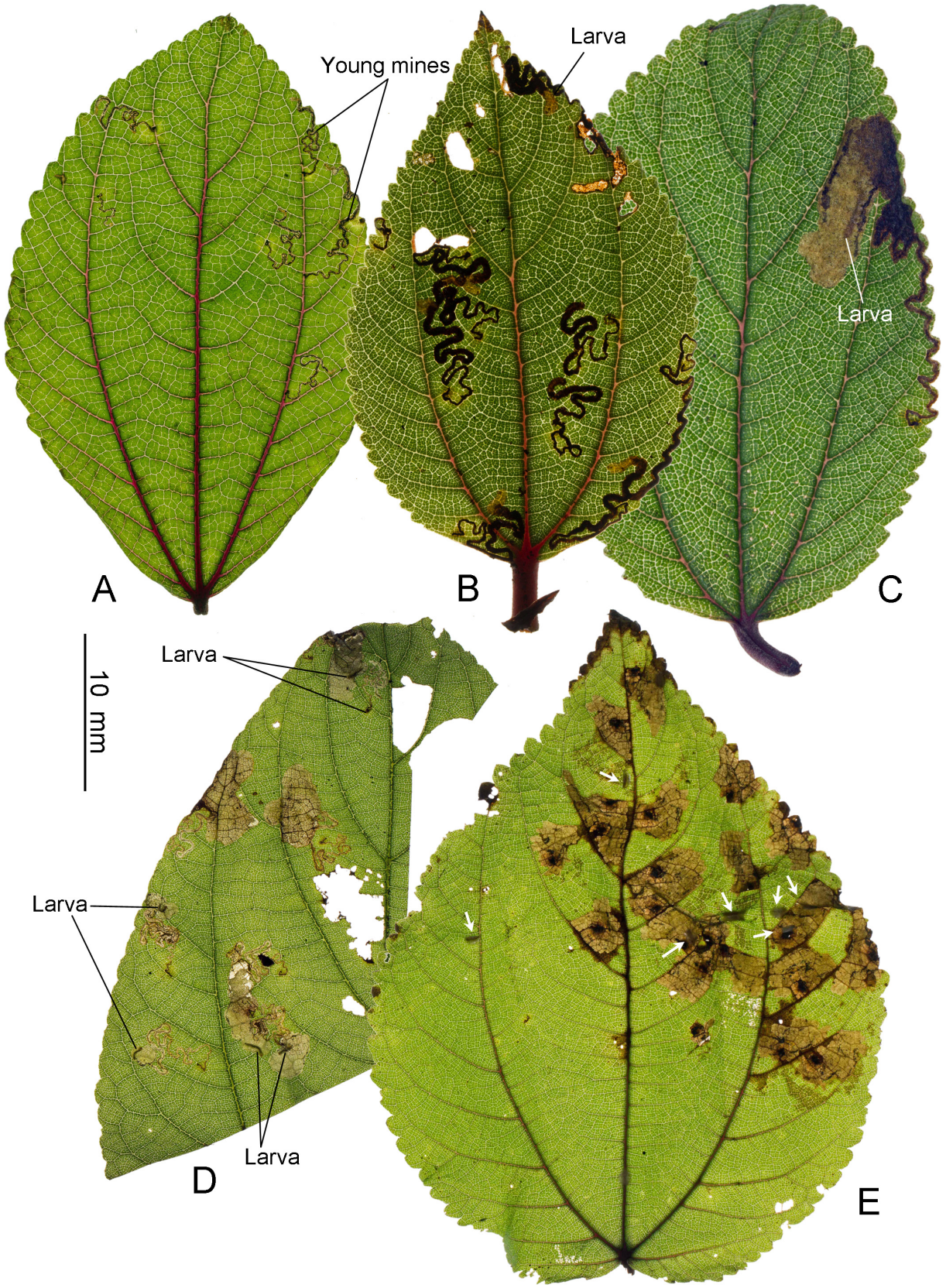

FIGURE 85. *Philodoria* species on leaves of the host plant, *Pipturus*. **A–D**: *Philodoria* sp. nr. *P. haelaauensis* or *P. floscula*, **E**: *P. neraudicola* A: Molokai, **B**, **D**: Hawaii (Big Island), **C**, **E**: West Maui, **B**: Kohala Forest Reserve, **C**: Waihe'e Forest Reserve **D**: Puu Makaala Natural Area Reserve, **E**: Iao Valley, same series of CJ336, 360, 361, 369. Host plants: **A** *Pipturus* sp. 1, **B** *Pipturus* sp. 4, **C**, **D** *Pipturus* sp. 2, **E** *Pipturus albidus*. Arrows point to cocoons.

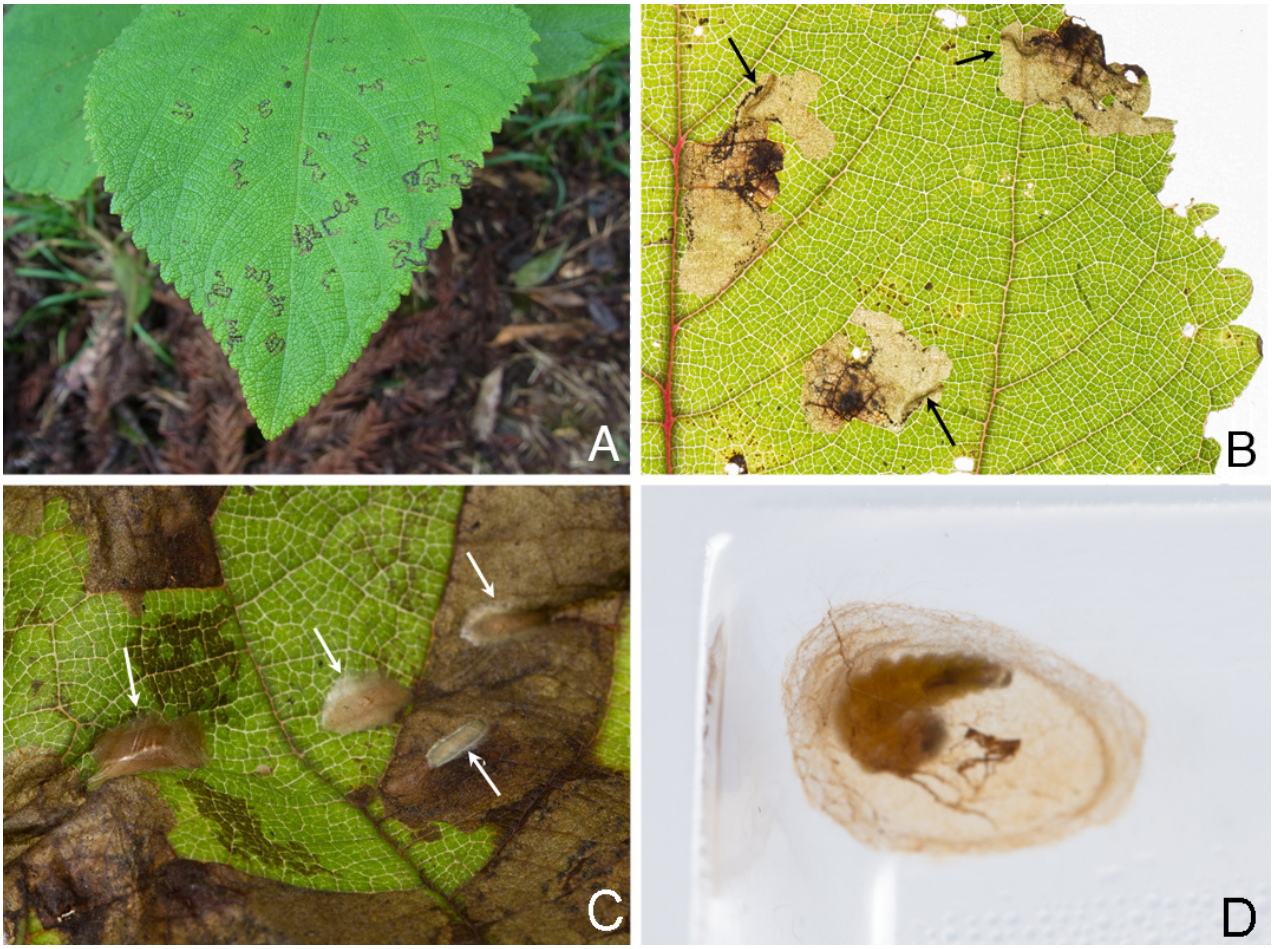

FIGURE 86. *Philodoria* species on leaves of the host plant, *Pipturus*. **A**, **D**: Unidentified *Philodoria* species, **B**: *Philodoria* sp. nr. *P. haelaauensis* or *P. floscula*, **C**: *P. neraudicola*. **A** West Oahu, **B**, **C**: Waihee Valley, West Maui, **D**: Kula Forest Reserve, East Maui, same series of CJ219, 222, 224, 230. Host plants: **A**: *Pipturus albidus*, **B**: *Pipturus* sp. 5, **C**: *Pipturus* sp. 4, **D**: *Pipturus rockii*. **A** Young mines, **B** Mine of late instar larva, **C** Cocoons on abaxial side of leaf, **D** Cocoon by final instar larva. Arrows show late instar larva (**B**) and cocoon (**C**).

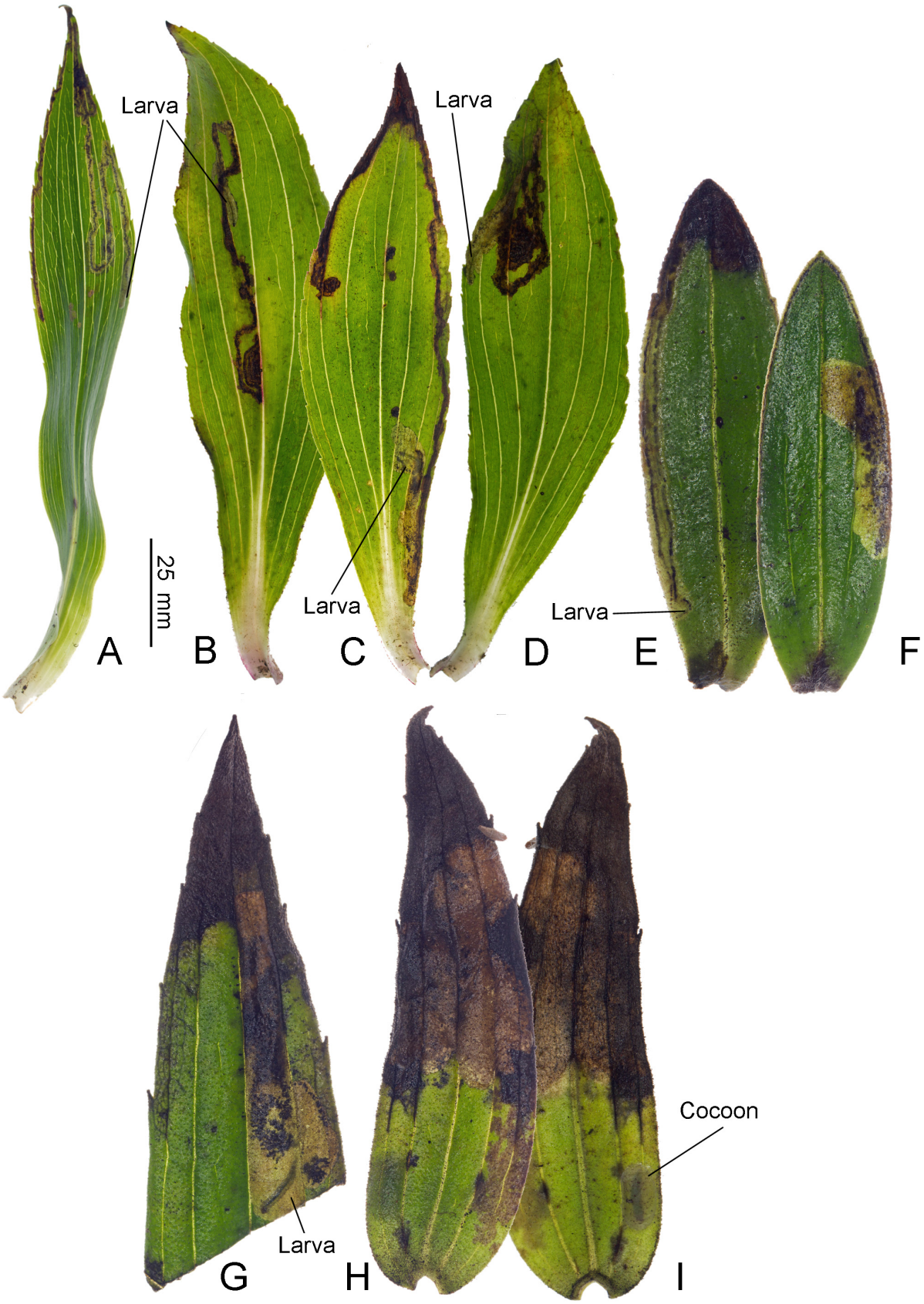

FIGURE 87. *Philodoria* species on leaves of the host plant, *Dubautia*. **A–D**: Unidentified *Philodoria* species, nr. *P. naenaeiella* or related species. **E**, **F**: *P.* sp. 1 of Johns *et al*. (2018), Maui, host: *Dubautia menziesii* **G–I**: *P. platyphylliella*, Maui, host: *Dubautia platyphylla*. **A** *D. plantaginea* Waihee Valley, Maui, CJ371, one adult (sex unknown) did not emerge, **B–D** *D. laxa* Konahuanui, Oahu, all larvae were consumed by parasitoids, CJ208, 242, 248.

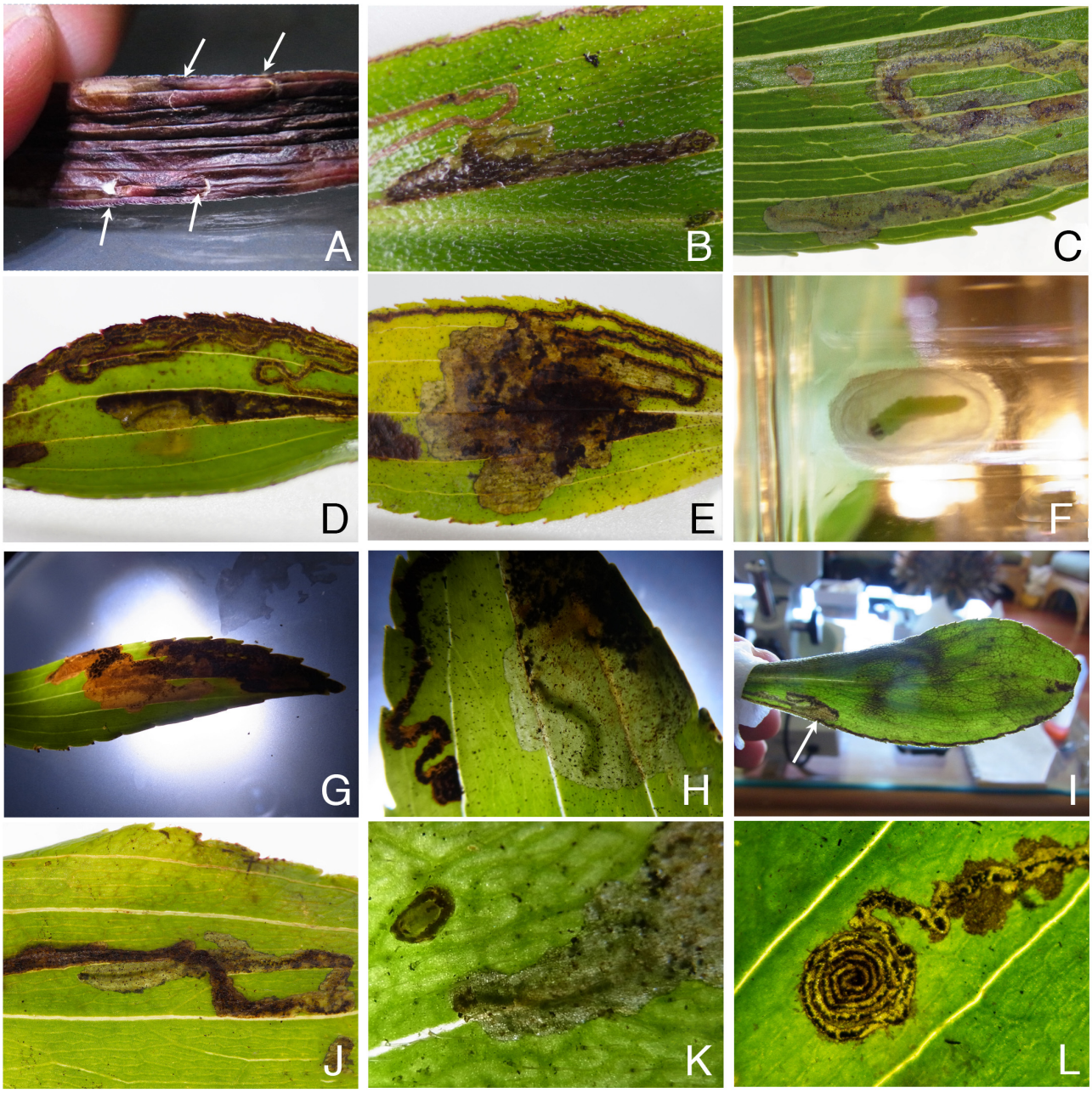

FIGURE 88. Asteraceae-mining *Philodoria* with thier host plants. **A**: *P. wilkesiella*, West Maui, host: *Argyroxiphium grayanum*, **B–F**: *P. dubauticola*, Haelaau, Maui, same series as CJ073, 074, 077 079, 080, 082–084, 094,111, 255, 256, host: *Dubautia laxa*, **G**, **H**: *P. naenaeiella* Poamoho, Oahu, same series as CJ130, 131, 140, 142, host: *Dubautia* sp. 1, **I–L**: Unidentified *Philodoria* species, **J**, **K**: East Oahu, host: *Dubautia* sp. 2, **I**: Eke, Maui, host: *D. laxa*, **L**: Kamakou, Molokai. **A** Old mines and cocoons, **B**, **L** Young mine, **C**, **H**, **J**, **K** Mine of late instar larva, **G**, **D**, **E**, **I** Mature mine, **F** Cocoon by final instar larva. Arrows point to cocoon (**A**) and mine (**I**).

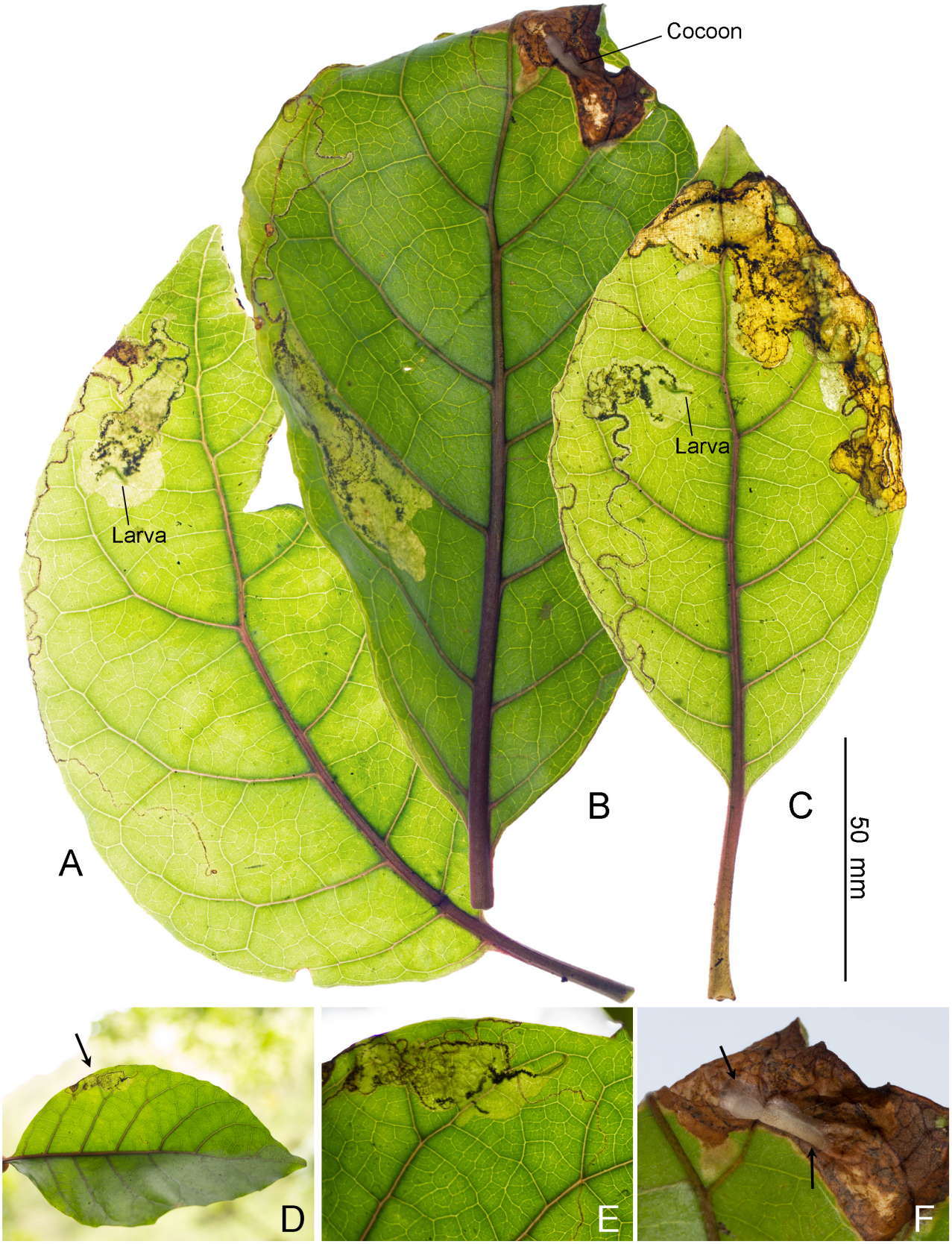

FIGURE 89. *Philodoria hesperomanniella* leaf mines on its host plant, *Hesperomannia arborescens* subsp. *opuhe*, West Maui. **A**, **C** Mines of latar larva, **B** Old mines and cocoon, **D** Young mine, **E** Mine of late instar larva, **F** Cocoon. Arrows point to mine (**D**) and cocoon (**F**).

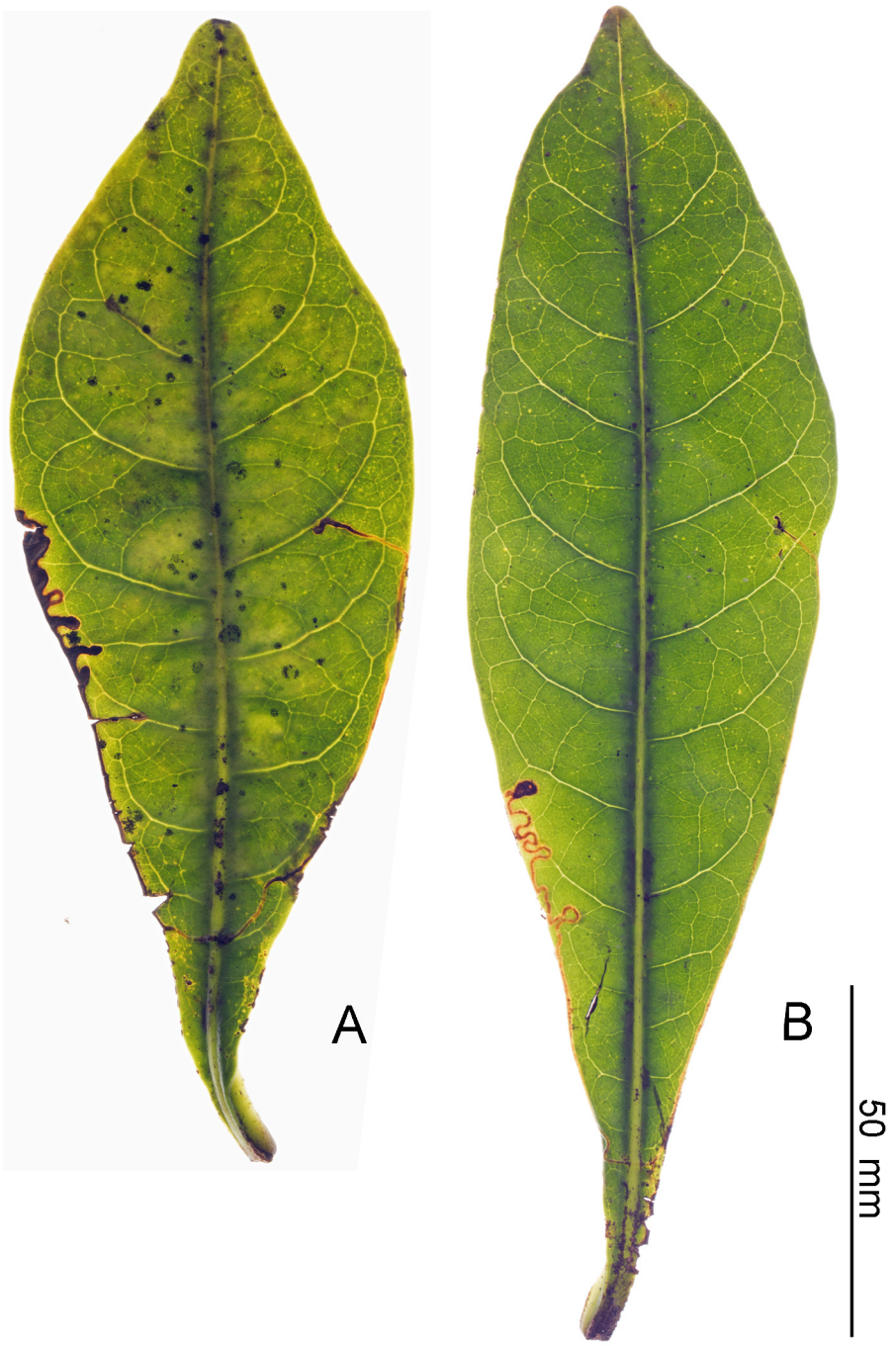

FIGURE 90. Mines of *Philodoria* sp. 2 on its host plant, *Hesperomannia lydgateyi*, Kauai. **A**, **B** Old mine.

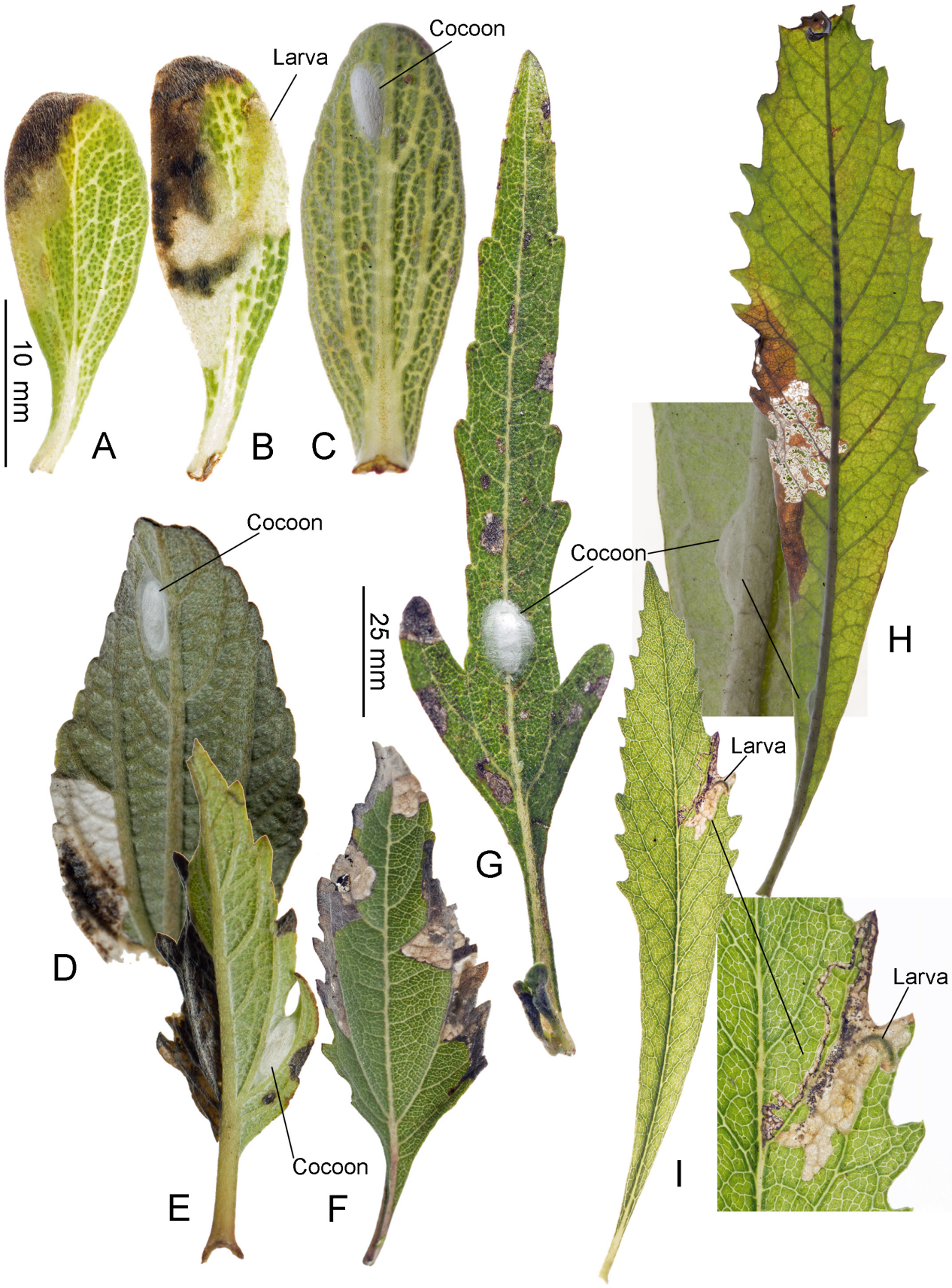

FIGURE 91. *Philodoria* species on leaves of Asteraceae host plants. **A–G**: *P. sciallactis*, **H**, **I**: *P. keahii*. Host plants: **A–C** *Melanthera integrifolia*, West Oahu, **D–F** *Lipochaeta rockii*, East Maui, **G** *Melanthera kamolensis*, East Maui, **H**, **I** *Remya mauiensis*, Maui.

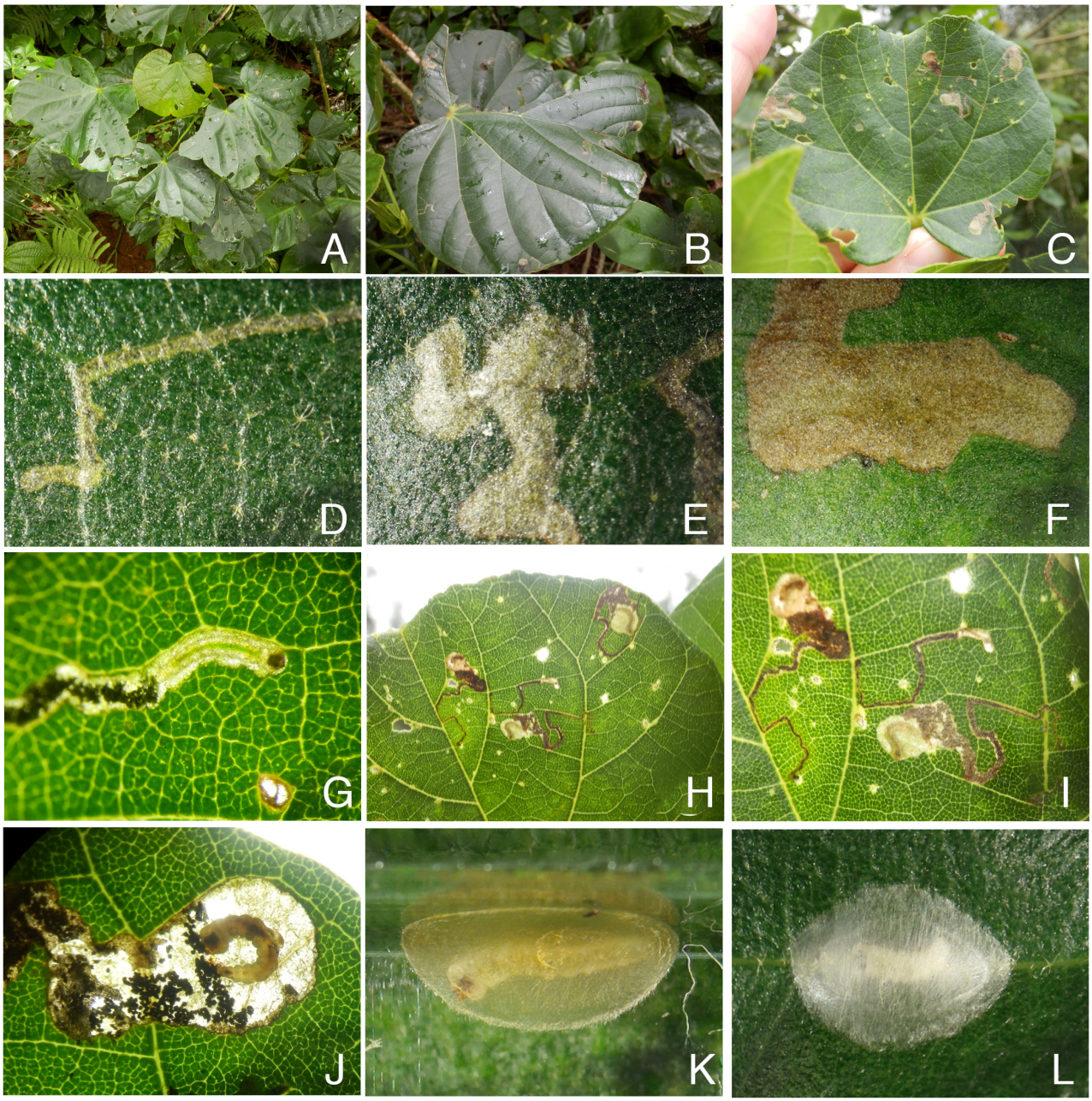

FIGURE 92. *Philodoria hauicola* and its host plant, *Hibiscus tiliaceus*, Nuuanu Pali, Oahu. **A–C** Host plant leaves and mines, **D**, **E** Young mine, **F** Later mine, **G** Mine of young instar larva, **H**, **I** Mine of late instar larva, **J** Late instar with parasitoid larva, **K**, **L** Cocoon spinning by final instar larva.

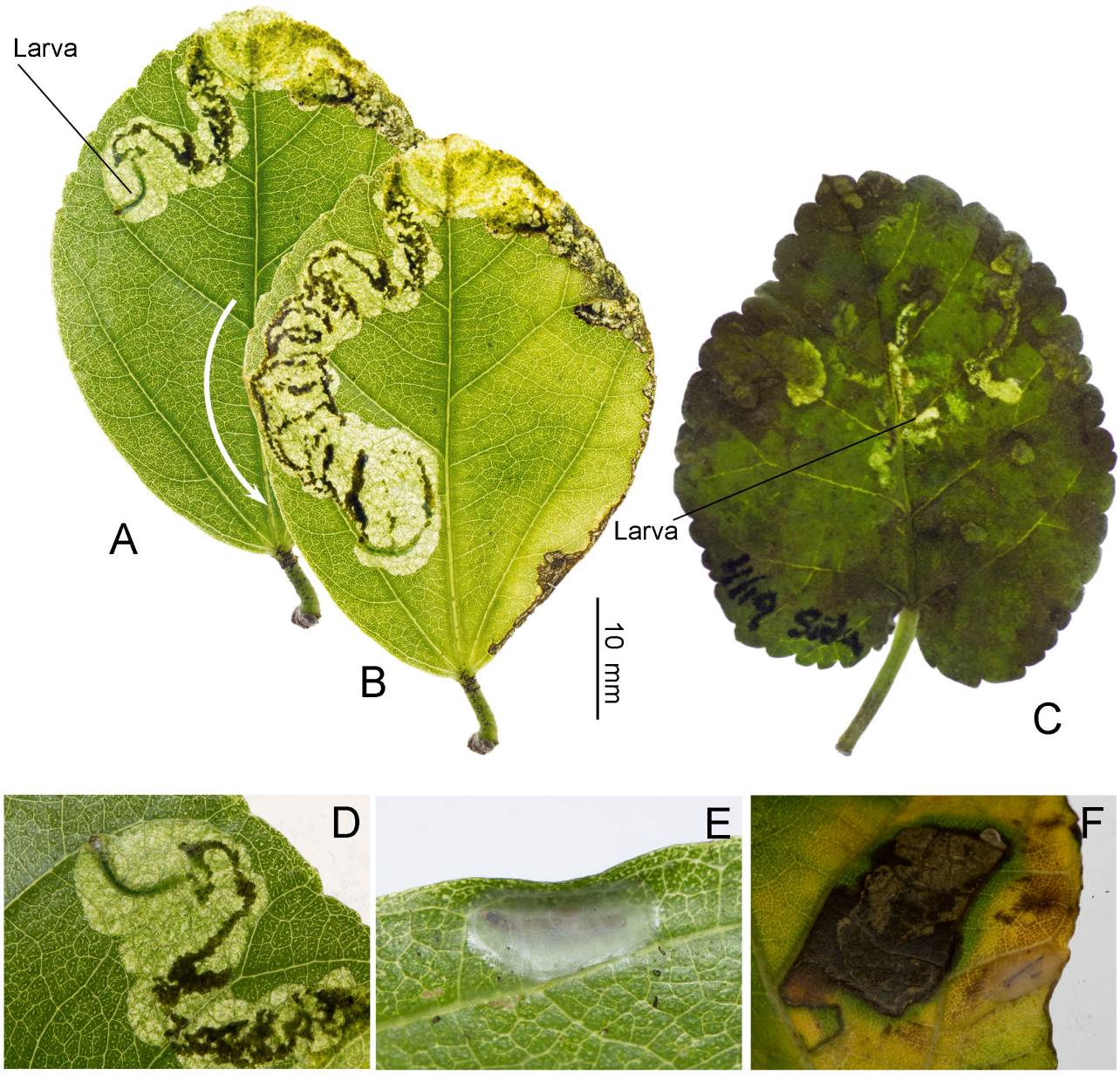

FIGURE 93. Mines of *Philodoria* species with thier Malvaceae host plants, Oahu. **A**, **B**, **D**, **E**: *P. hibiscella*, host: *Hibiscus arnottianus*, **C** *P. marginestrigata*, host: *Sida fallax*, **F** *P. hauicola*, host: *Hibiscus tilaceus*, **D** Mine of late instar larva, **E** Cocoon on the adaxial side of leaf, **F** Old mine.

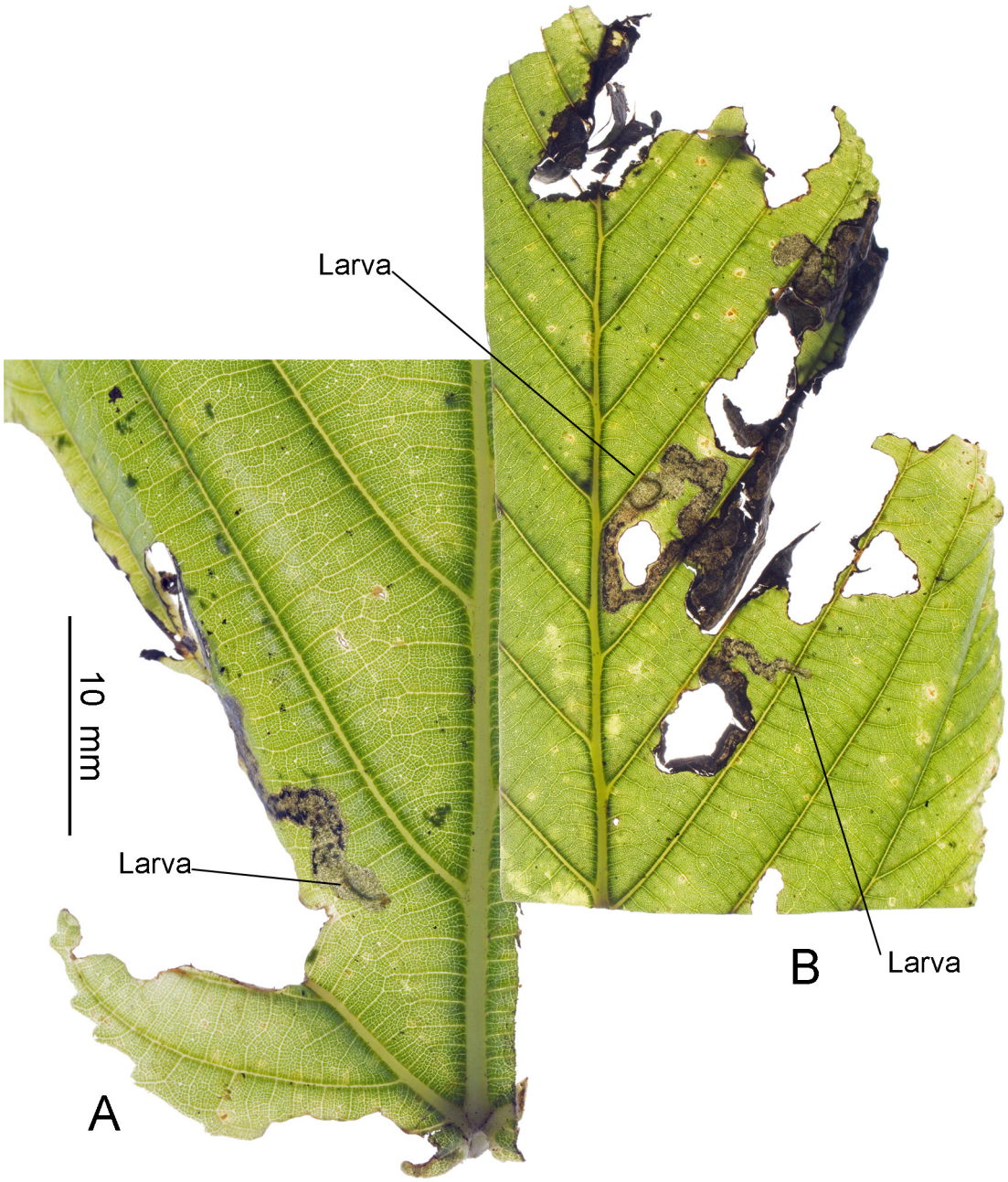

FIGURE 94. Mines of *Philodoria touchardiella* on the leaf of its host plant, *Touchardia latifolia*. **A**, **B** Mine of late instar larva.

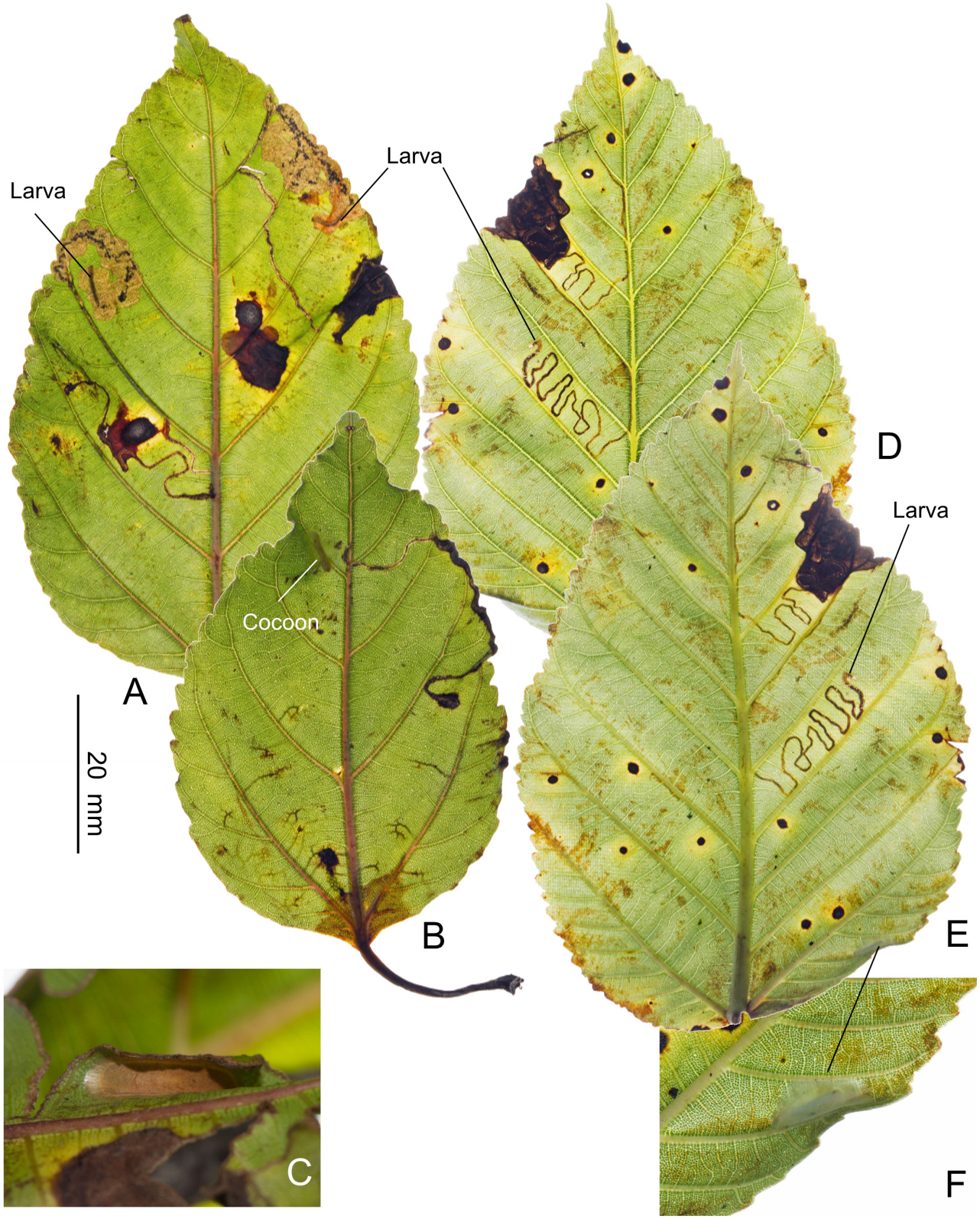

FIGURE 95. Mines of *Philodoria* on *Urera glabra*. **A–C**: *P. urerana*, Oahu, **D–F**: *P. ureraella*, Maui, CJ307, **A**, **D** Mines of late instar larvae, **B**, **E** Mines and cocoon, **C**, **F** Cocoon.

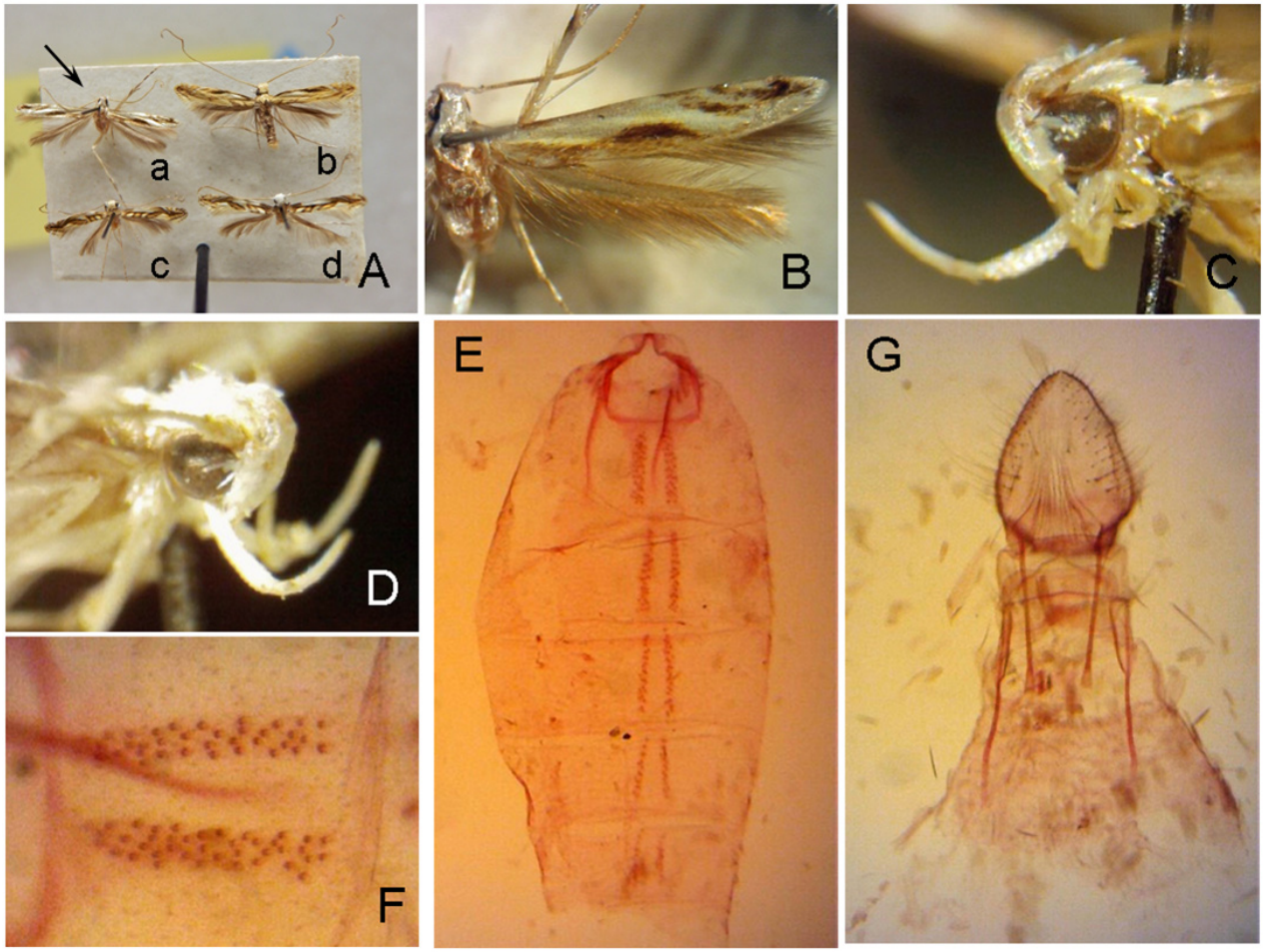

FIGURE 96. Adult morphology of *Chedra* sp., a genus of Batrachedridae that has been frequently been confused with *Philodoria*. **A** Adult of *Chedra* sp. (upper left specimen on mount with arrow, specimen was thought to be part of the '*P. ureraella*' syntype series, USNM). The specimen mount contains the paratype of *Philodoria opuhe* (upper right specimen on mount), paralectotype of *P. ureraella* (bottom two specimens on mount, SK742). The *Chedra* specimen has been here excluded from the '*P. ureraella*' syntype series (USNM). **B–G**: *Chedra* sp., **B** Forewing, **C**, **D** Head, lateral view, **E** Sockets of spiniform setae of tergum of A2–6, F Setae of A2, **G** Female genitalia, missing corpus bursae, ventral view.

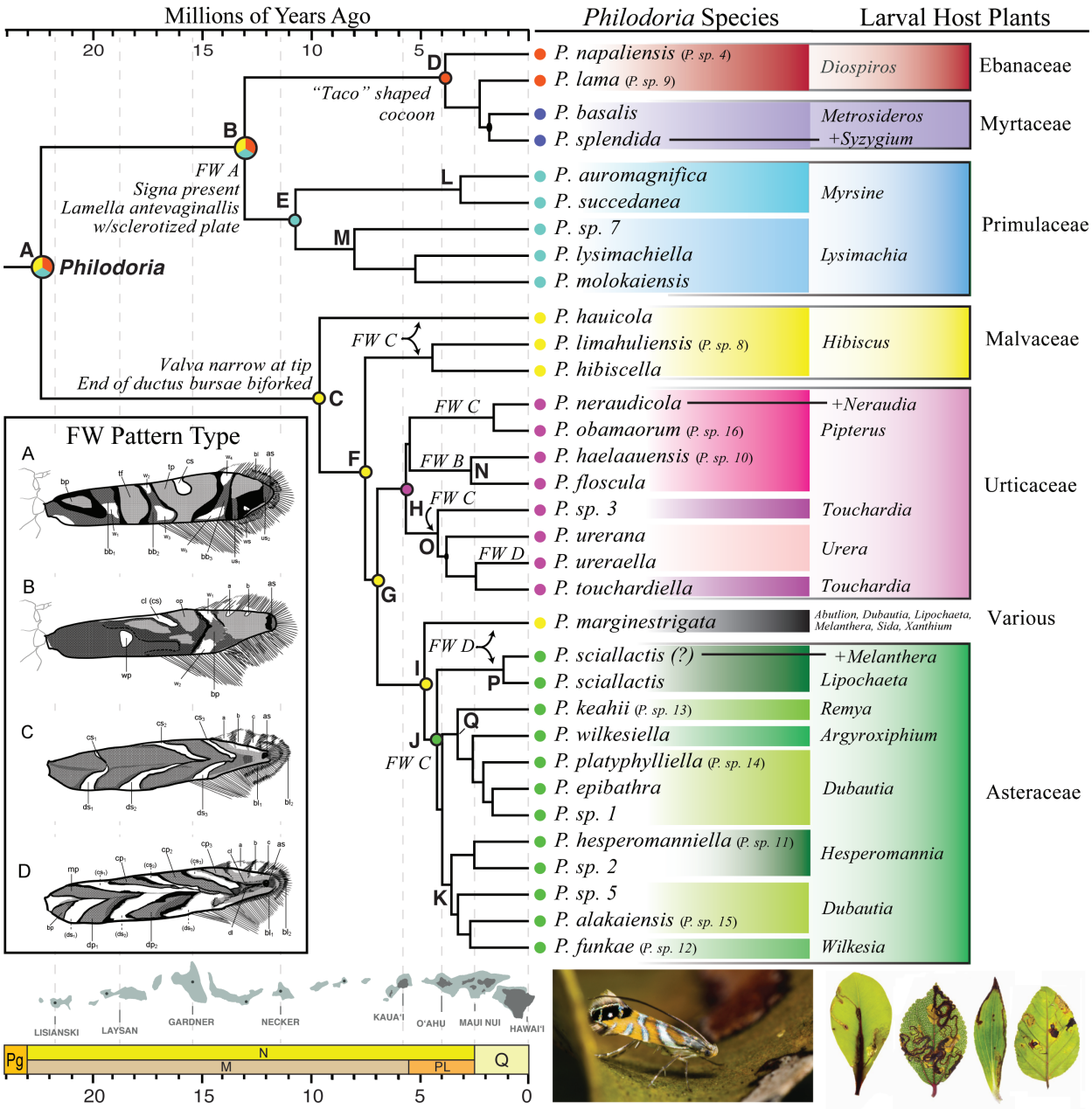

FIGURE 97. Dated evolutionary tree of *Philodoria* from Johns *et al*. (2018) based on 507 loci, with exemplar morphological traits and larval host plants mapped. Based on the morphology examined in the present study, we hypothesize that the following species, not in the study of Johns *et al*. (2018), belong to the following clades: **K**: *P. dubauticola*, *P. dubautiella*, *P. knudseniella*, *P. naenaeiella*, **L**: *P. kauaulaensis*, *P. kolea*, **M**: *P.* sp. A, **N**: *P. costalis*, *P. micropetala*, *P. pipturiella*, *P. pipturicola*, *P. spilota*, **O**: *P. opuhe*, **P**: *P. lipochaetaella*, *P.* sp. B, **Q**: *P. pittosporella*, *P. keaensis*, *P. nigrelloides*. There were 15 unnamed *Philodoria* species in the tree of Johns *et al.* (2018), these are noted in parentheses after their approprite names, at tree tips. The five species that remain unnamed in the tree are: "sp. 1–3" (codes: CJ344, CJ149/AHE_016, CJ494 respectively), which have no available adult specimens as they were all sacrificed for molecular analysis in the study of Johns *et al*. Species 5 ("sp. 5") is an unknown species that feeds on *Dubautia,* collected from a larval specimen from Tantalus, Oahu (code: CJ051), which lacks a morphological voucher. Species 7 ("sp. 7") is an unknown species (code: CJ451/AHE_20) in which the forewing is in poor condition and therefore could not be formally described in the present study.

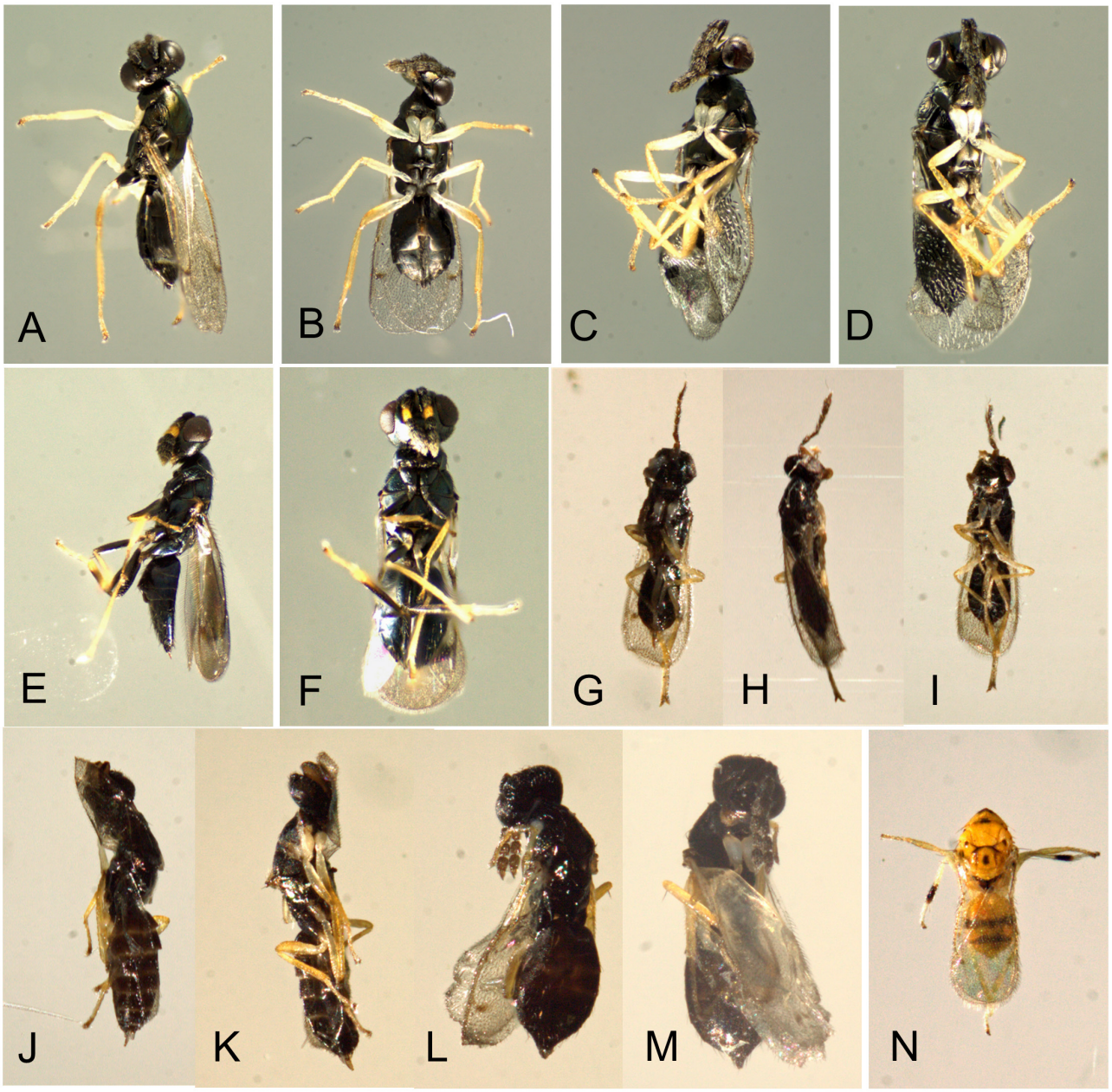

FIGURE 98. Parasitoid wasps that emerged from *Philodoria* that mine *Myrsine lessertiana*. **A–F**: Chalcidoidea from *P. auromagnifica* or *P. succedanea*, Oahu, **G–N**: unidentified species from *P. auromagnifica*, *P. kolea* or *P. succedanea*, Hawaii (Big Island). **A**, **B** CJ062-1, **C**, **D** CJ062-2, **E**, **F** CJ062-3, **G–I** SKH-10A, **J**, **K** SKH-10B, **L**, **M** SKH-10C, **N** SKH-1/SKH-15, Hawaii (Big Island).

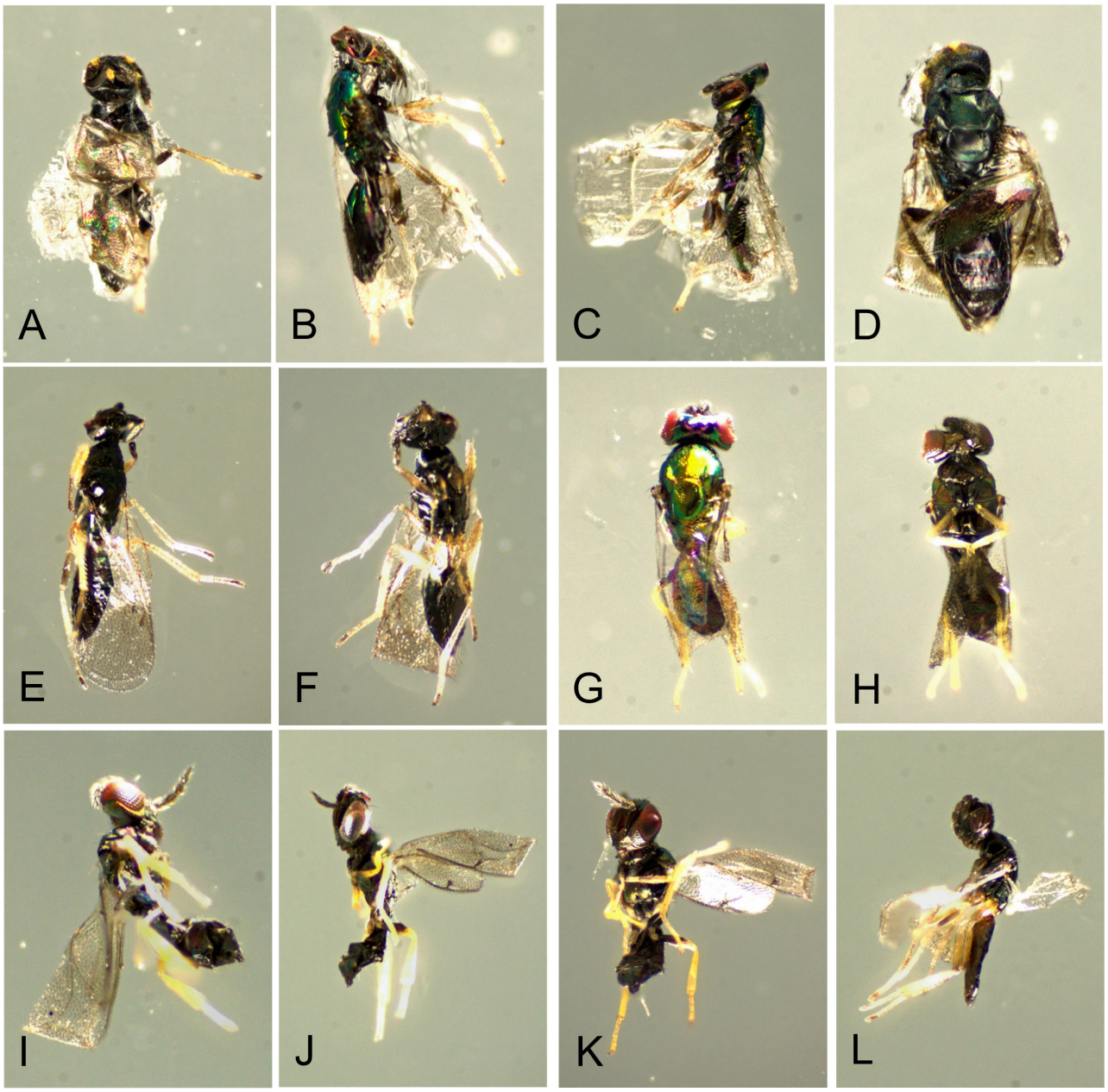

FIGURE 99. Parasitoid wasps that emerged from *Philodoria* that mine Primulaceae. **A–D**: unidentified wasps from *Philodoria* species (possibly *P. succedanea*) on *Myrsine linearifolia*, Kauai, **E–L**: Chalcidoidea from *P. molokaiensis* on *Lysimachia hillebrandii*, Molokai. **A**, **B** 511-1, 2/CJ511, **C**, **D** 511-3, 4/CJ511, **E**, **F** CJ201, **G**, **H** CJ203-1, **I**, **J** CJ203-2, **K**, **L** CJ203-3.

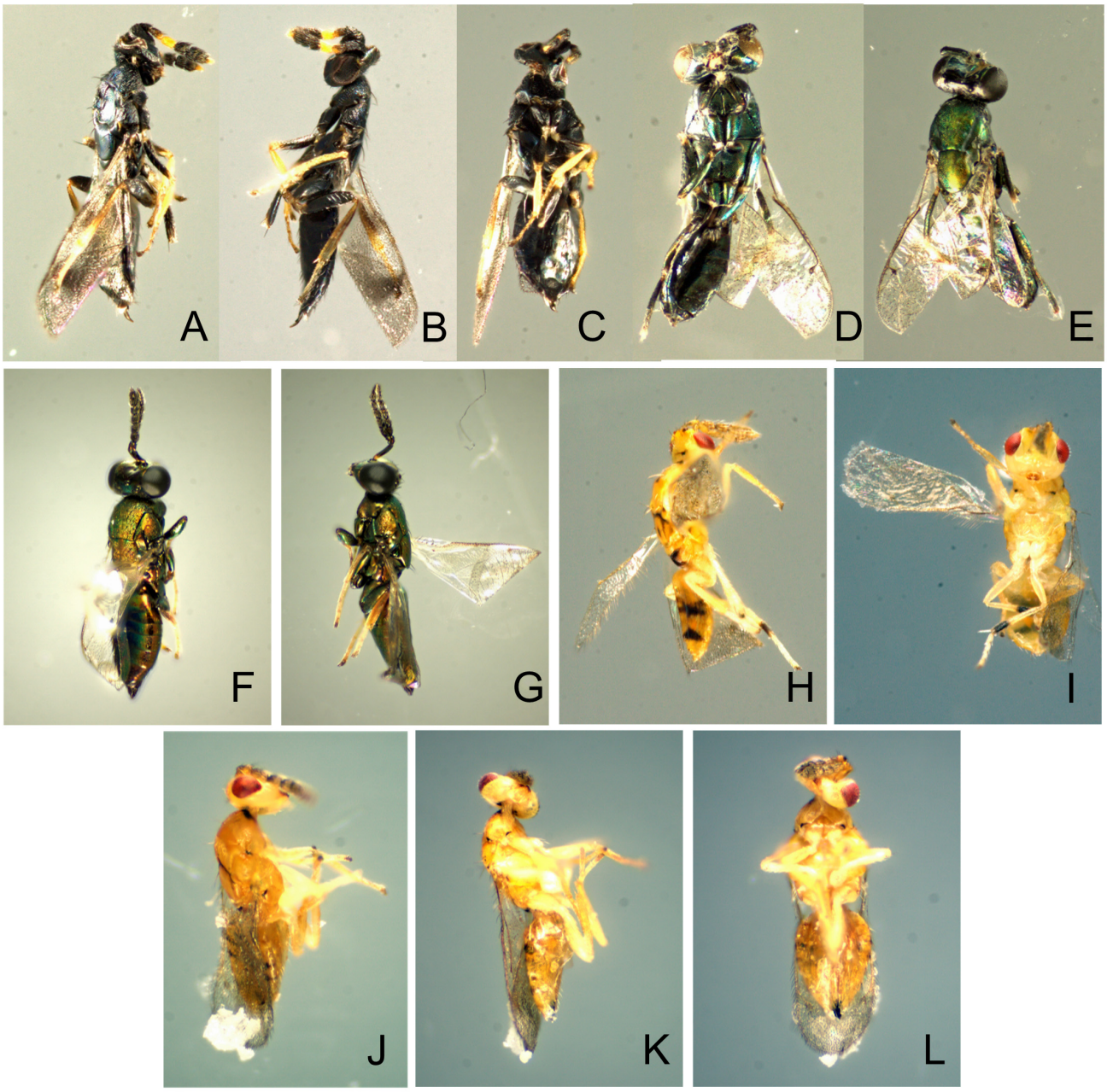

FIGURE 100. Parasitoid wasps (Chalcidoidea) that emerged from *Philodoria basalis* or *P. splendida* on *Metrosideros polymorpha*, Oahu. **A–C** CJ044, **D**, **E** CJ113, **F**, **G** CJ298, **H**, **I** CJ290, **J–L** CJ292.

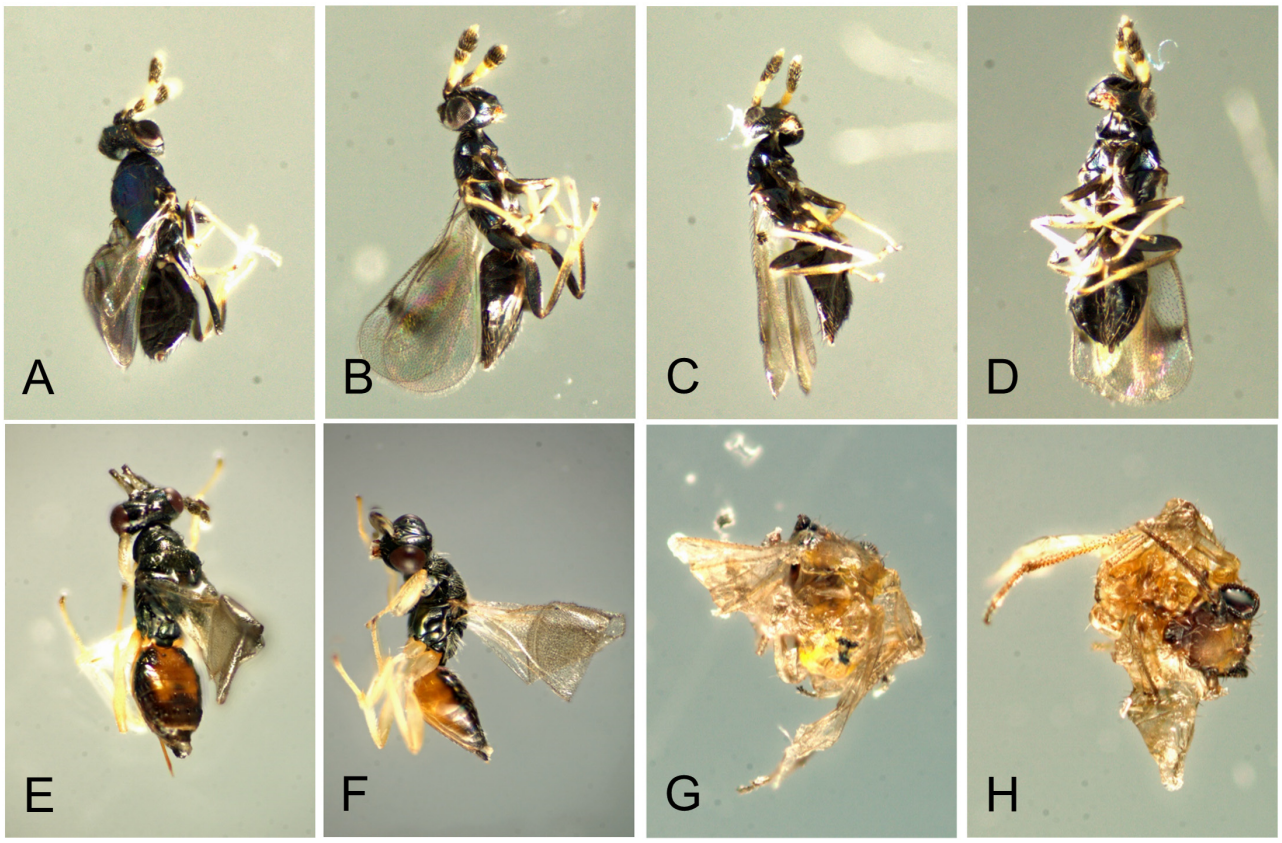

FIGURE 101. Parasitoid wasps (Chalcidoidea) that emerged from *Philodoria basalis* or *P. splendida*. **A–F**: from *P. basalis* or *P. splendida* on *Metrosideros polymorpha*. **A**, **B** CJ123-1, Maui, **C**, **D** CJ123-2, **E**, **F** CJ417, Hawaii (Big Island), **G**, **H** CJ515 from *P. splendida* on *Syzygium* sp., Kauai.

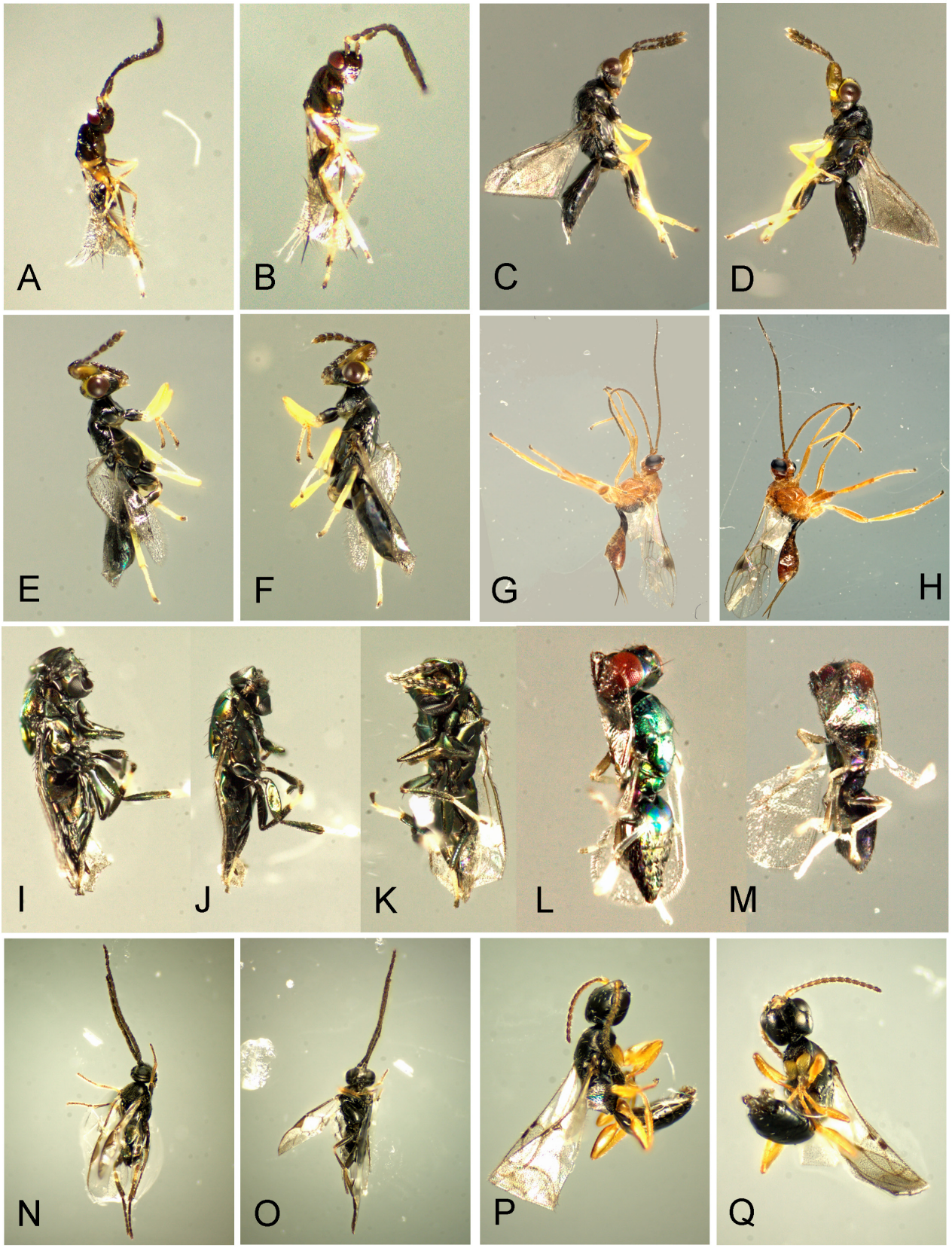

FIGURE 102. Parasitoid wasps that emerged from *Philodoria* that mine *Pipturus*. **A–F**, **I–Q**: Chalcidoidea, **G**, **H** Ichneumonidae, **N**, **O** Braconidae, **P**, **Q** Bethylidae male. **A**, **B** CJ206 from *Philodoria* sp. on *Pipturus rockii*, Maui, **C**, **D** CJ224-1 from *Philodoria* sp. on *P. rockii*, Maui, **E**, **F** CJ224-2, **G**, **H** CJ235 from *Philodoria* sp. on *Pipturus hawaiiensis*, Maui, **I**, **J** CJ289-1 from *Philodoria* sp. on *Pipturus* sp., Oahu, **K–M** CJ289-2, **N**, **O** CJ295 from *Philodoria* sp. on *P. albidus*, Oahu, **P**, **Q** CJ415 from *Philodoria* sp. on *Pipturus* sp., Hawaii (Big Island).

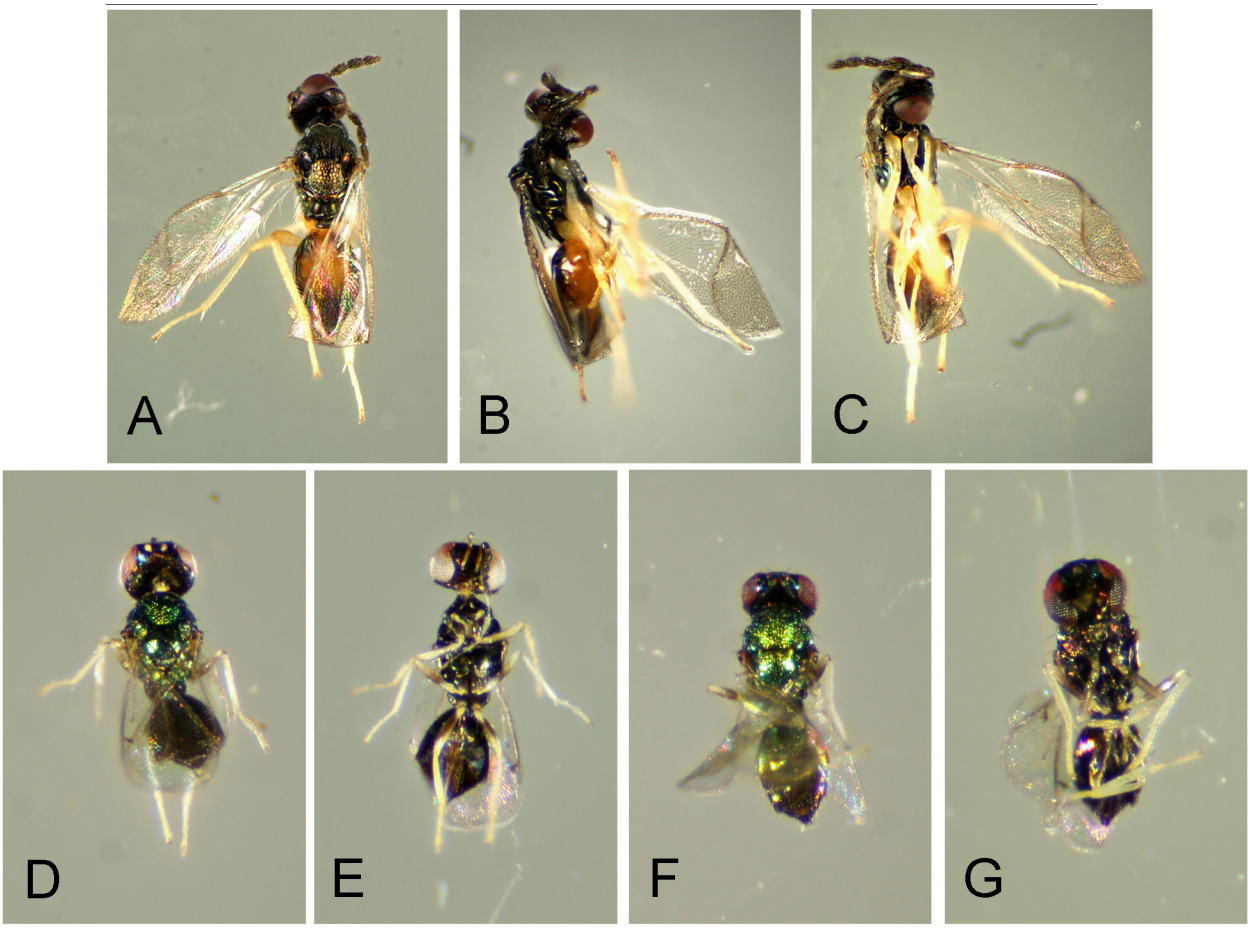

FIGURE 103. Parasitoid wasps that emerged from *Philodoria* that mine *Pipturus*, Hawaii (Big Island). **A–C** Chalcidoidea (CJ420) from *Philodoria* sp. on *Pipturus* sp., **D–G**: unidenitified species from *P. obamaorum* or *P. floscula* on *Pipturus* sp., **D**, **E** CLV017-1, 2, **F**, **G** CLV017-3, 4.

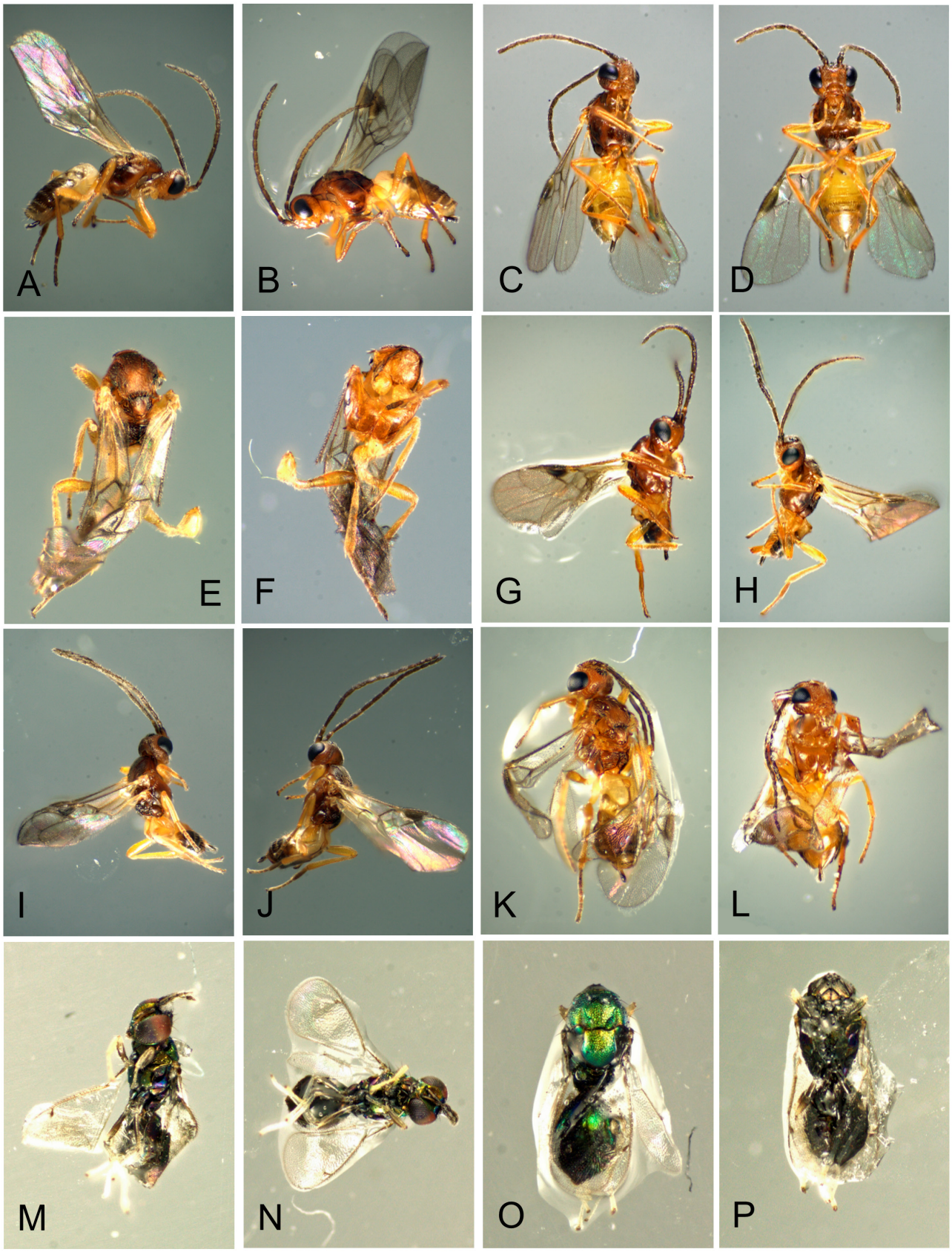

FIGURE 104. Parasitoid wasps that emerged from *Philodoria* that mine *Dubautia*, Oahu. **A–L**: Braconidae, **M–P**: Chalcidoidea, **A–H**: from *P. naenaeiella* or closely related species, **I–N**: from *Philodoria* sp., **A–D**, **M–P**: on *Dubautia plantaginea*, **E–L**: on *Dubautia* sp. **A**, **B** CJ208 **C**, **D** CJ242, same data as CJ208, **E**, **F** CJ248-1, **G**, **H** CJ248-2, **I**, **J** CJ140, **K**, **L** CJ313, **M**, **N** CJ502-1, **O**, **P** CJ502-2.

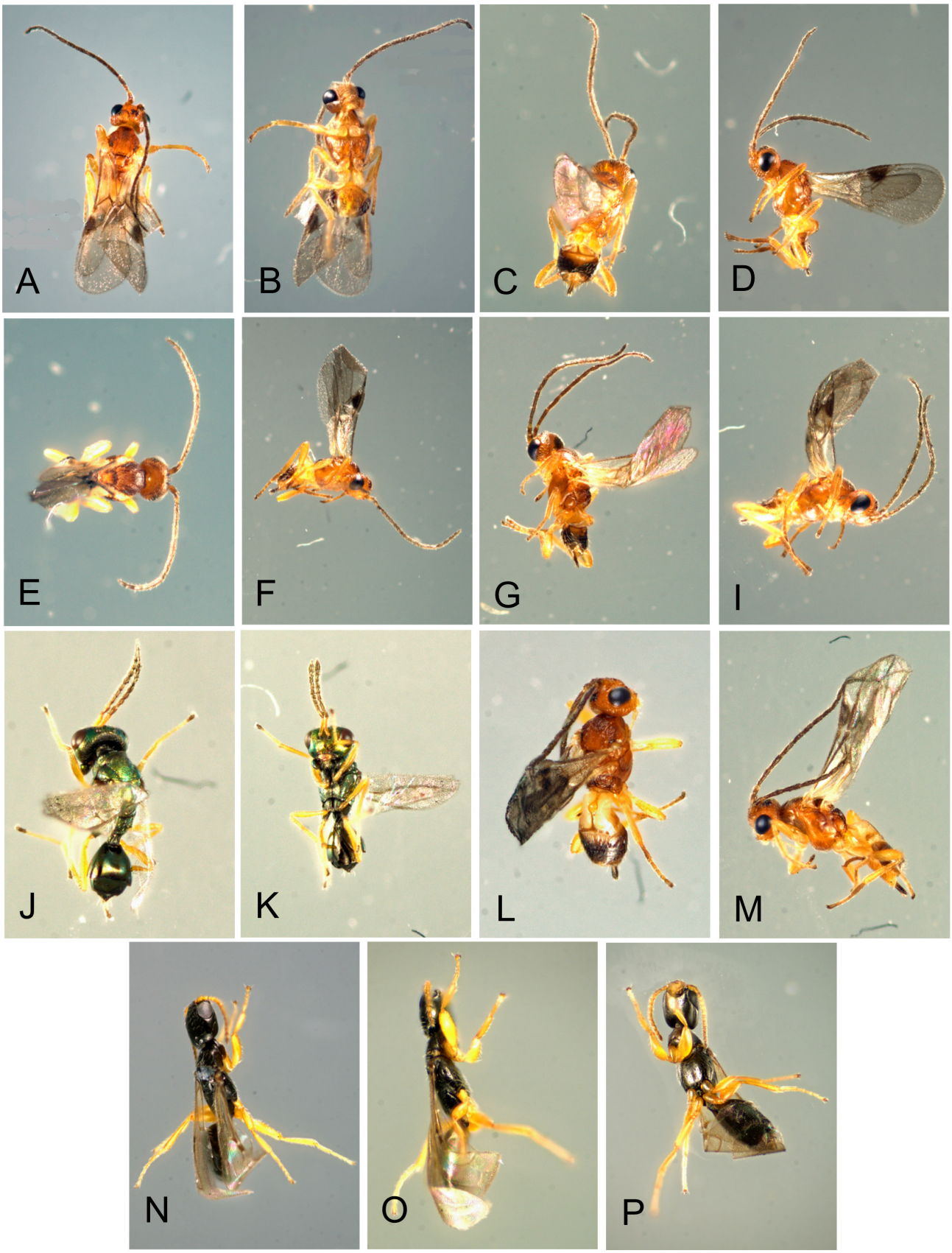

FIGURE 105. Parasitoid wasps that emerged from *Philodoria* that mine Asteraceae, Kauai. **A–H**, **M**, N: Braconidae, **I**, **J**: unidentified species, **M–O**: Bethylidae. **A–L**: from *P. alakaiensis*? on *Dubautia* sp. [*laxa*?], Kauai. **A**, **B** CJ453, **C**, **D** CJ458-1, **E**, **F** CJ458-2, **G**, **H** CJ458-3, **I**, **J** CJ458-4, **K**, **L** CJ458-5, **M–O** CJ522 from *P. funkae* on *Wilkesia gymnoxiphium*.

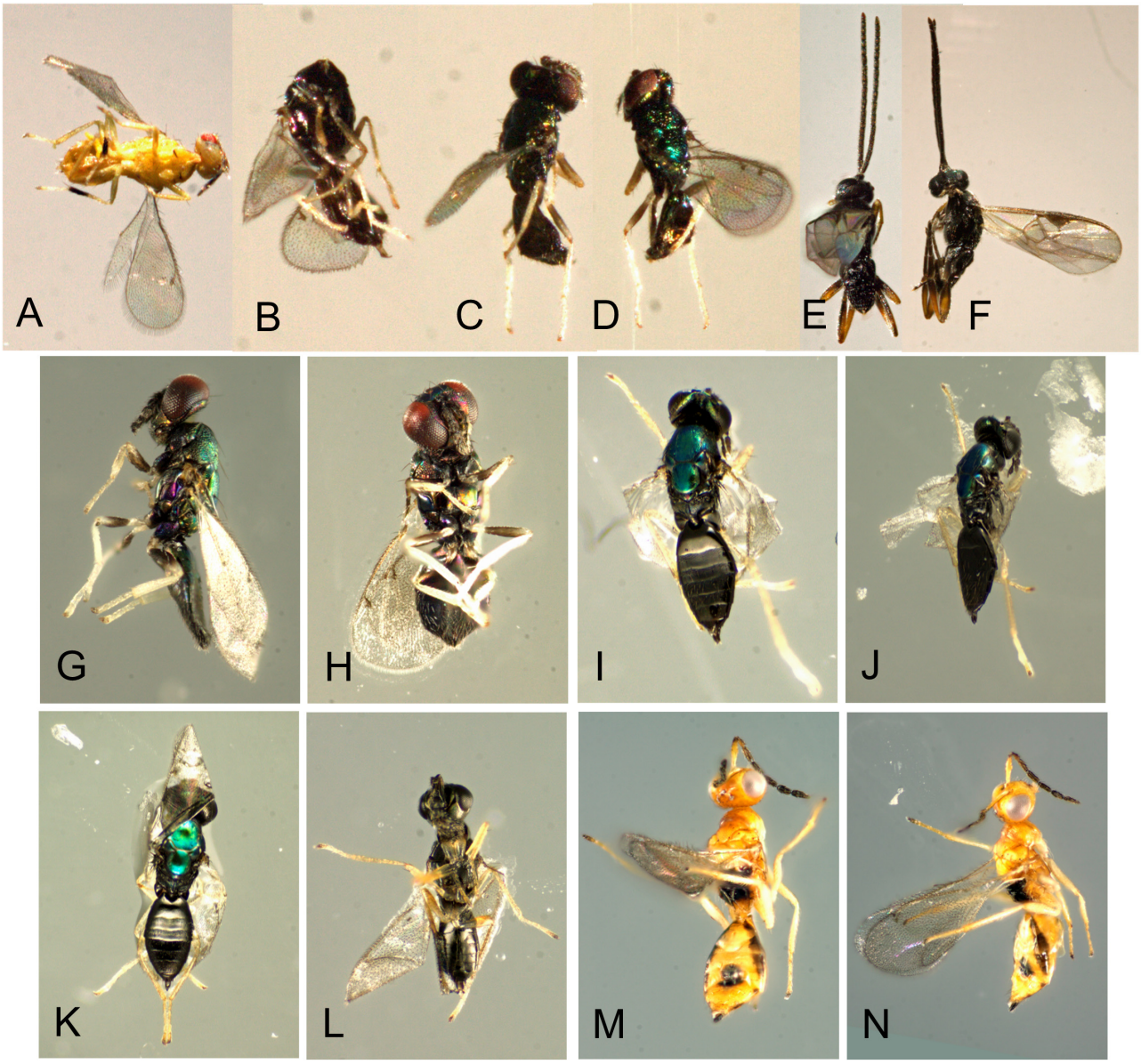

FIGURE 106. Parasitoid wasps that emerged from *Philodoria* that mine *Hibiscus*. **A–D**, **G**, **H**: unidentified species, **E**, **F**: Braconidae, **I–N**: Chalcidoidea. **A** SKH8-3-A from *P. hauicola* on *Hibiscus tilaceus*, Oahu, **B** SKH-8-3-B, **C, D** SKH-8-3-C, **E**, **F** SKH-8-11-A, same data as SKH-8-3, **G**, **H** CJ272 from *P. hauicola* or *P. hibiscella* on *H. tilaceus*, Oahu, **I**, **J** CJ236-1 from *P. hibiscella* on *H. arnottianus*, Oahu, **K** CJ236-2, **L** CJ236-3, **M**, **N** CJ469 from *P. limahuliensis* on *H. waimaeae* subsp. *haneri*, Kauai.

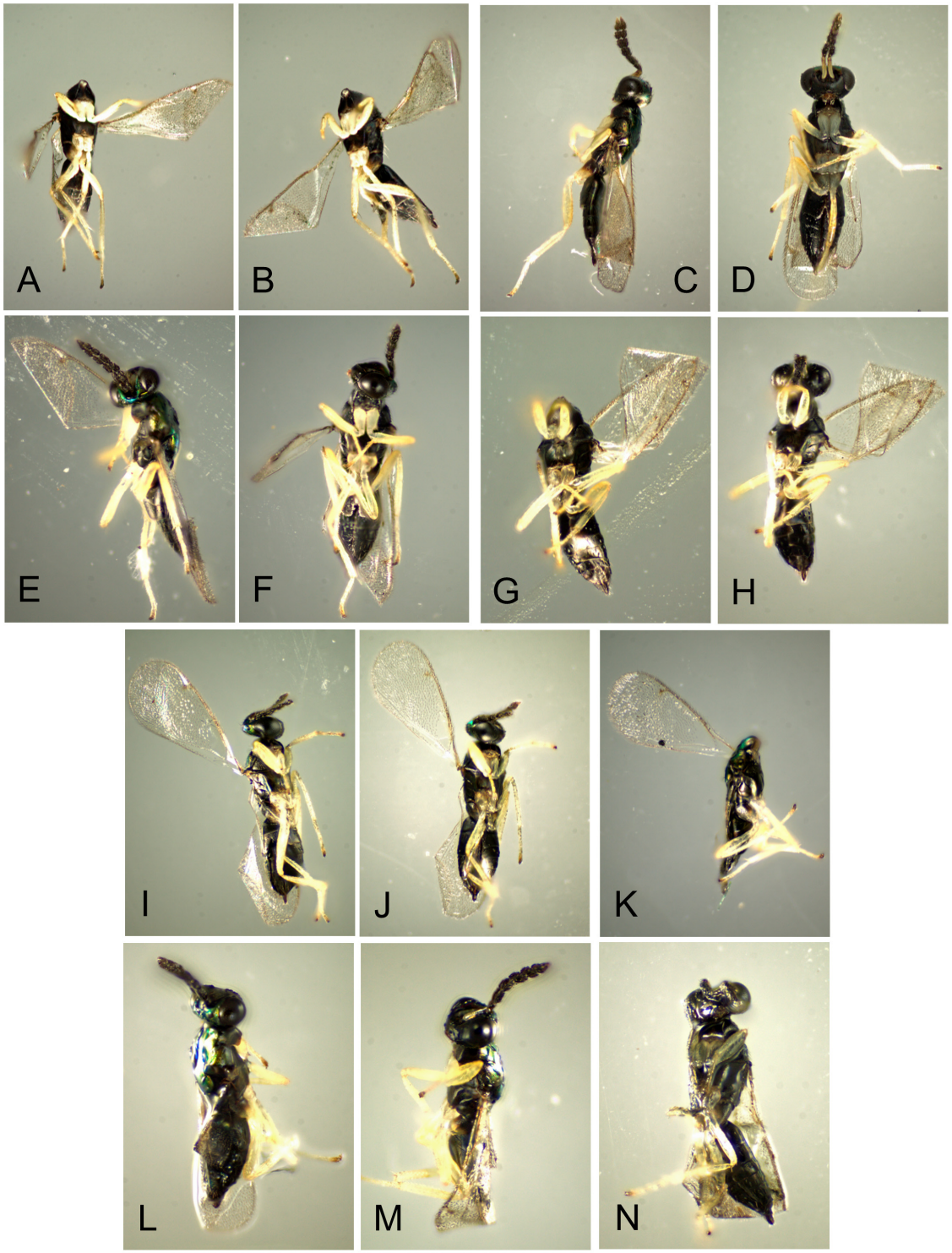

FIGURE 107. Parasitoid wasps (possibly family Scelionidae) that emerged from *Philodoria* sp. 3 of Johns *et al*. (2018) on *Touchardia latifolia*, Kauai. **A**, **B** CJ449-1, **C**, **D** CJ449-2, **E**, **F** CJ449-3, **G**, **H** CJ449-4, **I**, **J** CJ449-5, **K** CJ449-6, **L**, **M** CJ449-7, **N** CJ449-8.

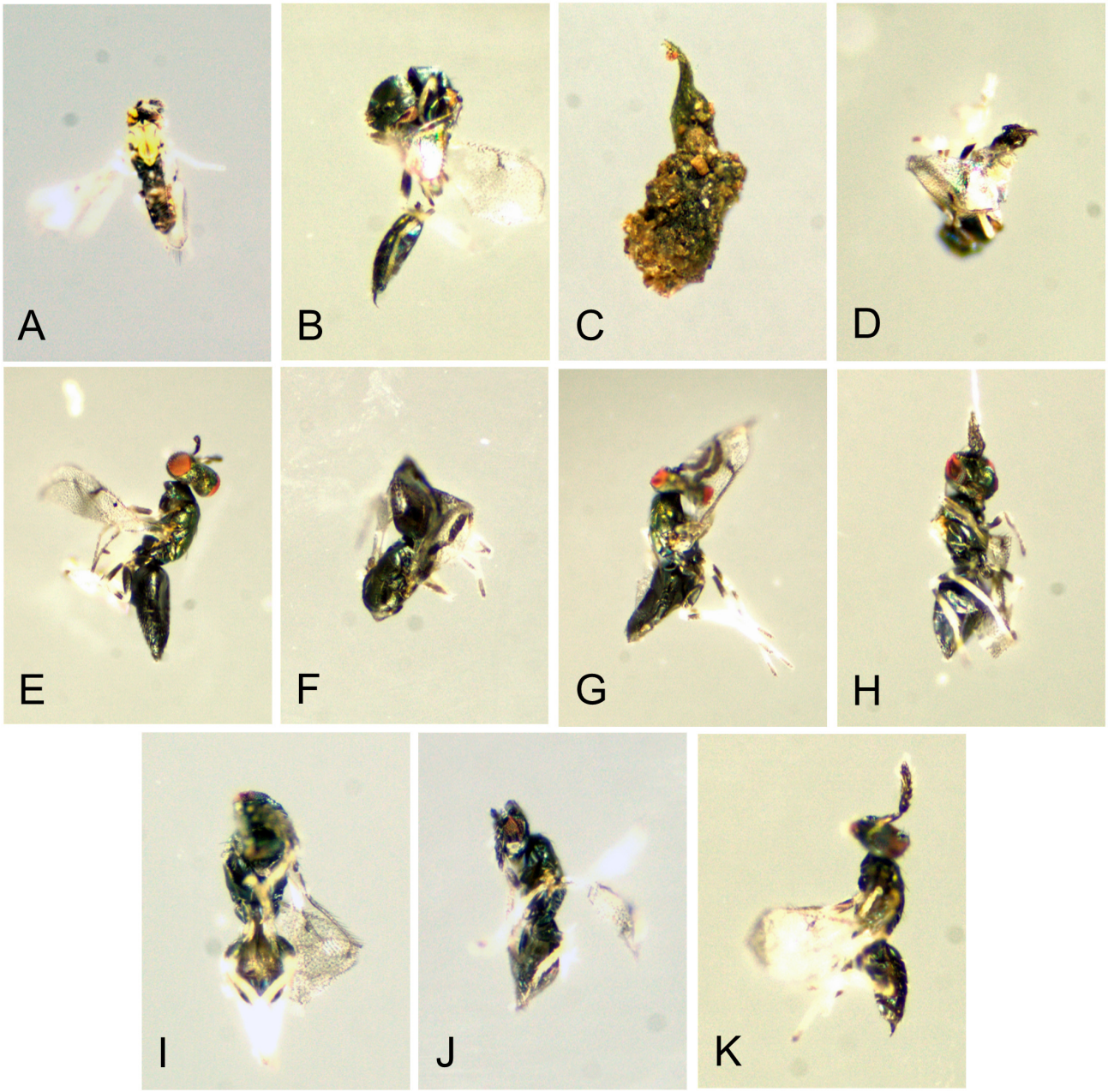

FIGURE 108. Parasitoid wasps (Chalcidoidea) that emerged from *Philodoria marginestrigata* on *Sida fallax*, Kaena point, Oahu. **A** CJ137-1, **B** CJ137-2, **C** CJ137-3, **D** CJ137-4, **E** CJ137-5, **F** CJ137-6, **G** CJ137-7, **H** CJ137-8, **I** CJ137-9, **J** CJ137-10, **K** CJ137-11.

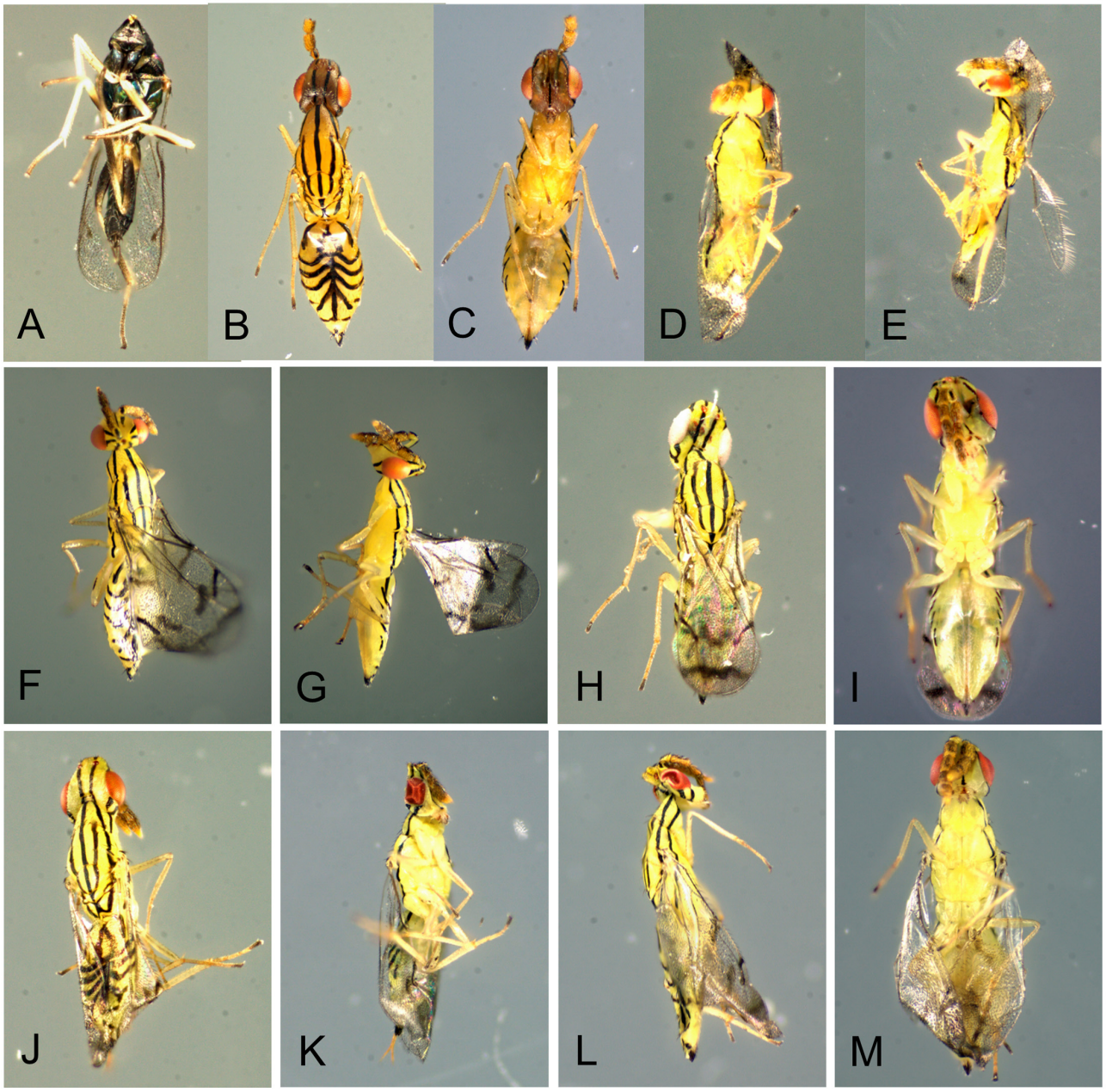

FIGURE 109. Parasitoid wasps that emerged from *Philodoria marginestrigata* on *Sida fallax*. **A**: Chalcidoidea, **B–M**: Eulophidae. **A** CJ055 Maui, **B**, **C** CJ056 Maui, **D**, **E** CJ193, Maui, **F**, **G** CJ205, Maui, **H**, **I** CJ378, Lanai, **J**, **K** CJ407-1, Hawaii (Big Island), **L**, **M** CJ407-2.

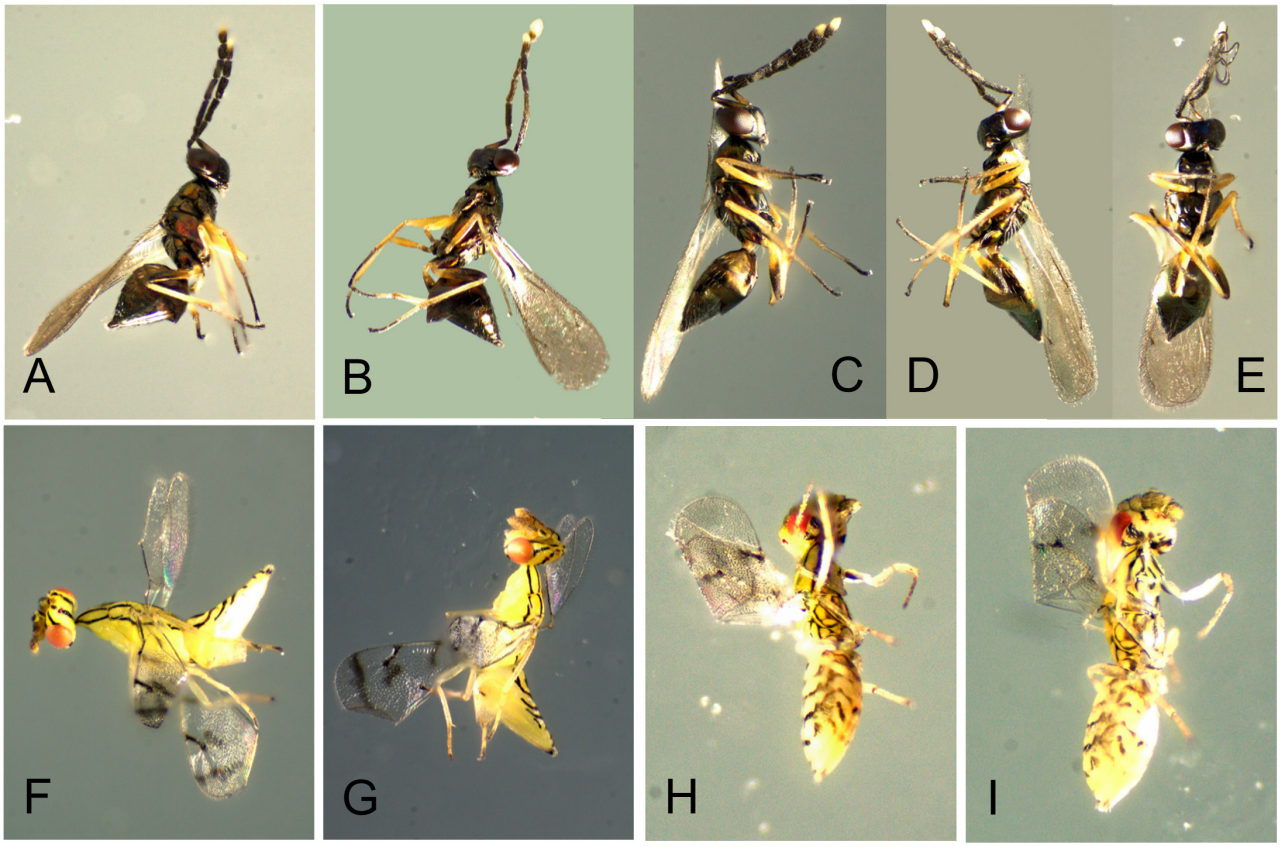

FIGURE 110. Parasitoid wasps that emerged from *Philodoria sciallactis* or *P. marginestrigata* on *Lipochaeta rockii*, Mokio, Molokai. **A**, **B** CJ180-1, **C**, **D**, **E** CJ180-2, **F, G** CJ196, **H**, **I** CJ207.

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