

The Systematics, Evolution, and Ecology of Hawaiian *Cydia* (Lepidoptera: Tortricidae)

by

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A dissertation submitted in partial satisfaction of the

Requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy and Management

in the

Graduate Division

of the

University of California, Berkeley

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Fall 2011

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## Abstract

*Cydia* Hübner 1825 is a genus of moths in the family Tortricidae with 231 named species and subspecies and is distributed on all continents except Antarctica. As larvae, many species feed within reproductive structures, such as fruits, seeds, and flowers, under bark, or within fleshy stems of at least 65 host-plant species including angiosperms and conifers. Many species, including codling moth, pea moth, spruce seed moth, pine seedworms, filbertworm, and hickory shuckworm are considered pests of agriculture and forestry. As a result, the biology, natural enemies, and pheromones of several species have been well-studied.

The nomenclature and classification of *Cydia* has also been well-studied but is less resolved. Nineteen different genus names have been proposed for species in this genus, with *Laspeyresia* Hübner, and *Carpocapsa* Treitschke being in common usage until relatively recently. Following the rules governing the International Code of Zoological Nomenclature, *Cydia* is the valid genus name for all species congeneric with the codling moth, *Cydia pomonella* (Linnaeus), the type species of the genus. The relationship of *Cydia* to other genera in the tribe Grapholitini is a topic of continued debate. Some authors have suggested that the tribe is an evolutionary grade while others have presented evidence that Grapholitini is a monophyletic clade. Although some secondary sexual characters have been proposed, the genus *Cydia* can claim no synapomorphies that can be found in all *Cydia* species. To better understand the systematics and evolution of this group more detailed morphological, molecular, and ecological data are needed for non-pest species.

At least 21 endemic species of *Cydia* are known from the Hawaiian Islands. Males of most species have a ventral pouch below the cubital vein of the hindwings similar to *C. latiferreana* (Walsingham), *C. maackiana* (Danilevsky), and several other *Cydia* species to a lesser extent, although this feature appears to have arisen independently in the Hawaiian group. Larvae, where known, feed on endemic plants in the family Fabaceae. Identification of species is made difficult by extreme polymorphism of wing patterns for some widespread species and a general reduction of morphological features in the genitalia of male moths, while some features of female genitalia, particularly the antrum and lamella postvaginalis, have diagnostic value. Eight new species of Hawaiian *Cydia* are described (*C. mauiensis* n.sp., *C. velocilimitata* n.sp., *C. haleakalaensis* n.sp., *C. makai* n.sp., *C. koaiae* n.sp., *C. hawaiiensis* n.sp., *C. acaciavora* n.sp., and *C. anomalousa* n.sp.) based on wing patterns and features of male and female genitalia. The thirteen previously known species are redescribed because original descriptions were inconsistent among authors and based solely on wing patterns. Distributions, host-plant affinities, and natural enemies for each species are discussed.

A molecular phylogeny of 66 specimens representing 14 Hawaiian *Cydia* species plus 20 outgroup species was constructed using nuclear and mitochondrial DNA to assess the relative importance of host-plant affinities and geographic isolation in their diversification. Hawaiian

*Cydia* is monophyletic and nested well-within the genus. They appear to have arrived in the Hawaiian Islands after the rise of Maui based on the basal position of several Maui and Hawaii Island species throughout the phylogeny. The earliest diverging species feed on *Canavalia* and dispersed across the high islands. Subsequent shifts to feeding on *Sophora chrysophylla* then *Acacia koa* were followed by speciation and the filling of these niches across the islands. The origin of Hawaiian *Cydia* remains obscure, but appears to be a separate colonization of remote Oceania from *Cydia pseudomalesana* Clarke in French Polynesia.

It is likely that several more species of Hawaiian *Cydia* await discovery while several others probably have gone extinct in the 100 years since they were first collected. A broader survey of outgroup taxa from Asia and the Americas, and more informative genes in a molecular phylogeny may help resolve the origins of Hawaiian *Cydia*.

## Dedication

To my family: My father Peter and mother Patricia for encouraging me to follow my own path, my sister Paula for being a sympathetic ear, my brother Michael for making me tough enough for any fieldwork, and my brother John for sharing my enthusiasm for nature. And to my dog, Willie, who has been with me since I started studying *Cydia* moths in Hawaii.

“Entomology extends the limits of being in a new direction, so that I walk in nature with a sense of greater space and freedom.” Henry David Thoreau

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## Acknowledgements

I thank my committee members, George Roderick, Rosemary Gillespie, Jerry Powell, and Bruce Baldwin for their guidance, advice, and encouragement, and Paul Banko and Greg Brenner for introducing me to Hawaiian *Cydia*. Many members of the Roderick-Gillespie lab, particularly Luke Hasty, Joe Spagna, Jeff Lozier, and Sean Schoville, were instrumental in teaching me molecular techniques. This work could not have been completed without the assistance in the laboratory and field by Marie Franc, Katie Roggeveen, Zac Hannah, Matt Strauser, Aviva Goldmann, Jiao “Joyce” Xue, Shannon Nguyen, and Athena Lam. I thank Richard Brown, Jesse Eiben, Will Haines, Laurent Jauze, Furumi Komai, Matt Medeiros, Quentin Paynter, David Pollock, Jerry Powell, Dan Rubinoff, and John Slotterback for collecting specimens. I also thank Kevin Tuck of the British Museum of Natural History, Keith Arakaki of the B.P. Bishop Museum, Dan Rubinoff of the University of Hawaii, Manoa, John Brown of the U.S. National Museum, Richard Brown of the Mississippi Entomological Museum, and David Foote of Hawaii Volcanoes National Park for access to specimens. Land access was granted by the Hawaii Department of Land and Natural Resources, Hawaii Volcanoes National Park, Haleakala National Park, The Nature Conservancy of Hawaii, Kokee State Park, and the US Army Garrison, Hawaii. Thank you to Betsy Gagne of the Department of Land and Natural Resources for facilitating permits to work in Hawaii. This research was funded in part by travel grants from the Entomology Students Organization at UC Berkeley, the Margaret C. Walker Fund, and the Joan Mosenthal DeWind Award from the Xerces Society.



## CHAPTER 1

Review of *Cydia* Hübner (Lepidoptera: Tortricidae: Olethreutinae: Grapholitini)

## INTRODUCTION

The moth family Tortricidae includes over 1,000 genera and nearly 10,000 named species distributed throughout all the continents except Antarctica (Brown *et al.* 2005, Baixeras *et al.* 2010). The only family in the superfamily Tortricoidea, Tortricidae is second only to the Gelechioidea in species diversity within the “microlepidoptera” grade (Horak and Brown 1991, Horak 1999, 2006). Tortricids are also numerically abundant in many habitats and are often important economic and ecological pests (Van Der Geest and Evenhuis 1991). For example, larvae of the spruce budworm complex (*Choristoneura* spp.) are well-known defoliators of conifer forests, creating wildfire hazards and reducing timber harvest and regeneration (Sanders 1991).

Likewise, the genus *Cydia* Hübner, whose larvae often bore into plant reproductive structures, includes several pests of agriculture and forestry. For example, the codling moth (*Cydia pomonella* Linnaeus) is a world-wide pest of apples, a \$1.5 billion average annual production value crop in the U.S. from 1997-2003 (N.A.S.S. 2010). Larvae bore into the fruit of apples, pears, walnuts, and several other species, costing millions of dollars in monitoring and pesticide application in addition to lost yield. In 2009 in California alone, 186,000 acres of apples were treated with 469,000 pounds of pesticide (Kegley *et al.* 2010). Because of their pest status, the biology and distribution of several *Cydia* species have been studied extensively (Van Der Geest and Evenhuis 1991). However, for many non-pest species, little biological information is available.

The purpose of this review is to summarize our current knowledge of the taxonomy, distribution, and biology of the genus *Cydia*. Recent collections of Neotropical tortricids indicate that many more *Cydia* species remain to be described (J.W. Brown & J.A. Powell, unpublished data), while several species currently included as *Cydia* may later prove to belong to other genera. Moreover, the biology of many species remains unknown and their importance in foodwebs and ecosystem function underappreciated. This review does not aspire to remedy these issues, but rather to provide an historical perspective on our understanding of this genus, a guide to navigating the taxonomic literature, and a foundation from which further coordinated studies of biology and ecology may be launched.

## DIVERSITY & DISTRIBUTION

The genus *Cydia* includes 231 named species and subspecies distributed worldwide (Brown *et al.* 2005, Baixeras *et al.* 2010). The greatest diversity of known species is in the Holarctic, with ~113 species in the Palaearctic and ~56 species in the Nearctic (Obraztsov 1959, Danilevsky and Kuznetsov 1968, Powell 1983, Razowski 2003, Brown *et al.* 2005) (Figure 1). However, native species are also known from South America (Schönherr 1987), Madagascar (Diakonoff 1988), the South Pacific (Clarke 1986), and other southerly locations (Clarke 1958). Habitats span boreal to tropical forest, and range from sea level to high elevation tree line. Most species are tightly coupled with the distribution of their host plants.

## TAXONOMY & MORPHOLOGY

Species assigned to *Cydia* have a confusing history in both nomenclature and systematic classification (Brown 1979, Wearing *et al.* 2001, Brown 2006). Since 1825, at least nineteen different genus names plus misspellings have been proposed for species currently assigned to *Cydia* (see below). Hübner (1825) proposed the genus *Cydia* (p. 375) to include *pomonana* Linnaeus (= *Cydia pomonella* (Linnaeus)), *aspidiscana* Hübner (= *Eucosma aspidiscana* (Hübner)), and *monetulana* Hübner (= *Eucosma cana* (Haworth)), but he did not designate a type species. In the same publication, Hübner proposed *Laspeyresia* (p. 381) to include *stagnana* Denis & Schiffermüller (= *Rhopobota stagnana* (Denis & Schiffermüller)), *cinereana* Haworth (= *Epinotia nisella* (Clerck)), and *corollana* Hübner (= *Cydia corollana* (Hübner)), with no type designations. Some authors have argued that Hübner's (1825) *Verzeichniss Bekannter Schmettlinge* [sic] is not a valid systematic treatise, that his genera are “childish guesses,” and should “never be quoted as an authority for genera” (Edwards 1873:31-32).

Nonetheless, Hübner's generic names were adopted by taxonomists and eventually designated by type species. The first restricted use of a *Cydia* species was by Kirby and Spence (1826) in reference to the larval mouthparts of *Erminea pomonella* (Linnaeus), thus making *pomonella* type species of *Erminea* by monotypy. However, *Erminea* was preoccupied by *Erminea* Haworth (1811) (Yponomeutidae), and therefore not available. It is unclear why Kirby and Spence used *Erminea* when referring to the figure of “*les chenilles des pommes*” from Réaumur (1734), unless they were misapplying *Erminea* Haworth. Treitschke (1830) proposed the genus *Carpocapsa* to include *pomonana* L. and four other species with no type designation. Curtis (1831) subsequently designated *pomonella* as type species for *Carpocapsa*, and Walsingham (1897) designated *pomonella* as the type species for *Cydia*. Busck (1903) argued that Curtis' type designation for *Carpocapsa* was the first (valid) restricted use of a genus name for *pomonella* and therefore has priority. But as Brown (1979) points out, Walsingham's designation made *Cydia* and *Carpocapsa* objective synonyms, giving priority to the older name: *Cydia*.

Fernald (1908) designated *aspidiscana* Hübner as type for *Cydia*, and *corollana* Hübner as type for *Laspeyresia* Hübner, the first restricted use of *Laspeyresia*. Walsingham (1914) concluded *pomonella* and *corollana* were congeneric, thus making *Cydia* the senior synonym to *Laspeyresia*, *Carpocapsa*, and any subsequent genera proposed for species congeneric with *C. pomonella*. Adding further confusion, Fletcher (1929) listed *Enarmonia* Hübner (1825) as senior synonym to *Cydia* and *Laspeyresia* based partly on notes from Meyrick and Durrant (Fletcher 1929 p. i), a synonymy followed by several workers in the early 20<sup>th</sup> century. However, *Enarmonia* is now considered a distinctly separate lineage from *Cydia* (Brown *et al.* 2005).

Although Obratzov (1959) treated *Cydia* and *Carpocapsa* as junior synonyms of *Laspeyresia*, priority dictates that *Cydia* remain the senior synonym. Kuznetsov and Kerzhner (1984) petitioned the International Commission on Zoological Nomenclature to suppress *Cydia* in favor of *Laspeyresia* due to greater usage (ICNZ, 2000, article 23.9), which incited some debate (Bradley *et al.* 1985, Hodges 1985, Miller 1985, Bradley and Hamilton 1986, Kerzhner and Kuznetsov 1986), but no decision was rendered. Therefore, as a result of differing regional preferences, both *Cydia* and *Laspeyresia* (and to a lesser degree *Carpocapsa*) remained in common usage for species of *Cydia* into the 1970's and 1980's. Regardless of regional

preferences, however, the above arguments are irrelevant because, as Walsingham (1914) indicated, *Laspeyresia* Hübner is preoccupied by *Laspeyresia* R.L. (1817), a justified emendation of *Laspeyria* Germar (1811), a genus of Noctuidae. Therefore, current workers follow Brown's (1979) conclusion that *Cydia* is the proper generic name for *pomonella* and congeneric species.

The systematic history of *Cydia* has been equally confusing. *Cydia* belong to the monophyletic subfamily Olethreutinae which is characterized as Tortricidae with a single row of scales per antennal flagellomere (as opposed to two rows in most other Tortricidae); male with modified genitalia, including the fusion of the juxta and caulis into a single structure, absence of transtilla, and reduced gnathos; and hindwing usually with a cubital pecten or cluster of long hair-like scales along the base of the cubital vein (absent in most other Tortricidae) (Horak 1999, 2006). Within the Olethreutinae, *Cydia* belong to the tribe Grapholitini Guenée 1845 (Razowski 1977, Brown 1979, Komai 1999, Komai and Horak 2006). Heinrich's (1923, 1926) concept of the subfamily Laspeyresiinae ( $\approx$  tribe Grapholitini), with hindwing veins M2 and M3 parallel and distant from each other, and male genitalia with uncus and socii absent or very reduced, was adopted by most workers for the tribe Laspeyresiini. This conception included *Laspeyresia* (= *Cydia*) plus 15 other Nearctic genera (Figure 2) and 14 Palearctic genera (Figure 3). However, some genera currently placed within Grapholitini (e.g. *Acanthoclita* Diakonoff, *Thaumatotibia* Zacher, and some *Cryptophlebia* Walsingham) include species which have M2 base curved towards M3 (as in tribe Eucosmini), while some species placed within Olethreutini and Enarmoniini have venation consistent with typical Grapholitini (Komai and Horak 2006). Horak and Brown (1991) considered these characters indicative of a polyphyletic grade rather than a monophyletic clade. Komai (1999), however, proposed that males with abdominal sternite 8 shortened and posterior margin straight (versus sternite 8 as long as tergite 8 and posterior margin bilobed) is a synapomorphy uniting Grapholitini (Figure 4). For a more thorough discussion of the monophyly and diagnosis of Grapholitini see Komai & Horak (2006).

The genera included in Grapholitini, whether they represent a grade or a clade, have changed little since Heinrich (1926), while relationships among genera have undergone many permutations. In Heinrich's concept, *Grapholita* Treitschke was derived from *Cydia*, with *Pammene* Hübner as "a higher development" of *Cydia* (Figure 2). Following this concept, some British workers (e.g. Bradley 1972) considered *Grapholita* a subgroup within *Cydia*. Komai (1999, Komai and Horak 2006), however, proposed three synapomorphies for a *Cydia* genus group, including *Cydia*, *Leguminivora* Obraztsov, *Fulcrifera* Danilevsky & Kuznetsov, *Lathronympha* Meyrick, *Notocydia* Komai & Horak, and *Apocydia* Komai & Horak; and two for a separate and distinct *Grapholita* genus group, including *Grapholita* and 31 other genera (Figure 4). For the *Grapholita* group Komai noted that all species possess a specialized scent organ (coremata) between abdominal segments 8 and 9, a character previously noted by other authors (Pierce and Metcalfe 1922, Heinrich 1926, Obraztsov 1960, 1961) and discussed by Danilevsky and Kuznetsov (1968); and male genitalia with tegumen strongly curved at its base. For the *Cydia* genus group, Komai noted that most species have male genitalia with sacculus ventral margin concave near base; male hindwing with anal fold; and male hindwing A3 close to anal edge (Komai 1999, Komai and Horak 2006). However, these characters are absent in several *Cydia* species, perhaps as secondary losses (Danilevsky and Kuznetsov 1968, R.L. Brown, unpublished data).

The genus *Cydia* can claim few, if any, synapomorphies (Komai and Horak 2006). Hübner's (1825) original description of *Cydia*, “*Die Schwingen mit einem golden bezeichneten Eckfleck geziert*” [wings with a golden distinct corner marking], referring to the light-colored ocellar patch near the “anal angle” of the forewing, has little diagnostic value. Danilevsky and Kuznetsov (1968) recognized two features consistent in most *Cydia*: males with hindwing vein A3 bordered dorsally by small glandular thecae or androconia (Figure 5), and female corpus bursae with a diverticulum (Figure 6), though the latter is found in some other Grapholitini genera (Komai 1999). R.L. Brown (unpublished) also suggested the division of sternum VII of females into three sections by weakly sclerotized lines may represent another synapomorphy, although, like the two former characters, it is absent in several *Cydia* species. The lack of consistent synapomorphies across all species may be an indication that *Cydia* is polyphyletic, but may also be the result of secondary losses, particularly for secondary sexual characters that may be under selection. Although molecular data are not immune to the problems of homoplasy and secondary gains and losses, ongoing DNA sequencing efforts is it hoped will contribute new insights to the relationships among species and genera by adding new character systems to larger and combined morphological analyses (e.g. Oboyski Chapter 3).

As a taxonomic convenience and to aid in biological understanding of the genus, authors have divided *Cydia* into subgenera and/or species groups. Danilevsky and Kuznetsov (1968) divided the genus *Laspeyresia* Hübner into three subgenera, *Endopisa*, *Laspeyresia* (*sensu stricto*), and *Kenneliola*, based on secondary sexual characters and host preferences. According to their concept, *Endopisa* are associated with herbaceous plants, particularly legumes (Fabaceae); *Laspeyresia* with gymnosperms; and *Kenneliola* with woody angiosperms. Morphologically, species of the subgenus *Endopisa* have hindwing vein A3 located near the wing edge; males with small glandular androconia (thecae) along vein A3 and small, deciduous cornuti on the aedeagus; and females with the lamellae postvaginalis sclerotized and sometimes with a proximally-directed sharp protrusion, ostium with a sclerotized half-ring separated from the lamellae antevaginalis and converging on the lamellae postvaginalis, and with the ductus bursae weakly sclerotized. Species of the subgenus *Laspeyresia* have hindwing vein A3 not located near the wing edge; males without androconia along vein A3 and with (usually non-deciduous) cornuti on the aedeagus; and females with the lamellae postvaginalis heavily sclerotized, ostium sclerotized with a half-ring converging on the lamellae postvaginalis, and spines within the ductus bursae. And species of the subgenus *Kenneliola* have hindwing vein A3 not located near the wing edge; males do not have androconia along vein A3 and no cornuti on the aedeagus; and females have lamellae postvaginalis elongate and weakly sclerotized, ostium not encircled by a sclerotized ring, and ductus bursae without internal spines. However, these characteristics are neither unique to each group nor apparent in all members, making them of limited use in classification. Instead they may reflect a phylogenetic grade, or represent highly labile characters.

Bradley (1972, Bradley et al. 1979) divided *Cydia* into four subgenera: *Euspila*, *Grapholita*, *Coccyx*, and *Cydia* *sensu stricto*, but made no indication of the characters used to separate each subgenus. Bradley's subgenus *Cydia* includes species from all three of Danilevsky and Kuznetsov's (1968) subgenera, while Bradley's *Coccyx* and *Euspila* include one and four species, respectively, which are not included in Danilevsky and Kuznetsov (1968). Furthermore, most workers treat *Grapholita* as a separate genus rather than as a subgenus of *Cydia* (e.g. Danilevsky and Kuznetsov 1968, Powell 1983, Komai and Horak 2006). Therefore, few taxonomists have followed these subgeneric assignments. Similarly, some workers have

designated species groups within *Cydia* (e.g. Danilevsky and Kuznetsov 1968, Sauter 1968, Miller 1990), for species with similar biology and morphology, but these have not been widely adopted.

## BIOLOGY

### Host-plants

*Cydia* species have been recorded from at least 65 host-plant genera in 20 families (table 1). While adults of both sexes of diurnal species visit flowers for nectar, those of nocturnal species are not known to do so. However, adult host records and effectiveness as pollinators have not been well documented. While larval host plants range from herbaceous and woody angiosperms to conifers (Heinrich 1926, Danilevsky and Kuznetsov 1968, Bradley et al. 1979, Miller 1987, 1990, Razowski 2003), *Cydia* are not known to feed on grasses or ferns. Most species as larvae feed within generative tissues of plants such as seeds, fruits, flowers, apical buds, fleshy stems, and under bark (cambium). Consequently, many species are considered agricultural or ecological pests (Van Der Geest and Evenhuis 1991). The codling moth, *Cydia pomonella*, is a notorious pest of apples (*Malus* spp.), Pears (*Pyrus* spp.), and walnuts (*Juglans* spp.) in almost all regions where they are grown. The pea moth, *C. nigricana* (Fabricius), destroys the beans of many legume species including green (*Pisum sativum*) and sweet peas (*Lathyrus odoratus*). Other agricultural pests include the hickory shuckworm, *Cydia caryana* (Fitch), which bores into fruits of walnuts and hickory (*Carya* spp.), and the filbertworm, *Cydia latiferreana* (Walsingham), which infest filberts or hazel nuts (*Corylus* spp.), walnuts, and pomegranates (*Punica granatum*) as well as the acorns and cynipid galls of oaks (*Quercus* spp.) (Peacock et al. 1988).

Several *Cydia* species are considered pests of forest ecosystems. The spruce seed moth, *Cydia strobilella* (Linnaeus), infests the seeds of several species of spruce (*Picea* spp.), and several species of pine seedworms, including *Cydia piperana* (Kearfott), infest the seeds of ponderosa and Jeffrey pines (*Pinus* spp.) (Otvos 1991). In Europe, the spruce bark tortrix, *Cydia pactolana* (Zeller) girdles small stems of Norway spruce (*Picea abies*), *Cydia illutana* (Herrich-Schäffer) infests the cones of several species of spruce and larch (*Larix* spp.), and the acorn moth, *Cydia splendana* (Hübner), infest the fruits of oaks, walnuts, and beech (*Fagus* spp.) (Bogenschütz 1991).

While most *Cydia* species appear to be host specialists (monophagous or narrowly oligophagous), a few species, such as *Cydia latiferreana* and *C. leguminana* (Zeller) have a more catholic diet (Peacock et al. 1988, Miller 1990). This same propensity for host-plant specialization and feeding on reproductive structures makes some *Cydia* species attractive as potential biological control agents. For example, *Cydia succedana* (Denis and Schiffermüller) was successfully introduced into New Zealand for the control of gorse, *Ulex europaeus* (Hill and Gourlay 2002), although some non-target feeding was observed (Paynter et al. 2008).

Each *Cydia* species tends to specialize on a particular host substrate (i.e. seeds, flowers, under bark, etc.), although some species show plasticity in their substrate use. Comparing food resources among 78 *Cydia* species, Miller (1990) found that seeds provided higher crude protein than leaves, flowers, cambium, and other substrates, and adults of seed-feeding species are on average larger than species feeding on other substrates. Among seed-feeders, average adult moth size also was positively correlated with average seed size (Miller 1990), even though some

species are known to infest new seeds as old ones are depleted (e.g. Hill and Gourlay 2002). Other species appear to take advantage of alternate substrates when primary substrates are unavailable. For example, *Cydia walsinghamii* (Butler) have been bred from seeds, twigs, and rust galls of *Acacia koa* in Hawaii (Swezey 1954). *Cydia latiferreana*, particularly in early summer, often are found in the large oak galls of *Adricus quercuscalifornicus* Bassett (Hymenoptera: Cynipidae) as well as oak acorns (Miller 1990, Joseph et al. 2011). Similarly, *C. "makai"* [Oboyski mss.] typically feed within the seeds of *Sophora chrysophylla* in Hawaii, but on the island of Kauai where *S. chrysophylla* trees are few, stunted, and produce few seeds, larvae feed within apical buds (Oboyski Chapter 2).

### Seasonality & Diapause

The life cycle of *Cydia*, particularly seed-feeding species, is correlated with the fruiting period of their host plants and often includes a period of diapause. In temperate regions, diapause usually occurs overwinter in late instar larvae with pupation and adult eclosion timed with the onset of fruits in the spring or early summer. For example, the hickory shuckworm, *Cydia caryana*, emerges in the spring at a time when hickory and pignut fruits are beginning to develop and again when pecans begin development (Calcote and Hyder 1979). Diapause is assumed to have evolved as a mechanism for organisms to escape harsh environmental conditions, such as cold winters or seasonal droughts (Andrewartha 1952, Tauber et al. 1986, Danks 1987), but may also play a role in synchronizing organisms with seasonally available food resources and with potential mates (Powell 1986, Tauber et al. 1986, Danks 1987, Powell 1989, Saunders 2002). Diapause has been studied most extensively in temperate regions where seasonal patterns of daylight hours are pronounced. Not surprisingly, photoperiod is the cue most studied in detail (see reviews by Tauber et al. 1986, Danks 1987, 1992, Denlinger 2002, Saunders et al. 2004). Temperature, independently or in concert with photoperiod, has also been shown to trigger a diapause response in some insect species (e.g. Bakke 1970, Denlinger 1974, Sieber and Benz 1980, Steinberg et al. 1992). Many temperate insects also require a period of cold during diapause, sometimes referred to as "cold conditioning," in order to complete diapause.

Among *Cydia* species, the cues for diapause are best understood for codling moth, *C. pomonella*. In apples grown in warm climates with long growing seasons codling moth may produce two or more generations with direct development. However, facultative diapause is induced when larvae are exposed to decreasing day-length (Sieber and Benz 1980, Ashby and Singh 1990). Along with photoperiod and temperature, the food quality of the host can also influence whether a particular generation is likely to diapause (e.g. Brown 1985, Steinberg et al. 1992, Van Steenwyk et al. 2004). Photoperiod and temperature cues for both the onset and termination of diapause have been studied for conifer seed-infesting species *C. strobilella* (Bakke 1970, Nesin 1984). Prolonged diapause – diapause extending into a second season or longer – is thought to be a mechanism to cope with erratic or unreliable food supplies such as seeds or fruits (Hedlin et al. 1982, Powell 1986, Danks 1987) and has been noted for *C. strobilella* (Nesin 1984).

### Predators & Parasitoids

Predators and parasitoids for some economically and ecologically important *Cydia* species are well known. For example, eggs of the codling moth, *C. pomonella*, are parasitized by species of trichogrammatid wasps, particularly *Trichogramma platneri* Nagarkatti in North America (Hassan 1989, Mansfield and Mills 2002), which may be massed released as part of integrated

control programs (Mills et al. 2000). Codling moth larvae are parasitized by a suite of wasps, including *Hyssopus pallidus* (Askew) (Hymenoptera: Eulophidae) (Zaviezo and Mills 1999, Hausmann et al. 2005). Overwintering larvae are subject to predation by birds and parasitism by *Elodia morio* (Fallen) (Diptera: Tachinidae), *Pristomerus vulnerator* (Panzer) (Ichneumonidae) and *Ascogaster quadridentata* Wesmael (Braconidae), as well as fungal pathogens (Subinprasert 1987), and parasitized in the cocoon by *Mastrus ridibundus* (Gravenhorst) (Ichneumonidae) (Mills 2005).

Larvae of the filbertworm, *C. latiferreana*, in North America are parasitized by *Calliephialtes nucicola* Cushman and *Lissonota* sp. (Ichneumonidae), *Macrocentrus ancylicivorus* Roh, *Phanerotoma tibialis* (Haldeman), and *Bassus nucicola* Muesebeck (Braconidae), *Elachertus evetriae* Girault (Chalcidae), and *Phorocera* sp.nr. *erecta* Coquillett (Tachinidae) (Dohanian 1940). Similarly, larvae of the hickory shuckworm, *C. caryana*, are parasitized by *Calleiphialtes grapholithae* (Cresson), *Phanerotoma fasciata* Procanther and *Mastrus carpocapsae* (Cushman) (Ichneumonidae) (Calcote and Hyder 1979). In Hawaii, *Cydia* species are parasitized by a suite of wasps, including *Calliephialtes grapholitha*, *Diadegma blackburni* (Cameron), *Pristomerus hawaiiensis* Perkins (Ichneumonidae), and *Euderus metallicus* (Ashmead) (Eulophidae), that attack “concealed” larvae of several lepidopteran families (Zimmerman 1978, Brenner et al. 2002, Oboyski et al. 2004). Likewise, parasitoids of many other *Cydia* species around the world have been recorded (Cheema and Syed 1973, Ghani and Cheema 1973, Ahmad et al. 1977, Schwenke 1978, Hassan 1989, Katovich and Kulman 1991, Spitzer and Jaros 2006).

### Pheromones and Kairomones

Female-produced sex attractant pheromones have been characterized for nearly 50 *Cydia* species (El-Sayed 2011). As with many Olethreutinae, the base component of most known *Cydia* female pheromones is a 12-carbon acetate chain, often with a double bond in the 8<sup>th</sup>, 9<sup>th</sup>, or 10<sup>th</sup> position (e.g. E8,E10-12Ac). For this reason there is often cross-reactivity in the field when only a generic formulation is used (Witzgall et al. 1996). Probably most pheromone bouquets contain a number of synergistic and/or antagonistic compounds that, in specific proportions, reduce interspecific reactivity (Witzgall et al. 1996, El-Sayed et al. 1999, Stephens et al. 2008, Witzgall et al. 2010). However, these adjuncts have been characterized for only a few *Cydia* species (McDonough et al. 1972, Witzgall et al. 1993, Witzgall et al. 1996, Stephens et al. 2008, Witzgall et al. 2010). For the most recent catalog of identified *Cydia* pheromones and literature references see [www.pherobase.com](http://www.pherobase.com) and [www.pherolist.slu.se/pherolist.php](http://www.pherolist.slu.se/pherolist.php).

Tortricid pheromones are most commonly used for monitoring and mating disruption in agricultural systems (e.g. Riedl et al. 1976, Cardé and Minks 1995, Welter et al. 2005, Witzgall et al. 2008). Monitoring crops with pheromones and kairomones can aid in calculating the timing and intensity of pesticide applications (e.g. Riedl et al. 1976, Witzgall et al. 2008). Lure and capture traps use pheromones to reduce pest abundance, while mating disruption employs pheromone dispensers to saturate local areas with female sex pheromones that prevent males from finding mates (Welter et al. 2005).

In addition to their practical use in integrated pest management, pheromones offer a great opportunity for ecological and evolutionary research. As a mate recognition system, pheromones offer an independent character set for the identification of species to complement genitalia



characters, which are often simplified and reduced in the Grapholitini. Combined with a well-resolved phylogeny, pheromones can further elucidate patterns and processes of speciation (Roelofs and Brown 1982, Cardé 1986, Löfstedt 1993, Newcomb and Gleeson 1998, Johansson and Jones 2007, Symonds and Elgar 2008, Gould et al. 2010, Loxdale 2010). For example, one might expect that closely related species in geographic proximity would experience character displacement (Schluter 2000) in the form of pheromone bouquet differences that prevent hybridization or introgression, compared to species that are not likely to interact due to geographic isolation.

Male tortricid pheromones, however, are less well-known. Secondary sexual structures in Lepidoptera are often used in courtship (Birch 1974, Weatherston and Percy 1977). In the Tortricidae these include modified scales within forewing costal folds, hindwing anal folds and cubital pouches, abdominal coremata, and leg hair pencils (Horak and Brown 1991, Horak 1999, 2006). Male *Cydia* species in particular often have the anal margin of the hindwing curled dorsally (anal roll) enclosing modified scales (Figure 8) presumed to be associated with pheromone dispensing (Brown and Miller 1983). In other *Cydia* species (particularly *C. latiferreana* (Walsingham), *C. maackiana* (Danilevsky), most Hawaiian species, and to a lesser extent *C. pomonella* and *C. caryana* (Fitch)), a dorsally-opening ventral pouch below the cubital vein encloses modified pecten scales (Brown 1983, Brown and Miller 1983, Oboyski Chapter 2) (Figure 9). However, the chemical signatures of the pheromones dispensed by these scales have not yet been characterized.

Host plant volatiles, particularly those from ripening fruits, are known to attract *Cydia* moths (Light and Knight 2005). For codling moth, host plant esters, sesquiterpenes, and other volatiles from apple, pear, and walnut aggregate moths for mating and oviposition (Wearing et al. 1973, Yan et al. 1999, Light et al. 2001), as well as attract neonate larvae to fruits (Sutherland and Hutchins 1972, 1973). Some of these volatiles also have been successfully used in monitoring and calibrating pesticide application schedules (Knight and Light 2004). Likewise for *Cydia strobilella*,  $\alpha$ -pinene and related compounds from spruce cones elicit antennal responses from both male and female moths (Bédard et al. 2002). While it is clear that host volatiles are involved in host plant seeking, host acceptance, and mate seeking, the particular host kairomone components that elicit responses for most *Cydia* species are yet to be documented.

## DISCUSSION

There appears to be no single morphological character or combination of uniquely derived characters that can be found in all species of *Cydia*. There are several possibilities for this: 1) *Cydia* is polyphyletic, 2) *Cydia* represents a grade of evolutionary development, 3) Synapomorphies include highly labile sexual characters that have been gained and lost secondarily within several species groups, or 4) Incomplete lineage sorting has resulted in the inclusion of characters found in related genera. Therefore, new character systems, such as genomic data, pheromones, and evolutionary development are needed to support or challenge current morphological systematics and to further resolve inter- and intrageneric relationships.

Due to the pest status of many *Cydia* species, continued research on several fronts, including ecology, behavior, physiology, genomics, and phylogenetic relationships, is critical. Although biological research on prominent pests, such as the codling moth, have provided great insights into development, diapause, and chemical communication, little is known about the biology of

most species. Continued research on predators, parasitoids, and pathogens will benefit integrated pest management programs and reduce non-target impacts, while characterization of synergistic/antagonistic components of pheromone bouquets will increase the efficiency of mating disruption programs.

## ANNOTATED TAXONOMY

### Journal abbreviations

Hist. nat. gen. part. crustacés, insects	Histoire naturelle générale et particulière des crustacés et des insectes, tome 3
Trans. Entomol. Soc. London	Transactions of the Entomological Society of London
Ann. Soc. Entomol. Fr.	Annales de la Société Entomologique de France
Gen. gr. Tortr. Lep. Br. Is.	Genitalia of the group Tortricidae of the Lepidoptera of the British Islands
U.S.N.M. Bull.	United States National Museum Bulletin (Smithsonian Institution)
Z. Wien. Entomol. Ges.	Zeitschrift der Wiener Entomologischen Gesellschaft
Verz. bek. Schmett.	Verzeichniss bekannter Schmettlinge
Intro. Entomol.	An introduction to entomology: or Elements of the natural history of insects
Schmett. Eur.	Die schmetterlinge von Europa
Nom. Br. Insects	The Nomenclature of British Insects

### FAMILY: **Tortricidae**

Tortrices Latreille 1803. Hist. nat. gen. part. crustacés, insects:415.

### SUBFAMILY: **Olethreutinae** Walsingham

Olethreutinae Walsingham 1895. Trans. Entomol. Soc. London 1895(4):500.

### TRIBE: **Grapholitini** Guenée

Grapholithidi Guenée 1845. Ann. Soc. Entomol. Fr. (2)3:169.

Ephippiphoridii Pierce & Metcalf 1922. Gen. gr. Tortr. Lep. Br. Is.:xxi, 74.

Lipoptychidii Pierce & Metcalf 1922. Gen. gr. Tortr. Lep. Br. Is.:xxi, 93.

Laspeyresiinae Heinrich 1923. U.S.N.M. Bull. 123:10. Razowski (1976) pointed out that because its type genus, *Laspeyresia* Hübner is a junior homonym of *Laspeyresia* R. L., it is invalid and proposed the use of Grapholitini based on the oldest family group name, Grapholithidi Guenée 1845.

Laspeyresiini Obraztsov 1946. Z. Wien. Entomol. Ges. 30: 23.

### GENUS: **Cydia** Hübner

*Cydia* Hübner (1825:375). Type species: *Phalaena (Tortrix) pomonella* Linnaeus (1758:538), by subsequent designation by Walsingham (1897:130).

*Laspeyresia* Hübner (1825:381). Type species: *Tortrix corollana* Hübner (1823:pl. 45, fig. 282), by subsequent designation by Fernald (1908:57). *Laspeyresia* Hübner

preoccupied by *Laspeyresia* R. L. (1817:291) [author “R. L.” unknown], an emendation of *Laspeyria* Germar (1811:13) (Lepidoptera: Noctuidae). *Laspeyresia sensu* Hübner a junior subjective synonym of *Cydia* Hübner (Walsingham 1914). Conservation of *Laspeyresia* Hübner proposed to ICZN by suppression of *Cydia* Hübner due to common usage (Kuznetsov and Kerzhner 1984) – no decision rendered.

*Erminea* Kirby and Spence (1826:123). Type species: *Phalaena pomonella* Linnaeus (1758:538), by monotypy. *Erminea* Kirby and Spence preoccupied by *Erminea* Haworth (1811). *Erminea pomonella* (Linnaeus) Kirby & Spence a junior objective synonym of *Cydia pomonella* (Linnaeus) (Walsingham 1897).

*Semasia* Stephens (1829:47). Type species: *Phalaena pomonella* Linnaeus (1758:538), by subsequent designation by Fernald (1908:23). *Semasia pomonella* (Linnaeus) Stephens a junior objective synonym of *Cydia pomonella* (Linnaeus) (Walsingham 1897).

*Coccyx* Treitschke (1830:230). Type species: *Tortrix strobilana* Hübner [1799]:pl. 12, fig. 70 (an emendation of *Phalaena strobilella* Linnaeus 1758:539), by subsequent designation by Desmarest (1857:224). [*Phalaena*] *tedella* Clerck, 1759:plate 10, figure 13, later designated as type species for *Coccyx* by Fernald, 1908. *Coccyx* Treitschke a junior subjective synonym of *Cydia* Hübner (Bradley 1972).

*Carpocapsa* Treitschke (1830:231). Type species: *Phalaena pomonella* Linnaeus (1758:538), by subsequent designation by Curtis (1831:352). *Carpocapsa pomonella* (Linnaeus) Treitschke a junior objective synonym of *Cydia pomonella* (Linnaeus) (Walsingham 1897).

*Strobila* Sodoffsky 1837:92. An unnecessary replacement name for *Coccyx* Treitschke. *Strobila* Sodoffsky preoccupied by *Strobila* Sars (1829:17) (Coelenterata).

*Carpocampa* Harris (1841:351). An unnecessary emendation of *Carpocapsa* Treitschke.

*Cerata* Stephens (1852:77). Type species: *Penthina servillana* Duponchel (1836 [1834]:503), by (virtual) monotypy. *Cerata* Stephens a junior subjective synonym of *Cydia* Hübner (Bradley 1972).

*Melissopus* Riley (1882:322). Type species: *Carpocapsa latiferreana* Walsingham (1879:xi, 70), by monotypy. *Melissopus* Riley a junior subjective synonym of *Cydia* Hübner.

*Melisopus* Riley (1882:322). Misspelling of *Melissopus* Riley.

*Mellisopus* Fernald (1892:54). Misspelling of *Melissopus* Riley.

*Melliopus* Packard (1890:219). Misspelling of *Melissopus* Riley.

*Adenoneura* Walsingham (1907:677). Type species: *Adenoneura falsifalcellum* Walsingham (1907:677), by original description. *Adenoneura* Walsingham a junior subjective synonym of *Cydia* Hübner (Zimmerman 1978).

- Melissopus* Fernald (1908:60). Misspelling of *Melissopus* Riley.
- Crobylophora* Kennel (1908:50). Type species: *Tortrix inquinatana* Hübner [1799]:pl. 8, fig. 43, by original description. *Crobylophora* Kennel preoccupied by *Crobylophora* Meyrick 1880:177 (Lepidoptera: Lyonetidae). *Crobylophora sensu* Kennel a junior subjective synonym of *Cydia* Hübner (Bradley *et al.* 1972).
- Hedulia* Heinrich, 1926:6, 65. Type species: *Hedulia injectiva* Heinrich, 1926:65, by original description. *Hedulia* Heinrich a junior subjective synonym of *Cydia* Hübner (Bradley *et al.* 1972).
- Lasperesia* Wu 1938:57. Incorrect spelling of *Laspeyresia* Hübner.
- Kenneliola* Paclt 1951:127. Type species: *Tortrix inquinatana* Hübner [1799]:pl. 8, fig. 43. as replacement name for *Crobylophora* Kennel. *Kenneliola* Paclt is a junior subjective synonym of *Cydia* Hübner (Bradley *et al.* 1972). *Kenneliola* Paclt also a subgenus of *Laspeyresia* (= *Cydia*) (Danilevsky and Kuznetsov 1968).
- Lespeyresia* Gozmany 1957:133. Incorrect spelling of *Laspeyresia* Hübner.
- Pseudotomoides* Obraztsov 1959:200. Type species: *Phalaena strobilella* Linnaeus 1758:539, by original designation. *Pseudotomoides* Obraztsov a junior subjective synonym of *Cydia* Hübner (Bradley *et al.* 1972).
- Erminia* Obraztsov 1959:175. Incorrect spelling of *Erminea* Kirby and Spence.
- Crobilophora* Obraztsov 1959:176. Incorrect spelling of *Crobylophora* Kennel.
- Collicularia* Obraztsov 1960:134. Type species: *Catoptria microgrammana* Guenée 1845:188, by original designation. *Collicularia* Obraztsov a junior subjective synonym of *Cydia* Hübner.
- Phanetoprepa* Obraztsov 1968:236. Type species: *Phanetoprepa agenjoi* Obraztsov 1968:237 [= *Cydia strigulatana* (Kennel)], by original designation. *Phanetoprepa* Obraztsov a junior subjective synonym of *Cydia* Hübner (Baixeras & Dominguez 1994).
- Danilevskia* Kuznetsov 1970:446. Type species: *Danilevskia silvana* Kuznetsov 1970:446, by original designation. *Danilevskia* Kuznetsov a junior subjective synonym of *Cydia* Hübner.
- Dicraniana* Diakonoff 1984:162. Type species: *Semasia seriana* Kennel 1901:270 [= *Cydia strigulatana* (Kennel)], by original designation. Originally proposed as a subgenus of *Cydia* Hübner. *Dicraniana* Diakonoff a junior subjective synonym of *Cydia* Hübner (Baixeras & Dominguez 1994).
- [Genus *Endopisa* Guenée 1845:182 considered a junior subjective synonym of *Cydia* Hübner based on the type designation *Pyralis nigricana* Fabricius by Fernald 1908. However, as Brown (1979) points out, *Grapholitha nebritana* Treitschke is the earliest type designation for *Eudopisa* Guenée, a misspelling of *Endopisa*, by Desmarest, 1857. Therefore, *Endopisa* Guenée a junior subjective synonym of *Grapholita* Treitschke, not *Cydia* Hübner.]

Table 1. Host plants of *Cydia*.

Family	Genus	Plant Part					
<b>Aceraceae</b>	<i>Acer</i>	Cortex	<b>Fagaceae</b>	<i>Castanea</i>	fruits		
		Seeds		<i>Fagus</i>	cortex		
<b>Araucariaceae</b>	<i>Araucaria</i>	cones			fruits		
		cortex		<i>Juglans</i>	fruits		
<b>Arecaceae</b>	<i>Coccothrinax</i>	seeds		<i>Quercus</i>	fruits		
<b>Betulaceae</b>	<i>Betula</i>	cortex	<b>Juglandaceae</b>	<i>Carya</i>	seed husk		
	<i>Corylus</i>	fruits		<i>Juglans</i>	seed husk		
	<i>Populus</i>	cortex		<i>Punica</i>	fruits		
<b>Boraginaceae</b>	<i>Cordia</i>	stems	<b>Lythraceae</b>	<i>Ficus</i>	fruits		
<b>Cupressaceae</b>	<i>Cryptomeria</i>	seeds	<b>Moraceae</b>	<i>Peganum</i>	flowers		
	<i>Cupressus</i>	cortex	<b>Nitrariaceae</b>	<i>Ochna</i>	foliage		
	<i>Juniperus</i>	sapwood	<b>Ochnaceae</b>	<i>Fraxinus</i>			
			<b>Oleaceae</b>	<i>Abies</i>	cone		
<b>Fabaceae</b>	<i>Abrus</i>	seeds	<b>Pinaceae</b>		cortex		
	<i>Acacia</i>	cortex		<i>Larix</i>	cones		
		flowers			cortex		
		rust galls			twigs		
		seeds		<i>Picea</i>	cones		
		twigs			cortex		
		<i>Adenocarpus</i>	seeds		Stems		
		<i>Bauhinia</i>	cortex		cortex		
		<i>Butea</i>	stems		Dioryctria		
		<i>Canavalia</i>	seeds		galls		
			stems		Petrova galls		
		<i>Cassia</i>	flowers		Retinia		
			seeds		tunnels		
		<i>Cytisus</i>	seeds		seeds		
		<i>Genista</i>	seeds	<b>Rosaceae</b>	<i>Pseudotsuga</i>	cortex	
		<i>Lathyrus</i>	seeds		<i>Cydonia</i>	fruits	
		<i>Lotus</i>	seeds		<i>Malus</i>	fruits	
		<i>Lupinus</i>	seeds		<i>Prunus</i>	fruits	
		<i>Lysiloma</i>			<i>Pyrus</i>	fruits	
		<i>Maackia</i>	seeds		<i>Rosa</i>	Diplolepis	
		<i>Medicago</i>	seeds			galls	
		<i>Ononis</i>	seeds			fruits	
		<i>Oxytropis</i>	seeds		<b>Salicaceae</b>	<i>Salix</i>	dipterous
		<i>Parkinsonia</i>	seeds				galls
		<i>Pisum</i>	seeds			twigs	
		<i>Pithecellobium</i>	seeds	<b>Sapondaceae</b>	<i>Dodonaea</i>	fruits	
		<i>Pongamia</i>	seeds	<b>Theaceae</b>	<i>Camellia</i>	foliage	
		<i>Prosopis</i>	seeds	<b>Ulmaceae</b>	<i>Ulmus</i>	cortex	
		<i>Retama</i>	seeds				
		<i>Sarothamnus</i>	seeds				
		<i>Sesbania</i>	seeds				
		<i>Sophora</i>	seeds				
	<i>Strongylodon</i>	seeds					
	<i>Ulex</i>	seeds					
	<i>Vicia</i>	seeds					

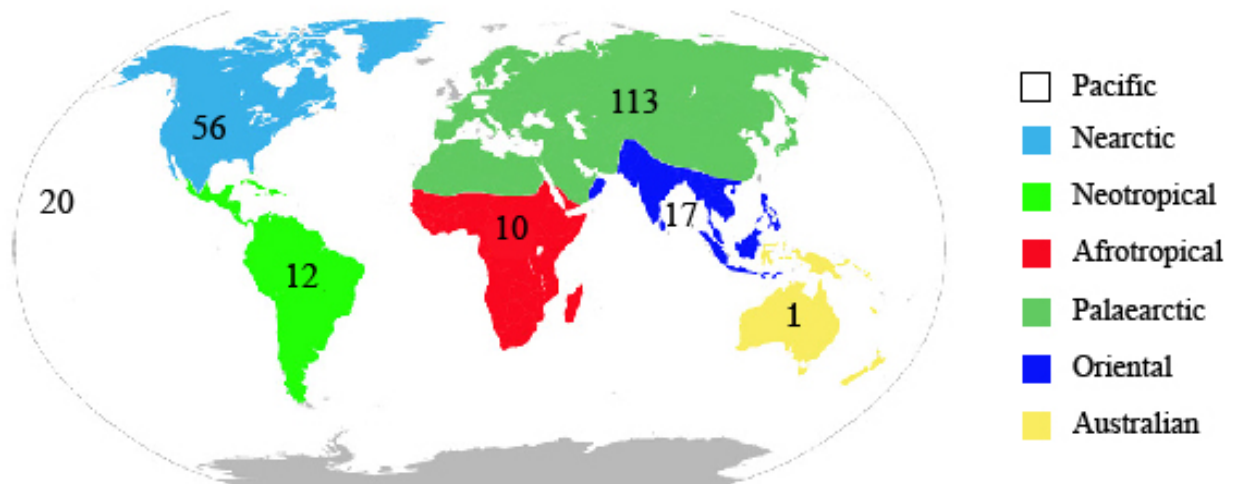


Figure 1. Zoogeographic regions and numbers of *Cydia* species. Numbers of species per region based on type localities and other published distribution records for species currently recognized as *Cydia* (Brown et al. 2005, Baixeras et al. 2010).

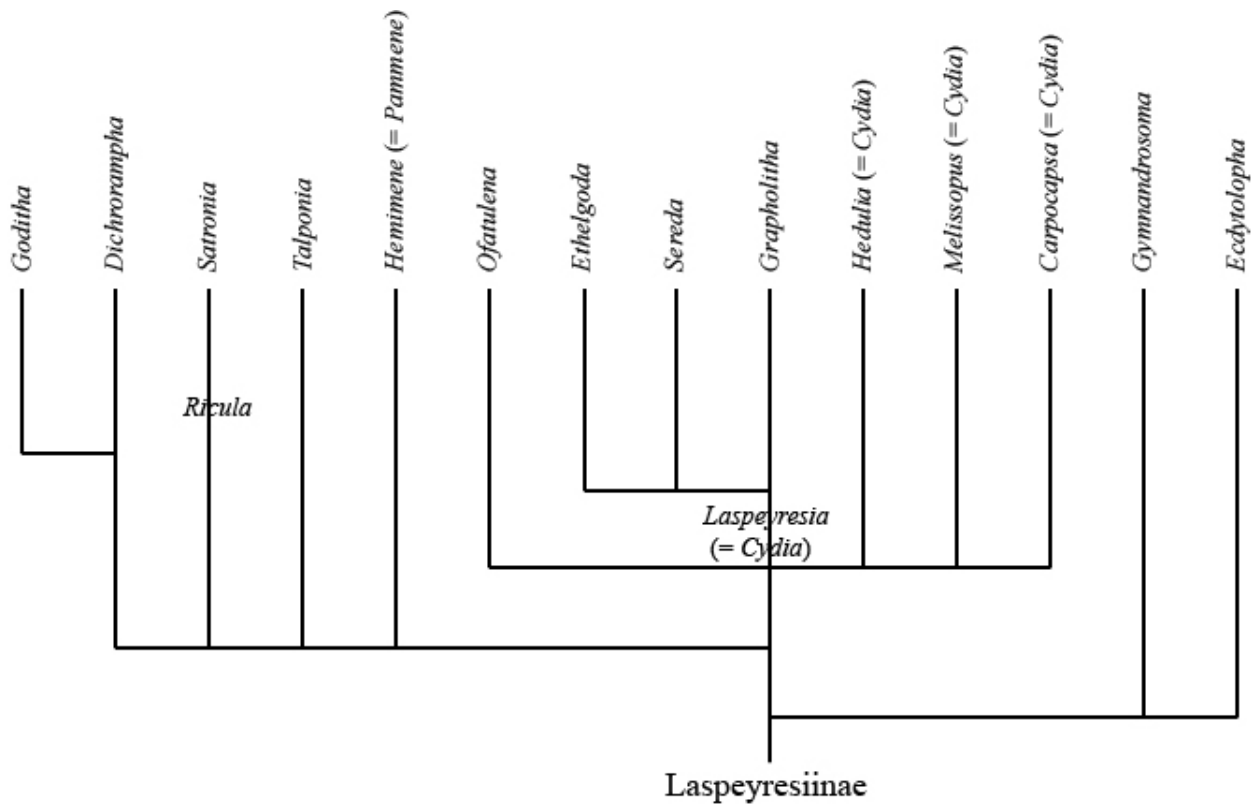


Figure 2. Phylogenetic tree of Nearctic Laspeyresiinae ( $\approx$  Grapholitini) redrawn from Heinrich (1926). Note that *Sereda* and *Ethelgoda* are derived from *Grapholita*, which is derived from *Laspeyresia* (= *Cydia*), while *Hemimene* (= *Pammene*) constitutes a “higher development” of *Laspeyresia* (Heinrich 1926).

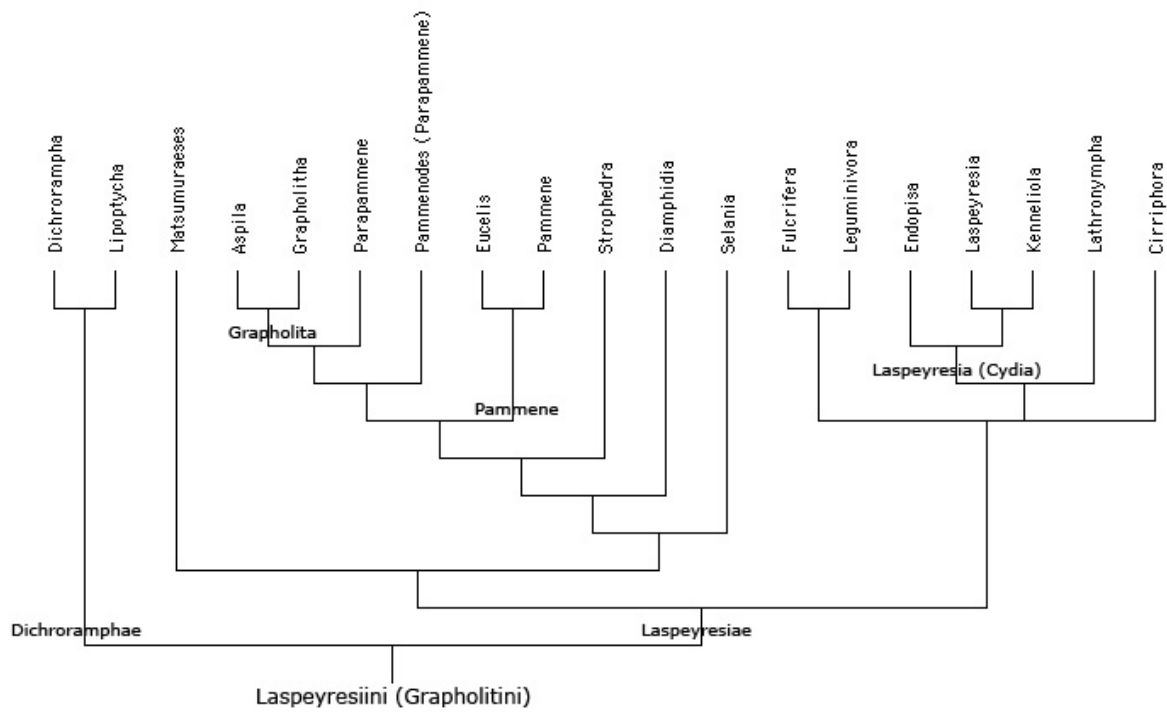


Figure 3. Phylogenetic tree of Palearctic Laspeyresiinae (≈ Grapholitini) redrawn from Danilevsky & Kuznetsov (1968). Note that *Cydia* is divided into three subgenera and fits within the subtribe of *Laspeyresiae*.



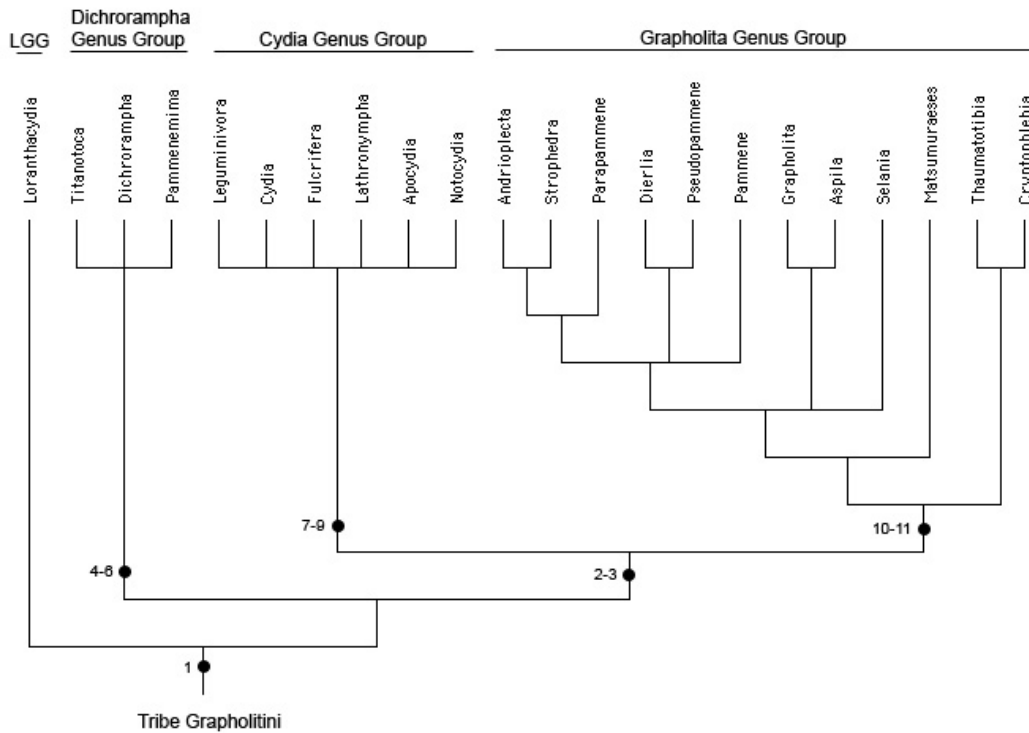


Figure 4. Cladogram of (palearctic) Grapholitini redrawn from Komai (1999). Mapped apomorphic character as follows: 1. S8 in male shortened with posterior margin straight (vs. posterior margin bilobed), 2. Bulbus ejaculatorius crescent-shaped (vs. fist-shaped), 3. Corpus bursae with diverticulum (vs. without), 4. Rs and M1 of hindwing separate and parallel (vs. approximate at base), 5. Forewing with row of dots along termen (vs. without), 6. Sterigma, 7<sup>th</sup> sternite, and sclerotized section of ductus bursae fused (vs. not fused), 7. Ventral margin at base of sacculus concave (vs. smooth/straight), 8. Male hindwing with anal fold (vs. without), 9. Male hindwing vein 3A close to anal edge (vs. distant), 10. Tegumen base (pedunculus) strongly curved (vs. straight), 11. Coremata present between 8<sup>th</sup> and 9<sup>th</sup> segments of male abdomen (vs. absent).

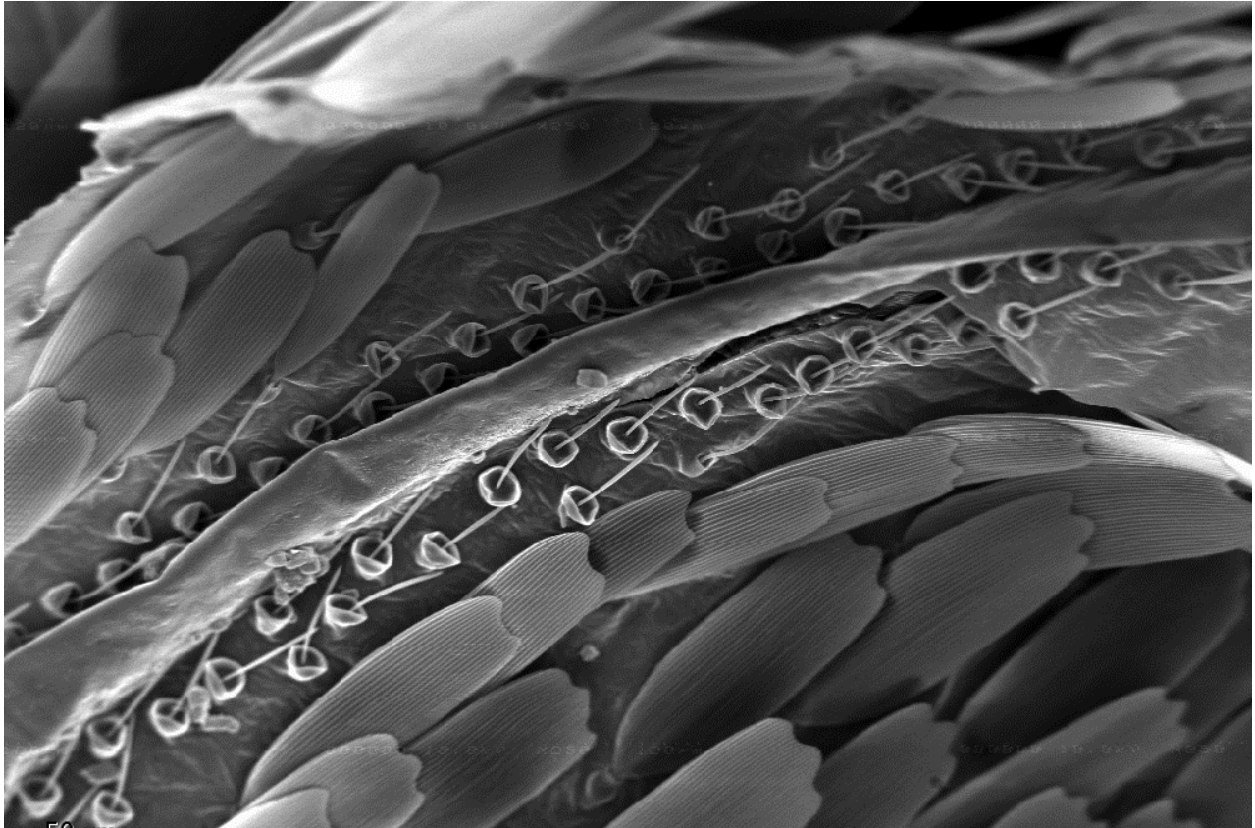


Figure 5. Thecae (andricornal scales) lining either side of vein A3 in male hindwing of *Cydia latiferreana* (Walsingham).

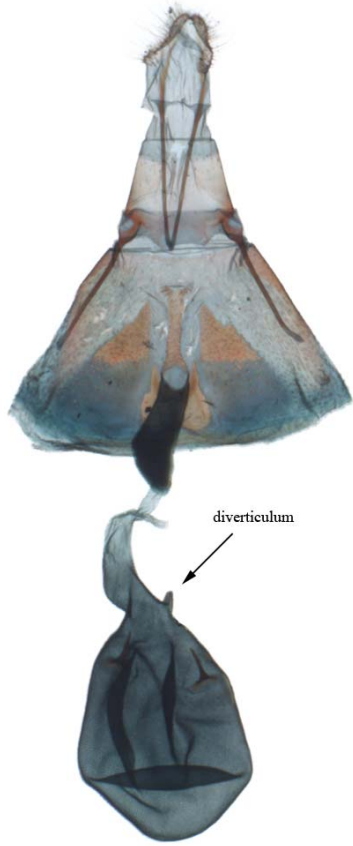


Figure 6. Female genitalia of *Cydia plicata* (Walsingham 1907). Membranous and lightly sclerotized tissues stained blue-black by Cholorsol-E black, more heavily sclerotized tissues stained red with Eosin-Y. Diverticulum of bursa copulatrix indicated by arrow. Oboyski slide pto-s143.



Figure 7. Male genitalia of *Cydia hawaiiensis* Oboyski. Oboyski slide pto-s302.

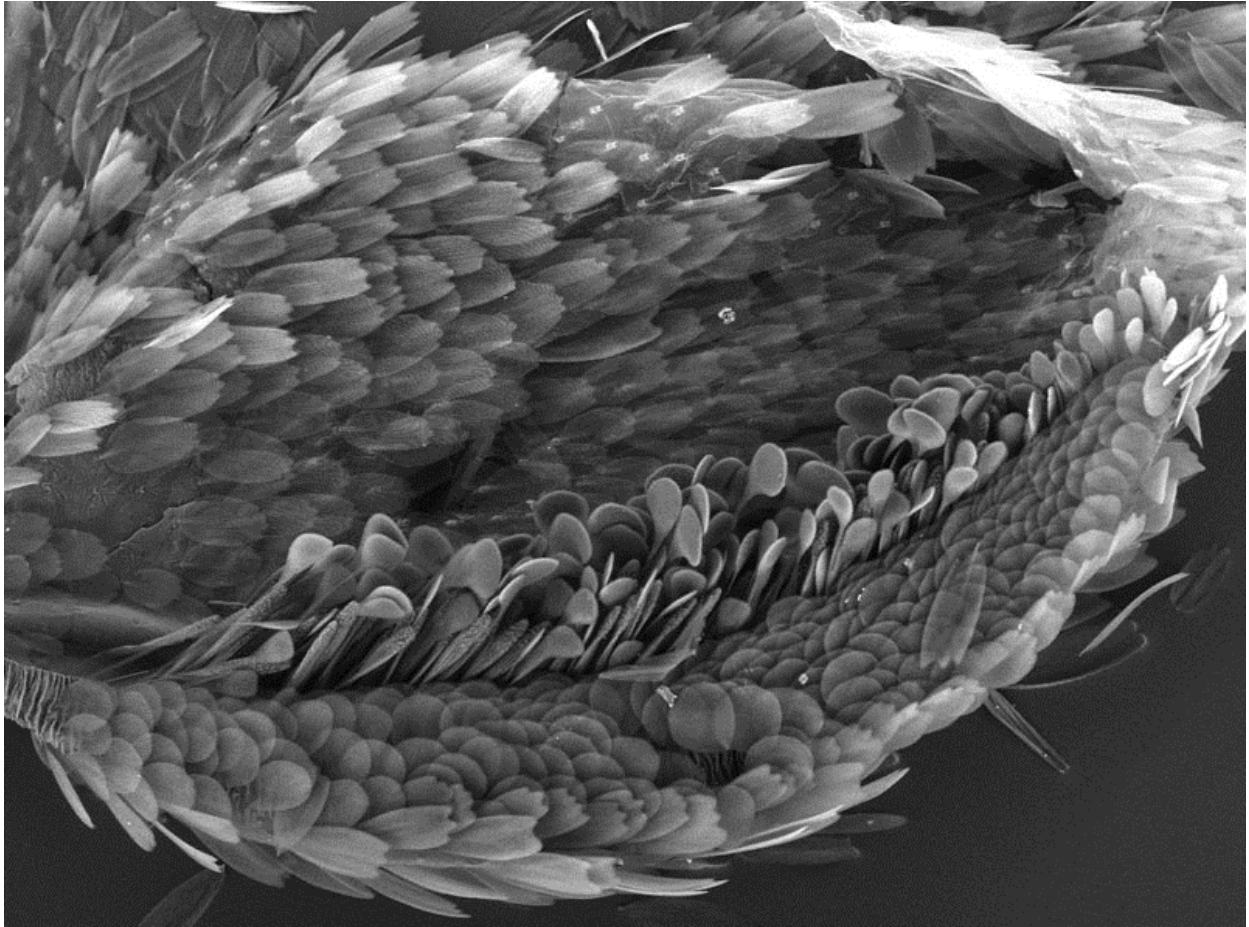


Figure 8. Hindwing “anal roll” of *Cydia latiferreana*. The dorsal curl of the anal margin encloses phylliform and fusiform scales probably associated with pheromone dispensing.

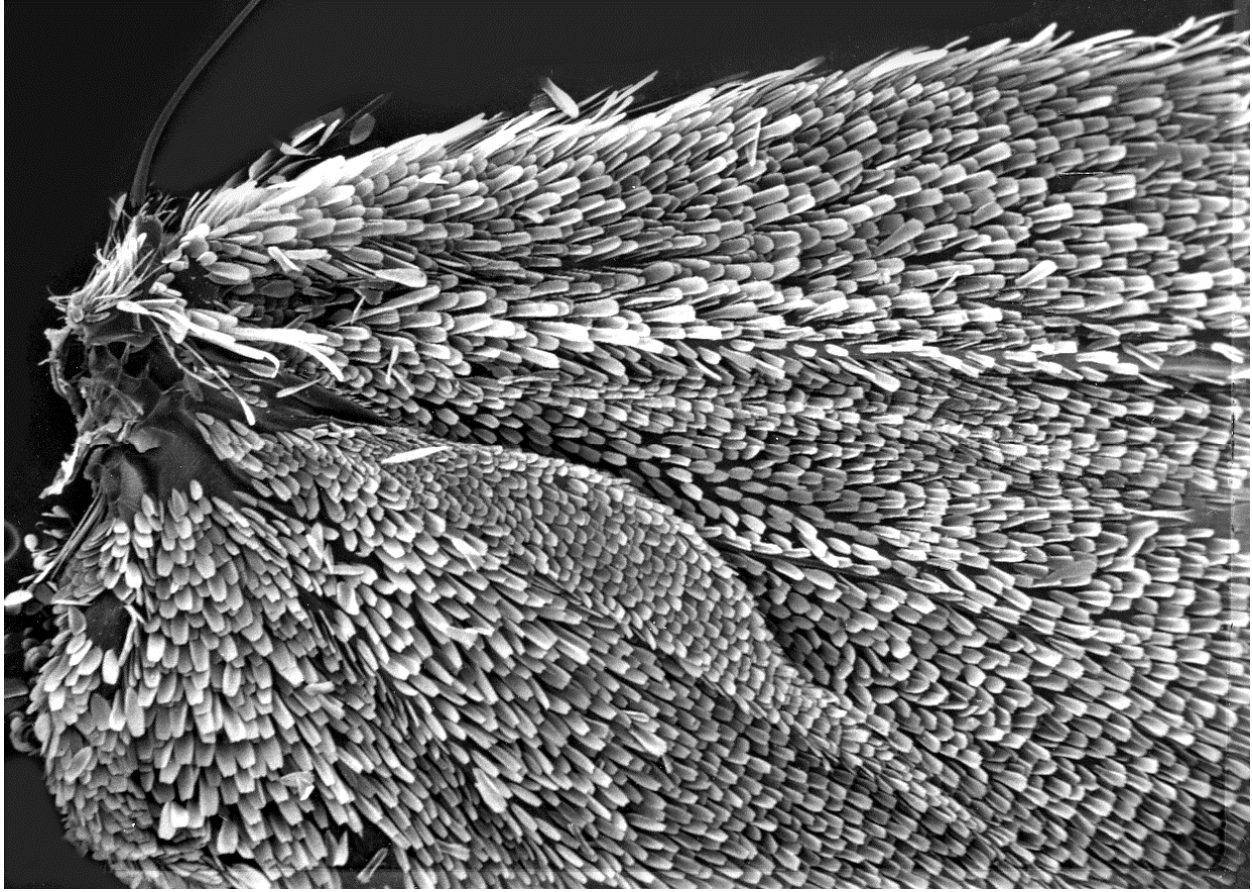


Figure 9. Hind wing pouch of *Cydia latiferreana*. Ventral view of male hindwing showing elongate pouch cloaked in smaller scales than the rest of the wing surface. The pouch opens dorsally and encloses modified pectin scales.

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## CHAPTER 2

Taxonomy of Hawaiian *Cydia* (Lepidoptera: Tortricidae),  
including descriptions of eight new species.

## ABSTRACT

Thirteen species of endemic *Cydia* have been described from the Hawaiian Islands under various genera between 1881 and 1932. Descriptions were based on wing colors and patterns, and noted distributions and host-plant affinities where known. Hawaiian *Cydia* has a small number of wing pattern elements that are common across most species and vary within species making specific determinations problematic. The taxonomic affinities of these species were not well-understood until brought together under the genus *Cydia* and presented with genitalia dissections in Zimmerman's Insects of Hawaii series. Males of most Hawaiian *Cydia* possess a ventral pouch on the hindwing surface and a general reduction in features of the genitalia. Females of Hawaiian *Cydia* display greater variation in genitalia morphology, particularly in the shape of the antrum and lamellae postvaginalis. Here I describe eight new species, (*Cydia mauiensis* n.sp., *C. velocilimitata* n.sp., *C. haleakalaensis* n.sp., *C. makai* n.sp., *C. koaiae* n.sp., *C. hawaiiensis* n.sp., *C. acaciavora* n.sp., and *C. anomalosa* n.sp.), and redescribe the original thirteen based on wing markings, presence or absence of the hindwing pouch, and features of both male and female genitalia. Larvae of Hawaiian *Cydia* feed on reproductive structures such as seeds, flowers, or buds and within twigs, under bark, or in rust galls of endemic Hawaiian plants in the family Fabaceae. Distributions, natural enemies, and host-plant associations are presented where known.

## INTRODUCTION

*Cydia* Hübner, a worldwide genus in the tribe Grapholitini (Olethreutinae), is represented by at least 21 species in the Hawaiian Islands. Found from shoreline to treeline on the main Hawaiian Islands (Kauai, Oahu, Molokai, Maui, and Hawaii), *Cydia* plays an important role in native forest ecosystems. The larvae of Hawaiian *Cydia* are associated with the native plants *Acacia koa* A.Gray, *A. koaia* Hillebr., *Canavalia* spp., *Sophora chrysophylla* (Salis.) Seem., *Strongylodon ruber* Vogel, and *Vicia menziesii* Spreng. in the family Fabaceae, feeding in generative structures (Figures 1-8) such as seeds, flowers, terminal buds, and under bark (Swezey 1954, Zimmerman 1978). As seed predators, Hawaiian *Cydia* can have a dramatic impact on the contributions of particular plant species to the seed bank (Zimmerman 1978). By feeding under the bark of dead and dying branches, larvae expose the wood to other invertebrate colonizers and decay fungi. And for several rare and endangered forest bird species in Hawaii that glean insects from seeds, flowers, and under bark, *Cydia* are an important protein-rich food resource (Banko et al. 2002, Pratt et al. 2009).

The appreciation of *Cydia* species diversity in Hawaii has been hampered, however, by a lack of conspicuous taxonomically useful characters and by extreme polymorphism in wing color patterns (Figures 9-12). The genus *Cydia* is characterized by a reduction in ornamentation in the male genitalia (i.e. loss of uncus, socii, and gnathos); characters that are often diagnostic for species in other groups of Lepidoptera (Komai 1999). Although subtle differences in the shape of the male valvae, aedeagus, and tegumen, and the female antrum and "ostial plate" (lamellae ante- and postvaginalis) can be used for identification, careful preparation and examination of genitalia are necessary to appreciate these differences. Conversely, whereas many Lepidoptera species have very characteristic wing patterns, some Hawaiian *Cydia* species vary widely in both color and wing pattern elements. The three most variable species, *C. plicata*, *C. makai*, and *C.*



*walsinghamii*, also have the broadest distribution in the islands, making superficial identifications problematic.

The thirteen named endemic *Cydia* species recognized from Hawaii were described between 1881 and 1932, and appear to be closely allied (Zimmerman 1978). Butler (1881, 1882) described the first Hawaiian species, *C. rufipennis* and *C. walsinghamii*, from the island of Oahu based on collections by the reverend Thomas Blackburn. Walsingham (1907) later described *C. conspicua*, *C. crassicornis*, *C. falsifalcella*, *C. latifemoris*, *C. montana*, *C. obliqua*, *C. plicata* and *C. storeella* from the monumental Fauna Hawaiiensis collections of R.C.L. Perkins (1913). Meyrick (1932), in his Exotic Microlepidoptera series, described three more species, *C. chlorostola*, *C. gypsograptus*, and *C. parapteryx*. An additional species, *Cydia* “new species 1”, was known from collections before the publication of the Insects of Hawaii microlepidoptera volume, but remained undescribed (Zimmerman 1978). Several species are known from only one to three individuals used in the original descriptions: *C. chlorostola* (1♀), *C. crassicornis* (2♂), *C. gypsograptus* (1♂), *C. obliqua* (3♀), and *C. storeella* (1♀). Although each of these appears to be unique species, the lack of specimens is a concern because of known variation in wing color patterns, which were the basis of all the original descriptions.

The affinity of the Hawaiian species to *Cydia* outside of Hawaii remains obscured (Oboyski Chapter 3). Butler (1881) described *C. rufipennis* in the genus *Phoxopterus* Treitschke (= *Ancylis* Hübner), which is assigned to the tribe Enarmoniini. A year later, Butler (1882) described *C. walsinghamii* in the genus *Proteopteryx* Walsingham (= *Epinotia* Hübner), which is in the tribe Eucosmini. Walsingham (1907) proposed a new genus, *Adenoneura*, based on the presence of a glandular pouch along the cubital vein in the hindwing of males (*Adeno* = gland, *neura* = nerve) (Figures 13-18). He placed four of his new species in this genus, stating it was allied to *Thiodia* Hübner (Eucosmini), and tentatively placed the rest, (males lacking the glandular pouch or species known only from females), in *Enarmonia* Hübner (Enarmoniini). Meyrick (1932) was the first to recognize the affinity of Hawaiian species to other *Cydia* when he described *C. chlorostola* in the genus *Laspeyresia* Hübner (= *Cydia*). The use of genitalic characters in microlepidopterology did not come into vogue until the early 20<sup>th</sup> century. All previous descriptions had been based on external features, particularly wing venation and color patterns. Zimmerman (1978) presented genitalia preparations of the type specimens of Hawaiian *Cydia* and brought the twelve (plus one undescribed) species together under the name *Cydia* and tentatively suggested they derived from a broadly distributed legume-feeder.

Here I describe eight new species of Hawaiian *Cydia* and redescribe the thirteen previously known species. Previous treatments of Hawaiian *Cydia* are inconsistent in their descriptions and none includes descriptions of genitalia. A comprehensive treatment of the currently known species will 1) provide a common framework for identifying specimens and recognizing new species, and 2) synthesize our current knowledge of Hawaiian *Cydia* diversity.

## MATERIALS AND METHODS

### Material Examined

I examined freshly prepared field-caught specimens as well as historical material from several museum collections, as follows:

BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii
BMNH	The Natural History Museum, London
CAS	California Academy of Sciences, San Francisco, California
EMEC	Essig Museum of Entomology, University of California, Berkeley
HAVO	Hawaii Volcanoes National Park, Volcano, Hawaii
HDOA	Hawaii Department of Agriculture, Honolulu, Hawaii
MEM	Mississippi Entomology Museum
UHMA	University of Hawaii at Manoa, Honolulu, Hawaii
USNM	United States National Museum, Washington, D.C.

Holotypes of all previously described Hawaiian *Cydia* species and slide preparations of their genitalia are housed at the Natural History Museum, London. Well-prepared series of Hawaiian *Cydia* collected by Dr. Klaus Sattler in 1973, 1976, and 1982 are not yet integrated into the BMNH collections but were available for examination. The Bernice P. Bishop Museum and Hawaii Department of Agriculture collections each hold paratypes and short series of some species, and the Hawaii Volcanoes National Park and University of Hawaii, Manoa collections each hold short series of particular species. A small number of specimens exist in other institutional and private collections, such as the California Academy of Sciences, the Mississippi Entomology Museum, and the United States National Museum. The remainder of the material examined I collected and prepared between 1998 and 2008. Voucher specimens were deposited in the BPBM, HDOA, and EMEC.

### Field collections

Hawaiian *Cydia* species were collected on all the main islands (Hawaii, Maui, Molokai, Oahu, and Kauai), but not from Kahoolawe, Lanai, and Niihau. Because the Island of Kahoolawe was virtually denuded of native vegetation by ungulate grazing, it is unlikely that any native *Cydia* survive there. Five to ten *Sophora chrysophylla* trees remain on the island of Lanai along with planted *Acacia koa* trees, but I failed to find larval or moth specimens. However, examination of historic collections from Lanai of *S. chrysophylla* in the Bishop Museum herbarium revealed emergence holes from seedpods similar to *Cydia* emergence holes from other islands. I also visited the island of Nihoa, the youngest and most pristine in the Northwest Hawaiian Islands chain, but found no *Cydia* despite the presence of an abundant potential host legume, *Sesbania tomentosa* Hook. & Arn.

Field-collected specimens were taken either as adults at ultraviolet lights or as larvae from host plant material. Adults collected at lights were killed either in the field with potassium cyanide, or in a refrigerator freezer (-20°C). Prior to pinning and spreading adults, I removed and placed into 95% EtOH 1-3 legs from a subset of moths for subsequent DNA analysis (Oboyski Chapter 3). Field collected larvae were reared in plastic containers fitted with mesh lids (Brenner et al. 2002) in order to confirm host-plant and parasitoid relationships.

## Dissections

Zimmerman (1978) dissected the genitalia of type specimens housed at the BMNH. I examined each of these preparations and found certain features difficult to discern due to the orientation and weak staining of the genitalia. Zimmerman (1978) states, “there are obvious differences in the genitalia, but they are not clearly shown in all of my illustrations.” Therefore, where possible, I made additional dissections from conspecific specimens. I prepared dissections following Robinson (1976) as follows: Abdomens were removed from the thorax of dry specimens and briefly “wetted” in 70% EtOH and placed in sub-boiling 10% KOH for 3 to 5 minutes, or until sclerotized tissues were pliable. The entire abdomen was then placed in distilled water for cleaning which consisted of brushing away scales with an ultra-fine paintbrush, gently “squashing” the abdomen with blunt soft forceps to squeeze out macerated soft tissues, and flushing with distilled water using a fine syringe. Male genitalia were pulled free from the rest of the abdomen (or “pelt”) with forceps, naturally separating between the 8<sup>th</sup> and 9<sup>th</sup> segments. As the female lamellae antevaginalis and postvaginalis (or “ostial plate”) are located on the 8<sup>th</sup> segment, female genitalia were pulled free from the pelt between the 7<sup>th</sup> and 8<sup>th</sup> segments. Further cleaning of loose tissue and scales was done in distilled water using a fine brush and curled tip of a minuten pin. Both the pelt and genitalia were then dipped for one to two minutes in concentrated Chlorozol Black E stain and rinsed in distilled water. Next the pelt and genitalia were dipped in concentrated Eosin-Y stain for approximately 5-10 minutes then rinsed with distilled water. The combination of Chlorozol Black E and Eosin-Y creates a contrast between the weakly sclerotized tissues (stained blue-gray by the Chlorozol Black E) and the more-strongly sclerotized tissues (stained red by the Eosin-Y). Next the genitalia were positioned in a series of baths of 70%, then 95% EtOH, for 10-15 minutes, often held in position by a small shard of microscope slide. Genitalia were then placed in Euparal Essence<sup>®</sup> until mounted in Euparal<sup>®</sup> mounting medium (BioQuip Products, Rancho Dominguez, CA) on glass slides with cover slips.

The juxta of male *Cydia* genitalia, like those of many Olethreutinae, is fused with the caulis and anellus forming a stout, inflexible substrate to which the aedeagus is attached (Horak 2006). This poses a challenge in positioning the valvae and aedeagus, resulting in features, particularly the valvae, aedeagus, and tegumen, being distorted or in different planes of focus. For this reason it was sometimes preferable to separate the valvae and aedeagus before mounting them on glass slides. It is also common practice in the study of some lepidopteran taxa to evert the vesica of the aedeagus in order to better view its shape and any cornuti present. None of the specimens examined appeared to have cornuti (deciduous or otherwise), so no attempt was made to evert the vesica to avoid potentially damaging the preparations.

Wings were prepared for examination of venation patterns following Zimmerman (1978). Wings (usually right side) were broken or cut free from the body and “wetted” with 70% EtOH. The wings were then placed in pure household bleach (6% sodium hypochlorite) for 30-60 seconds, or until small bubbles began to form. The now soft and delicate wings were transferred to distilled water for cleaning with a fine brush and the hooked tip of a minuten pin. Wings were then stained with acid fuchsin to visualize the veins. The stained wings were then rinsed in 70% EtOH and passed through 95% EtOH to drive away excess moisture. Still in 95% EtOH, the

wings were then floated onto glass slides and mounted with Euparal<sup>®</sup>, once the EtOH had evaporated to the edges of the wings.

### Illustrations

Slide preparations (wings and genitalia) were photographed with a Leica<sup>®</sup> digital camera and microscope using Automontage<sup>®</sup> software (Syncroscopy, Cambridge, UK and Maryland, USA). These digital images were then traced and shaded in Adobe Illustrator<sup>®</sup> and Photoshop<sup>®</sup> (San Jose, California, USA). Similarly, figures from Zimmerman (1978) were redrawn after examining the original slides and taking note of features difficult to discern in the published photographs.

### Morphological Characters

The following characters were considered for diagnosing and describing *Cydia* species.

**Colors:** Descriptive colors follow the language of the original descriptions for consistency and comparison, and can be translated as follows: buff (yellowish beige), cinereous (ash-gray), ferruginous (reddish-brown, rust), fuliginous (sooty, dusky), fuscous (dark gray, grayish-brown), ochreous (earthy reddish-yellow), olivaceous (olive green, dusky yellowish green), plumbaginous (lead gray), testaceous (dull brick red).

**Scales:** Many species have head, thorax, and leg scales with light-colored tips that contrast with their darker bases. Although not used here as a diagnostic character, the presence of these contrasting scales contributes to the overall color patterns.

**Head:** The antennae, palpi, and vestiture of the head are typical of most *Cydia* species and consistent for all Hawaiian species, and therefore not of diagnostic value.

**Thorax:** Wing expanse (exp.) was measured to the nearest half-millimeter from wing tip to wing tip (including fringe) of fully spread specimens. Wing expanse is variable and often related to larval food quantity and quality (Miller 1990) but is diagnostic for some species. Wing venation is nearly uniform for all Hawaiian *Cydia* species (Figure 9), except as noted where the presence of a hindwing pouch displaces vein A3 towards the anal area. Scale color of the thorax and banding patterns on the legs are often useful in confirming identifications, but not consistent enough to be diagnostic. Wing patterns are limited to a small number of pattern elements (Figure 10) that are variably present or absent on individuals within a species. The combination of pattern elements and their colors can be used to identify many species, but with caution because of the high degree of polymorphism found within many species. Species within the *Canavalia*-feeding group all appear to have a sinuous termen and crescent-shaped apical patch on the forewing (Figure 11) as opposed to termen straight and subtriangular-shaped apical patch of other Hawaiian *Cydia* (Figure 12). The absence of a ventral pouch within the hindwing of males (Figure 13) is diagnostic for four species, and the presence of an anal roll in male hindwings is known only in *C. anomalosa* n.sp. (Figures 19-24). Variations in wing patterns are illustrated by photographs (Figures 25-51).

**Abdomen:** Male (Figures 52-69) and female (Figures 70-86) genitalia have the most consistent diagnostic value in Hawaiian *Cydia*. The invagination of the ventral margin at the base of the male cucullus is variable among species but of limited value, and potentially deceptive, because perceiving it is dependent on the orientation of the genitalia in the slide preparation. Similarly, the shape of the caudal ridge, or crista, of the tegumen (in the absence of a developed uncus) can be diagnostic for some species when the preparation allows the proper view of this structure. For males, the most diagnostic feature is the tip of the aedeagus which may be flared, spatulate, or

excavated. For females, the shape of the lamellae postvaginalis and antrum (i.e. basal sclerotization at the junction of the ductus bursae with the ostium) are diagnostically more informative than characters in the male genitalia for this group. Zimmerman (1978) noted that the proximity of the signa in the female corpus bursae was a character indicative of some species, but closer inspection of his slide preparations revealed this was an illusion caused by orientation of signa on opposite sides of the corpus bursae.

## TAXONOMY

### Genus *Cydia* Hübner, 1825

*Cydia* species are easily separated from other Hawaiian Tortricidae using the keys in Zimmerman (1978) based on wing venation, labial palpi, and some secondary sexual characters. The synonymies and general morphology of the genus *Cydia* are reviewed elsewhere (Oboyski Chapter 1, Komai 1999, Komai and Horak 2006). Hawaiian *Cydia* conforms to the general description of other *Cydia* with a few notable exceptions. Males of Hawaiian *Cydia* lack the hindwing anal roll and associated sex scales (Figures 22, 24), and thecae along hindwing vein A3 (Figure 20) found in most other *Cydia* species (Komai and Horak 2006), with the exception of *C. anomalosa* n.sp., which possess an anal roll and phylliform scales only (Figures 21, 23). Where males are known, 15 of 18 species of Hawaiian *Cydia* have a glandular ventral pouch that opens dorsally along the path of the CuP vein (Figures 9, 13, 14), which encloses modified cubital pecten scales (Figure 15, 17). A similar structure occurs in *C. latiferreana* (Walsingham) (Figures 16, 18), *C. maackiana* (Danilevsky), and several other *Cydia* species to a lesser degree, but appear to be derived independently in Hawaiian *Cydia* based on the microstructure of the modified pecten scales (Figures 15-18). The presence of the hindwing ventral pouch is accompanied by a shift in vein A3 towards the anal margin (Figure 9).

### *Cydia chlorostola* (Meyrick 1932) (Figure 70)

*Laspeyresia chlorostola* Meyrick 1932:226

*Cydia chlorostola*. – Zimmerman 1978:585, Figures 378 (moth), 389 (genitalia)

**DIAGNOSIS:** The most pale of all the Hawaiian *Cydia*, nearly uniform whitish. Distinguished from other Hawaiian *Cydia* by the complexity of the antrum sclerotization (Figure 70). Most similar to, and likely to be confused with, very pale forms of the *Canavalia*-feeding Hawaiian species (*C. falsifalcella*, *C. mauiensis*, *C. parapteryx*, *C. velocilimitata*), which have similarly complex antra (Figures 71-73).

**DESCRIPTION:** (exp. 16 mm, n=1) **Head:** Antennae and labial palpi uniformly buff-white. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Head buff-white, slightly darker laterally. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsally and ventrally buff-white (holotype partly denuded), tegulae somewhat lighter. Legs uniformly white-cinereous. No discernable sex scales (e.g. hair pencils). **Forewings:** Slightly dilated distally, costa gently arched, apex obtuse, termen somewhat sinuate. Nearly uniform buff-white with no distinguishable striae or fascia, ocellus consisting of three black dots of one scale

each, bordered distally by faint silvery-whitish line, fringe white-cinereous. Ventrally somewhat darker ochreous-white basally grading to buff-white distally. **Hindwings:** White-cinereous, faintly gray along fold and above cell. Fringe and ventral hindwing uniformly white-cinereous. **Abdomen:** (removed for dissection). **Male genitalia:** (male not known). **Female genitalia:** (Figure 70) Lamellae postvaginalis nearly as broad as long and somewhat centrally constricted, antrum with complex sclerotization pattern, extending well beyond the junction with ductus bursae. Corpus bursae with diverticulum, two long falcate signa with rounded tips. Ductus bursae slightly longer than width of corpus bursae, tapering gradually from corpus bursae to ostium.

TYPE MATERIAL: *Laspeyresia chlorostola* Meyrick – ♀ holotype (BMNH): Hawaiian Islands, Oahu, Waialua, P. 09 [RCL Perkins 1909]; genitalia slide BM 9546 Clarke.

ADDITIONAL MATERIAL: The female type is the only known specimen of this species.

BIOLOGY: There is no information available regarding larval biology, host plants, habitat, predators, or parasitoids.

DISTRIBUTION: Perkins' label includes only the general description of "Waialua, Oahu." Meyrick (1932) suggested this species was introduced along with a legume host, probably of Asiatic origins, but is not known from any other locations. Zimmerman (1978) disagreed and considered the species endemic to Hawaii. In the absence of more specimens I decline to conjecture any further than to suggest this is an endemic Hawaiian species.

REMARKS: This species is probably extinct. The type location, Waialua region of Oahu, no longer contains native habitats, and sampling of the nearby native forests has not produced any new specimens. Aspects of the female genitalia (see description above) suggest that this is a member of the Hawaiian *Cydia* group, and not an introduced species as Meyrick suggests.

*Cydia gypsograpt* (Meyrick 1932)  
(Figure 52)

*Adenoneura gypsograpt* Meyrick 1932:222

*Cydia gypsograpt*. – Zimmerman 1978:591; Figures 379 (moth), 384 (♂ genitalia)

DIAGNOSIS: A mostly white species with dark gray strigulae and pretornal blotch, but without costal triangle and distinct medial fascia common in other Hawaiian species. Male genitalia difficult to discern from *Canavalia*-feeding species group (*C. falsifalcella*, *C. mauiensis*, *C. parapteryx*, *C. velocilimitata*).

DESCRIPTION: (exp. 13 mm, n=1) Colored scales on head, body, and legs mostly shades of grayish-brown with whitish tips. **Head:** Antennae brownish-cinereous, head and labial palpi dorsum white, palpi with fuscous lateral streak. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsally and ventrally generally whitish, mid-dorsum light brown scales with white tips, tegulae light brown anteriorly grading to longer white scales posteriorly. Without dorsal tuft of scales. Legs whitish, foretibia banded brown and white, midtibia less so. No discernable sex scales (e.g.

hair pencils). **Forewings:** Slightly dilated distally, costa gently arched, apex obtuse, termen somewhat sinuate. Ground color buff white. Costal strigulae distinct, directed distally towards termen, striae fragmented through cell but prominent again from fold to dorsal margin as dark streaks between dorsal strigulae. No triangular costal patch. Distinct, broadly rounded-triangular fuscous pretornal blotch. Pale ocellar area with one or two distinct ocellar spots, bounded distally by light fuscous then silvery crescent. Apex with a fuscous patch probably extending into fringe (fringe worn away). Continuation of fuscous stria to central termen extends into fringe. Ventrally uniform light fuscous. **Hindwings:** Fuscous, lighter anteriorly, with silvery-white fringe. Ventrally uniform light fuscous. Males with glandular ventral pouch below cubital vein opening dorsally and enclosing elongate modified pecten scales. Vein A3 in male displaced towards the anal margin. Males without an anal role or androconial scales (thecae) along vein A3. **Abdomen:** (abdomen removed). **Male genitalia:** (Figure 52) Tegumen simple with broadly rounded caudal ridge, lacking gnathos, socii, and uncus. Valvae with excavation in basal third, costa gently concave, ventral margin with moderate invagination. Sacculus slightly sinuous, with slight concavity near base. Cucullus elongate rounded with dense short setae along ventral and distal margin, interspersed with fewer long setae. Aedeagus simple, curved, without cornuti, spatulate tip excavated dorsally for 1/5<sup>th</sup> of length of aedeagus. **Female genitalia:** (females not known).

TYPE MATERIAL: *Adenoneura gypsograpt* – ♂ holotype (BMNH): Oahu, Honolulu, P. 08 [RCL Perkins 1908]; genitalia slide BM 9543 Clarke.

ADDITIONAL MATERIAL: This species is known only from the male holotype.

BIOLOGY: There is no information available regarding larval biology, host plants, habitat, predators, or parasitoids.

DISTRIBUTION: Endemic to Hawaiian Islands: This species is known only from a single specimen collected by RCL Perkins near Honolulu, Oahu.

REMARKS: This species is probably extinct. The Honolulu region of Oahu no longer contains native habitats, and sampling of nearby native forests has not turned up any new specimens. The presence of the hindwing pouch in the male suggests that this is a member of the Hawaiian *Cydia* group.

*Cydia mauiensis* n. sp.  
(Figures 11, 25, 53, 71)

DIAGNOSIS: Most closely allied with *C. falsifalcella*, *C. parapteryx*, and *C. velocilimitata*, being the Maui Island taxon of the *Canavalia*-feeding species group, with wing patterns similar. Differentiated from these other species by its distribution and the shape of the female antrum (Figure 71).

DESCRIPTION: (exp. 15-17 mm, n=5) **Head:** Antennae, head, and labial palpi light ochreous. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsally light ochreous, tegulae same. Without dorsal tuft of scales. Ventrally lighter. Legs light brown-ochreous. No discernable sex scales (e.g.

hair pencils). **Forewings:** (Figures 11, 25) Slightly dilated distally, costa gently arched, apex obtuse, termen somewhat sinuous. Ground color light ochreous. Costal strigulae distinct, silvery light brown basally, whitish-buff distally, directed towards termen, striae indistinct except near apex. Basal area light brown-ochreous to buff, mottled with occasional brown or fuscous scales. No triangular costal patch. Oblique medial fascia extending from end of cell towards basal dorsum brown-ochreous with darker brown distal border. Whitish discal patch present and extending along medial fascia. Brown-ochreous pretornal patch vaguely present. Ocellar patch light ochreous with three distinct ocellar spots, bordered distally by a silvery-white crescent. Apex with wide crescent-shaped light brown-ochreous patch extending into fringe as dark brown-ochreous. Continuation of light brown-ochreous stria to central termen extends as dark brown-ochreous into fringe. Fringe otherwise light brown-ochreous. Ventrally uniform brown-cinereous. **Hindwings:** Dorsal and ventral light bronze-ochreous, somewhat lighter basally and ventrally. Males with glandular ventral pouch along path of CuP, opening dorsally and enclosing elongate modified pecten scales. Vein A3 in males displaced towards anal margin. Males without anal roll or androconial scales (thecae) along vein A3. **Abdomen:** light brown-ochreous dorsally, lighter ventrally. **Male genitalia:** (Figure 53) Tegumen simple with bilobed crista along caudal ridge, lacking gnathos, socii, and uncus. Valvae with excavation in basal third, costa gently concave, ventral edge with somewhat deep invagination. Sacculus slightly sinuous, with slight concavity near base. Cucullus elongate rounded with dense short setae along ventral and distal margin interspersed with longer setae distally. Aedeagus simple, curved, without cornuti, and with tip spatulate and excavated dorsally for approximately one-third the length of aedeagus. **Female genitalia:** (Figure 71) Lamellae postvaginalis nearly as wide as long and slightly constricted centrally. Antrum with prominent dorsal lobe near ostium and ventral lobe extending well beyond the dorsal junction with ductus bursae. Corpus bursae with diverticulum, two moderately long falcate signa. Ductus bursae shorter than width of corpus bursae, slightly wider at junction with corpus bursae than junction with antrum.

TYPE MATERIAL: *Cydia mauiensis* - ♂ holotype (BPBM): Hawaiian Islands, Maui, Kipahulu Valley, Oheo campground, 10.VII.2005, PT Oboyski; UV light; Oboyski specimen PTO-544.1. ♀ allotype (BPBM): Hawaiian Islands, Maui, Kipahulu Valley, Oheo campground, 10.VII.2005, PT Oboyski; UV light; Oboyski specimen PTO-544.4; genitalia slide PTO-s154. 7♂ paratypes (EMEC): Hawaiian Islands, Maui, Kipahulu Valley, Oheo campground, 2 m., UV light nr. *Canavalia* vines 10.VII.2005, PT Oboyski. Oboyski specimen PTO-544.2, genitalia slide PTO-s254.

ADDITIONAL MATERIAL: This species is known only from a single collection of nine specimens from the type locality.

BIOLOGY: Adults were collected at UV lights in proximity to *Canavalia* vines. Although no larvae were found within seedpods, like its close relatives, *C. falsifalcella*, *C. parapteryx*, and *C. velocilimitata*, this species probably feeds opportunistically within flower peduncles and stems of *Canavalia* spp.

DISTRIBUTION: Endemic to Hawaiian Islands: Maui. Possibly widespread and locally common where *Canavalia* is abundant, but known only from the type locality at Oheo campground, Haleakala National Park, Maui.



REMARKS: In molecular phylogenetic analyses (Oboyski Chapter 3), this species appears most basal in the Hawaiian *Cydia* clade or forms a basal clade with the three other *Canavalia*-feeding species.

*Cydia falsifalcella* (Walsingham 1907)  
(Figures 26, 27, 54, 72)

*Adenoneura falsifalcellum* Walsingham 1907:677; Plate 10, Figure 17 (moth)

*Cydia falsifalcella*. – Zimmerman 1978:586; Figures 371 (head, wing venation), 373 (wing venation), 379 (moth), 384 (♂ genitalia)

DIAGNOSIS: Most closely allied with *C. mauiensis*, *C. parapteryx*, and *C. velocilimitata*, being the Hawaii Island taxon of the *Canavalia*-feeding species group, with wing patterns similar. Differentiated from these other species by its distribution and the shape of the female antrum (Figure 72).

DESCRIPTION: (exp. 13-18 mm, n=6) Colored scales on head, body, and legs mostly shades of grayish-brown with whitish tips. **Head:** Antennae and labial palpi uniformly light brown-cinereous. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Head uniformly light brown-cinereous. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsally and ventrally light brown-cinereous, tegulae same. Without dorsal tuft of scales. Legs light brown-cinereous, fore- and mid-tibiae banded with fuscous bases and lighter distally, hindleg tarsi likewise banded. No discernable sex scales (e.g. hair pencils). **Forewings:** (Figures 26-27) Slightly dilated distally, costa gently arched, apex obtuse, termen somewhat sinuate. Ground color ochreous-white, overlaid by variable pattern elements. Costal strigulae distinct, directed distally towards termen, striae vague below costa in basal area, more distinct and ferruginous distally. Occasionally with a distinct triangular costal patch suffused from base to 2/3 length of costa, posteriorly overlapping the fold, ranging in color from dark fuscous to ferruginous. Costal patch often not fully suffused anterior and basal leaving an oblique medial fascia extending from end of cell towards basal dorsum (as in ♂ holotype), bordered distally by a distinct whitish discal patch at end of cell. Light brown pretornal patch sometimes vaguely evident. Pale ocellar patch with three distinct ocellar spots, bordered distally by a silvery-white crescent. Apex with a crescent-shaped ferruginous patch extending into fringe. Continuation of ferruginous stria to central termen extends into fringe. Ventrally strigulae apparent along costal margin, otherwise uniformly brown-cinereous. **Hindwings:** Uniformly light brown-cinereous dorsally, ventrally vague light brown maculations on fuscous background. Males with glandular ventral pouch along path of CuP, opening dorsally and enclosing elongate modified pecten scales. Vein A3 in male displaced towards the anal margin. Males without an anal role or androconial scales (thecae) along vein A3. **Abdomen:** Uniformly light brown-cinereous. **Male genitalia:** (Figure 54) Tegumen simple, occasionally with single lobed crista along the caudal ridge, lacking gnathos, socii, and uncus. Valvae with excavation in basal third, costa gently concave, ventral edge with deep invagination. Sacculus slightly sinuous, with slight concavity near base. Cucullus elongate rounded with dense short setae along ventral and distal margin, interspersed with fewer long setae. Aedeagus simple, curved, without cornuti, flared spatulate tip excavated dorsally for one-fifth length of aedeagus. **Female genitalia:** (Figure 72) Lamellae

postvaginallis slightly longer than wide, hourglass-shaped, antrum with complex sclerotization pattern, extending beyond junction with ductus bursae. Corpus bursae with diverticulum, two long falcate signa. Ductus bursae approximately as long as width of corpus bursae, tapering gradually from corpus bursae to antrum.

TYPE MATERIAL: *Adenoneura falsifalcellum* Walsingham – ♂ holotype (BMNH): Hawaii: Olaa, VII. 1895, RCL Perkins; Walsingham specimen 27506; genitalia slide BM 2051. 1♂ paratype (BMNH): Hawaii, Olaa, ix.1896, RCL Perkins; Walsingham specimen 28043. 3♂ paratype. (BMNH): Hawaii, Olaa, 2000 ft, RCL Perkins; Walsingham specimens 28630, 28638, 28640. 2♂ (BPBM): Hawaii, Olaa, 2000 ft, xi.1896, RCL Perkins; Walsingham specimens 28642, 28648; genitalia & wings (28648), “slide 79, ecz Oct 1940.”

ADDITIONAL MATERIAL: 1♂ (BPBM): Hawaii, Mauna Loa, Kaeuhou road, 5900ft, reared: *Vicia menziesii*, 5-27.iii.1979, C Hodges; USFS #79-1; genitalia slide PTO-s182. 1♀ (BPBM): Hawaii, Mauna Loa, Keauhou road, 5900ft, reared: *Vicia menziesii*, 5-27.iii.1979, C Hodges; USFS #79-1; genitalia slide PTO-s183. 2♂ (EMEC): Hawaii, Mauna Loa, Manuka State Park, loop trail, 560 m, UV light nr. *Canavalia hawaiiensis*, 28.viii.2005, PT Oboyski; genitalia slide PTO-s251.

BIOLOGY: According to Zimmerman (1978), descriptions of larval biology attributed to *C. falsifalcella* prior to 1932, when *C. parapteryx* was described from Oahu, belong to the latter species. Probably, like *C. parapteryx*, *C. falsifalcella* larvae feed on *Canavalia* species. Inspection of the few seedpods of *Canavalia hawaiiensis* growing at Manuka, Hawaii Island showed no indication of larval feeding; however, two adults were collected at an ultraviolet light positioned amid the *Canavalia* vines. Larvae probably develop opportunistically in the flower peduncles, seedpods, or vines of this plant. While *Canavalia hawaiiensis* is rare in nature, *Canavalia galeata*, the type host of *C. parapteryx* on Oahu, is common at low elevations. However, UV light trapping and seedpod inspection of *Canavalia galeata* have not produced any *Cydia* specimens on Hawaii Island. Two specimens of *C. falsifalcella* also were reared from the seeds of *Vicia menziessii* at Keauhou, Hawaii, by C. Hodges, suggesting that this species may have a somewhat varied diet. *Vicia menziesii* is a critically endangered plant represented by less than a dozen mature, naturally growing plants, and dozens of struggling out-planted seedlings. None of these plants has set seed in many years (Kealii Bio, USGS-BRD, personal communication). However, *Vicia* plants were once more common in this area and may have been an alternate host-plant for this species, and the source for Perkins' original collections in Olaa.

DISTRIBUTION: Endemic to Hawaiian Islands: Hawaii – uncommon and very localized.

REMARKS: *C. falsifalcella* closely resembles its sister species *C. parapteryx* from Oahu and has been confused with this latter species in the literature (Zimmerman, 1978) (see notes under Biology above).

*Cydia parapteryx* (Meyrick 1932)  
(Figures 9, 28, 55, 73)

*Enarmonia* sp. Swezey 1908:15

*Adenoneura falsifalcella* (sensu Perkins 1913:clxviii, not Walsingham 1907)

*Adenoneura parapteryx* Meyrick, 1932:222

*Cydia parapteryx*. – Zimmerman 1978:608; Figures 374 (wing venation), 381 (moth), 386 (♂ genitalia), 395 (♀ genitalia)

DIAGNOSIS: Most closely allied with *C. falsifalcella*, *C. mauiensis*, and *C. velocilimitata*, being the Oahu Island taxon of the *Canavalia*-feeding species group, with wing patterns similar. Differentiated from these other species by its distribution, the lack of excavation of the tip of the male aedeagus (Figure 55), and the shape of the female antrum (Figure 73).

DESCRIPTION: (exp. 14-24 mm, n=23) **Head:** Antennae, head, and labial palpi light brown-ochreous. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsally light brown-ochreous, tegulae same. Without dorsal tuft of scales. Ventrally lighter, somewhat darker around coxae. Legs light brown-ochreous. No discernable sex scales (e.g. hair pencils). **Forewings:** (Figure 28) Slightly dilated distally, costa gently arched, apex obtuse, termen somewhat sinuous, nearly vertical. Ground color light brown-ochreous. Costal strigulae distinct, silvery light brown basally, whitish-buff distally, directed distally towards termen, striae indistinct in basal half creating mottled appearance or obscured by suffusion of ferruginous to fuscous triangular costal patch. Oblique medial fascia along distal edge of costal triangle extending from end of cell towards basal dorsum dark ferruginous often with dark brown-fuscous distal border. Whitish discal patch present and often distinct. Pretornal patch absent or very vague. Ocellar patch mottled light and dark brown with three distinct ocellar spots, bordered distally by a silvery-white crescent. Apex with wide crescent-shaped ferruginous patch extending into fringe as fuscous-ferruginous. Continuation of ferruginous stria to central termen extends as fuscous-ferruginous into fringe. Fringe otherwise light brown-buff. Ventrally strigulae apparent along costal margin, otherwise uniform brown-cinereous. **Hindwings:** Dorsal and ventral ferruginous, somewhat lighter basally and ventrally, maculation somewhat apparent ventrally. Males with glandular ventral pouch along path of CuP, opening dorsally and enclosing elongate modified pecten scales. Vein A3 in males displaced towards anal margin. Males without anal roll or androconial scales (thecae) along vein A3. **Abdomen:** light brown-ferruginous dorsally, lighter ventrally. **Male genitalia:** (Figure 55) Tegumen simple with broadly flattened caudal ridge, lacking gnathos, socii, and uncus. Valvae with excavation in basal third, costa gently concave, ventral edge with somewhat deep invagination. Sacculus slightly sinuous, with slight concavity near base. Cucullus elongate rounded with dense short setae along ventral and distal margin interspersed with longer setae distally. Aedeagus simple, curved, without cornuti, and tip bilobed. **Female genitalia:** (Figure 73) Lamellae postvaginalis somewhat longer than wide, slightly constricted centrally. Antrum relatively shortened with prominent dorsal lobe near ostium and ventral lobe extending just beyond dorsal junction with ductus bursae. Corpus bursae with diverticulum, two long falcate signa. Ductus bursae shorter than width of corpus bursae, only slightly wider at junction with corpus bursae than junction with antrum.

TYPE MATERIAL: *Adenoneura parapteryx* – ♂ lectotype (BMNH): Oahu, Honolulu, P. 09 [1909], bred from *Canavalia galeata*, RCL Perkins; genitalia slide BM 9544. 2♀ paralectotype (BMNH): Oahu, Honolulu, P. 09, bred from *Canavalia galeata*, RCL Perkins; genitalia slide BM 7549. 3♂ paralectotype (BMNH): Oahu, Honolulu, P. 09 [RCL Perkins 1909], bred from *Canavalia galeata*; wing slide BM 7532.

ADDITIONAL MATERIAL: 1♀ (BPBM): Oahu, Mt Kaala, ex: *Canavalia galeata* seeds, 14.x.1928, OH Swezey. 3 (HDOA): Oahu, Mt Kaala, ex: *Canavalia galeata* seeds, (11.xi.1926, 14.x.1928, 23.i.1929), OH Swezey. 4 (HDOA): Oahu, Honolulu, (10.viii.1907, 27.i.1908, 1.ii.1908, 28.iv.1908). 1 larva (HDOA): Oahu, Honolulu, ex: *Canavalia tursida*, 31.vii.1907. 2 (HDOA): Oahu, Honolulu, ex: *Canavalia microcarpa*, 9.viii.1907. 1 (HDOA): Oahu, HPSA station, ex: beans, 22.vii.1907. 1 (HDOA): Oahu, Piko trail, ex: *Canavalia*, 30.xii.1933, OH Swezey. 1 (HDOA): Oahu, Kahaluu, light trap, vii.1969, W Au. 1 (HDOA): Oahu, Nuuanu, ex: *Strogylydon*, 1.i.1916. 3♂ (EMEC) Oahu, S. Waianae Mtns., Honouliuli TNC Preserve, Kaluaa section, 585 m., UV light nr. *Strongylydon* vines, 24.vii.2005, PT Oboyski, Oboyski specimens PTO-563.1,2,3. 2♀ (CAS) Oahu, Mt Kaala, ex: *Canavalia galeata* seeds, 14.x.1928, OH Swezey. 2 (CAS) Oahu, Honolulu, 27.i.1908. 4 (USNM) Oahu, Honolulu.

BIOLOGY: Larvae feed in the unripe seeds, fleshy walls of developing seedpods, flower cluster peduncles, leaf petioles, and vining branches of *Canavalia galeata* (Fabaceae) (Swezey, 1908 as *Enarmonia* sp.; Perkins, 1913 as *Adenoneura falsifalcella*), as well as *Canavalia microcarpa*, *Canavalia tursida*, (and likely other *Canavalia* spp.), and *Strongylydon ruber* (Fabaceae) (Swezey 1936, 1954, Zimmerman 1978). Swezey ((1908); also quoted in Zimmerman (1978)) provides a detailed description of larval and pupal morphology, and of the biology of this species, paraphrased as follows: eggs are laid singly or in small groups on the seedpod surface; upon hatching larvae bore into the seedpod feeding first on the fleshy walls, then on the ripening seeds; before pupation the larva creates a silken tube to the outer wall of the pod, out of which it eats a hole except for the outermost layer; through which the pupa will protrude to enable adult emergence. Although *Cryptophlebia illepida* can also be bred from *Canavalia* seedpods, the larvae are fairly easily distinguished by the darkly sclerotized thorax of *Cryptophlebia illepida* (Namba 1957, Zimmerman 1978). The ichneumonid wasp, *Trathala flavoorbitalis* Cameron, parasitizes larvae of *C. parapteryx* Swezey (1954). The adults are attracted to lights.

DISTRIBUTION: Endemic to Hawaiian Islands: Oahu – widespread, but only locally common where host plants occur.

REMARKS: Observations of larval biology (Swezey 1908, Perkins 1913) attributed to other *Canavalia*-feeding larvae on Oahu before Meyrick described *C. parapteryx* in 1932, rightly belong to this species (Zimmerman 1978). This is the largest of the Hawaiian species, although adult size varies considerably depending on the quality of the larval diet.

*Cydia velocilimitata* n. sp.  
(Figures 29, 30, 56)

DIAGNOSIS: Most closely allied with *C. falsifalcella*, *C. mauiensis*, and *C. parapteryx*, being the Kauai Island taxon of the *Canavalia*-feeding species group, with wing patterns similar. Differentiated from these other species by its distribution, and aedeagus of male with tip excavated for much shorter distance than in *C. mauiensis*.

DESCRIPTION: (exp. 13-18 mm, n=8) Colored scales on head, body, and legs mostly shades of light ochreous-brown with whitish tips. **Head:** Antennae, head, and labial palpi light brown. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsally light brown, tegulae same. Without dorsal tuft of scales. Ventrally lighter. Legs light brown. No discernable sex scales (e.g. hair pencils). **Forewings:** (Figures 29-30) Slightly dilated distally, costa gently arched, apex obtuse, termen somewhat sinuous. Ground color silvery-white. Costal strigulae distinct, plumbaginous, directed towards termen, striae vague below costa in basal area creating a brown-ochreous and white mottled appearance, more distinct and ferruginous distally. Some specimens with a distinct triangular costal patch suffused dark fuscous from base to 2/3 length of costa, posteriorly overlapping the fold. If no costal patch, ferruginous oblique medial fascia extending from end of cell towards basal dorsum, bordered distally by distinct whitish discal patch at end of cell. Ferruginous pretornal patch evident. Ferruginous ocellar area with three distinct ocellar spots, bordered distally by a plumbaginous crescent. Apex with a crescent-shaped ferruginous patch extending into fringe. Continuation of ferruginous stria to central termen extends into fringe, fringe along termen otherwise light ochreous. Venter uniformly light brown-ferruginous. **Hindwings:** Uniformly light brown-ferruginous dorsally, ventrally lighter. Males with glandular ventral patch along path of CuP, opening dorsally and enclosing elongate modified pecten scales. Vein A3 in male displaced towards anal margin. Males without an anal roll or androconial scales (thecae) along vein A3. **Abdomen:** Uniformly light brown. **Male genitalia:** (Figure 56) Tegumen simple, with gently rounded caudal ridge, lacking gnathos, socii, and uncus. Valvae with excavation in basal third, costa gently concave, ventral edge with deep invagination. Saccus slightly sinuous, with slight concavity near base. Cucullus elongate rounded with dense short setae along ventral and distal margin interspersed with longer setae distally. Aedeagus simple, curved, without cornuti, and with tip somewhat spatulate and excavated dorsally for approximately one-fifth length of aedeagus. **Female genitalia:** (females not known).

TYPE MATERIAL: *Cydia velocilimitata* – ♂ holotype (BPBM): Kauai, Hanalei, Waipa Valley, along Hwy 560, UV light nr. *Canavalia* vines, PT Oboyski, 28.vi.2005, Oboyski specimen PTO-519.2, genitalia slide PTO-s170. 7♂ paratypes (EMEC): Kauai, Hanalei, Waipa Valley, along Hwy 560, UV light nr. *Canavalia* vines, PT Oboyski, 28.vi.2005

ADDITIONAL MATERIAL: This species is known only from a single collection of eight male specimens.

BIOLOGY: Adults were collected at ultraviolet lights in proximity to *Canavalia* vines. Like its close relatives, *C. falsifalcella*, *C. mauiensis*, and *C. parapteryx*, this species probably feeds opportunistically within flower peduncles, stems, and seeds of *Canavalia* spp.

**DISTRIBUTION:** Endemic to Hawaiian Islands: Kauai. Possibly widespread and locally common where *Canavalia* is abundant, but known only from the type locality at Waipa Valley near Hanalei, Kauai.

**REMARKS:** Collected along a roadside, where *Canavalia* vines were growing into trees, using an ultraviolet light suspended between a telephone pole and speed limit sign. This type location is the inspiration for the specific epithet.

***Cydia plicata*** (Walsingham 1907)  
(Figures 1-4, 15, 17, 31-33, 57, 74)

*Adenoneura plicatum* Walsingham 1907:678; Plate X, Figure 19 (moth). Swezey & Williams 1932:187, Swezey 1936:198, 1954:204

*Cydia plicata*. – Zimmerman 1978:609; Figures 374 (wing venation), 382 (moth), 387 (♂ genitalia), 396 (♀ genitalia). Stein 1983a:318, Brenner et al. 2002:101

*Cydia crassicornis* (sensu Brenner et al. 2002:104, not Walsingham 1907) - misidentification

*Cydia falsifalcella* (sensu Brenner et al. 2002:104, not Walsingham 1907) - misidentification

*Cydia obliqua* (sensu Brenner et al. 2002:104, not Walsingham 1907) - misidentification

*Cydia storeella* (sensu Brenner et al. 2002:104, not Walsingham 1907) - misidentification

**DIAGNOSIS:** This is a highly polymorphic species in both wing patterns and adult size, and therefore difficult to distinguish from *Cydia makai*, *C. montana*, *C. obliqua*, and *C. storeella*. This species typically is found at higher elevations than *C. makai*, another *Sophora chrysophylla*-feeding species, while *C. montana* is associated with *Acacia koa*. Females can be distinguished from other Hawaiian *Cydia* by the shape of the antrum and lamellae postvaginalis (Figure 74). In males (Figure 57), the tip of the aedeagus is excavated similarly to that of the *Canavalia*-feeding species group and unlike others in the *Sophora*-feeding group.

**DESCRIPTION:** (exp. 15-20 mm, n=30) Colored scales on head, body, and legs mostly shades of grayish-brown ochreous with whitish tips. **Head:** Antennae, labial palpi, and head light brown-ochreous, head somewhat lighter anteriorly. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsally and ventrally light brown ochreous, tegulae same. Without dorsal tuft of scales. Legs light brown ochreous, tibiae somewhat darker. No discernable sex scales (e.g. hair pencils). **Forewings:** (Figures 31-33) Slightly dilated distally, costa gently arched, apex obtuse, termen straight. Ground color ochreous-white, overlaid by highly variable pattern elements. Costal strigulae usually distinct white cinereous but sometimes obscured in specimens with costal suffusion, directed distally towards termen, striae often indistinct in basal half creating mottled appearance or obscured by suffusion of ochreous- to ferruginous-brown triangular costal patch. Oblique medial fascia of ochreous-brown along distal edge of costal triangle extending from end of cell towards basal dorsum sometimes absent. Whitish discal patch usually present and distinct. Pretornal patch of ochreous-brown present or absent, sometimes replaced by whitish scales between dorsal margin and triangular costal patch to ocellar patch. Ocellar patch usually light ochreous-brown grading darker distally with 0, 2, 3 or 4 dark ocellar spots, bordered distally by a silvery-white crescent. Apex often with subtriangular ochreous-brown patch

extending into fringe. Continuation of ochreous-brown stria to central termen extends into fringe. Fringe otherwise light brown-buff. Ventrally uniformly fuscous-brown. **Hindwings:** Dorsally and ventrally light ochreous-brown, darker distally, fringe grayish-white. Males with glandular ventral pouch along path of CuP, opening dorsally and enclosing elongate modified pecten scales. Vein A3 in males displaced towards anal margin. Males without anal roll or androconial scales (thecae) along vein A3. **Abdomen:** Dorsally olivaceous-brown, light brown ventrally. **Male genitalia:** (Figure 57) Tegumen simple with rounded sub-triangular caudal ridge, lacking gnathos, socii, and uncus. Valvae with excavation in basal third, costa gently concave, ventral edge with deep invagination. Sacculus slightly sinuous, with slight concavity near base. Cucullus elongate rounded with dense short setae along ventral and distal margin interspersed with longer setae. Aedeagus simple, curved, without cornuti, with somewhat spatulate tip excavated for one-eighth to one-fifth of the length of aedeagus. **Female genitalia:** (Figure 74) Lamellae postvaginalis long and narrow flared into two small lobes caudally. Antrum simple, elongate cylindrical, extending anteriorly into abdominal segment VI with a slight curve. Junction with ductus bursae at anterior end of antrum. Corpus bursae with diverticulum, two long falcate signa. Ductus bursae slightly shorter than width of corpus bursae, with broad tapering junction with corpus bursae to junction with ductus seminalis, narrower from ductus seminalis to antrum.

TYPE MATERIAL: *Adenoneura plicatum* – ♂ holotype (BMNH): Hawaii, Kona, 4000 ft, 13.viii.1892, RCL Perkins; Walsingham specimen 25717; genitalia slide BM 1885. ♀ holotype (BMNH): Hawaii, Kona, over 6000 ft., 30.viii.1892, RCL Perkins; Walsingham specimen 25615. ♂ paratype (BMNH): Hawaii, summit crater of Mt. Hualalai, Kona, 8000 ft, 15.viii.1892, RCL Perkins; Walsingham specimen 28663; F.H. 370. ♂ paratype (BPBM): Hawaii, Mt Kilauea, xii.1896, RCL Perkins; Walsingham specimen 28662; genitalia Busck slide 222; wing slide BM 7570 [there is some confusion about this slide since the specimen still has both pairs of wings]. ♀ allotype (BMNH): Hawaii, Kona, over 6000 ft, 30.viii.1892, RCL Perkins; genitalia slide BM 1886. ♂ homotype (BMNH): Hawaiian Islands, Hawaii, Mauna Loa, 4000 ft, (from seeds of native *Acacia* – [clearly a mistake]), excl. 1900, RCL Perkins; Walsingham specimen 29270; F.H. 679.370.

ADDITIONAL MATERIAL: 2♂, 2♀ (BPBM): Maui, Haleakala, ex: mamane seeds [= *Sophora chrysophylla*], 25.viii.1918, OH Swezey. 1♂, 5♀ (BPBM): Maui, Haleakala, 7000 ft, ex: *Sophora*, 18.viii.1929, OH Swezey; (1♀ abdomen missing). 1♂ (BPBM): Maui, Haleakala, 8000 ft, ex: *Sophora* seeds, 26.ii.1935, OH Swezey. 1 (CAS) HAVO, 5500 ft, 22.v.1986. 3 (UHMA) Hawaii, Mauna Kea. 6♂, 8♀ (EMEC): Hawaiian Islands, Maui, Haleakala N.P., “crater”, 2240 m., reared from *Sophora chrysophylla* seeds, 10.ix.1999, PT Oboyski. 2♀ (EMEC): Hawaiian Islands, Maui, Polipoli, boundary tr., 1830 m., reared from *Sophora chrysophylla* seeds, 31.vii.2002, PT Oboyski. (HAVO) Hundreds of specimens were reared from *Sophora chrysophylla* on Mauna Kea, Hawaii Island between 1995 and 2002 as part of parasitism research (Brenner et al. 2002, Oboyski et al. 2004).

BIOLOGY: Larvae feed within the green (unripe) seeds of *Sophora chrysophylla* (Swezey and Williams 1932, Swezey 1936, 1954, Zimmerman 1978) (Figure 2). Following R.C.L. Perkins’ field notes, Walsingham (1907) mistakenly suggests, “Larva in the seeds of native *Acacias* (Perkins I : 1900).” Eggs are laid singly or in small clusters on the outside of the seedpod (Figure 1), first instar larvae bore into the endosperm. In both the laboratory and the field, larvae may

feed on a single seed, or may tunnel within a seedpod to consume several seeds, and occasionally exit one seedpod and enter another hanging in the same cluster. Occupied seedpods are often detectable by a silk and frass plug covering a hole from the seed to the outside of the pod (Figure 5). Pupation occurs within the seed and the mature pupa protrudes part way out of the silk-covered opening for eclosion of the imago (Figure 4). In the laboratory, some larvae survived for over 18 months in drying seeds and emerged as adults shortly after the application of a moist tissue, suggesting the capacity for facultative diapause. Similarly in the field, I have found live mature larvae in hollowed-out dry mature seeds. Larvae are commonly parasitized by *Pristomerus hawaiiensis*, *Diadegma blackburni*, *Calliephaltes grapholithae* (Ichneumonidae), and *Euderus metallicus* (Eulophidae) (Figure 3) (Brenner et al. 2002, Oboyski et al. 2004). Larvae of this species are also important insect prey of the ‘palila’ (Fringillidae: *Loxioides bailleui*), an endangered Hawaiian honeycreeper bird (Banko et al. 2002). Some aspects of biology are also reviewed by (Swezey 1954, Zimmerman 1978, Oboyski et al. 2004).

**DISTRIBUTION:** Endemic to Hawaiian Islands: Hawaii – Mauna Kea, Mauna Loa, Hualalai; Maui – Haleakala. Common above 2000 m in *Sophora chrysophylla* forest and shrubland, sympatric with *C. haleakalaensis* and *C. latifemoris* on Maui.

**REMARKS:** Wing color and patterns are highly variable in this species (Figure 31-33). The high degree of polymorphism resulted in this species being mistakenly identified as several species (*C. crassicornis*, *C. falsifalcella*, *C. obliqua*, and *C. storella*) by Brenner et al. (2002). However, genitalia dissections and DNA sequencing (Oboyski Chapter 3) of specimens obtained by extensive rearing efforts (Brenner et al. 2002, Oboyski et al. 2004) confirm that this is a single variable species. O.H. Swezey (pers. comm. in Zimmerman 1978) notes he has witnessed up to 70% of *Sophora chrysophylla* seeds damaged by *C. plicata* larvae. However, *C. haleakalaensis*, *C. latifemoris* and *C. makai* also feed on *S. chrysophylla* seeds and may be partly responsible for Swezey’s observation. The adult moths are attracted to ultraviolet lights.

***Cydia obliqua*** (Walsingham 1907)  
(Figure 75)

*Enarmonia* (?) *obliqua* Walsingham 1907:686; Plate XI. Figure 4 (moth)

*Adenoneura obliqua*. – Meyrick 1932:222

*Cydia obliqua*. – Zimmerman 1978:608; Figures 381 (moth), 394 (♀ genitalia)

*Cydia oblique*. – Stein 1983a:318 (misspelling of *C. obliqua* Walsingham)

**DIAGNOSIS:** *Cydia obliqua*, known from only three female specimens, closely resembles a form of the polymorphic *C. plicata* found on Hawaii and Maui. However, the short, stout, female antrum and wide lamellae postvaginalis of *C. obliqua* (Figure 75) is distinctly different from other Hawaiian *Cydia*.

**DESCRIPTION:** (exp. 14-17 mm, n=3) **Head:** Antennal scales fuscous with lighter tips, labial palpi and head buff white. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsal scale light brown-cinereous with lighter tips, mid-dorsum somewhat darker, tegulae light brown-cinereous becoming lighter with longer scales posteriorly. Without dorsal tuft of scales. Ventral body and



legs light brownish-buff. No discernable sex scales (e.g. hair pencils). **Forewings:** Slightly dilated distally, costa gently arched, apex obtuse, termen nearly straight. Ground color whitish-cinereous. Costal strigulae somewhat obscured basally, distally distinct directed distally towards termen, striae indistinct in basal half. Mid-basal area buff white. No triangular costal patch. Oblique medial fascia light olivaceous-brown extending from end of cell towards basal dorsum ending in a darker dorsal blotch. Whitish discal patch distinct. Pretornal patch light olivaceous-brown basally, darker distally. Ocellar patch light brown-cinereous with two or three indistinct ocellar spots, bordered distally by a silvery-brown crescent. Apex with a light olivaceous-brown patch extending into fringe. Continuation of olivaceous-brown stria to central termen extends into fringe. Fringe otherwise buff white. Ventrally uniform dark brown-cinereous, ventral fringe matching dorsum. **Hindwings:** Dorsally brown-cinereous, darker distally, buff gray costal margin, fringe buff gray. Ventrally similar to dorsum but somewhat lighter. It is not known whether males have a glandular ventral pouch. **Abdomen:** Light brown-cinereous dorsally, lighter ventrally. **Male genitalia:** (males not known). **Female genitalia:** (Figure 75) Lamellae postvaginalis somewhat wider than long, dilated posteriorly. Antrum funnel-shaped with two lightly sclerotized longitudinal bands, direct anterior junction with ductus bursae. Corpus bursae with diverticulum, two long falcate signa. Ductus bursae somewhat shorter than width of corpus bursae, wider between corpus bursae and ductus seminalis than between ductus seminalis and antrum.

TYPE MATERIAL: *Enarmonia (?) obliqua* – ♀ holotype (BMNH): Hawaii, Hualalai (Kona), 5000 ft., 15.VIII.1892, RCL Perkins; Walsingham specimen 25828; genitalia slide BM 1882. ♀ paratype (BMNH): Hawaii, Hualalai (Kona), 5000 ft., 15.VIII.1892, RCL Perkins; Walsingham specimen 25832.

ADDITIONAL MATERIAL: 1♀ (BMNH): Hawaii, Kona, 4000 ft., 10.VIII.1892, RCL Perkins; Walsingham specimen 25271; (with determination label: *Enarmonia* sp. Drnt.).

BIOLOGY: There is no information available regarding larval biology, host plants, habitat, predators, or parasitoids.

DISTRIBUTION: Endemic to Hawaiian Islands: Hawaii – Known only from three female specimens collected 1200-1500 m on Hualalai volcano.

REMARKS: If not an extinct species (or nearly so), it is possible that the three specimens of *C. obliqua* represent an aberrant form of the highly polymorphic *C. plicata* found commonly at higher elevations (> 2000 m) on Hawaii and Maui. But without further material showing greater similarity to the type specimens I shall resist synonymizing these two species. Specimens misidentified as *C. obliqua* by Brenner et al. (2002) are correctly referred to *C. plicata*.

***Cydia storeella*** (Walsingham 1907)  
(Figure 77)

*Enarmonia* (?) *storeella* Walsingham 1907:686; Plate XI. Figure 3 (moth)

*Adenoneura storeella*. – Meyrick 1932:222

*Cydia storeella*. – Zimmerman 1978:609; Figures 383 (moth), 398 (♀ genitalia)

**DIAGNOSIS:** Color and pattern of wings similar to morphs of *Cydia plicata* (e.g. Figure 33). Distinguished from all other female Hawaiian *Cydia* by the elongate antrum and shape of the lamellae postvaginalis. Males not known.

**DESCRIPTION:** (exp. 14 mm, n=1) Colored scales on head, body, and legs mostly shades of brown-cinereous with whitish tips. **Head:** Antennae, head, and labial palpi light brown-cinereous, head somewhat lighter anteriorly. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsally light brown-cinereous, tegulae same. Ventrally whitish-buff (although largely denuded of scales). Without dorsal tuft of scales. Legs light brown-cinereous. No discernable sex scales (e.g. hair pencils). **Forewings:** Slightly dilated distally, costa gently arched, apex obtuse, termen straight. Ground color whitish-buff. Costal strigulae not apparent. Distinct triangular costal patch suffused brown-olivaceous from base to 2/3 length of costa, posteriorly overlapping fold, bordered distally by a lighter band of scales and distinct whitish discal patch at end of cell. Pretornal patch only vaguely evident as light brown-cinereous. Ocellar patch indistinct and with no discernable ocellar spots or distal border, and no discernable apical patch. Distal area instead speckled light brown olivaceous, with thin brown-olivaceous line along termen. Fringe uniformly light plumbaginous. Ventrally light brown-cinereous. **Hindwings:** Uniformly brown-cinereous dorsally, ventrally lighter. It is unknown whether males of this species possess a ventral pouch. **Abdomen:** (removed). **Male genitalia:** (males not known). **Female genitalia:** (Figure 77) Lamellae postvaginalis slightly longer than wide, constricted centrally and widely flared posteriorly. Antrum very long and slender relative to other Hawaiian *Cydia*, projecting with a lightly sclerotized ventral lobe just beyond junction with ductus bursae. Corpus bursae with diverticulum. Two long, falcate signa on opposite sides of corpus bursae (not proximate as suggested by Zimmerman 1978). Ductus bursae shorter than width of corpus bursae, sharply tapering from corpus bursae, then uniformly slender to junction with antrum.

**TYPE MATERIAL:** *Enarmonia* (?) *storeella* – ♀ holotype (BMNH): Hawaiian Islands, Maui, Haleakala, 5000 ft, v.1896, RCL Perkins; Walsingham specimen 28185; genitalia slide BM 1881.

**ADDITIONAL MATERIAL:** This species is known only from the female holotype.

**BIOLOGY:** There is no information available regarding larval biology, host plants, habitat, predators, or parasitoids.

**DISTRIBUTION:** Endemic to Hawaiian Islands: Maui – Haleakala, 5000 ft. Known from a single female specimen.

REMARKS: If not extinct, this species is very rare. There remains ample native forest around 5000 ft on Haleakala, Maui, so it is doubtful that this species was lost due to habitat destruction, although many species of forest understory plants have become rare or extirpated due to ungulate and rat feeding. Zimmerman (1978:607) suggested the approximation of the signa in the corpus bursae is a diagnostic characteristic for this species. However, closer examination of the holotype slide (BM 1881) reveals that the signa are on opposite sides of the corpus bursae giving the appearance of proximity. The antrum of the female genitalia appears unique and not likely to be an aberrant form of another more common polymorphic species (e.g. *C. plicata*). However, *C. crassicornis* (Hawaii) and *C. gypsograptia* (Oahu) are known from only male holotypes. Specimens misidentified as *C. storeella* by Brenner et al. (2002) are correctly referred to *C. plicata*.

*Cydia haleakalaensis* n. sp.  
(Figures 34, 58, 77)

DIAGNOSIS: This species is uniformly dark (mottled dark brown and charcoal), which is unique among Hawaiian *Cydia*.

DESCRIPTION: (exp. 12-17 mm, n=6) Colored scales on head, body, and legs fuscous with whitish tips. **Head:** Head scales fuscous tipped with silvery-white giving a frosted appearance. Labial palpi pale cinereous, lighter towards tips. Antennae banded fuscous and pale cinereous. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsal color same as head, tegulae same. Ventrally similar. Without dorsal tuft of scales. Legs slightly darker. No discernable sex scale (e.g. hair pencils). **Forewings:** (Figure 34) Slightly dilated distally, costa gently arched, apex obtuse, termen nearly straight. Ground color fuscous. Costal strigulae vague, fuscous tipped with light cinereous, interspersed with dark brown-ferruginous streaks, directed towards termen, striae indistinct giving a mottled appearance throughout. No triangular costal patch. Oblique medial fascia of dark brown-ferruginous extending from end of cell towards basal dorsum. Discal patch absent. Dark brown-ferruginous pretornal patch vaguely present. Ocellar patch indistinct and without ocellar spots. Termen, from apex to tornus, with a band of brown-ferruginous mottled with fuscous. Fringe at apex light brown-ferruginous, dark brown fuscous below apex. Ventrally uniform dark-brown fuscous. **Hindwings:** Dorsal and ventral dark brown fuscous. Males with glandular ventral pouch along path of CuP, opening dorsally and enclosing elongate modified pecten scales. Vein A3 in males displaced towards anal margin. Males without anal roll or androconial scales (thecae) along vein A3. **Abdomen:** Dark brown-fuscous. **Male genitalia:** (Figure 58) Tegumen simple with central point between short lobes that create a somewhat parallel-sided crista along caudal ridge, lacking gnathos, socii, and uncus. Valvae with excavation in basal third, costa gently concave, ventral edge with deep invagination. Sacculus slightly sinuous, with slight concavity near base. Cucullus elongate rounded with dense short setae along ventral and distal margin interspersed with longer setae distally. Aedeagus simple, curved, without cornuti. Tip of aedeagus with two dorsal ridges and often a short, sharp ventral projection. **Female genitalia:** (Figure 77) Lamellae postvaginalis longer than wide, constricted through middle, and flared posteriorly. Antrum forms a stout cylinder as wide as ostial opening directly into ductus bursae. Corpus bursae with diverticulum, two long falcate signa. Ductus bursae longer than width of corpus, tapering gradually from corpus bursae to antrum.

TYPE MATERIAL: *Cydia haleakalaensis* - ♂ holotype (BPBM) Maui, Haleakala N.P. nr. Hosmer grove, 2105 m., aerial netting, 1.vii.2005, PT Oboyski. Specimen PTO-521.1, genitalia slide pto-s146. ♀ allotype (BPBM) Maui, Haleakala N.P., nr. Oilipuu, 2040 m., reared: *Sophora chrysophylla* pods, 8.vii.2005, PT Oboyski. Specimens PTO-538.22, genitalia slide pto-s337. 3♂ paratypes (EMEC) Maui, Haleakala N.P. nr. Hosmer grove, 2105 m., aerial netting, 1.vii.2005, PT Oboyski. Specimens PTO-521.2,3,4.

ADDITIONAL MATERIAL: 1♂ (EMEC) Maui, Haleakala N.P., nr. Hosmer grove, 2105 m., reared: *Sophora chrysophylla* pods, 29.vii.2002, PT Oboyski. Specimen greasy. 1♀ (EMEC) Maui, Haleakala N.P., Kaupo Gap, 1591 m., reared: *Sophora chrysophylla* pods, 5.viii.2002, PT Oboyski. Specimen greasy. 5♂, 1♀ (EMEC) Maui, Haleakala N.P., Halemauu Trail, 2240 m., reared: *Sophora chrysophylla* pods, 6.viii.2002, PT Oboyski. Specimens greasy.

BIOLOGY: Larvae feed within the ripening seeds of *Sophora chrysophylla*. Four adult male specimens of this species were captured flying during the day. It is unclear whether this is a diurnal species, or if these individuals were flushed from the vegetation. However, each was observed from some distance, suggesting they were not flushed, and none has been collected at lights.

DISTRIBUTION: Endemic to Hawaiian Islands: Maui – Haleakala, 1900-2240 m., along the outer slopes and within the summit “crater,” sympatric with *C. latifemoris* and *C. plicata*.

REMARKS: Molecular evidence places *C. haleakalaensis* sister to *C. latifemoris* (Oboyski Chapter 3), with which it is sympatric.

***Cydia latifemoris*** (Walsingham 1907)  
(Figures 35, 59, 78)

*Adenoneura latifemoris* Walsingham 1907:679; Plate X. Figure 20 (moth). Swezey 1936:198, 1954: 204

*Cydia latifemoris*. – Zimmerman 1978:592; Figures 373 (wing venation), 380 (moth), 385 (♂ genitalia), 392 (♀ genitalia)

*Cydia latefemoris*. – Miller 1990:126 (misspelling of *latifemoris*)

DIAGNOSIS: The rich, dark brown and black coloring of fresh specimens of this species and *C. haleakalaensis* are distinct among Hawaiian *Cydia*. This species can be distinguished from its sympatric sister-species, *C. haleakalaensis* (uniformly dark), by its distinct pretornal blotch (Figure 35), the excavated tip of the male aedeagus (Figure 59), and the more distinct ventral lobe of the female antrum (Figure 78).

DESCRIPTION: (exp. 11-16, n=10) Colored scales on head, body, and legs mostly shades of dusky-brown with whitish tips. **Head:** Antennae, head and labial palpi dark brown-cinereous. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsally dark brown-cinereous, tegulae same. Without dorsal tuft of scales. Ventrally lighter, somewhat ochreous around coxae. Legs light

brown-cinereous. No discernable sex scales (e.g. hair pencils). **Forewings:** (Figure 35) Slightly dilated distally, costa gently arched, apex obtuse, termen nearly straight. Ground color light brown-cinereous. Costal strigulae distinct, directed distally towards termen, striae indistinct in basal half creating mottled appearance. No triangular costal patch. Oblique medial fascia extending from end of cell towards basal dorsum. Whitish discal patch present but indistinct. Pretornal patch light brown-ochreous basally with distal margin dark brown-cinereous. Ocellar patch light brown-ochreous with three distinct ocellar spots, bordered distally by a silvery crescent. Apex with a light brown-ochreous patch with dark brown-cinereous distal edge. Continuation of light brown-ochreous stria streaked dark brown-cinereous to central termen along termen edge to tornus, bordered distally by dark brown-cinereous. Fringe silvery-bronze. Ventrally uniformly light brown-cinereous, lighter along anal margin. **Hindwings:** Dorsal and ventral dark brown-cinereous distally grading to lighter brown basally. Males with glandular ventral pouch along the path of CuP opening dorsally and enclosing elongate modified pecten scales. Vein A3 in males displaced towards anal margin. Males without anal roll or androconial scales (thecae) along vein A3. **Abdomen:** Uniformly dark brown-cinereous. **Male genitalia:** (Figure 59) Tegumen simple with single-lobed crista along caudal ridge, lacking gnathos, socii, and uncus. Valvae with excavation in basal third, costa gently concave, ventral margin with a deep invagination. Sacculus slightly sinuous, with slight concavity near base. Cucullus elongate rounded with dense short setae along ventral and distal margin. Aedeagus simple, curved, without cornuti, dilated distally with somewhat spatulate tip excavated dorsally for one-eighth of the length of aedeagus. **Female genitalia:** (Figure 78) Lamellae postvaginalis somewhat longer than wide, tightly constricted centrally and wider posteriorly than at ostium. Antrum elongate cylindrical with ventral lobe extending beyond junction with ductus bursae. Corpus bursae with diverticulum, two long falcate signa. Ductus bursae slightly shorter than width of corpus bursae, only slightly wider at junction with corpus bursae than junction with antrum.

TYPE MATERIAL: *Adenoneura latifemoris* – ♀ holotype (BMNH): Hawaiian Islands, Maui, Haleakala crater, X.1896, RCL Perkins; Walsingham specimen 28127; genitalia slide BM 2054. ♂ allotype (BMNH): Hawaii: Hualalai (Kona), summit of crater, 8000 ft., 15.VII.1892, RCL Perkins; Walsingham collection 28665; genitalia slide BM 2053. ♀ paratype (BPBM): Hawaii: Hualalai (Kona), summit of crater, 8000 ft., 15.VII.1892, RCL Perkins; Walsingham collection 28664; (abdomen missing); “Both sexes occurred at the summit of Hualalai but the ♀ is in poor condition” and therefore used as a paratype rather than the holotype (Walsingham 1907:679).

ADDITIONAL MATERIAL: 3♂ (BPBM): Maui, Haleakala, ex: mamane seeds [= *Sophora chrysophylla*], 25.viii.1918, OH Swezey; missing parts – (1♂ abdomen, antennae, hindwing sexpouchs; 1♂ head; 1♂ left hindwing sexpouch). 1♀ (BPBM): Maui, Haleakala, ex: mamane seeds [= *Sophora chrysophylla*], 25.viii.1918, OH Swezey; (abdomen missing). 2♂ (BPBM): Maui, Haleakala, 8000 ft, ex: *Sophora* seeds, 26.ii.1935, OH Swezey. 5♀ (EMEC): Hawaiian Islands, Maui, Haleakala N.P., “crater”, 2240 m., reared from *Sophora chrysophylla* seeds, 10.ix.1999, PT Oboyski. 1♀ (EMEC): Hawaiian Islands, Maui, Polipoli, boundary tr., 1830 m., reared from *Sophora chrysophylla* seeds, 31.vii.2002, PT Oboyski.

BIOLOGY: Larvae feed within the ripening seeds of *Sophora chrysophylla* (Swezey 1936, 1954, Zimmerman 1978) at mid to high elevations (> 2000 m). O.H. Swezey (pers. comm. in Zimmerman, 1978) noted that the larvae of *C. latifemoris* can destroy nearly half of the seed crop

of *Sophora*. On Maui (Haleakala), *C. latifemoris* is sympatric with *C. plicata* and *C. haleakalaensis*, which also feed in the seeds of *Sophora*. It is unclear, therefore, if Swezey was referring specifically to *C. latifemoris*. I also observed terminal twigs of *Sophora chrysophylla* with past feeding damage (*i.e.* split in terminal twigs) similar to those on Kauai from which *C. makai* were reared. However, no larvae have been found in twigs on Maui. Adults were collected after sunset at ultraviolet lights (compare with *C. haleakalaensis*). Larvae are parasitized by the ichneumonid wasps *Pristomerus hawaiiensis* Perkins, *Diadegma blackburni* Cameron, and *Calliephialtes grapholithae* Cresson, as well as the eulophid wasp *Euderus metallicus* Ashmead.

**DISTRIBUTION:** Endemic to Hawaiian Islands: Maui – *C. latifemoris* is particularly abundant in the *Sophora* shrublands of Haleakala volcano, both on the outer slopes and within the “crater,” sympatric with *C. haleakalaensis* and *C. plicata*. Despite targeted collection efforts, no other specimens of this species have been collected on Hawaii Island since the two specimens collected by Perkins in 1892. This species is probably not a persistent resident of Hawaii Island. However, given the proximity (~100 km) of Haleakala and Hualalai it would not be surprising for *C. latifemoris* to periodically establish small populations in the subalpine *Sophora* forests of Hualalai.

**REMARKS:** Specimens misidentified as *C. latifemoris* by Brenner et al. (2002) are correctly referred to *C. plicata*.

***Cydia makai* n. sp.**  
(Figures 36, 37, 60, 79)

**DIAGNOSIS:** *Cydia makai* is polymorphic. Forms of *C. makai* are nearly identical to forms of the highly polymorphic *C. plicata*. A slight difference in the shape of the tip of the male aedeagus can be used to separate these species. *Cydia makai* is found at elevations lower than other *Sophora*-feeding species (<2000 m), although *C. makai* distributions overlap with *C. plicata* on Hawaii Island. Regarding molecular data, *C. makai* and *C. plicata* are consistently divergent for the mitochondrial genes cytochrome oxidase I and II (2.9-4.3% and 2.3-3.8% uncorrected P, respectively) when comparing specimens pooled across islands or within individual islands separately (Oboyski Chapter 3).

**DESCRIPTION:** (exp. 11-17 mm, n=8) Colored scales on head, body, and legs mostly shades of light brown-ferruginous with whitish tips. **Head:** Antennae, head, and labial palpi light brown-ferruginous. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Ocelli and chaetosemata conspicuous. **Thorax:** Similar color to head, tegulae tending more ferruginous posteriorly. Without dorsal tuft of scales. Legs light brown-ferruginous. No discernable sex scales (e.g. hair pencils). **Forewings:** (Figures 36-37) Slightly dilated distally, costa gently arched, apex obtuse, termen straight. Ground color light brown-buff. Most commonly (Figure 36), costal strigulae distinct, light brown-ferruginous, basally interspersed with dark ferruginous becoming lighter distally, directed towards termen, striae indistinct except near apex. Basal area light brown-buff, mottled with light brown-ferruginous. No triangular costal patch, oblique medial fascia, discal patch or pretornal patch. Ocellar patch vaguely defined by light brown ferruginous with three somewhat distinct ocellar spots, bordered distally by a plumbaginous crescent. Apical patch indistinct. Termen below apex to tornus with a

ferruginous band. Fringe ferruginous, becoming fuliginous towards tornus. An alternative form on Kauai (Figure 37) with ferruginous triangular costal patch bordered distally by light brown-ferruginous. A dark fuscous streak runs through the cell. Termen, from apex through tornus, bordered by dark fuscous band. Fringe ferruginous mixed with fuscous. Ventrally uniform light brown-ferruginous. **Hindwings:** Dorsal and ventral light bronze-ferruginous, somewhat lighter basally and ventrally. Males with glandular ventral pouch along path of CuP, opening dorsally and enclosing elongate modified pecten scales. Vein A3 in males displaced towards anal margin. Males without anal roll or androconial scales (thecae) along vein A3. **Abdomen:** light brown-ferruginous dorsally, lighter ventrally. **Male genitalia:** (Figure 60) Tegumen simple with rounded caudal ridge, lacking gnathos, socii, and uncus. Valvae with excavation in basal third, costa gently concave, ventral edge with deep invagination. Sacculus slightly sinuous, with slight concavity near base. Cucullus elongate rounded with dense short setae along ventral and distal margin densely intersperse with longer setae. Aedeagus simple, curved, without cornuti, and with tip excavated dorsally approximately one-eighth the length of aedeagus. **Female genitalia:** (Figure 79) Lamellae postvaginalis long and narrow flared into two small lobes caudally. Antrum simple, elongate cylindrical, extending anteriorly into abdominal segment VI with a slight dorsal curve. Junction with ductus bursae at anterior end of antrum. Corpus bursae with diverticulum, tow long falcate signa. Ductus bursae slightly shorter than width of corpus bursae, with broad tapering junction with corpus bursae to junction of ductus seminalis, narrower from ductus seminalis to antrum.

TYPE MATERIAL: *Cydia makai* – ♂ holotype (BPBM): Hawaii Islands, Molokai, TNC Kamakou Preserve, nr. Onini gulch, northern branch, 902 m., 25.vii.2003, PT Oboyski. Specimen PTO-197.7. ♀ holotype (BPBM): Hawaii Islands, Molokai, TNC Kamakou Preserve, nr. Onini gulch, northern branch, 902 m., 25.vii.2003, PT Oboyski. Specimen PTO-197.56. 1♂ paratype (EMEC) Hawaii Islands, Molokai, TNC Kamakou Preserve, nr. Onini gulch, southern branch, 881 m., 25.vii.2003, PT Oboyski. Specimen PTO-197.11, genitalia slide pto-s311. 1♂ paratype (EMEC) Hawaii Islands, Molokai, TNC Kamakou Preserve, nr. Onini gulch, southern branch, 881 m., 25.vii.2003, PT Oboyski. Specimen PTO-198.21, genitalia slide pto-s148. 2♀ paratypes (EMEC) Hawaii Islands, Molokai, TNC Kamakou Preserve, nr. Onini gulch, northern branch, 902 m., 25.vii.2003, PT Oboyski. Specimen PTO-197.25, genitalia slide pto-s147; specimen PTO-197.31, genitalia slide pto-s152.

ADDITIONAL MATERIAL: 1♀ (EMEC): Hawaiian Islands, Kauai, Kokee State Park, Awaawapuhi trail, 1101 m, at UV light, 26.ii.2005, PT Oboyski. 1♂ (EMEC): Hawaiian Islands, Kauai, Kokee State Park, Nualolo trail, 1049 m., reared from *Sophora chrysophylla* live terminal twig, 27.ii.2005, PT Oboyski. 2♂, 1♀ (EMEC): Hawaiian Islands, Hawaii, Kohala, Kawaihae Uka, *Acacia koaia* sactuary, 965 m., reared from *Sophora chrysophylla* seeds, 5.vii.2003, PT Oboyski. 2♂, 2♀ (EMEC): Hawaiian Islands, Hawaii, Kilauea, HAVO N.P., Ainahou, 930 m., reared from *Sophora chrysophylla* seeds, 6.vii.2003, PT Oboyski.

BIOLOGY: Larvae feed within the ripening seeds of *Sophora chrysophylla*, and are parasitized by *Calliephialtes grapholithae*, *Diadegma blackburni*, *Pristomerus hawaiiensis*, and *Euderus metallicus*. A non-native species of *Araecerus* (Anthribidae) beetle also feeds within seeds of *Sophora* at low elevations. It is unclear if *Cydia makai* compete directly with beetles, which are

more often found in mature, hardened seeds. However, very few intact seeds are added to the local seed bank in areas with beetle infestation (PT Oboyski, personal observation).

**DISTRIBUTION:** Endemic to Hawaiian Islands: low elevations (< 2000 m) on Kauai, Molokai, and Hawaii, and probably occurred on Oahu, Lanai, and Maui. Bishop Museum herbarium specimens of *Sophora chrysophylla* seedpods from Oahu and Lanai have exit holes similar to those made by *Cydia* species.

**REMARKS:** The specific epithet *makai* in the Hawaiian language means towards the sea, as opposed to *mauka*, meaning towards the mountains. This species is found at elevations lower than other *Sophora*-feeding species, and is difficult to identify where their ranges overlap. *Cydia makai* will likely go extinct within the next 100 years as the number of low elevation *Sophora* trees continues to decline, particularly on the older islands, and as the alien seed beetle, *Araecerus* sp., expands its range.

*Cydia koaiae* n. sp.  
(Figures 10, 38, 39, 63)

*Cydia* new species 1 Zimmerman 1978:610; Figures 377 (feeding damage), 386 (♂ genitalia)

**DIAGNOSIS:** *Cydia koaiae*, endemic to Hawaii Island, is a gray and black species likely to be confused with its sister-species, *C. conspicua*, known only from the older islands. For most male specimens of *C. koaiae* the cucullus has an abrupt angle not present in *C. conspicua*.

**DESCRIPTION:** (exp. 11-21 mm, n=12) Scale colors on head, body, and legs mostly shades of grayish-brown with whitish tips. **Head:** Antennae, head, and labial palpi uniformly light brown-cinereous, head and palpi somewhat lighter on top. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsally and ventrally light brown-cinereous, lighter ventrally, tegulae the same. Without dorsal tuft of scales. Legs whitish-fuscous, fore- and middle-legs tibia and tarsomeres banded with fuscous bases and lighter tips. No discernable sex scales (e.g. hair pencils). **Forewings:** (Figures 10, 38, 39) Slightly dilated distally, costa gently arched, apex obtuse, termen somewhat sinuate. Ground color light cinereous. Costal strigulae distinct, directed distally towards termen, but somewhat obscured when triangular costal patch is present. Distinct triangular costal patch present or absent. If present, fuliginous-brown suffused from base to two-thirds length of costa, posteriorly overlapping the fold. If absent, basal area streaked with striae, and oblique medial fascia of fuliginous-brown extending from end of cell towards basal dorsum. Distal end of cell with a conspicuous white discal patch. Costal patch with a fuliginous-brown projection from below discal patch connecting to a vague pretornal blotch. Ocellar patch light cinereous with three distinct ocellar spots, bordered distally by a silvery-white crescent. Apex with a subtriangular fuliginous-brown patch extending into fringe. Continuation of fuliginous-brown stria to central termen extends into fringe. Fringe otherwise silvery-white. Ventrally light fuliginous-brown. **Hindwings:** Dorsally light brown-cinereous, somewhat lighter basally and ventrally. Males with a ventral glandular pouch below cubital vein opening dorsally and enclosing elongate modified pecten scales. Vein A3 in males displaced towards anal margin. Males without an anal roll or androconial scales (thecae) along vein A3. **Abdomen:** Mottle



brown-cinereous and cinereous, somewhat lighter ventrally. **Male genitalia:** (Figure 63) Tegumen simple, lacking gnathos, socii, and uncus, with crista of caudal ridge broadly rounded with central point. Valvae with excavation in basal third, costa gently concave, ending at an abrupt angle, ventral edge with deep invagination. Sacculus slightly sinuous, with slight concavity near base. Cucullus elongate, rounded below abrupt angle at end of costal edge, with dense short and long setae along ventral and distal margin. Aedeagus simple, curved, without cornuti, spatulate tip excavated dorsally for one-fifth length of aedeagus. **Female genitalia:** (females not known).

TYPE MATERIAL: *Cydia koaiae* – ♂ holotype (BPBM): Hawaiian Islands, Hawaii, Kohala, Kawaihae Uka, Acacia koaia sanctuary, 970 m., at UV light, 18.vii.2004, PT Oboyski; Oboyski specimen PTO-323.13, genitalia slide pto-s333. 11♂ paratypes (EMEC): Hawaiian Islands, Hawaii, Kohala, Kawaihae Uka, Acacia koaia sanctuary, 970 m., at UV light, 18.vii.2004, PT Oboyski.

ADDITIONAL MATERIAL: 2♂ (HDOA): Hawaii, Kawaihae Uka, ex: *Acacia koaia* dead twig, 3.iii.52, C.J. Davis collector. 3♂ (HDOA): Hawaii, Kawaihae Uka, ex: *koaia*, 17.ii.65, C.J. Davis collector, H-65-1. 1♂ (HDOA): Hawaii, Kawaihae Uka, ex: *Acacia koaia*, 30.i.68, C.J. Davis collector.

BIOLOGY: The larvae of *C. koaiae* feed in the senescing terminal branches of *Acacia koaia*, along with *C. walsinghamii*. It is unclear whether larvae cause the senescence or infest already senescing branches. Larvae are most likely attacked by the suite of *Cydia* parasitoids in Hawaii, although I know of none that has been reared. Host trees at the *Acacia koaia* sanctuary on Hawaii Island are interspersed with *Sophora chrysophylla* from which I have reared *Cydia makai* and its parasitoids, *Pristomerus hawaiiensis*, *Diadegma blackburni*, *Calliephialtes grapholithae* (Ichneumonidae), and *Euderus metallicus* (Eulophidae). The adults of *C. koaiae* are attracted to lights.

DISTRIBUTION: Endemic to Hawaiian Islands: Hawaii – Kohala, 950-1000 m. Appears to be limited to a small, protected population of *Acacia koaia* trees in the Kohala district of Hawaii Island. Although a small population of *Acacia koaia* exists on Molokai, a single *Cydia* specimen reared from these trees is clearly *C. walsinghamii*. *Acacia koaia* also grows on Maui, but I have not seen these trees, nor do I know of any moths that have been collected in association with them.

REMARKS: Zimmerman (1978) qualified this as a new species that may have been confused with *C. walsinghamii* by past researchers, but declined to name it. Unlike *C. walsinghamii*, however, *C. koaiae* has the sex pouch in the male hindwing. This species was discovered by the late entomologist C.J. Davis in 1965, who first investigated the senescing branches of *Acacia koaia* at its sanctuary enclosure in Kohala, Hawaii (see photo in Zimmerman 1978: figure 377).

*Cydia conspicua* (Walsingham 1907)  
(Figures 40, 41, 64, 82)

*Enarmonia* (?) *conspicua* Walsingham 1907:684; Plate X. Figure 28 (moth)

*Adenoneura conspicua*. – Meyrick 1928:98; 1932: 222. Swezey 1954:4

*Cydia conspicua*. – Zimmerman 1978:585; Figures 372 (wing venation), 376 (pupa), 378 (moth), 385 (♂ genitalia), 390-391 (♀ genitalia)

**DIAGNOSIS:** Most closely allied with *C. koaiae* from Hawaii Island, sharing similar black, gray, and white color patterns on the forewings. Males of *C. conspicua* with cucullus elongate rounded while most males of *C. koaia* have an angle near the apex of cucullus. Alternate forms of *C. conspicua* on Oahu (Figure 41) more closely resemble the color patterns of *C. walsinghamii*, but males of *C. walsinghamii* lack the hindwing pouch.

**DESCRIPTION:** (exp. 12-20 mm, n=27) Scale colors on head, body, and legs mostly shades of grayish-brown with whitish tips. **Head:** Antennae and labial palpi uniformly brownish-cinereous, palpi somewhat lighter on top. Head uniformly whitish-brown. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsally and ventrally brownish-cinereous, lighter ventrally, tegulae somewhat ferruginous. Without dorsal tuft of scales. Legs whitish-fuscous, tibia darker than femur, tarsomeres banded with fuscous bases and lighter tips. No discernable sex scales (e.g. hair pencils). **Forewings:** (Figures 40-41) Slightly dilated distally, costa gently arched, apex obtuse, termen somewhat sinuate. Ground color ochreous-white, overlaid by variable pattern elements. Costal strigulae distinct, directed distally towards termen. Most often with a distinct triangular costal patch suffused from base to two-thirds length of costa, posteriorly overlapping the fold, ranging in color from fuscous to ferruginous. Costal patch sometimes not fully suffused anterior-basal leaving an indistinct basal suffusion or an oblique medial fascia extending from end of the cell towards basal dorsum. Distal end of cell with a conspicuous white discal patch. Occasionally costal patch with a fuscous projection from below discal patch towards tornus (as in ♀ holotype) or a triangular fuscous pretornal blotch. Pale ocellar area with three or four ocellar spots not always visible, bordered distally by a lighter brownish-white crescent. Apex with a subtriangular fuscous-ferruginous patch extending into fringe. Continuation of fuscous-ferruginous stria to central termen extends into fringe. Ventrally brown-fuscous with pale basal anal area. **Hindwings:** Uniformly brown-fuscous, somewhat paler ventrally. Males with glandular ventral pouch along path of CuP opening dorsally and enclosing elongate modified pecten scales. Vein A3 in males displaced towards the anal margin. Males without an anal roll or androconial scales (thecae) along vein A3. **Abdomen:** Uniformly fuscous. **Male genitalia:** (Figure 64) Tegumen simple, with bilobed or rounded crista along the caudal ridge, lacking gnathos, socii, and uncus. Valvae with excavation in basal third, costa slightly concave, ventral margin with shallow invagination. Sacculus slightly sinuous, with slight concavity near base. Cucullus elongate rounded with dense short setae along ventral and distal margin, interspersed with fewer long setae. Aedeagus simple, strongly curved, without cornuti, spatulate tip excavated dorsally for one-fifth length of aedeagus. **Female genitalia:** (Figure 82) Lamellae postvaginalis slightly longer than wide, hourglass-shaped. Antrum without complex sclerotization pattern, elongate with a lobe extending just beyond junction with ductus bursae. Corpus bursae with diverticulum. Two long, falcate signa on opposite side of corpus bursae (no proximate as suggested by

Zimmerman 1978). Ductus bursae short, joined broadly to corpus bursae, quickly tapering to antrum.

TYPE MATERIAL: *Enarmonia (?) conspicua* Walsingham – ♀ holotype (BMNH): Hawaiian Islands, Maui, Haleakala, 5000 ft., x.1896, RCL Perkins; Walsingham specimen 28134; genitalia slide BM 2052. ♂ paratype (BMNH): Oahu, Honolulu, P. 08, RCL Perkins. 2♂, 2♀ paratypes (BMNH): Oahu, Kahauiki, bred [*Acacia koa*], OH Swezey, 28.ix.1924; [includes 2♂ pupal cases, 1♀ head in a vial].

ADDITIONAL MATERIAL: 1♂ (BPBM): Oahu, Sugarloaf hill, ex: koa seeds [= *Acacia koa*], 15.xi.1922, OH Swezey. 3♀ (HDOA): Oahu, Kahauiki, ex: koa bark, 28.ix.1924, OH Swezey; (determined by Meyrick). 4 (HDOA): Oahu, Kahauiki, ex: koa, 14.ix.1930, OH Swezey. 2♂ (HDOA): Oahu, Tantalus, 25.x.1930, FC Hadden; (determined by Meyrick). 1♀ (EMEC): Hawaiian Islands, Kauai, Kokee State Park, Canyon trail, trail head, 1052 m., at UV light, 28.ii.2005, PT Oboyski. 2♂ (EMEC): Hawaiian Islands, Kauai, Kokee State Park, Canyon trail, trail head, 1052 m., at UV light, 5.iii.2005, PT Oboyski. 3♂ (EMEC): Hawaiian Islands, Kauai, Kokee State Park, Makaha road, 1040 m., at UV light, 17.vi.2005, PT Oboyski. 1♂, 1♀ (EMEC): Hawaiian Islands, Kauai, Kokee State Park, Kumuwela ridge, 1113 m., at UV light, 20.vi.2005, PT Oboyski. 1M (EMEC): 1♂, 1♀ (EMEC): Hawaiian Islands, Kauai, Kokee State Park, Awaawapuhi trail, 1027 m., at UV light, 21.vi.2005, PT Oboyski. 3♂ (EMEC): Hawaiian Islands, Kauai, Kokee State Park, Awaawapuhi trail, 1171 m., at UV light, 23.vi.2005, PT Oboyski. 1♂ (EMEC): Hawaiian Islands, Kauai, Kokee State Park, 4WD road off Canyon road, 887 m., at UV light, 26.vi.2005, PT Oboyski. 1♂, 3♀ (EMEC): Hawaiian Islands, Oahu, S. Waianae Mtns., TNC Honouliuli preserve, Kaluaa section, 607 m., at UV light, 22.vii.2005, PT Oboyski. 1♂, 1♀ (UHMA): HI: Oahu, Koolau Mtns, Wiliwilinui Trail, UV light trap, 6 June 2006, J. Eiben & W. Haines.

BIOLOGY: Larvae feed in the seeds and decaying bark of *Acacia koa* (Meyrick 1928, Swezey 1954), and are parasitized by the ichneumonid wasp *Pristomerus hawaiiensis* Perkins (Zimmerman 1978). Adults are readily attracted to ultraviolet lights, typically several hours after sunset, in dense or mature *Acacia koa* forests with senescing branches.

DISTRIBUTION: Endemic to Hawaiian Islands: Maui, Oahu, Kauai. The type specimen is the only known specimen from Maui. This species may persist at low densities on Maui, but probably would be in competition with *C. acaciavora*. This species is relatively common in dense mature *Acacia koa* stands on Kauai.

REMARKS: The forewing patterns in this species are somewhat variable requiring genitalia preparations for conclusive identification. Zimmerman (1978:599) suggested the approximation of the signa in the corpus bursae is a diagnostic characteristic for this species. However, closer examination of the holotype slide (BM 2052) reveals that the signa are on opposite sides of the corpus bursae giving the appearance of proximity. Zimmerman's own slide preparation (Z-XII-62-5) appears to be misplaced (at BPBM) and therefore unavailable for examination, but illustrates the same illusion (Zimmerman, 1978, Figure 391). The male genitalia slide figured by Zimmerman (1978, Figure 385) is also misplaced (at BPBM), but shows a bilobed uncus margin not seen in other specimens of this species.

*Cydia rufipennis* (Butler 1881)  
(Figures 42, 43, 61, 80)

*Phoxopteris rufipennis* Butler 1881:395

*Adenoneura rufipennis*. – Walsingham 1907:680; Plate X. Figure 22 (moth), Swezey 1936:198, 1954:4

*Cydia rufipennis*. – Zimmerman 1978:609; Figures 375 (wing venation), 382 (moth), 388 (♂ genitalia), 397 (♀ genitalia), Plate 2:8 (moth). Stein 1983a:318, 1983b:300. Miller 1990:136

**DIAGNOSIS:** *Cydia rufipennis*, from Oahu and Kauai and its sister, *C. montana*, from Hawaii and Maui, are the two smallest species of Hawaiian *Cydia*. They appear to be in the early stages of diversification and may represent an evolutionary grade rather than two separate clades. The size and reddish hue of *C. rufipennis* is unique among Hawaiian *Cydia*.

**DESCRIPTION:** (exp. 6-10 mm, n=26) **Head:** Head testaceous, labial palpi buff with testaceous flecks and testaceous third segment, antennae banded ferruginous and buff. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsally ferruginous scales with buff tips, mixed with occasional testaceous scales, particularly in scutellar area, tegulae same. Without dorsal tuft of scales. Ventrally whitish-buff. Fore- and middle-legs ferruginous scales with buff tips, middle-tibia testaceous, middle and hind-tarsi banded fuscous and buff. No discernable sex scales (e.g. hair pencils). **Forewings:** (Figures 42-43) Slightly dilated distally, costa gently arched, apex obtuse, termen nearly straight. Ground color fuscous-brown. Costal strigulae distinct interspersed with testaceous streaks, directed distally towards termen, striae indistinct in basal half creating mottled appearance. No triangular costal patch. Testaceous oblique medial fascia extending from end of cell towards basal dorsum, bordered distally by small whitish discal patch. Testaceous streak extending from medial fascia below discal patch, connecting with vague testaceous pretornal blotch. Ocellar patch light ferruginous with 2-3 ocellar spots, bordered distally by a plumbaginous crescent and anteriorly by oblique testaceous streak ending in the central termen. Testaceous subtriangular apical patch extends along termen as a thin band. Fringe ferruginous. Ventrally costal strigulae apparent along costal margin, otherwise uniform dark brown. **Hindwings:** Dorsally and ventrally dark brown, fringe light brown-buff. Males with glandular ventral pouch along path of CuP opening dorsally and enclosing elongate modified pecten scales. Vein A3 in males displaced towards anal margin. Males without anal roll or androconial scales (thecae) along vein A3. **Abdomen:** Uniformly dark brown, caudal area sometimes ringed by light brown-buff scales. **Male genitalia:** (Figure 61) Tegumen simple with small central point along caudal ridge, lacking gnathos, socii, and uncus. Valvae with excavation in basal third, costa gently concave, ventral edge with somewhat shallow invagination. Sacculus slightly sinuous, with slight concavity near base. Cucullus elongate rounded with short setae along ventral and distal margin sparsely intersperse with longer setae. Aedeagus simple, curved, without cornuti, tip with a slight dorsal notch. **Female genitalia:** (Figure 80) Lamellae postvaginalis longer than wide, constricted centrally and flared into two lobes on the caudal end. Antrum narrow elongate cylindrical with no obvious sclerotization, not extending past junction with ductus bursae. Corpus bursae with diverticulum, two falcate signa. Ductus bursae shorter

than width of corpus bursae, with broad junction to corpus bursae, but otherwise narrow as antrum.

TYPE MATERIAL: *Phoxopterus rufipennis* – ♀ holotype (BMNH): Hawaiian Islands, 81.7 109 [Blackburn code on other specimens indicating “the mountains of Oahu” Zimmerman (1978: 609)]. ♂ cenotype (BMNH): Oahu, Waianae Mtns., 2000 ft, IV.1892, RCL Perkins; Walsingham specimen 25094. ♀ cenotype (BMNH): Oahu, Waianae Mtns., 2000 ft, IV.1892, RCL Perkins; Walsingham specimen 25097.

ADDITIONAL MATERIAL: 1♂ (BMNH): Hawaiian Islands, Kauai, Lihue, 4000 ft, VII.1896, RCL Perkins; Walsingham specimen 28032; genitalia slide BM 2058. 1♀ (BMNH): Hawaiian Islands, Kauai, Kaholuamano, 4000 ft, IV.1895, RCL Perkins; Walsingham specimen 27734. 1♂ (BMNH): Hawaiian Islands, Oahu, Halemano, c. 2000 ft, XII.1892; RCL Perkins; Walsingham specimen 25822. 1♀, 1? (BMNH): Oahu, Waianae Mtns., 2000 ft, IV.1892, RCL Perkins; Walsingham specimens 25096, 25100 respectively. 2 (BMNH): Hawaiian Islands, 1899, Blackburn. 3♀ (BPBM): Oahu, Waianae Mtns., 2000 ft, IV.1892, RCL Perkins; Walsingham specimen 25095, 25098, 25099; (abdomen missing from 25095 & 25098). 1♂ (BPBM): Oahu, Honolulu, 21.iii.1917, JC Bridwell. 1♀ (BPBM): Oahu, Tantalus, OH Swezey; (right FW missing). 1♂, 1♀ (BPBM): Oahu, Kahili, ex: *Acacia koa* seeds, OH Swezey; (♀ abdomen missing). 1♂ (EMEC): Hawaiian Islands, Kauai, Kokee State Park, Awaawapuhi trail, 1101 m., at UV light, 23.vi.2005, PT Oboyski. 3♀ (EMEC): Hawaiian Islands, Kauai, Kokee State Park, 4WD road off Canyon road, 889 m., at UV light, 25.vi.2005, PT Oboyski. 1♂ (UHMA): HI: Kauai Island, Na Pali - Kona F.R., Mohihi Rd @ Waiakoali Stream, 3400 ft., V-17-05, D. Rubinoff et al. 1♂ (UHMA): HI: Oahu, Koolau Mtns., Wiliwilinui Trail, 6 June 2008, UV light trap, J. Eiben & W. Haines.

BIOLOGY: Larvae of *C. rufipennis* feed on *Acacia koa* within developing seeds, flowers, and flower buds (Swezey 1936, 1954, Zimmerman 1978, Stein 1983a, b). Bridwell (1919) reports that last instar larvae emerge from seedpods to pupate elsewhere. The adults I have collected on Kauai at ultraviolet lights were only amid flowering *Acacia koa* trees.

DISTRIBUTION: Endemic to Hawaiian Islands: Kauai (particularly around Kokee State Park) and Oahu – widely distributed but only locally abundant where *Acacia koa* grows.

REMARKS: *Cydia rufipennis* from the older islands (Kauai and Oahu) is sister to *C. montana* on the younger islands (Maui and Hawaii), and appears to occupy a similar niche.

*Cydia montana* (Walsingham 1907)  
(Figures 44, 45, 46, 62, 81)

*Adenoneura montanum* Walsingham 1907:679; Plate X. Figure 21 (moth). Swezey & Williams 1932:187, Swezey 1936:198, 1954:204

*Cydia montana*. – Zimmerman 1978:595; Figures 373 (wing venation), 381 (moth), 385 (♂ genitalia), 393 (♀ genitalia). Stein 1983a:318

**DIAGNOSIS:** *Cydia montana*, from Hawaii and Maui, and its sister *C. rufipennis*, from Oahu and Kauai, are the two smallest species of Hawaiian *Cydia* (exp. 8-11 mm and 6-10 mm, respectively). They appear to be in the early stages of diversification and may represent an evolutionary grade rather than two separate clades. The light brown mottled coloring of *C. montana* resembles a diminutive *C. storeella* or *C. plicata*, compared to the reddish hue of *C. rufipennis*. However, larger species, such as *C. plicata*, can have diminutive forms under poor food resource conditions (Oboyski, personal observation), as has been noted for other *Cydia* species (Miller 1990). *Cydia montana* is easily distinguished from *C. rufipennis* by the distribution and red hue of the latter, and from *C. storeella* and *C. plicata* by the shape of the female antrum.

**DESCRIPTION:** (exp. 8-11 mm, n=25) Colored scales on head, body, and legs mostly shades of ferruginous-brown with whitish tips. **Head:** Antennae, head and labial palpi light brown-cinereous. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsally light ferruginous-brown, tegulae same. Without dorsal tuft of scales. Ventrally lighter ferruginous-brown. . Legs light brown-ochreous, tarsomeres banded dark brown-cinereous at bases, lighter distally. No discernable sex scales (e.g. hair pencils). **Forewings:** (Figure 44-46) Slightly dilated distally, costa gently arched, apex obtuse, termen nearly straight. Ground color light brown-ochreous. Costal strigulae distinct, directed distally towards termen, striae indistinct in basal half creating mottled appearance. No triangular costal patch. Oblique medial fascia and pretornal blotch indistinct. Whitish discal patch faint. Ocellar patch light brown-ochreous with three ocellar spots, bordered distally by a light bronze crescent. Apex often with a light ferruginous-brown patch extending into fringe. Continuation of ferruginous-brown stria to central termen extends into fringe. Fringe otherwise ferruginous-white. Ventrally dark brown-cinereous, lighter along anal margin. **Hindwings:** Dorsally cinereous-brown basally, ferruginous-brown distally. Males with glandular ventral pouch along path of CuP opening dorsally and enclosing elongate modified pecten scales. Vein A3 in males displaced towards anal margin. Males without anal roll or androconial scales (thecae) along vein A3. **Abdomen:** Uniformly dark brown-cinereous dorsally, lighter ventrally. **Male genitalia:** (Figure 62) Tegumen simple with somewhat bilobed crista along caudal ridge, lacking gnathos, socii, and uncus. Valvae with excavation in basal third, costa gently concave, ventral edge with somewhat shallow invagination. Sacculus slightly sinuous, with slight concavity near base. Cucullus elongate rounded with relatively sparse short setae along ventral and distal margin intersperse with longer setae relative to other Hawaiian *Cydia*. Aedeagus simple, curved, without cornuti, and somewhat bilobed at tip. **Female genitalia:** (Figure 81) Lamellae postvaginalis slightly longer than wide, hardly constricted centrally. Antrum narrow elongate cylindrical with no obvious sclerotization, not extending past junction with ductus bursae. Corpus bursae with diverticulum, two long falcate signa. Ductus

bursae much shorter than width of corpus bursae, with broad junction to corpus bursae, but otherwise narrow as antrum.

TYPE MATERIAL: *Adenoneura montanum* – ♂ holotype (BMNH): Hawaii, Mt Kilauea, vii.1895, RCL Perkins; Walsingham specimen 27483; genitalia slide BM 2055. ♀ holotype (BMNH): Hawaii, Kona, 4000 feet, 10.viii.1892, RCL Perkins; Walsingham specimen 25275. 2♂, 2♀ paratypes (BMNH): Hawaii, Mt Kilauea, vii.1895, RCL Perkins; Walsingham specimens 27423, 27396, 27398, 27405, respectively; ♂ wing slide BM 7531; ♀ genitalia slide BM 2056. ♀ paratype (BMNH): Hawaii, Kona, 4000 ft, 8.ix.1892, RCL Perkins; Walsingham specimen 25561. 3♂ paratypes (BPBM): Hawaii, Mt Kilauea, vii.1895 (2 specimens), viii.1896 (1 specimen), RCL Perkins, Walsingham specimens 27412, 27403, 28083, respectively. 1♀ paratype (mistakenly labeled by Walsingham as ♂) (BPBM): Hawaii, Mt Kilauea, viii.1895, RCL Perkins, Walsingham specimens 27464. ♀ allotype (BMNH?): Hawaii, Kona, 4000 feet; (abdomen lost).

ADDITIONAL MATERIAL: 1 (HDOA): Hawaii, Nauhi gulch, 5000-6000 ft, koa?, 30.ix.1931, OH Swezey & FX Williams; determined by Swezey. 3 (HDOA): Hawaii, Kilauea, HAVO, ex: light trap, ix.1946, CJ Davis; determined by Swezey. 1♀ (EMEC): Hawaiian Islands, Hawaii, Mauna Kea, Hakalau N.W. R., Nauhi cabin, 1640 m., at mercury vapor light, 8.viii.2003, PT Oboyski. 1♀ (EMEC): Hawaiian Islands, Hawaii, Kilauea, HAVO N.P., residential quarters 20, 1150 m., at mercury vapor light, 5.vii.2004, PT Oboyski. 4♂,6♀ (EMEC): Hawaiian Islands, Hawaii, Mauna Loa, HAVO N.P., Mauna Loa strip road, 1885 m., at UV light, 2.viii.2005, PT Oboyski. 3♂ (EMEC): Hawaiian Islands, Hawaii, Kilauea, HAVO N.P., crater rim trail nr. military camp, 1200 m., at UV light, 4.viii.2005, PT Oboyski. 3♀ (EMEC): Hawaiian Islands, Hawaii, Hualalai, top of Kaloko Drive, 1485 m., at UV light, 5.viii.2005, PT Oboyski. 2♀ (EMEC): Hawaiian Islands, Hawaii, Mauna Loa, Kipuka Puu Huluhulu (west side), 2010 m., at UV light, 10.viii.2005, K. Roggeveen. 5♂,2♀ (EMEC): Hawaiian Islands, Hawaii, Mauna Loa, Saddle Road Kipuka mp 21, 1695 m., at UV light, 12.viii.2005, K. Roggeveen. 1♂,1♀ (EMEC): Hawaiian Islands, Hawaii, Mauna Loa, HAVO N.P., Mauna Loa strip road, 1940 m., at UV light, 17.viii.2005, K Roggeveen.

BIOLOGY: Zimmerman (1978) and Stein (1983a), following Swezey (1936, 1954), lists *Sophora chrysophylla* seeds as the host of *C. montana*. I have not been able to locate the specimens Swezey claims to have reared from *Sophora* and suspect that he was mistaken. In fact, one specimen collected by O.H. Swezey and F.X. Williams from Nauhi Gulch, Hawaii Island includes “koa?” on the collection label. Although I have not reared this species, I have observed large numbers of *C. montana* adults at ultraviolet lights located amid mature *Acacia koa* trees, but never among *Sophora* trees. I have also swept adults of this species from the canopy of *Acacia koa* at 1715 m elevation at Keauhou Ranch, Mauna Loa. Extensive efforts to rear larvae from *Acacia koa* seedpods and rust galls have produced mostly *Cryptophlebia illepada* (Butler) and few *Cydia walsinghamii* (Butler), but no *C. montana*. Less effort was spent rearing larvae from *Acacia* flowers, a known substrate for *C. rufipennis*, the sister to *C. montana*. Based on this strong circumstantial evidence, I suspect *C. montana* feeds on *Acacia koa*, particularly on flowers.

DISTRIBUTION: Endemic to Hawaiian Islands: Hawaii – distributed around the island along the “koa belt” (600-1200 m). One specimen collected from 1290 m on Haleakala, Maui.

REMARKS: Although previously thought to feed on *Sophora*, this species is associated with *Acacia koa* and is the Hawaii Island (and Maui) sister-species of *C. rufipennis* found on the older islands (Oboyski Chapter 3). The one specimen I collected on Maui has a reddish hue similar to *C. rufipennis* but the mitochondrial DNA haplotype of *C. montana* (Oboyski Chapter 3), and appears to represent an intermediate form. Specimens misidentified as *C. montana* by Brenner et al. (2002) are correctly referred to *C. plicata*.

*Cydia hawaiiensis* n. sp.  
(Figures 47, 65, 83)

DIAGNOSIS: *Cydia hawaiiensis* is easily confused with *C. walsinghamii* based on size, markings, and habitat, and probably is a close relative. Males of *C. hawaiiensis* have a very shallow pouch on the hindwing relative to other Hawaiian *Cydia*. Males of *C. walsinghamii* lack a hindwing pouch. The genitalia of *C. hawaiiensis* females are nearly identical to *C. walsinghamii*.

DESCRIPTION: (exp. 18-22 mm, n=11) **Head:** Antennae light brown-ferruginous. Head and labial palpi pale ochreous-buff. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsally pale ochreous-buff mottled with fuscous and ferruginous, tegulae with ferruginous bases grading to ochreous caudally. Without dorsal tuft of scales. Venter whitish-buff. Forelegs fuliginous, fore- and midtibia and tarsi banded fuliginous and ochreous. No discernable sex scales (e.g. hair pencils). **Forewings:** (Figure 47) Slightly dilated distally, costa gently arched, apex obtuse, termen nearly straight. Ground color buff. Costal strigulae distinct, directed distally towards termen. Striae in basal area indistinct, mottled ochreous, fuscous, and ferruginous. Triangular costal patch absent. Oblique medial fascia interrupted, represented by dark brown-fuscous patch towards end of cell and oblique patch from fold to dorsum, bordered distally by small white discal patch and whitish oblique band. Costal strigulae in distal half of costa sometimes suffused with dark brown-fuscous patch connecting to dark patch at end of cell. Pretornal blotch reaching to dark patch at end of cell, bordered by dark brown-fuscous with ferruginous center. Ocellar patch light brown-ochreous, ocellar spots indistinct, bordered distally by thin plumbaginous crescent. Dark brown apical patch suffused over much of apical area extending into fringe. Fringe at mid-termen and tornus light brown-ochreous. Ventrally, costal strigulae apparent along costa, otherwise uniformly fuscous-brown. **Hindwings:** Uniformly brown dorsally and ventrally. Males with a very shallow glandular ventral pouch along path of CuP opening dorsally and enclosing elongate modified pecten scales. Vein A3 in males displaced towards the anal margin. Males without an anal roll or androconial scales (thecae) along vein A3. Abdomen: Uniformly dark brown. **Male genitalia:** (Figure 65) Tegumen simple, with broadly rounded caudal ridge, lacking gnathos, socii, and uncus. Valvae with excavation in basal third, costa slightly concave, ventral margin with deep invagination. Sacculus slightly sinuous, with slight concavity near base. Cucullus elongate rounded with dense short and long setae along ventral and distal margin. Aedeagus simple, curved, without cornuti, tip split by two dorsal ridges. **Female genitalia:** (Figure 83) Lamellae postvaginalis slightly longer than wide, with slight central constriction.



Antrum elongate funnel-shaped with small sclerotized line near junction with ductus bursae. Corpus bursae with diverticulum and two falcate signa. Ductus bursae shorter than width of corpus bursae, broadly joined with corpus bursae, quickly tapering to antrum.

TYPE MATERIAL: *Cydia hawaiiensis* – ♂ holotype (BPBM): Hawaiian Islands, Hawaii, Mauna Loa, HAVO N.P., Mauna Loa trail, *Acacia koa* forest, 2035 m., at UV light, 5.vii.2004, PT Oboyski; Oboyski specimen PTO-279.8, genitalia slide pto-s304. ♀ allotype (BPBM): Hawaiian Islands, Hawaii, Mauna Loa, HAVO N.P., Mauna Loa strip road top, *Acacia koa* forest, 2180 m., at UV light, 17.vii.2004, PT Oboyski; Oboyski specimen PTO-322.2, genitalia slide pto-s042. 1♂ paratype (EMEC): Hawaiian Islands, Hawaii, Mauna Loa, Papaloa (upslope of Kona), *Acacia koa* forest, 1560 m., at UV light, 9.vii.2003, PT Oboyski; Oboyski specimen PTO-218.2, genitalia slide pto-s301. 10♂ paratypes (EMEC): Hawaiian Islands, Hawaii, Kilauea, HAVO N.P., Kipuka Puauulu, *Acacia koa* forest, 1195 m., at UV light, 15.i.2004, PT Oboyski. Oboyski specimens PTO-238.1-10, genitalia slides pto-s302, s303.

ADDITIONAL MATERIAL: This species is known only from the type material although some female specimens labeled as *Cydia walsinghamii* in existing collections may be *C. hawaiiensis*.

BIOLOGY: This species is known only from adults collected at ultraviolet lights in *Acacia koa* forest. Probably larvae feed on *Acacia koa*.

DISTRIBUTION: Endemic to Hawaiian Islands: Hawaii.

REMARKS: Adults are attracted to ultraviolet lights.

*Cydia acaciavora* n. sp.  
(Figures 48, 66, 84)

DIAGNOSIS: *Cydia acaciavora* is one of four *Cydia* species in Hawaii (*C. acaciavora*, *C. anomalosa*, *C. crassicornis*, *C. walsinghamii*) that lack the pouch in the male hindwing. Males of *C. acaciavora* can be separated from these other three species by the genitalia, particularly by the long slender shape of the aedeagus. Females of *C. crassicornis* are not known and *C. anomalosa* differ in the shape of the antrum. Females of *C. acaciavora* and *C. walsinghamii* are difficult to distinguish, although the antrum of *C. acaciavora* is more narrow than that of *C. walsinghamii*.

DESCRIPTION: (exp. 13-17 mm, n=4) **Head:** Antennae light brown, head and labial palpi pale ochreous, palpi becoming fuscous distally and ventrally. Palpi slightly upcurved, third segment projecting beyond vestiture of second segment. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsally dark brown-fuscous, tegulae pale ochreous. Without dorsal tuft of scales. Venter whitish-buff. Legs pale cinereous, fore- and midtibia and tarsi banded fuscous and pale ochreous. No discernable sex scales (e.g. hair pencils). **Forewings:** (Figure 48) Slightly dilated distally, costa gently arched, apex obtuse, termen nearly straight. Ground color whitish-buff. Costal strigulae distinct, directly distally towards termen. No triangular costal patch. Basally mottled pale fuscous above cell, cell and below buff mottled with thin fuscous streaks. Oblique medial fascia of light brown vague, with darker distal edge, bordered distally by whitish band and whitish discal patch. Pretornal blotch of dark brown-ferruginous broad and short. Subtriangular

apical patch dark brown-ferruginous extends into fringe. Ocellar patch whitish with 2-3 indistinct ocellar spots, bordered distally by silvery-white crescent. Continuation of brown-ferruginous stria to central termen extends into fringe. Fringe otherwise silvery-buff. Ventrally brown-ferruginous with costal strigulae somewhat apparent. **Hindwings:** Uniformly brown-ferruginous. Males without a glandular ventral pouch, anal roll, or androconial scales (thecae) along vein A3. **Abdomen:** Uniformly brown-ferruginous. **Male genitalia:** (Figure 66) Tegumen simple, with broadly rounded caudal ridge, lacking gnathos, socii, and uncus. Valvae with excavation in basal third, costa gently concave, ventral margin with deep invagination. Sacculus slightly sinuous, with slight concavity near base. Cucullus elongate rounded with dense short setae along ventral and distal margin interspersed with longer setae. Aedeagus simple, curved, long and slender with wider base, without cornuti, flared spatulate tip with dorsal excavation for one-fifth length of aedeagus. **Female genitalia:** (Figure 84) Lamellae postvaginalis longer than wide and relatively narrowed by central constriction. Antrum relatively short and narrow with sclerotized ring at junction with ductus bursae. Corpus bursae with diverticulum and two falcate signa. Ductus bursae short, joined broadly to corpus bursae, quickly tapering to antrum.

TYPE MATERIAL: *Cydia acaciavora* – ♂ holotype (BPBM): MAUI, Haleakala N.P., Kipahulu Vy., Delta Camp. UV light, 15 Jan 2004, D. Rubinoff, W. Haines; Oboyski specimen PTO-343.5, genitalia slide pto-s316. 2♀ paratypes (EMEC): MAUI, Haleakala N.P., Kipahulu Vy., Delta Camp. UV light, 15 Jan 2004, D. Rubinoff, W. Haines; Oboyski specimens PTO-343.1, genitalia slide pto-s315, PTO-343.2. 1♂ paratype (EMEC): Hawaiian Islands, Maui, Olinda, Makawao F.R., Kula pipeline trail, 1280 m., reared from dead *Acacia koa* branch, 27.vii.2002, PT Oboyski; Oboyski specimen PTO-95.20. 1♂ paratype (EMEC): Hawaiian Islands, Hawaii, Kohala, Kawaihae Uka, *Acacia koa* sanctuary, 975 m., sweeping *Acacia koa*, 5.vii.2003, PT Oboyski; Oboyski specimen PTO-149.1, genitalia slide pto-s307.

BIOLOGY: Larvae feed under bark of senescing branches and in *Uromyces koae* rust galls on *Acacia koa*. Although *Pristomerus hawaiiensis* emerged from rearing substrates, it was not possible to determine whether they were associated with *Cydia acaciavora*, *Cydia walsinghamii*, or *Cryptophlebia illepida* larvae, all of which produced adults from the same host material. Adults are attracted to ultraviolet lights.

DISTRIBUTION: Endemic to Hawaiian Islands: Maui – Haleakala. Hawaii – One specimen collected from Kawaihae Uka, *Koaia* sanctuary.

REMARKS: This species may be more widespread than realized, but dismissed as a form of *C. walsinghamii*. Mitochondrial DNA evidence corroborates these are two separate species (Oboyski Chapter 3).

*Cydia walsinghamii* (Butler 1882)  
(Figures 49, 67, 85)

*Proteopteryx walsinghamii* Butler 1882:43

*Enarmonia walsinghami*. – Walsingham 1907:684, 736; Plate XI. Figure 1 (moth). Swezey 1954:5

*Cydia walsinghamii*. – Zimmerman 1978:610; figures 375 (wing venation), 383 (moth), 388 (♂ and ♀ genitalia)

DIAGNOSIS: *Cydia walsinghamii* is one of four *Cydia* species in Hawaii (*C. acaciavora*, *C. anomalosa*, *C. crassicornis*, *C. walsinghamii*) that lack the pouch in the male hindwing. This species can be distinguished by the shape of the antrum in females and the tip of the aedeagus in males.

DESCRIPTION: (exp. 10-22 mm, n=37) **Head**: Antennae, head, and labial palpi light brown-cinereous. Palpi slightly upcurved, third segment projecting beyond vestiture of second segment. Ocelli and chaetosemata conspicuous. **Thorax**: Dorsally light brown-cinereous gradually becoming darker towards scutellum, tegulae same. Without dorsal tuft of scales. Venter light brown-buff. Legs light brown cinereous, hind tarsi paler. No discernable sex scales (e.g. hair pencils). **Forewings**: (Figure 49) Slightly dilated distally, costa gently arched, apex obtuse, termen slightly sinuous. Ground color whitish-buff. Costal strigulae distinct, directed distally towards termen. The following patterns variable in color and degree of suffusion. Triangular costal patch of light brown-ferruginous to dark brown sometimes present, suffusing through some of the following patterns. Basal area light brown cinereous mottle with streaks of dark brown-ferruginous. Oblique medial fascia ferruginous with dark brown-ferruginous streaks from end of cell towards basal dorsum, bordered distally by band of whitish-buff and whitish discal patch. Conspicuous pretornal blotch of ferruginous to dark brown-ferruginous nearly reaching to discal patch. Ocellar patch whitish-buff with three distinct ocellar spots, bordered distally by silvery-white crescent. Subtriangular apical patch ferruginous extending into fringe. Continuation of brown-ferruginous stria to central termen extends into fringe. Fringe otherwise pale cinereous. Ventrally brown-cinereous. **Hindwings**: Uniformly light brown-cinereous to fuscous. Males without a glandular ventral pouch, anal roll, or androconial scales (thecae) along vein A3. **Abdomen**: brown-cinereous. **Male genitalia**: (Figure 67) Tegumen simple, crista of broadly rounded caudal ridge with central point, lacking gnathos, socii, and uncus. Valvae with excavation in basal third, costa slightly concave, ventral margin with deep invagination. Sacculus slightly sinuous, with slight concavity near base. Cucullus elongate rounded with dense short and long setae along ventral and distal margin. Aedeagus simple, slightly curved, stout near base and middle tapering quickly to end with shallow dorsal excavation at tip, without cornuti. **Female genitalia**: (Figure 85) Lamellae postvaginalis slightly longer than wide, constricted centrally. Antrum funnel-shaped with one thin line of sclerotization on either side and a sclerotized ring at junction with ductus bursae. Corpus bursae with diverticulum and two falcate signa. Ductus bursae shorter than width of corpus bursae, broadly joined with corpus bursae, quickly tapering to antrum.

TYPE MATERIAL: *Proteopteryx walsinghamii* – ♀ holotype (BMNH): Hawaiian Islands, 89.2; 161 [Blackburn collecting code indicating “in the neighborhood of Honolulu” (Zimmerman, 1978:610)]; genitalia slide BM 3756. ♂ cenotype (BMNH): Mt Kilauea, Hawaii, VIII.1896, RCL Perkins; Walsingham specimen 28075; genitalia slide BM 1892. ♀ cenotype (BMNH): Kona, 4000 ft, Hawaii, 12.VIII.1892, RCL Perkins; Walsingham specimen 25765; genitalia slide BM 1893.

ADDITIONAL MATERIAL: 1♀ (BPBM): Hawaii, Hilo, 2000 ft, xii.1895, RCL Perkins; Walsingham specimen 28599. 1♀ (BPBM): Hawaii, Hualalai (Kona), 5000 ft, 5.viii.1892, RCL Perkins; Walsingham specimen 25830; (abdomen missing). 1♂ (BPBM): Hawaii, Kona, 4000 ft, 10.viii.1892, RCL Perkins; Walsingham specimen 25747. 4♂ (EMEC): Hawaiian Is: Hawaii, M. Loa, Kipuka Puu Huluhulu, *A. koa* forest – UV light, 2005 m., 12.viii.2005, K. Roggeveen. 4♂ (EMEC): Hawaiian Is: Hawaii, M.Loia, HAVO N.P., Mauna Loa strip rd, *A.koa* forest – UV light, 1885 m., 2.viii.2005, PT Oboyski. 5♂ (EMEC): Hawaiian Is: Hawaii, Hualalai, top of Kaloko Drive., *A.koa* forest – UV light, 1485 m., 5.viii.2005, PT Oboyski. 7♂ (EMEC): Hawaiian Is: Maui, Haleakala, upper Makawao F.R., *A.koa* forest – UV light, 1291 m., 3.vii.2005, PT Oboyski. 6♂,5♀ (EMEC): Hawaiian Is: Kauai, Kohee, Awaawapuhi trail, ~1.5 mi., *A.koa* forest – UV light, 1027 m., 21.vi.2005, PT Oboyski.

BIOLOGY: Larvae of *Cydia walsinghamii* feed on *Acacia koa* and *A. koaia* in dead twigs, living tips of twigs, and galls caused by *Uromyces koae* rust fungus (Swezey 1954), as well as *Acacia koa* seeds (Zimmerman 1978). Larvae compete for these resources with *Cryptophlebia illepada*, *Cydia rufipennis*, *C. montana*, and *C. conspicua*, although some resource partitioning likely takes place among species. *C. walsinghamii* larvae are parasitized by the ichneumonid *Pristomerus hawaiiensis* and probably other parasitoids that attack *Cydia* larvae in Hawaii. Adults are often abundant at lights in *Acacia* habitat.

DISTRIBUTION: Endemic to Hawaiian Islands: Common and abundant where mature *Acacia koa* trees can be found on Hawaii, Maui, Oahu, and Kauai islands. It probably occurred on Molokai and Lanai, but naturally growing *A. koa* no longer occurs on these islands. However, I reared one specimen from a dead twig of *Acacia koaia* from a senescing natural population of this tree within a protective enclosure fence in the Kamiloloa section of the Molokai Forest Reserve, Molokai.

REMARKS: This is a widespread and extremely variable species, both in size and color. Zimmerman (1978) suspected *C. walsinghamii* to be a species complex, but did not attempt to qualify the different forms. The collection of Dr. Klaus Sattler at the BMNH contains long series of morphologically variable specimens from Hawaii, Oahu, and Kauai that may represent new species. However, these specimens were not available for dissection and genitalia analysis. More than one species may exist within what is currently called *walsinghamii*, but this is obscured by the extreme variation within this species.

*Cydia crassicornis* (Walsingham 1907)  
(Figure 68)

*Enarmonia crassicornis* Walsingham 1907:685; Plate XI. Figure 2 (moth)

*Cydia crassicornis*. – Zimmerman 1978:585; Figures 373 (wing venation), 378 (moth), 384 (male genitalia)

**DIAGNOSIS:** *Cydia crassicornis* is one of four *Cydia* species in Hawaii (*C. acaciavora*, *C. anomalosa*, *C. crassicornis*, *C. walsinghamii*) that lack the pouch in the male hindwing. Although possibly a form of the widespread and polymorphic *walsinghamii*, the caudal ridge of the tegumen lacks the minute crista (Figure 68) found on *walsinghamii* (Figure 67). The tip of the aedeagus of male *C. crassicornis* (Figure 68) is not excavated as in *C. acaciavora* (Figure 66). Males of *C. crassicornis* also lack the hindwing anal roll and thecae along vein A3 as in *anomalosa*.

**DESCRIPTION:** (exp. 14 mm, n=2) **Head:** Antennae light brown-cinereous, labial palpi buff white dorsally, light brown-cinereous laterally. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Head buff white, post ocular scales light brown-cinereous, some scales with dark tips. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsally and ventrally buff white, mid-dorsum light brownish white, tegulae light ferruginous anteriorly, becoming lighter posteriorly. Without dorsal tuft of scales. Legs (very worn) light brown-cinereous with cinereous-white spurs and tarsi, midtibia darker with light-tipped scales. No discernable sex scales (e.g. hair pencils). **Forewings:** Slightly dilated distally, costa gently arched, apex barely obtuse, termen straight or slightly convex. Ground color buff white. Costal strigulae distinct, directed distally towards termen. Triangular costal patch mottled fuscous-ferruginous suffused from base to 2/3 length of costa, posteriorly overlapping the fold. Dorsal area light ochreous-white contiguous with white patch at distal end of cell, very light brown-cinereous suggestion of a pretornal patch. Ocellar patch with two or three indistinct ocellar spots bordered distally by silvery-bronze crescent. Apex with a light fuscous patch extending into fringe. Continuation of fuscous-ferruginous stria to central termen extends into fringe. Ventrally brown-fuscous. **Hindwings:** Uniformly light brown-cinereous dorsal and ventral, fringe whitish-gray. Males without glandular pouch, cubital pecten not modified. Vein A3 in males similar to females of other species, not displaced towards anal margin as in species with glandular pouch. Males without anal role or androconial scales (thecae) along vein A3. Abdomen: Uniformly brown-cinereous. **Male genitalia:** (Figure 68) Tegumen simple, broadly rounded along caudal ridge, lacking gnathos, socii, and uncus. Valvae with excavation in basal third, costa slightly concave, ventral margin with deep invagination. Sacculus slightly sinuous, with slight concavity near base. Cucullus elongate rounded with dense short setae along ventral and distal margin, interspersed with fewer long setae. Aedeagus simple, slightly curved, without cornuti, tip slightly excavated dorsally with short dorsal projection. **Female genitalia:** (females not known).

**TYPE MATERIAL:** *Enarmonia crassicornis* Walsingham – ♂ holotype (BMNH): Hawaii, Kona, above 4000 ft., ix.1892, RCL Perkins; Walsingham collection 25212; genitalia slide BM 1880. ♂ paratype (BMNH): Hawaii, Kona, above 4000 ft., ix.1892, RCL Perkins; Walsingham collection 25215.

**ADDITIONAL MATERIAL:** This species is known only from two males collected by R.C.L. Perkins in 1892.

**BIOLOGY:** Perkins' field notes for September 1892 indicate he "collected ... by sifting dead leaves at the foot of a big koa tree (4000 ft.)," and later that month in the "rain belt" at lower elevations above Kona (Evenhuis 2007). Perkins also collected the koa-feeding *C. montana* at 4000 ft. above Kona in August and September 1892. Although it is likely *C. crassicornis* was associated with *Acacia koa*, without further information, it is not possible to assign the proper host plant, habitat, larval biology, predators, or parasitoids for this species.

**DISTRIBUTION:** Endemic to Hawaiian Islands: Hawaii Island – known only from two specimens collected above Kona above 1200 m.

**REMARKS:** If not extinct, this species is very rare. The wing venation and genitalia confirm the placement of this species within *Cydia*, though it is unclear without more material whether it represents a separate lineage in Hawaii.

***Cydia anomalosa* n. sp.**  
(Figures 19, 21, 23, 50, 51, 69, 86)

**DIAGNOSIS:** Males of *C. anomalosa* are the only *Cydia* in Hawaii with an anal roll on the hindwing, a characteristic common among non-Hawaiian *Cydia* species. Males also lack the hindwing pouch found on many other Hawaiian *Cydia*. Females can be distinguished from the similar-looking *C. walsinghamii* by the shape of the female antrum.

**DESCRIPTION:** (exp. 10-13 mm, n=11) **Head:** Antennae, head, and labial palpi light brown-cinereous. Palpi slightly upcurved, third segment projecting forward beyond vestiture of second segment. Ocelli and chaetosemata conspicuous. **Thorax:** Dorsally and ventrally light brown-cinereous, tegulae same. Without dorsal tuft of scales. Legs light brown-cinereous. No discernable sex scales (e.g. hair pencils). **Forewings:** (Figures 50-51) Slightly dilated distally, costa gently arched, apex obtuse, termen somewhat sinuate. Ground color whitish-buff. Costal strigulae distinct, directed distally towards termen, sometimes obscured by triangular costal patch of brown-cinereous from base to two-thirds length of costa, posteriorly overlapping the fold. Oblique medial fascia of dark-brown cinereous extending from end of cell towards basal dorsum. Occasionally anal area below fold to pretornal blotch suffused whitish-buff. Pretornal blotch indistinct area of light brown to coppery-brown. Whitish discal patch often indistinct. Ocellar area olivaceous to light brown with three ocellar spots, bordered distally by silvery crescent. Subtriangular apical patch of light brown to coppery brown sometimes extending into fringe. Continuation of ferruginous-brown stria to central termen sometime extending into fringe. Termen with thin band of dark brown-ferruginous from apex through tornus, sometime interrupted. Fringe otherwise light brown-cinereous. Ventrally brown-fuscous. **Hindwings:** Ventrally brown-fuscous, lighter along costal area. Males with anal roll enclosing whitish scales within (Figure 19) and phylliform scales along anal margin (Figures 21, 23). Males without glandular ventral pouch or modified pecten scales. **Abdomen:** brown-cinereous. **Male genitalia:** (Figure 69) Tegumen simple, with broadly rounded caudal ridge, lacking gnathos, socii, and uncus. Valvae with excavation in basal third, costa slightly concave, ventral margin with deep

invagination. Sacculus slightly sinuous, with slight concavity near base. Cucullus elongate rounded with short and long setae intersperse along ventral and distal margin. Aedeagus simple, curved, relatively short and stout, tip mostly flat with a dorsal “hood”. **Female genitalia:** (Figure 86) Lamellae postvaginalis nearly as wide as long, constricted centrally. Antrum simple cylindrical connecting directly with ductus bursae. Corpus bursae with diverticulum and two falcate signa. Ductus bursae shorter than width of corpus bursae, broadly connecting with corpus bursae and tapering only slightly to antrum.

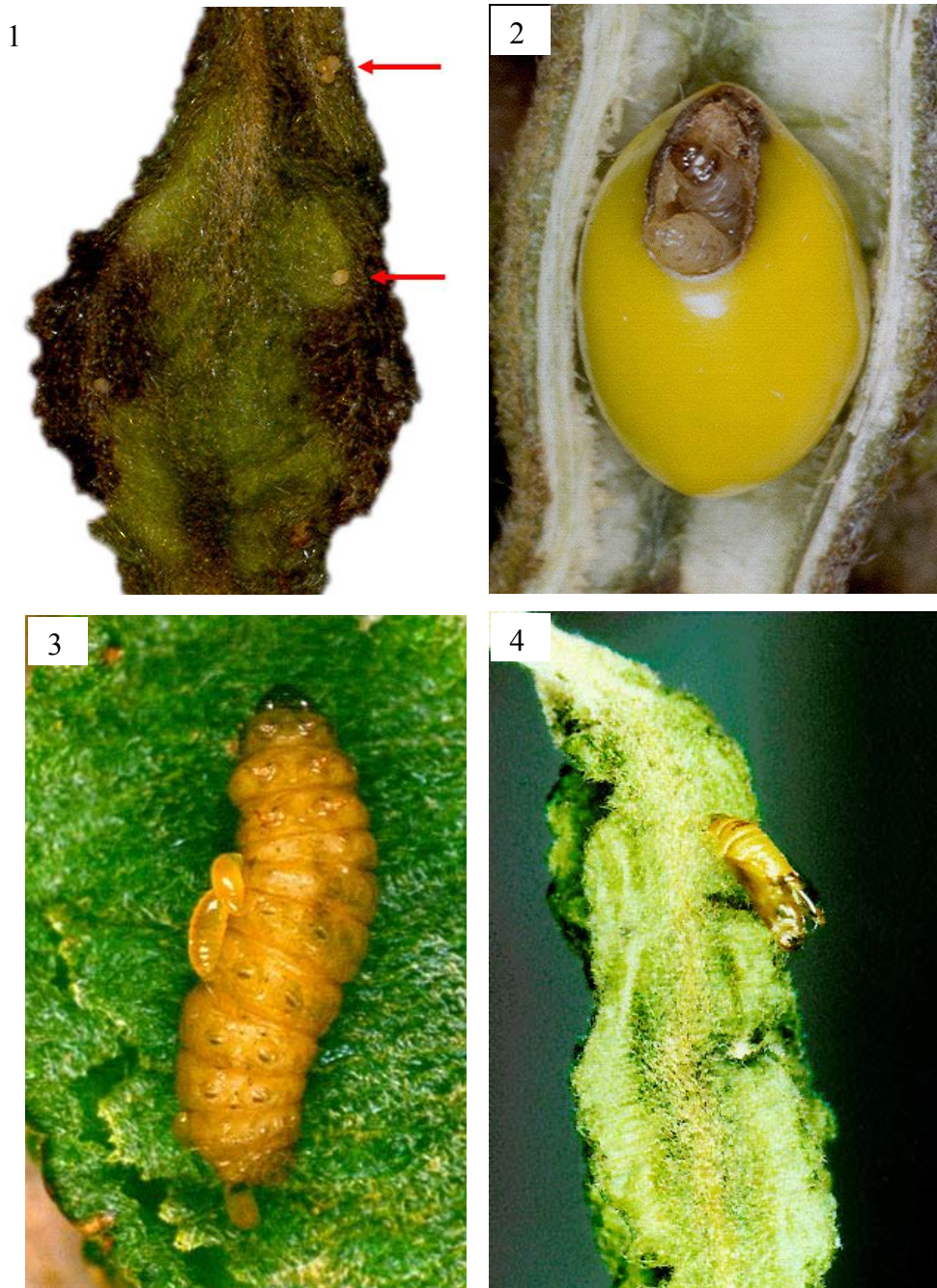
TYPE MATERIAL: *Cydia anomalosa* – ♂ holotype (BPBM): Hawaiian Islands, Kauai, Mt. Kahili State Forest Reserve, 354 m., at UV light, 24.vi.2005, PT Oboyski; Oboyski specimen PTO-513.3. 7♂,2♀ paratypes (EMEC): Hawaiian Islands, Kauai, Mt. Kahili State Forest Reserve, 354 m., at UV light, 24.vi.2005, PT Oboyski; Oboyski specimens PTO-513.1,2,4,5,6,7,8,9,14, genitalia slides pto-s163 (♂ PTO-513.1), pto-s164 (♀ PTO-513.2), pto-s169 (♀ PTO-513.5). 1♂ paratype (EMEC): Hawaiian Islands, Maui, Makawao F.R., Kula pipeline trail, 1280 m., reared from *Acacia koa* pods, 27.vii.2002, PT Oboyski; Oboyski specimen PTO-096.5. 1♂ paratype (EMEC): Hawaiian Islands, Maui, Haleakala N.P., Kaupo Gap, 1680 m., reared from *Acacia koa* pods, 5.viii.2002, PT Oboyski; Oboyski specimen PTO-129.8, genitalia slide pto-s342. 1♂ paratype (EMEC): Hawaiian Is: Maui, upper Makawao F.R., *Acacia koa* forest, 1291 m., at UV light, 3.vii.2005, PT Oboyski; Oboyski specimen PTO-529.8. 1♂ paratype (EMEC): Hawaiian Is: Maui, Haleakala N.P., Kaupo Gap, *A. koa* forest – UV light, 1680 m., 8.vii.2005, PT Oboyski; Oboyski specimen PTO-540.10.

BIOLOGY: Larvae feed within the seedpods of *Acacia koa*. Although *Pristomerus hawaiiensis* and *Euderus metallicus*, which parasitize other *Cydia* species, emerged from seedpods containing *C. anomalosa*, it was not possible to tell whether they emerged from these or *Cryptophlebia illepidia*, found in the same collection of pods. Adults are attracted to ultraviolet lights.

DISTRIBUTION: Endemic to Hawaiian Islands: Kauai – Mt Kahili, Kokee State Park; Maui – Haleakala. Sympatric with *C. conspicua*, *C. acaciavora*, and *C. walsinghamii* at some locations.

REMARKS: This species is typical of non-Hawaiian *Cydia* in having an anal roll and without a sex pouch on the hindwings. It is unlikely that these characters would re-evolve after being lost and appears to represent a separate lineage of *Cydia* in Hawaii. However, mitochondrial and nuclear DNA evidence suggest this species is closely related to other *Acacia*-feeding Hawaiian *Cydia* (Oboyski Chapter 3).



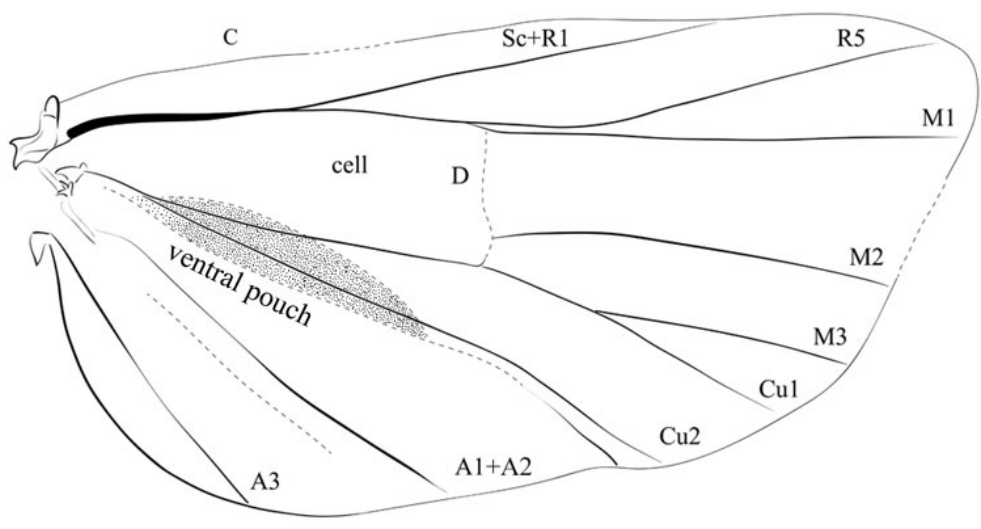
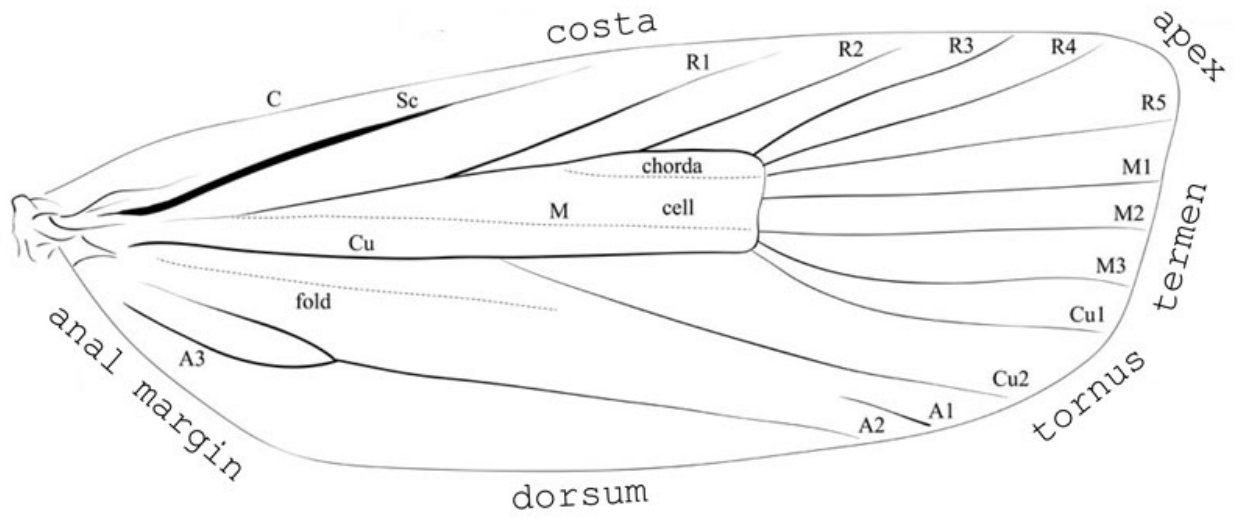


Figures 1-4. Eggs, larvae, parasitoids, and pupa of *Cydia plicata* (Walsingham). 1. Section of *Sophora chrysophylla* seedpod with arrows indicating a cluster of three eggs and a single egg. 2. Larva feeding inside *S. chrysophylla* seed. 3. Larvae of parasitoid *Euderus metallicus* (Ashmead 1901) feeding on *Cydia* larva. 4. Pupal exuvia partially protruding from *S. chrysophylla* seedpod.





Figures 5-8. Host plants of Hawaiian *Cydia*. 5. *Sophora chrysophylla* seedpods on Mauna Kea, Hawaii, arrow indicating silk plug made by *C. plicata* larva. 6. *S. chrysophylla* terminal twig at Kokee, Kauai, showing split from previous *C. makai* feeding. 7. *Acacia koa* at Kokee, Kauai, showing flowers and *Uromyces koae* rust gall. 8. *Canavalia galeata* flowers, seedpods, and stems from Punaluu, Hawaii.



Figures 9. Wing venation of *Cydia parapteryx* (Meyrick). The pouch hangs below the wing opening along a thin slit on the upper surface of the wing along the path of the obscured CuP vein.

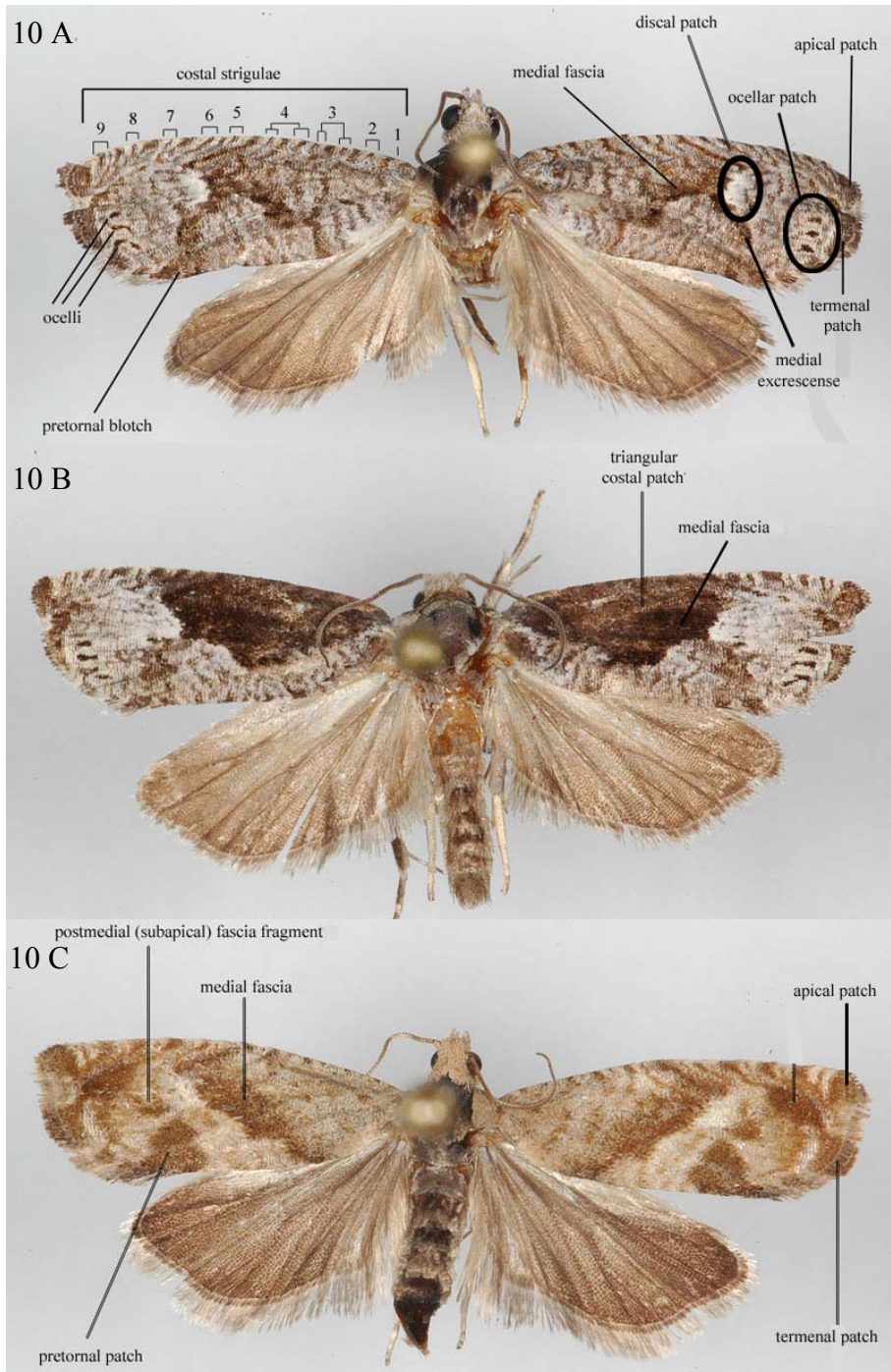


Figure 10. Hawaiian *Cydia* wing pattern elements. A and B. *C. koiiae* n.sp. Oboyski, *C. plicata* (Walsingham).

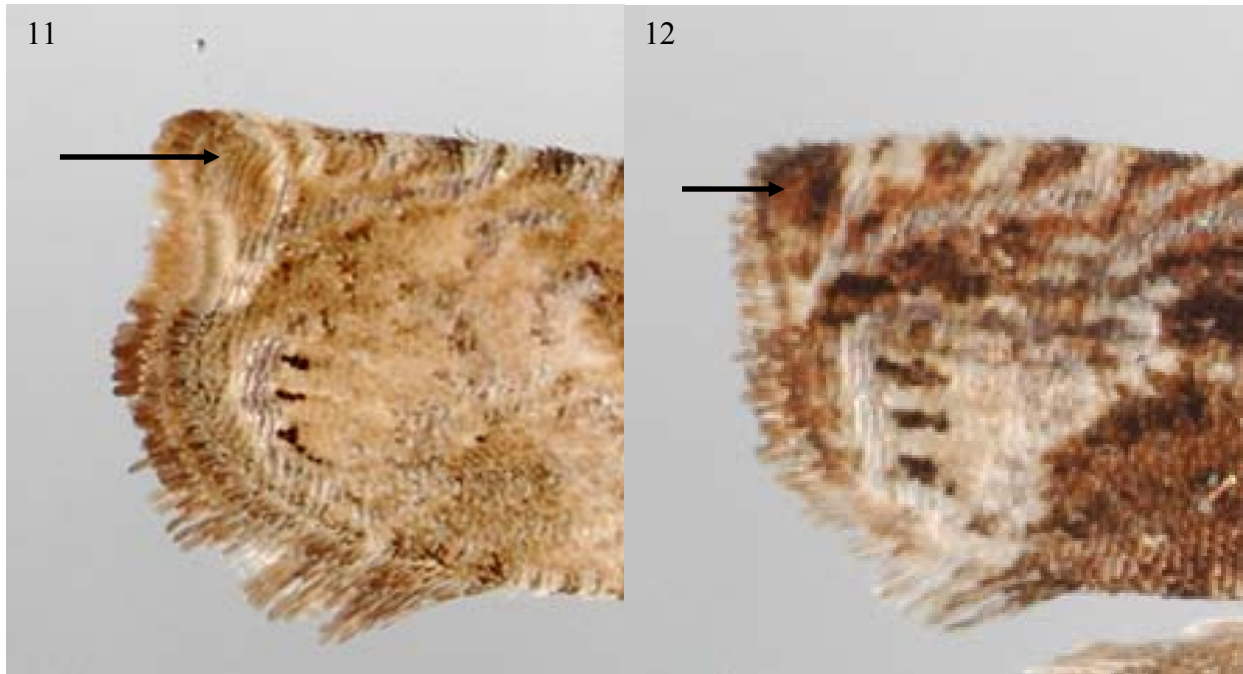
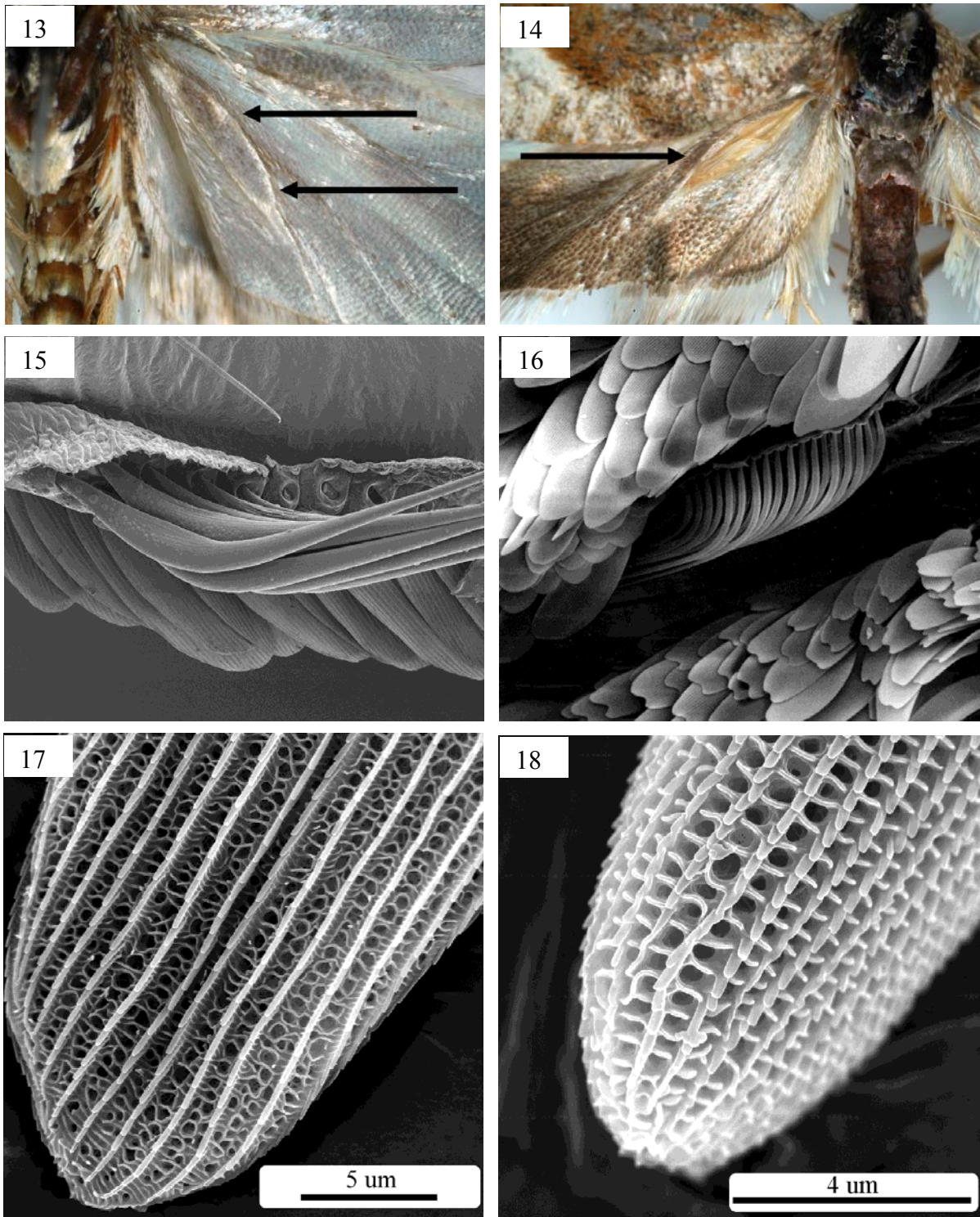
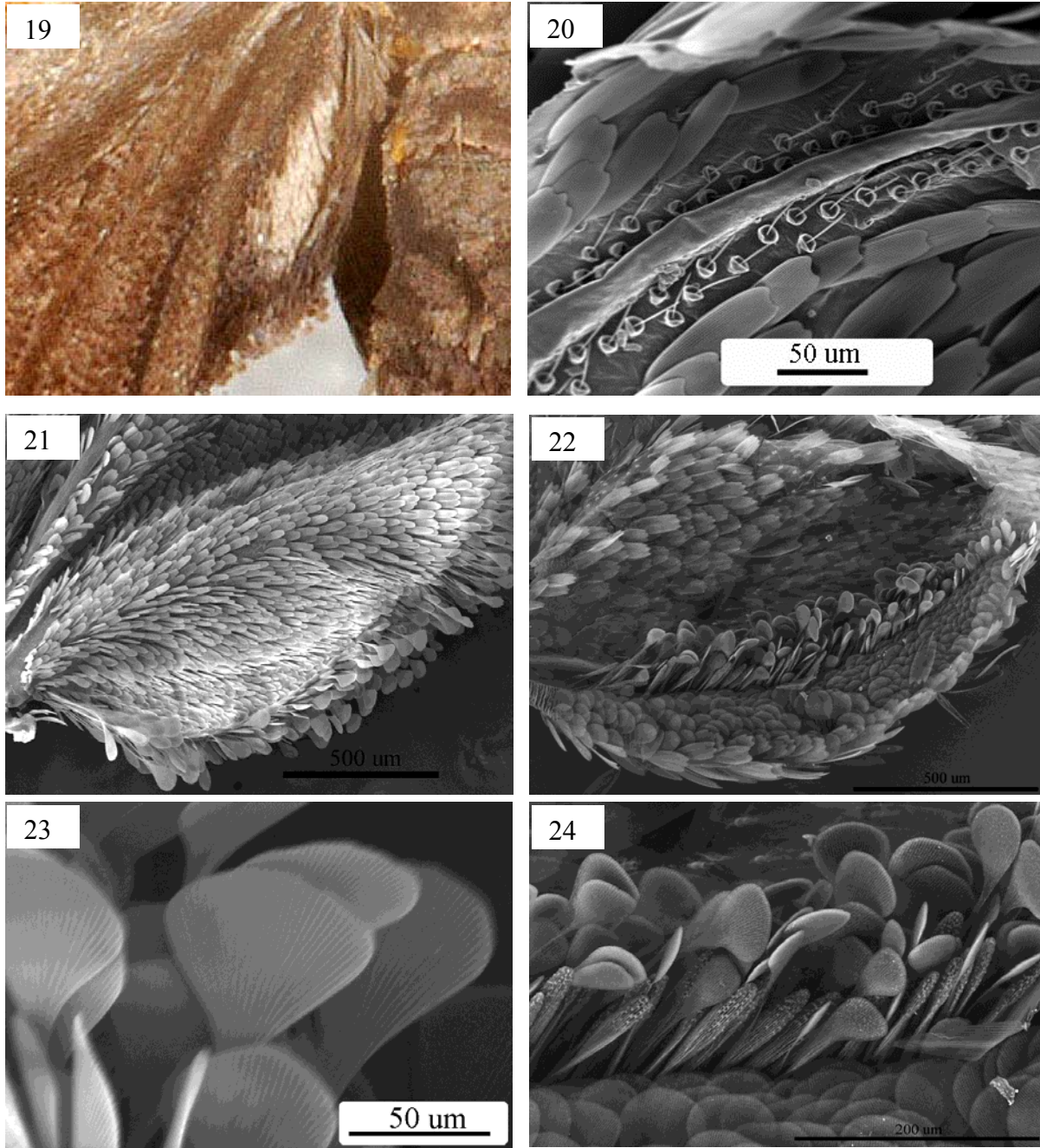


Figure 11-12. Forewing tips of Hawaiian *Cydia*. 11. Forewing tip of *Cydia mauiensis* showing sinuous termen and crescent-shaped apical patch (arrow) characteristic of the *Canavaliae* group of species. 12. Forewing tip of *Cydia walsinghamii* showing the nearly linear termen and subtriangular apical patch (arrow) typical of most Hawaiian *Cydia*.



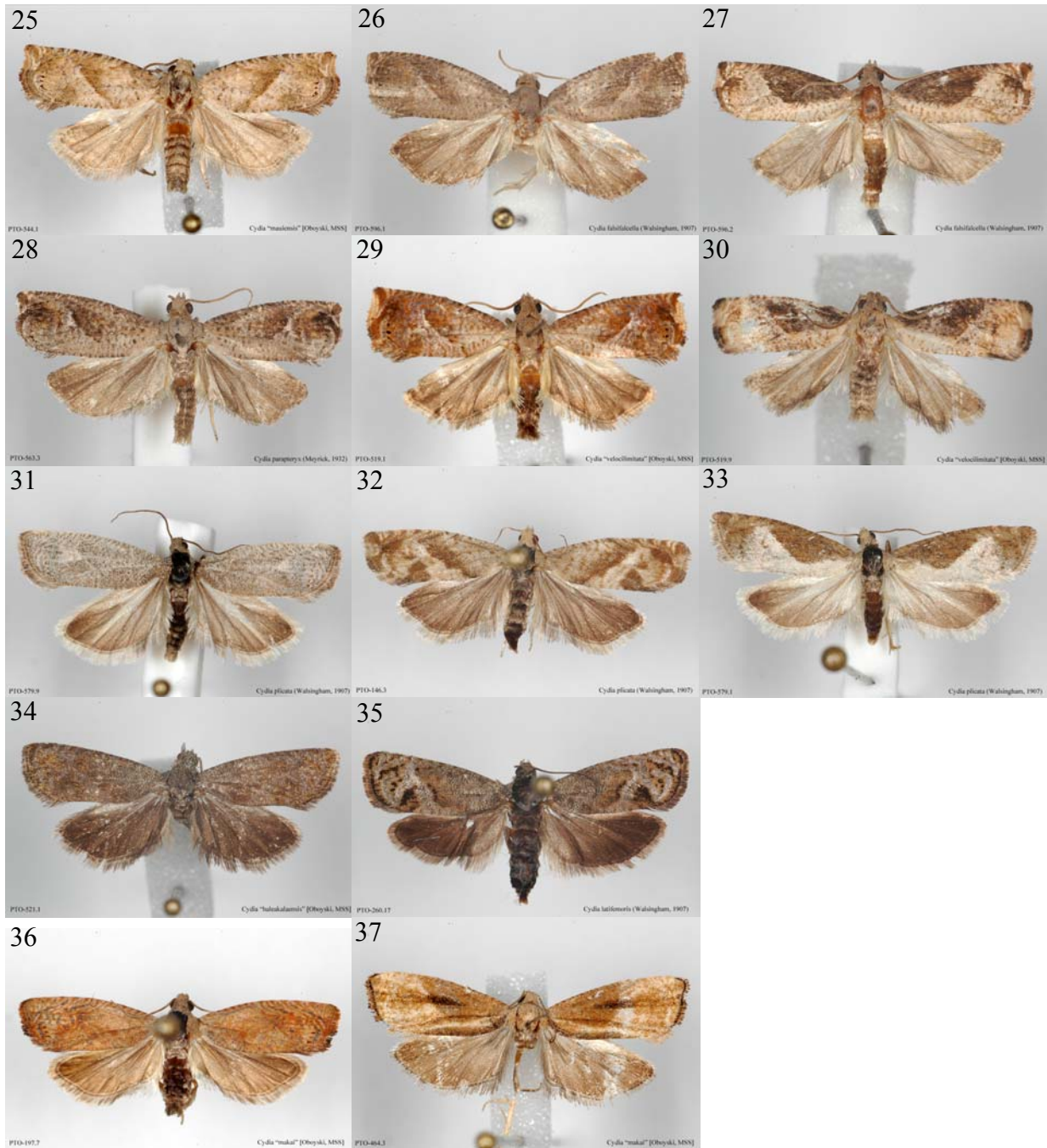


Figures 13-18. Hindwing ventral pouch and modified pecten scales. 13. Ventral view of hindwing pouch (arrows) of *Cydia plicata*, 14. Dorsal view showing opening to pouch (arrow) below cubital in *C. plicata*, 15. Base of modified pecten scales of *C. plicata* bending into pouch, 16. Base of modified pecten scales of *C. latiferreana* from California bending into pouch, 17. Tip of modified pecten scale of *C. plicata*, 18. Tip of pecten modified scale of *C. latiferreana*.

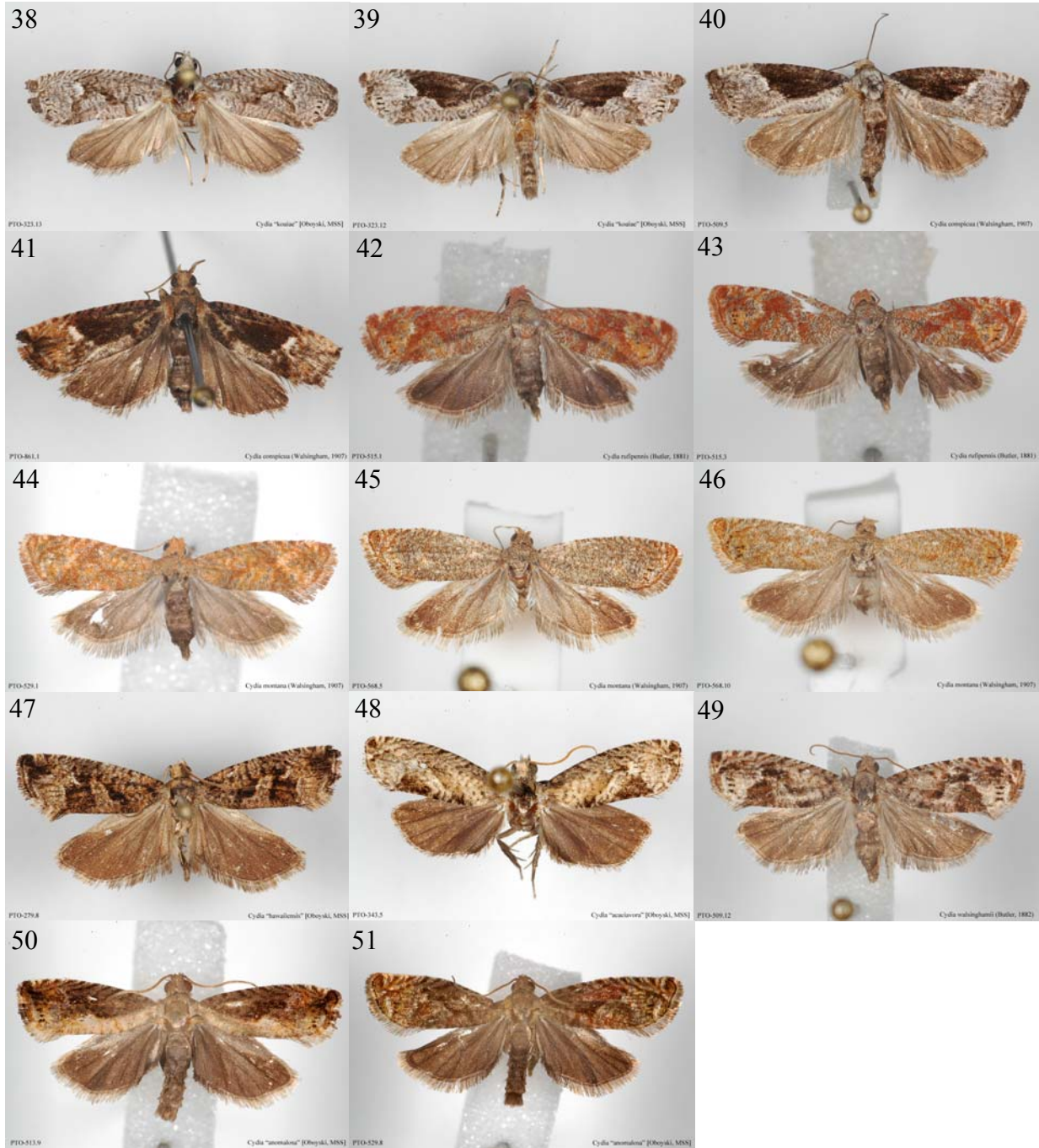


Figures 19-24. Hindwing anal roll with modified scales. 19. *C. anomalosa* showing white scales within dorsal pocket of hindwing anal roll. 20. SEM of thecae (androconial scales) along vein A3 in male hindwing of *C. latiferreana*. 21. SEM of hindwing anal roll of *C. anomalosa*. 22. SEM of hindwing anal roll of *C. latiferreana*. 23. SEM of modified scales along the margin of *C. anomalosa* anal roll showing phylliform sex scales. 24. SEM of modified scales along the margin of *C. latiferreana* anal roll showing phylliform and fusiform sex scales.





Figures 25-37. Hawaiian *Cydia* adult habitus. 25. *C. mauiensis*. 26. *C. falsifalcella*. 27. *C. falsifalcella*. 28. *C. parapteryx*. 29. *C. velocilimitata*. 30. *C. velocilimitata*. 31. *C. plicata*. 32. *C. plicata*. 33. *C. plicata*. 34. *C. haleakalaensis*. 35. *C. latifemoris*. 36. *C. makai*. 37. *C. makai*



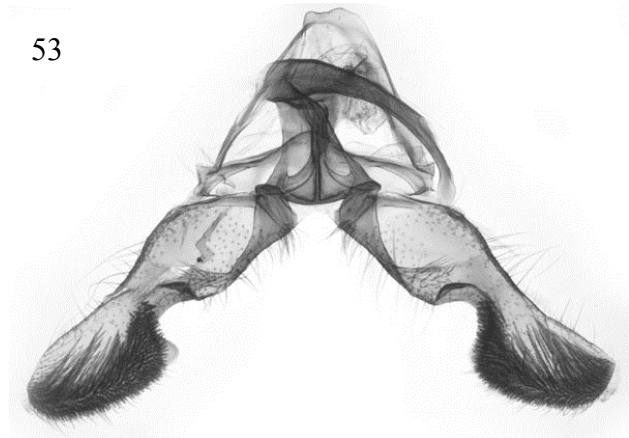
Figures 38-51. Hawaiian *Cydia* adult habitus (continued). 38. *C. koaiae*. 39. *C. koaiae*. 40. *C. conspicua*. 41. *C. conspicua*. 42. *C. rufipennis*. 43. *C. rufipennis*. 44. *C. montana*. 45. *C. montana*. 46. *C. montana*. 47. *C. hawaiiensis*. 48. *C. acaciavora*. 49. *C. walsinghamii*. 50. *C. anomalous*. 51. *C. anomalous*



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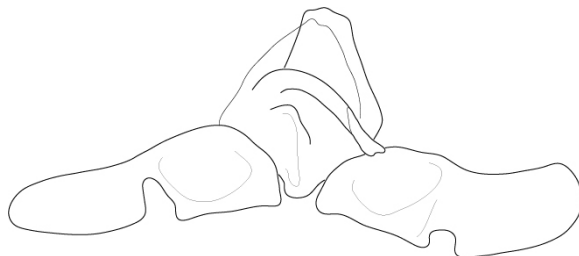
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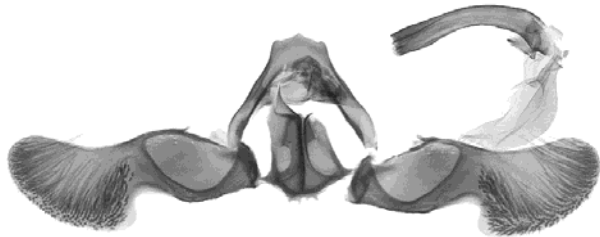


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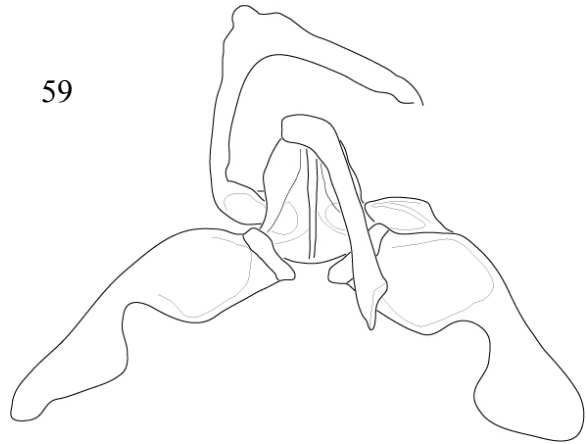


Figures 52-57. Male genitalia 52. *Cydia gypsograpti* – male holotype, slide BM 9543. 53. *C. mauiensis* – male holotype, slide PTO-s254. 54. *C. falsifalcella* – male holotype, slide BM 2051. 55. *C. parapteryx* – slide PTO-s252. 56. *C. velocilimitata* – slide PTO-s170. 57. *C. plicata* – male holotype, slide BM 1885.

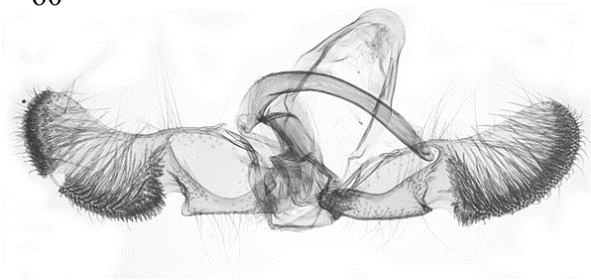
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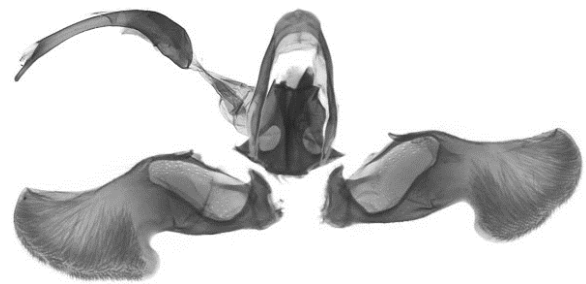
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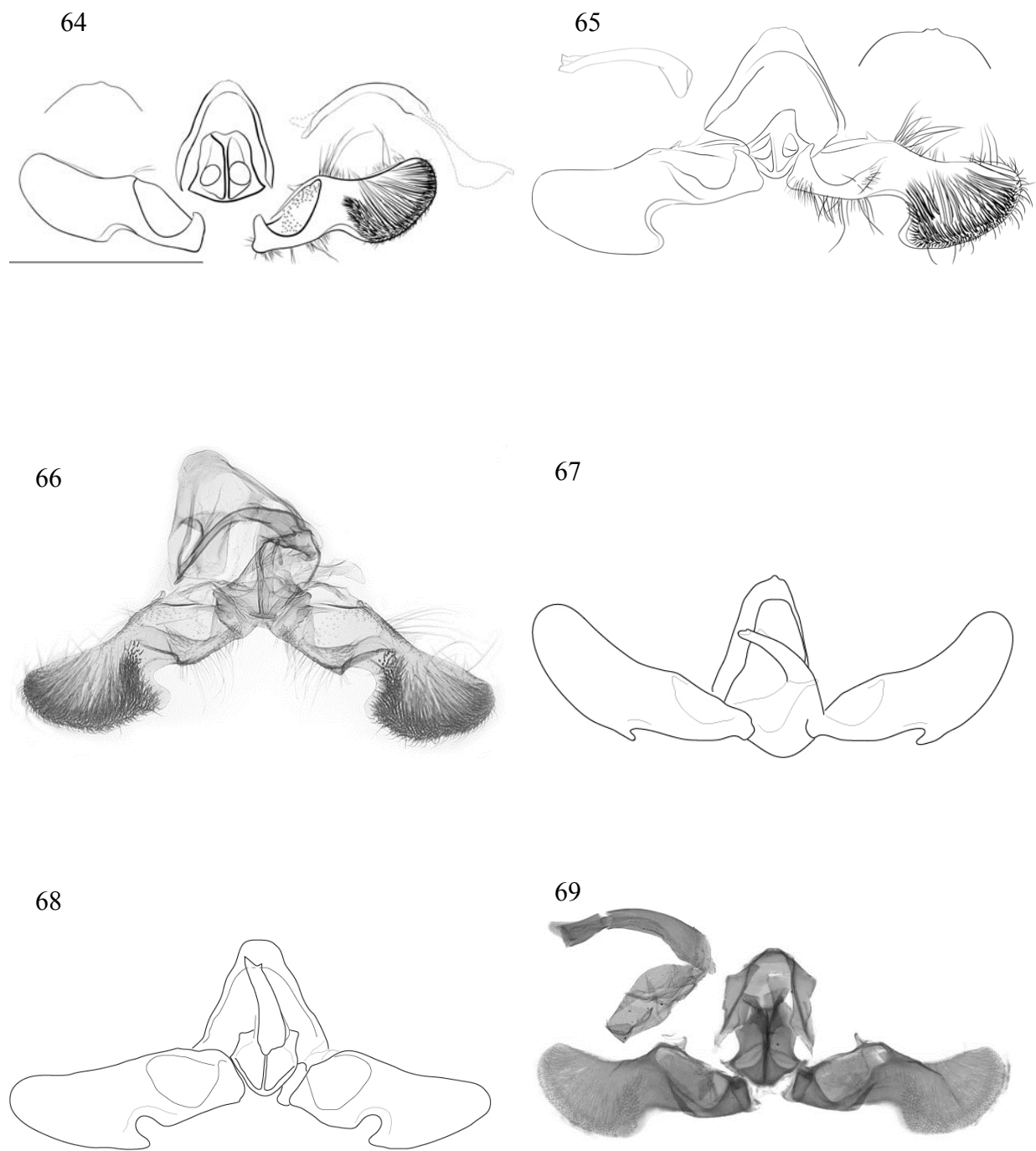
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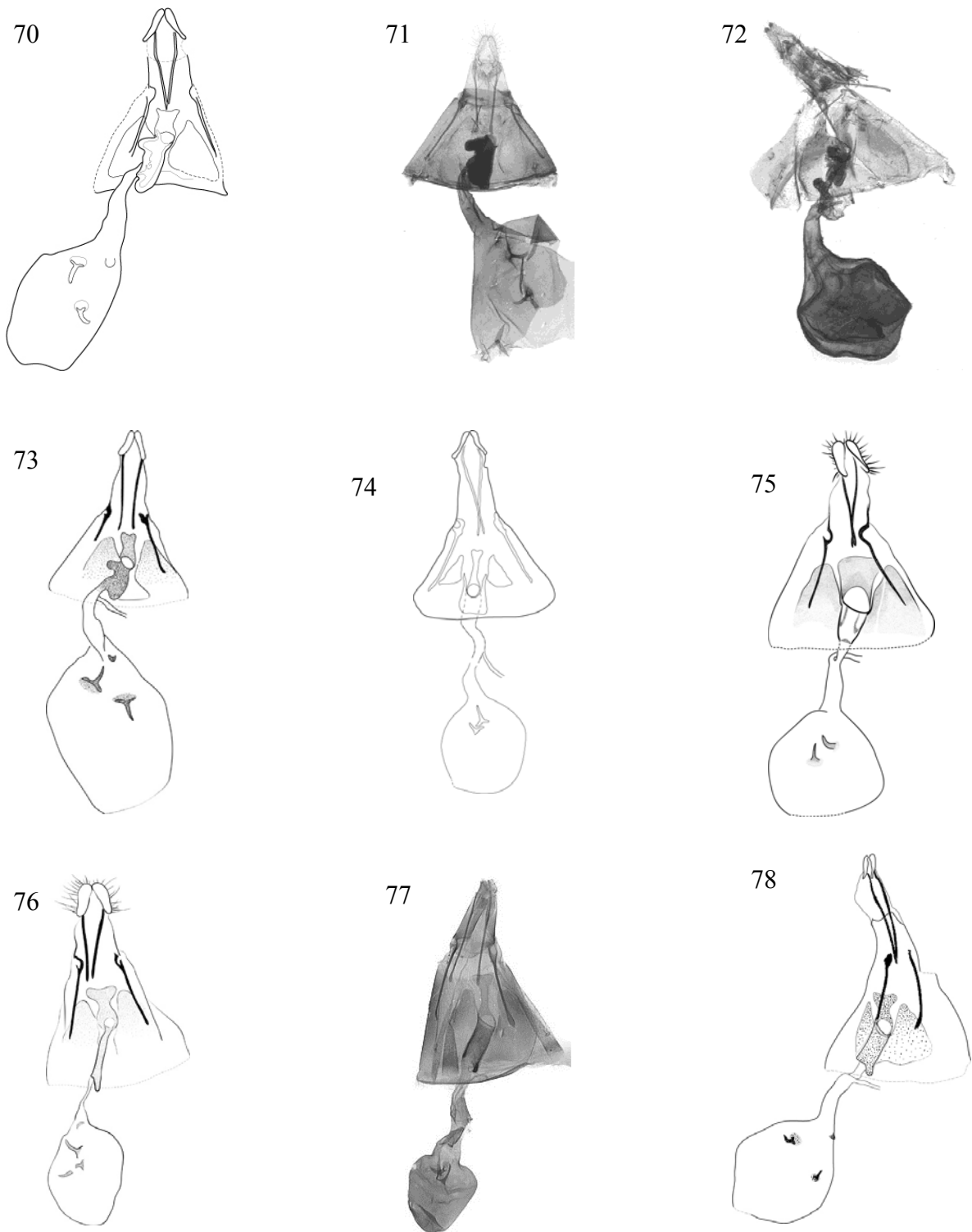
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Figures 58-63. Male genitalia (continued). 58. *Cydia haleakalaensis* – slide PTO-s339. 59. *C. latifemoris* – allotype, slide BM 2053. 60. *C. makai* – slide PTO-s311. 61. *C. rufipennis* – slide BM 2058. 62. *C. montana* – slide PTO-s323. 63. *C. koaiae* – slide PTO-s333.



Figures. 64-69. Male genitalia (continued). 64. *Cydia conspicua* – slide PTO-s335. 65. *C. hawaiiensis* – slide PTO-s302. 66. *C. acaciavora* – slide PTO-s307. 67. *C. walsinghamii* – slide BM 1892. 68. *C. crassicornis* – holotype, slide BM 1880). 69. *C. anomalousa* – slide PTO-s342.



Figures 70-78. Female genitalia. 70. *Cydia chlorostola* – holotype, slide BM 9546 Clarke. 71. *C. mauiensis* – slide PTO-s154. 72. *C. falsifalcella* – slide PTO-s183. 73. *C. parapteryx* – paralectotype, slide BM 7549. 74. *C. plicata* – allotype, slide BM 1886. 75. *C. obliqua* – holotype, slide BM 1882. 76. *C. storeella* – holotype, slide BM 1881. 77. *C. haleakalaensis* – slide PTO-s318. 78. *C. latifemoris* – holotype, slide BM 2054.

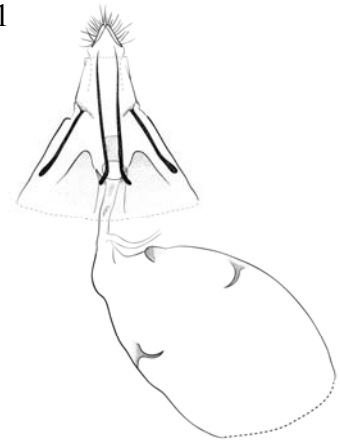
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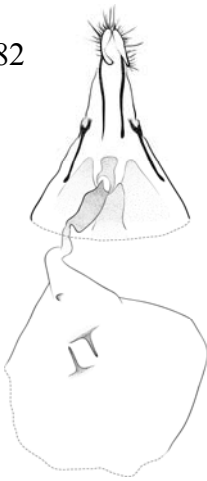
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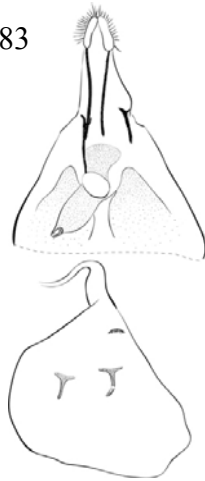
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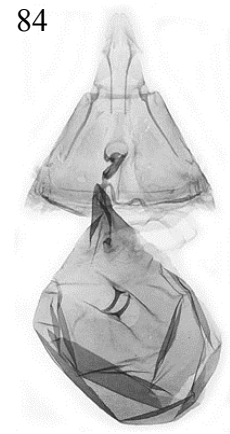
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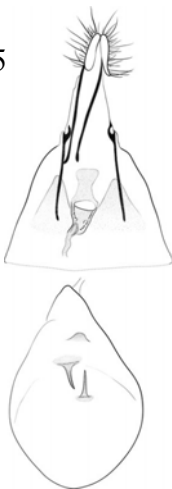
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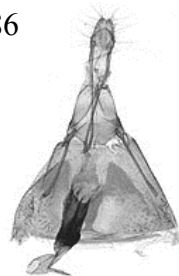
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Figures 79-86. Female genitalia (continued). 79. *Cydia makai* – slide PTO-s147. 80. *C. rufipennis* – slide BM 2057. 81. *C. montana* – slide PTO-s322. 82. *C. conspicua* – slide PTO-s336. 83. *C. hawaiiensis* – slide PTO-s42. 84. *C. acaciavora* – slide PTO-s315. 85. *C. walsinghamii* – slide PTO-s308. 86. *C. anomalousa* – slide PTO-s169.

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## CHAPTER 3

Host-plant shifts and interisland dispersal in the evolution  
of Hawaiian *Cydia* Hübner (Lepidoptera: Tortricidae)



## ABSTRACT

What drives diversification and speciation is a central topic of biodiversity research. Geographic isolation is thought to be one of the most important factors leading to new species formation, although renewed interest in ecological speciation has led to convincing evidence that niche partitioning and symbiotic relationships can play an equally important role in speciation in some biological systems. To evaluate the relative importance of geography and ecology in diversification I mapped the distribution and host-plant affinities of 14 species of Hawaiian *Cydia* moths on a molecular phylogeny constructed from nuclear and mitochondrial genes. The genus *Cydia* is represented by a monophyletic clade of at least 21 endemic species in the Hawaiian Islands and feed on endemic plants in the family Fabaceae. Diversification of this genus in Hawaii is associated with host-plant shifts followed by dispersal to similar niches on other islands. *Cydia pseudomalesana* Clarke in French Polynesia is a separate colonization of the Pacific from the Hawaiian species, stemming from the Austral-Asian region. The origins of Hawaiian *Cydia* remain obscured although of the outgroup taxa analyzed they appear most closely related to species in the Holarctic region.

## INTRODUCTION

The relative influence of geographic isolation and ecology in the diversification of lineages has long been debated, but has been recently rekindled through renewed interest in ecological speciation (Friar et al. 2007, Egan et al. 2008, Matsubayashi et al. 2010, Peccoud and Simon 2010, Rice et al. 2011, Thibert-Plante and Hendry 2011). Host plants of phytophagous insects, in particular, can act as aggregation sites for mating, facilitate differential developmental rates and success among populations, and result in genetic differentiation through adaptive selection or genetic drift (Berlocher and Feder 2002, Thomas et al. 2003, Egan et al. 2008, Nosil et al. 2008, Matsubayashi et al. 2010, Michael and Carolyn 2010, Peccoud and Simon 2010). More often, however, differentiation among populations of phytophagous insects probably is caused by a number of interacting factors including ecological opportunity, competitive displacement, specialization, sexual selection, and reproductive success, as well as the geographic structure of populations that can minimize gene flow (Turner and Burrows 1995, Berlocher and Feder 2002, Dres and Mallet 2002, Despres and Cherif 2004, Matsubayashi and Katakura 2009, Yoder et al. 2010). As molecular tools for identifying population structure continue to expand and improve, the nexus of ecology and geography in promoting speciation is becoming better understood. However, much of our understanding is based on a limited number of model systems.

Remote island ecosystems offer a fertile laboratory for contrasting the role of ecology and geography in speciation because of their discrete geographic units and the endemic radiations often found on them. The Hawaiian Islands are home to some 6000+ native insects and spiders (Nishida 2002, Eldredge and Evenhuis 2003) that are thought to have diversified from only 233-400 independent colonizations (Zimmerman 1948, Howarth 1990). While some genera, such as *Drosophila* flies (~1000 spp., O'Grady et al. 2011) and *Hyposmocoma* moths (300+ spp., Rubinoff 2008), have diversified extraordinarily from one or few initial colonizers, others such as *Manduca* moths and *Vanessa* butterflies are known

by only a single endemic species (for review, see Howarth 1990, Roderick and Gillespie 1998). Moreover, entire families of insects that are widespread and common on continents, such as ants, hover flies, and ladybird beetles, have no native representatives in Hawaii (Nishida 2002). While contingency probably has played an important role in the establishment of new lineages, the extreme isolation of the Hawaiian Archipelago likely is responsible for the lack of many taxonomic groups, attenuation of others, and fostering of the spectacular radiations for some of those fortunate enough to reach Hawaii (Perkins 1913, Zimmerman 1948, Gillespie and Roderick 2002, Gillespie and Baldwin 2010).

Of the 20 families of moths with native species in the Hawaiian Islands, the cosmopolitan and species-rich family Tortricidae (nearly 10,000 species, Brown et al. 2005) is represented by eleven native and eight non-native genera (Zimmerman 1978, Nishida 2002). The eight non-native genera, (*Acleris*, *Amorbia*, *Bactra*, *Epiphyas*, *Episimus*, *Lorita*, *Platynota*, and *Strepsicrates*), include both accidental introductions and purposefully released biological control agents (Funasaki et al. 1988). Of the eleven genera having native species, eight are endemic to Hawaii (*Eccoctocera*, *Macraesthetica*, *Mantua*, *Nuritamburia* [formerly *Bradleyella* (see Koçak and Kemal 2007)], *Panaphelix*, *Paraphasis*, *Pararrhaptica*, and *Spheterista*). Of the three remaining tortricid genera in Hawaii, *Cryptophlebia* includes one putatively native and one non-native species, *Crocidosema* includes three endemic species, and the genus *Cydia*, although it includes many widespread pests of legumes and conifers, is known only from 21 endemic species in Hawaii (Oboyski Chapter 2, Zimmerman 1978).

Hawaiian *Cydia* (Grapholitini) are distributed across all the high islands from shoreline to tree line and feed in the generative tissues of legumes (Fabaceae), thus forming an ubiquitous and important link in Hawaiian food webs (Table 2). Larvae of Hawaiian *Cydia* appear to be host-specific, feeding within the seeds, flowers, terminal twigs, or under bark of *Acacia koa* A. Gray, *Acacia koaia* Hillebr., *Canavalia* spp., *Sophora chrysophylla* (Salisb.) Seem., *Strongylodon ruber* Vogel, and *Vicia menziesii* Spreng. (Swezey 1954, Zimmerman 1978), consuming up to 70% of the seed crop in the case of *Sophora* (Swezey in Zimmerman 1978). Larvae also provide a rich protein source for rare endemic Hawaiian birds such as the akiapola'au (TK Pratt and PT Oboyski unpublished data) and palila (Banko et al. 2002b), and share a suite of parasitoid wasps with agricultural pests and other native moth species (Zimmerman 1978, Brenner et al. 2002, Oboyski et al. 2004). Despite their ecological importance, however, the evolutionary history of Hawaiian *Cydia* is largely unknown.

In addition to improving our taxonomic and ecological understanding of this group, resolution of the evolutionary history of Hawaiian *Cydia* would provide an opportunity to test hypotheses regarding modes of speciation within lineages of vagile, monophagous insects. Hawaii is an ideal natural laboratory for studying the processes of evolution due to the extreme isolation of the archipelago and the known ages of the linearly arranged high islands (Price and Clague 2002). Given the chronological arrangement of the islands, Funk and Wagner (1995) formalized a “progression rule” of diversification whereby lineages established on older islands gave rise to new species on younger islands. In contrast, Ehrlich and Raven (1964) suggested that a shift to new host plants could lead to speciation in tightly coupled plant-herbivore interactions. The legume hosts on which Hawaiian *Cydia* feed

represent diverse lineages within the Fabaceae, which typically produce a diverse array of secondary compounds including canavanine,  $\beta$ -cyanoalanine, and quinolizidine alkaloids thought to deter many herbivores (Bell 1972, Banko et al. 2002a). Therefore a shift to a new host plant accompanied by adaptations to detoxify or sequester host toxins could represent a “key innovation” that leads to diversification (Berenbaum et al. 1996).

Although Hawaii is rich with endemic, host-specific, insect herbivores, surprisingly few studies have sought to compare the relative influence of biogeography and host-plant use on speciation in a phylogenetic framework. Here I present a molecular phylogeny of Hawaiian *Cydia* to test hypotheses regarding the evolutionary history of this genus in the Hawaiian Islands. More specifically, using DNA sequence data from Hawaiian *Cydia* and their non-Hawaiian relatives I address the following questions: 1) Are Hawaiian *Cydia* a monophyletic lineage? 2) What are the likely origins of Hawaiian *Cydia*? 3) What are the biogeographic patterns of species groups relative to present-day distributions and host-plant usage? 4) What are the likely modes of diversification within Hawaiian *Cydia*?

## METHODS

### Taxon sampling

Specimens used in molecular analyses were collected in the Hawaiian Islands (Figure 1) between 2002 and 2006. Additional outgroup specimens were collected in California, Mississippi, Portugal, Reunion Island, Japan, Micronesia, and French Polynesia by the author or colleagues (Table 1). Adult moths were collected using 15W ultraviolet lights powered by 12v DC batteries in targeted habitats in Hawaii (i.e. habitats supporting the known host plants of Hawaiian *Cydia*) and opportunistically elsewhere. Some adult specimens were collected using an insect net by sweeping vegetation or aerial capture of day-flying individuals. Moths were dispatched at the time of capture using potassium cyanide or frozen alive within a few hours after capture. Shortly thereafter, the middle and hind legs on one side of each specimen were pulled free from the body and placed in 95% ethyl alcohol for subsequent analysis. Moths were then pinned for identification and morphological analysis (e.g. genitalia dissections to confirm identification).

Larvae were also collected for molecular analyses and to assess host plant affinities. Known and suspected host plants were inspected for evidence of larvae boring into seeds, flowers, and twigs, and under bark. Host plant material was placed in 240 ml clear plastic containers fitted with screen lids and checked periodically for emergence of adult moths or parasitoid wasps. Some larvae were sacrificed before pupation and preserved in 95% ethyl alcohol. Both sacrificed larvae and emerged adults from host plants were used for DNA sequence analysis. Although in some cases several individuals from each location were sequenced from either captured adults or reared larvae, specimens with identical sequences from the same island were not included in the following analyses.

### DNA sequencing

Total genomic DNA was extracted from one or two legs (adult moths) or a section of abdominal muscle (larvae) using a DNEasy<sup>®</sup> tissue kit (Qiagen Corporation) following the manufacturer’s protocol for animal tissue. Fragments of the mitochondrial (mtDNA) gene regions cytochrome c oxidase subunit I (COI) and subunit II (COII), the nuclear ribosomal

RNA (rRNA) gene region 28S (domain 'A'), and the nuclear gene (nDNA) regions elongation factor 1 alpha (EF1 $\alpha$ ) and wingless (WG) (Table 3) were amplified using the polymerase chain reaction (PCR) (Table 4). The PCR thermal profile consisted of 2 minutes at 95 °C; 35 cycles of 30 seconds at 95 °C, 45 seconds at X °C (where annealing temperature X = 50, 63, 64 °C for the mtDNA & 28S genes, EF1 $\alpha$ , and WG, respectively), and 90 seconds at 72 °C; and an extension cycle of 10 minutes at 72 °C. PCR products were purified using ExoSAP-IT<sup>®</sup> (USB Corporation, Cleveland, Ohio) following manufacturer's specifications but at one-tenth the recommended concentration. Cycle sequencing of purified PCR products was done in both forward and reverse directions for each specimen using BigDye<sup>®</sup> v3.1 sequencing kit (ABI) following the manufacturer's protocols and subsequently cleaned by EtOH / EDTA precipitation. Sequencing was performed on an ABI 3730 automated sequencer (Applied BioSystems). Sequence editing and alignment using Geneious<sup>®</sup> 5 (Drummond et al. 2009) was trivial since only one three-basepair (bp) insertion for COII and one three-bp insertion for WG were found.

### Analyses

Uncorrected genetic distances (uncorrected p) were calculated using PAUP\* (Swofford 2002) and visually depicted with heat maps using a Visual Basic script in Microsoft Excel<sup>®</sup> to assess the range of genetic distances between species and to distinguish genetic outliers (*i.e.* potential disagreement between taxonomy and genetic distance). Phylogenetic trees were generated using 2579 bp of sequence data from 66 specimens representing 14 Hawaiian *Cydia* plus 9 non-Hawaiian *Cydia*, 10 non-*Cydia* olethreutine tortricids, and a species of the sister subfamily (Tortricinae: Archipini), *Clepsis peritana* (Clemens), as the outgroup taxon (Table 1). Phylogenetic estimation criteria included maximum parsimony (MP) and Bayesian (BA) Markov Chain Monte Carlo (MCMC) analyses. Unweighted, unpartitioned MP analysis was performed using TNT (Goloboff et al. 2008) for each gene separately and all genes fragments combined using the new technology search option employing sectorial search, ratcheting, drift, and tree fusing. Two independent runs of 100 replicates with 10 random addition sequences contributed to the final strict consensus tree for each analysis, with 100 random addition bootstrap replicates to measure branch support. Bayesian analysis was performed by MrBayes (Huelsenbeck and Ronquist 2001) on CIPRES (Miller et al. 2009) for all data combined and for each gene fragment separately. Separate analysis of mtDNA and nDNA data followed a GTR model based on recommendations from ModelTest (Posada and Crandall 1998), and allowed bp frequencies for each codon position to vary independently using a partitioned dataset with nst=6 and rates=invgamma for each partition. The 28S analysis was run as a single partition with nst=6 and rates=propinv. For each analysis two independent runs of four chains each were run for 10,000,000 generations, with sampling every 1,000 generations. For each analysis a consensus tree was generated after discarding the first 25% of samples as burnin. Analyses of combined data included all partitions as listed above in a single analysis and combining partitions for mtDNA and nDNA. Combined analyses with partitions required 35,000,000 generations for convergence and adequate mixing of chains as estimated by split frequencies, potential scale reduction factors (PSRF), and tree mixing overlay plots. Branch support was assessed by posterior probability (PP). Bayesian consensus trees were then used to test alternative evolutionary models of progression rule and ecological speciation.

### Model Testing

Patterns of diversification within Hawaiian *Cydia* were tested by comparing Bayes factors derived from an unconstrained consensus tree (null model) with alternative hypotheses based on host-plant use and contemporary distribution (Kass and Raftery 1995, Nylander et al. 2004). To compare alternative hypotheses, phylogenies of the Hawaiian species were generated by Bayesian analysis using *Cydia latiferreana* as the outgroup and the following constraint trees: 1) in order to test the progression rule, whereby older lineages are found on older islands, a constraint tree forced monophyly for species found on progressively younger islands (*i.e.* derived from older-island species); and 2) in order to test if shifting to a new host acted as a “key innovation” (Ehrlich and Raven 1964, Berenbaum et al. 1996) that promoted subsequent speciation, constraint trees were constructed that forced species that feed on the same host plant to be either a clade or grade. Bayes factors from the constrained analyses were then compared with the unconstrained analysis. Bayes factors within one or two units indicate that there is no discernable difference between models, while a difference in Bayes factors greater than ten units indicates that the model with the greater Bayes factor (*i.e.* less negative) is “very strong” evidence in favor of that model (Kass and Raftery 1995, Nylander et al. 2004).

## RESULTS

### DNA Sequencing

Five gene fragments were successfully sequenced for specimens of Hawaiian *Cydia*, non-Hawaiian *Cydia*, and non-*Cydia* Tortricidae. However, the nDNA genes EF1 $\alpha$  and WG failed to amplify for some non-Hawaiian specimens (Table 1). The mtDNA genes, COI and COII, were A/T-rich (70% and 76%, respectively) compared to the rRNA gene, 28S, (48%), while the nDNA genes, WG and EF1 $\alpha$ , tended toward greater C/G content (64% and 57%, respectively). Overall, COI and COII had a comparable proportion of variable loci: 34% of 658 bp for COI, and 40% of 480 bp for COII. However, COII showed a far greater proportion of non-synonymous substitutions (24%) than COI (6%). This corresponds with proportionally greater first and second codon position substitutions for COII than for COI (Table 5). Within Hawaiian *Cydia* both COI and COII showed proportionally less variation than the overall trends (18% each), with COII continuing to show a greater proportion of non-synonymous substitutions (Table 5). The 28S gene fragment showed little variation (5 of 520 bp) within Hawaiian *Cydia*. Three variable loci within 28S were limited to one specimen (*walsinghami*\_56004), while the two other variable positions had widespread pyrimidine transitions. The 28S fragment did, however, show greater variation (38 of 520 bp) across the entire taxa set. The nDNA gene fragments, particularly WG, also showed considerable variation among outgroup species, and some informative variation within Hawaiian *Cydia* (Table 5, Figure 2).

The within and among species genetic distance for Hawaiian *Cydia* was greatest for COI followed by COII (Table 6). Within species distance (uncorrected P) ranged from 0 – 1.98% for COI, while among species distance ranged from 1.4 – 6.4%. *Cydia mauiensis* was the most different (4.6 – 6.4%) from the remaining Hawaiian *Cydia* species, while the least distance between species (1.4%) was between a specimen of *C. falcifalcella* and *C. conspiciua*. Consistent across all genes was the genetic similarity between *C. rufipennis* and

*C. montana*. Within species genetic distance of COI within the *C. rufipennis-montana* complex, treated as two separate species in this analysis, ranged from 0.8 – 0.9% and 0.2 – 1.5% for *C. rufipennis* and *C. montana*, respectively, while the between species distance ranged from 2.28 – 2.74%. Some taxa (*C. mauiensis*, *C. velocilimitata*, *C. falsifalcella*, *C. parapteryx*, *C. hawaiiensis*, *C. koaiae*, *C. latifemoris*) were represented by one to few specimens and are known from only one island (and in some cases were collecting during a single event), while others (*C. conspicua*, *C. makai*, *C. pseudanomalousa*, *C. plicata*, and *C. walsinghamii*) were represented by more specimens and/or were collected from two or more islands.

### Phylogenetic Analyses

Cladograms from each of the five genes analyzed separately provided differing levels of resolution and somewhat conflicting topologies. Therefore, each gene tree is presented separately along with a combined-analysis tree. Maximum parsimony and Bayesian topologies were largely in agreement for each gene. Therefore, only Bayesian phylograms are presented because they provide estimates of branch lengths and were used for model testing. Each of the mtDNA and nDNA gene trees strongly support (1.00 PP) the monophyly of a Hawaiian *Cydia* clade, while the 28S tree does not distinguish Hawaiian *Cydia* from other Grapholitini (Figures 3-7). The mtDNA genes, COI and COII, place most of the Hawaiian species in a polytomy with some sister-species relationships evident (Figures 3-4). Both genes recover a sister-relationship between *C. rufipennis* and *C. montana* (> 0.99 PP).

Other recovered clades appear particular to the genes analyzed, although the following weak patterns bear mentioning as they gain support in the analysis of the full dataset. COI weakly groups the *Canavalia*-feeding species *C. parapteryx*, *C. falsifalcella*, and *C. velocilimitata* as a clade (0.54 PP) with a weak sister-relationship to the *Acacia*-feeding *C. conspicua* (0.69 PP), but does not include the *Canavalia*-feeding *C. mauiensis*. COI also weakly groups the *C. rufipennis-montana* complex with *C. makai* (0.68 PP). And whereas COI places *C. koaiae* sister to *C. walsinghamii* (0.56 PP), COII places *C. acaciavora* sister to *C. walsinghamii* (0.56 PP). The nDNA gene trees separate the four *Canavalia*-feeding species (*C. mauiensis*, *C. parapteryx*, *C. falsifalcella*, *C. velocilimitata*) from the remaining species, forming a basal polytomy along with *C. conspicua* and *C. koaiae* as sister to the other species in the case of EF1 $\alpha$ , and as a separate clade (0.99 PP) within a broader polytomy for WG. Neither gene provides much resolution for the remaining Hawaiian species (Figures 6-7).

The combined analysis for all five genes provides greater resolution across the Hawaiian *Cydia* clade (Figure 8). The *Canavalia*-feeding species form a moderately supported clade (0.76 PP) sister to the remaining Hawaiian species (0.93 PP). The strict consensus maximum parsimony tree (not shown) supports a basal grade of these species, with *C. mauiensis* basally divergent to a clade of the other three species, which in turn are sister to the remaining species. The remaining species form a progression of nested polytomies of varying support (Figures 8-9), with the following notable sister group relationships: *C. haleakalaensis* sister to *C. latifemoris* (0.79 PP); *C. koaiae* sister to *C. conspicua* (0.89 PP); *C. rufipennis* sister to *C. montana* (1.00 PP); and *C. acaciavora* sister to *C. walsinghamii* (0.99 PP).

### Model testing and evolutionary patterns

Model testing using Bayes factors does not support a progression rule pattern of phylogeography, but does support successive host-plant shifts (Table 7). Constraining species from younger islands to be nested within older-island species resulted in a topology (not shown) that did not fit the data as well as the unconstrained analysis (107 log likelihood units difference) which scattered older island species throughout the Hawaiian *Cydia* clade (Figure 9). Further evidence against a progression rule pattern is the placement of *C. mauiensis* from Maui as sister-group to the rest of the Hawaiian species in many analyses.

Constraining clades by host-plant affinities, however, resulted in topologies that fit the data as well as unconstrained analyses (Table 7). Constraining species that feed on either *Canavalia*, *Sophora*, or *Acacia* to be monophyletic resulted in a topology (not shown) that fit the data almost as well as the unconstrained analysis (1.99 log likelihood units difference). Constraining each host group to successive nesting (*i.e.* *Acacia* feeders nested within *Sophora* feeders and together nested within *Canavalia* feeders) resulted in a topology indistinguishable from the unconstrained analysis (0.57 log likelihood units difference).

### Origins of Hawaiian *Cydia*

The relationship of Hawaiian *Cydia* to other species sampled is equivocal. The individual-gene and combined-data analyses consistently place the Hawaiian species well within *Cydia* with six non-Hawaiian species, including *C. latiferreana*, clustered as nearest relatives (Figures 3-8). However, none of these species consistently emerged as sister to the Hawaiian species, but rather they grouped more consistently with each other with varying levels of support. *Cydia pseudomalesana* from French Polynesia consistently grouped with *C. undosa* from the Indian Ocean for each gene separately and in combined-analyses (> 95% PP for each). Overall, the *Cydia* species analyzed nested within the tribe Grapholitini with the exception of *C. deshaisiana*, which grouped more closely with *Cryptophlebia* than *Cydia*.

## DISCUSSION

### Utility of molecular characters

Five gene fragments provided varying levels of phylogenetic resolution. The two mitochondrial genes, COI and COII, had the greatest amount of variation and consistently united morphologically determined species. However, these genes failed to resolve relationships among most of the Hawaiian species. COII had a greater proportion of non-synonymous first and second codon position changes resulting in more amino acid changes than in COI. COII also resulted in different sister-species pairings than COI for the few species that showed this level of resolution. The “barcode” region of COI (Folmer et al. 1994) used in the present study, therefore, was useful for assigning specimens to species using reciprocal monophyly but not for relationships among species. Furthermore, the 2-3% COI divergence threshold recommended for many animal groups (e.g. Hebert et al. 2004) could result in misidentification of species such as *C. conspicua* and *C. falsifalcella* (1.4 % divergence), consistent with the caution noted by other authors (e.g. Meyer and Paulay 2005) that arbitrary barcode thresholds are not appropriate for understudied taxa.

The nuclear rRNA gene 28S contained little phylogenetically informative variation for the species studied, while the two nuclear genes, EF1 $\alpha$  and wingless, provided resolution for among-species relationships. The 28S gene fragment from the 'A' domain used in this study showed variation at the tribe and subfamily level that may be useful for resolving relationships at these higher levels. However, its lack of variation below the tribal level marginalized its utility in the current study. Similarly, EF1 $\alpha$  and wingless were of limited value in assigning individuals to species, but variation in these genes among the basal Hawaiian and deeper nodes provided phylogenetic resolution not provided by the mitochondrial genes. Therefore, the combination of characters provided resolution throughout the phylogeny that the individual genes alone could not.

An examination of morphological characters does not refute the molecular phylogeny presented here. *Cydia* males have relatively simplified genitalia, (lacking developed socii, gnathos, or uncus), compared to most other Lepidoptera. Hawaiian *Cydia* are also relatively uniform in the proportional size of the wings and legs (Oboyski Chapter 2). One species, *C. anomalosa*, is an exception among the morphological uniformity of the Hawaiian species, calling into question its phylogenetic placement. *Cydia anomalosa* is typical of non-Hawaiian *Cydia* species in having the anal margin of male hindwings rolled dorsally enclosing specialized scales, characteristics suggested as synapomorphic for the genus *Cydia* (Danilevsky and Kuznetsov 1968, Brown and Miller 1983, Komai 1999, Komai and Horak 2006). No other *Cydia* in Hawaii possesses the anal roll, but instead most species possess a ventral pouch on the male hindwing below the cubital vein (along the path of CuP) containing modified cubital pecten scales, much like *C. latiferreana*, *C. maackiana*, and a few other species to a lesser degree (Brown 1983). However, both the mitochondrial and nuclear genes analyzed, together or separately, placed the morphologically divergent *C. anomalosa* well within Hawaiian *Cydia*. It appears that these secondary sexual characters are fairly labile, questioning their value as sources of synapomorphies for this genus (Brown 1983, Brown and Miller 1983).

#### *Cydia* in the Pacific

*Cydia pseudomalesana* Clarke (1986) from the Marquesas and Society archipelagos evidently represents a colonization into the Pacific islands separate from the Hawaiian clade. Of the species analyzed, *C. pseudomalesana* pairs consistently with *C. undosa*, reared from *Sophora denudata* Bory from Reunion Island, for all genes analyzed. The larvae of *C. pseudomalesana* in the Marquesas and Society islands feed on the seeds of *Dodonaea viscosa* Jacq. (Sapindaceae) (Oboyski, unpublished data), a widespread plant that is locally common on islands from Australia to Hawaii (West 1984). Recently, Komai & Horak (2006) reported a *Cydia* species ("sp. A") reared from *D. viscosa* in Australia that appears morphologically similar to *C. pseudomalesana*. Although specimens of the Australian species were not obtained for this study, it is likely these are close relatives, if not the same widespread species. Extensive efforts to rear tortricid larvae from *D. viscosa* seeds in Hawaii (Oboyski and The Nature Conservancy 1997, Oboyski et al. 2001) have resulted in only *Cryptophlebia illepida* (Butler). Therefore, the morphological, molecular, geographic, and behavioral differences between *C. pseudomalesana* and Hawaiian *Cydia* confirm that these two lineages are separate and distinct penetrations into the Pacific.



Several other Pacific Islands tortricid species are classified as *Cydia*. Little is known about *C. callizona* (Meyrick) from New Guinea. According to Clarke (1976), *C. celiae* (Clarke) and *C. doria* (Clarke) from Micronesia most closely resemble Indian species of *Cydia*. However, female *C. celiae* lack a diverticulum on the corpus bursae, while male *C. doria* have a somewhat developed uncus (see figures in Clarke 1976), calling into question the generic placement of these Micronesian species. According to Diakonoff (1967), *C. inflata* (Meyrick) from the Philippines is of questionable generic placement. Of the six species known from Japan (*C. infausta* (Walsingham), *C. japonensis* Kawabe, *C. kamijoi* (Oku), *C. kurokoi* (Amsel), *C. pactolana yasudai* (Oku), and *C. trasi* (Meyrick)), only *C. trasi*, reared from the seeds of *Sophora japonica* L., was available for inclusion in this study. Also included in the analyses were *Acanthoclita balanoptycha* (Meyrick) and *A. defensa* (Meyrick) from Micronesia, both considered by Clarke (1976) to be *Cydia* species (Diakonoff 1982). Considering these taxonomic uncertainties, as well as the long branch from the phylogenetic analyses, it is unlikely that any of the species above are close relatives of Hawaiian *Cydia* and do not provide evidence for island hopping to Hawaii. For the present, therefore, the origins of Hawaiian *Cydia* remain obscured.

#### Hawaiian *Cydia* origins and patterns of diversification

Hawaiian *Cydia* appears to represent a single endemic radiation restricted to the current “high islands” of Hawaii (Hawaii, Maui, Molokai, Oahu, Kauai). The relatively long branch separating the Hawaiian species from other *Cydia* suggests that this genus has a long history in Hawaii. However, the long branch is more likely an artifact of outgroup sampling. The genus *Cydia* currently includes 231 named species and subspecies with a worldwide distribution (Oboyski Chapter 1, Brown *et al.* 2005, Komai and Horak 2006). A few named species are known to both the New World and Old World tropics and Australia, although some of these regions have not been explored to the same extent as the temperate regions. Outgroups used in the present study include *Cydia* and other tortricid species from California, Mississippi, Japan, French Polynesia, Micronesia, Portugal, and Reunion Island, including two *Cydia* that feed on *Sophora* spp. (*C. trasi* and *C. undosa*) and one (*C. latiferreana*) with a pronounced male hindwing pouch superficially similar to Hawaiian *Cydia* (Oboyski Chapter 2, Brown 1983). Phylogenetic analyses placed six species, including *C. latiferreana* and *C. undosa*, near Hawaiian *Cydia*, but these six tended to group closer to each other than to the Hawaiian species, with the arrangement of species differing for each gene analyzed. The lack of agreement among analyses as to which species is most closely related to Hawaiian *Cydia* suggests that none is particularly close, resulting in a long branch to the Hawaiian clade.

Relationships among Hawaiian *Cydia* suggest a relatively recent arrival to Maui Island, with a geological date of 1.2 Mya or less (Price and Clague 2002). Relationships among the Hawaiian species were largely unresolved for individual genes analyzed separately, although a fairly well-supported and resolved phylogeny emerged from the full data set (Figure 8). *Cydia mauiensis*, collected in association with *Canavalia* along the Maui coast, appears basally divergent to taxa from Hawaii Island, Oahu, and Kauai in the sister clade to all other Hawaiian taxa in both maximum parsimony and Bayesian analyses of the full dataset. The early diverging positions of this Maui species and *C. falsifalcella* from Hawaii Island, and those of other taxa from Maui and Hawaii in successively diverging clades of

non-*Canavalia*-feeders, precludes a progression rule of speciation from older to younger islands (Figure 9). Moreover, the progression rule was not supported by analysis of constraints placed on the data to simulate a progression rule pattern.

This study does suggest, however, that speciation accompanied successive colonization of new host-plant genera (Figure 9). Larvae of Hawaiian *Cydia* are confined to three major host-plant genera (*Acacia*, *Canavalia*, and *Sophora*) and two minor host genera (*Strongylodon* and *Vicia*) in the family Fabaceae (Oboyski Chapter 2, Swezey 1954, Zimmerman 1978). None of these genera is endemic to Hawaii and each belongs to a different plant tribe, although each has evolved endemic species in Hawaii (Wagner et al. 1999). Therefore, *Cydia* did not track the diversification of their host-plants after arriving in Hawaii. Rather it appears likely that switching to new host genera acted as a key innovation (sensu Berenbaum et al. 1996, Schluter 2000) that promoted speciation within Hawaiian *Cydia*. Phylogenetic analyses place the *Canavalia*-feeding species most basally divergent in the Hawaiian clade, either as a clade or as a grade with *C. mauiensis* as the earliest diverging lineage. A subsequent shift to feeding on *Sophora chrysophylla* was accompanied by speciation and filling of this feeding niche across the islands. Another shift to *Acacia*-feeding appears to have accompanied another wave of speciation and filling of this niche across the islands (Figure 9).

Despite the distribution of *Canavalia* throughout the Pacific, including widespread coastal species and upland island endemics (Sauer 1964, St. John 1970), no *Cydia* species has been recorded from *Canavalia* outside of Hawaii (Brown et al. 2008). Nor do Hawaiian species appear to share a recent common ancestor with other *Sophora*- or *Acacia*-feeding species. Therefore, *Cydia* immigrants to Hawaii probably had to overcome the defenses of native plant species. Hawaiian species of *Canavalia* have not been assayed for canavanine, a toxic amino acid found in other species of *Canavalia* (Bell 1972), or for other toxic compounds. Apart from native *Cydia*, only a small number of non-native Anthribidae, Bruchidae, and Tortricidae have been reared from *Canavalia* seeds (Oboyski unpublished data), although it is unclear whether this is due to host-plant chemistry or a lack of generalist seed predators. *Sophora chrysophylla* seeds, however, are high in pyralizidine alkaloids (Banko et al. 2002a). Apart from one invasive species of anthribid beetle (Oboyski unpublished data), *S. chrysophylla* seeds are fed on by only endemic Hawaiian *Cydia* and palila birds, *Loxioides bailleui* Oustalet (Banko et al. 2002a). We can assume, therefore, unique physiological adaptations to feeding on these underutilized resources allowed *Cydia* species to spread rapidly across the islands.

Although Hawaiian *Cydia* appears constrained to feeding on species of Fabaceae, the three major host-plant genera are fed on by the same or closely related *Cydia* species on each island (Table 4). For example, *C. koaia*, an *Acacia* twig-feeder on Hawaii Island is sister to the twig-feeding *C. conspicua* found on the older islands. Similarly, the *Acacia* flower-feeding *C. rufipennis* of Kauai and Oahu is sister to the *Acacia* flower-feeding *C. montana* on Maui and Hawaii Islands. However, not all sister pairs are found on different islands. For example, *C. haleakalaensis* is sister to *C. latifemoris*, both *Sophora*-feeding Maui species, and *C. acaciavora* from Maui is sister to the widespread and polymorphic *C. walsinghamii*. A similar island-by-host-plant matrix of herbivorous Hawaiian insects was first noted for

cerambycid beetles (Gressitt 1978), but is obvious for many genera of herbivorous insects with endemic radiations where host-plant affinities are well-known (e.g. Swezey 1954, Asquith 1995, Roderick 1997, Polhemus 2002). As an increasing number of robust phylogenies are generated for Hawaiian insect radiations we can expect the interplay between geography and host-plant in promoting speciation to reveal some general patterns.

Southwood (1960) noted that the diversity of herbivores on Hawaiian trees was directly related to the relative abundance of each tree species, with *Metrosideros* and *Acacia*, the two most common and widespread tree species in Hawaii, supporting the greatest diversity of herbivores (see also Southwood 1961). Likewise, *Acacia*-feeding *Cydia* have the greatest number of species, both within and among islands (Table 2). Two species for which host affinities are unknown, *C. obliqua* and *C. storeella*, likely fed on *Sophora chrysophylla*, given the habitats from which they were collected, making *Sophora*-feeders the second most diverse. *Canavalia*, although not as abundant as the other two host plants, likely were more prominent in Hawaiian forests and waysides in the past, but are particularly vulnerable to browsing by ungulates and are now rare outside of protected areas (St. John 1970, 1972). The herbivore diversity host-plant abundance hypothesis is further supported by the addition of three *Sophora*-feeding *Cydia* on Hawaii Island and Maui, where the abundance of *Sophora*, rare on the other islands, is greatly increased by the addition of the subalpine habitat. And indeed, two *Sophora* seed-feeding *Cydia* species, *C. plicata* and *C. makai*, appear to differ only in their altitudinal limits, with *C. plicata* reaching peak abundance in the subalpine *Sophora* forests of Mauna Kea, Hawaii and Haleakala, Maui and *C. makai* found across all the high islands at low elevations (Oboyski Chapter 2).

Extinction may have played a role in the current distribution of species, although its signal is not obvious in the present analyses. If *Cydia* species existed at high elevations (> 3000 m) on the older islands, these earlier lineages would have gone extinct as those islands eroded and subsided. Such species might have been closer to the original forms that colonized the archipelago than any of the currently known species and might belong to a more basal position in the phylogeny. Several species of Hawaiian *Cydia*, including *C. chlorostola*, *C. crassicornis*, *C. gypsograptus*, *C. obliqua*, and *C. storeella*, each known from one to three individuals collected at the turn of the 20<sup>th</sup> century, may have gone extinct in recent times (Walsingham 1907, Zimmerman 1978). However, some of these “species” may be members of other more variable species such as *C. plicata* or *C. walsinghamii* (Oboyski Chapter 2). The phylogeny presented here is a hypothesis based on currently available data. Increased sampling, including better outgroup representation, inclusion of extinct species, and more sophisticated analyses can further refine this phylogeny in the future. However, the importance of host-shifting and ecological opportunity in the radiation of Hawaiian *Cydia* is unlikely to be discounted.

## CONCLUSIONS

Hawaiian *Cydia* appears to represent a single radiation in the Hawaiian Islands. However, the outgroup taxa used in this analysis provide little insight into the ancestral habits or origins of Hawaiian *Cydia*. A much larger analysis including better representation of Asian and American species is necessary to resolve the likely origins of this group. Given the

positions of *C. mauiensis* and *C. falsifalcella* in all phylogenetic analyses, and the early diverging positions of other Maui and Hawaii Island taxa in the larger clade exclusive of the *Canavalia*-feeding group, *Cydia* appears to have initially colonized Maui or Hawaii Island. Patterns of diversification do not follow a progression rule of speciation from older to younger islands, but do support the hypothesis of successive host-plant shifting from *Canavalia* to *Sophora* to *Acacia* associated with the formation of new species and filling of ecological niches across the high island chain. Geographic isolation appears to have played an important role in that nominal sister pairs are often found on different islands. This host-plant-by-island matrix pattern is not unusual for herbivorous insects in Hawaii and indicates the importance of both ecology and geography in diversification of vagile, host-seeking, Hawaiian endemics.

Table 1. List of specimens used for molecular phylogeny analysis. General location (Country, US State, or Island) is given for all specimens; particular location (Region) is only given for Hawaiian *Cydia*. All specimens were collected by the author except Mississippi specimens collected along with R.L. Brown, *C. succedana* collected by Q. Paynter, *C. trasi* collected by F. Komai, and *C. undosa* collected by L. Jauze. Specimens were reared from host plants except where noted by superscript<sup>1</sup>, which indicates that the host plant is assumed from published records and/or the habitat from which the specimen was collected.

Taxon	Specimen	Location	Host
Tortricinae			
Archipini			
<i>Clepsis peritana</i> (Clemens, 1860)	606.09	Mississippi	at light
Olethreutinae			
Olethreutini			
<i>Episimus argutana</i> (Clemens, 1860)	606.03	Mississippi	at light
Enarmoniini			
<i>Ancylis burgessiana</i> (Zeller, 1875)	606.15	Mississippi	at light
Eucosmini			
<i>Crociosema</i> sp.	505.17	Hawaii	at light
<i>Eccoctocera</i> n.sp.	505.05	Hawaii	at light
<i>Epiblema abruptana</i> (Walsingham, 1879)	605.11	Mississippi	at light
<i>Retinia gemistrigulana</i> (Kearfott, 1905)	606.07	Mississippi	at light
<i>Rhopobota finitimana</i> (Heinrich, 1923)	606.01	Mississippi	at light
Grapholitini			
<i>Acanthoclitia balanoptycha</i> (Meyrick, 1910)	670.10	Micronesia	at light
<i>Acanthoclitia defense</i> (Meyrick, 1922)	688.11	Micronesia	at light
<i>Cryptophlebia ombrodelta</i> (Lower, 1898)	688.14	Micronesia	at light
<i>Cydia caryana</i> (Fitch, 1856)	606.02	Mississippi	at light
<i>Cydia conspicua</i> (Walsingham, 1907)	351.02	Kauai (Kokee)	<i>Acacia</i>
<i>Cydia conspicua</i> (Walsingham, 1907)	470.03	Kauai (Kokee)	<i>Acacia</i>
<i>Cydia conspicua</i> (Walsingham, 1907)	482.01	Kauai (Kokee)	<i>Acacia</i>
<i>Cydia conspicua</i> (Walsingham, 1907)	560.01	Oahu (Waianae Mts)	<i>Acacia</i>
<i>Cydia conspicua</i> (Walsingham, 1907)	560.03	Oahu (Waianae Mts)	<i>Acacia</i>
<i>Cydia cupressana</i> Kearfott, 1907	621.01	California	<i>Cupressus</i>
<i>Cydia deshaisiana</i> (Lucas, 1858)	256.09	California	<i>Sebastiania</i>
<i>Cydia falsifalcella</i> (Walsingham, 1907)	596.01	Hawaii (Mauna Loa)	<i>Canavalia</i> <sup>1</sup>
<i>Cydia latifemoris</i> Walsingham, 1907	133.17	Maui (Haleakala)	<i>Sophora</i>
<i>Cydia latifemoris</i> (Walsingham, 1907)	133.34	Maui (Haleakala)	<i>Sophora</i>
<i>Cydia latifemoris</i> (Walsingham, 1907)	523.02	Maui (Haleakala)	<i>Sophora</i>
<i>Cydia latiferreana</i> (Walsingham, 1879)	601.01	California	<i>Quercus</i> <sup>1</sup>
<i>Cydia montana</i> (Walsingham, 1907)	226.03	Hawaii (Mauna Kea)	<i>Acacia</i> <sup>1</sup>
<i>Cydia montana</i> (Walsingham, 1907)	529.01	Maui (Haleakala)	<i>Acacia</i> <sup>1</sup>
<i>Cydia montana</i> (Walsingham, 1907)	573.02	Hawaii (Hualalai)	<i>Acacia</i> <sup>1</sup>
<i>Cydia montana</i> (Walsingham, 1907)	584.03	Hawaii (Mauna Loa)	<i>Acacia</i> <sup>1</sup>
<i>Cydia parapteryx</i> (Meyrick, 1932)	563.01	Oahu (Waianae Mts)	<i>Strongylodon</i> <sup>1</sup>
<i>Cydia parapteryx</i> (Meyrick, 1932)	563.02	Oahu (Waianae Mts)	<i>Strongylodon</i> <sup>1</sup>
<i>Cydia parapteryx</i> (Meyrick, 1932)	563.03	Oahu (Waianae Mts)	<i>Strongylodon</i> <sup>1</sup>
<i>Cydia plicata</i> (Walsingham, 1907)	097.09	Maui (Haleakala)	<i>Sophora</i>
<i>Cydia plicata</i> (Walsingham, 1907)	108.19	Maui (Haleakala)	<i>Sophora</i>
<i>Cydia plicata</i> (Walsingham, 1907)	112.01	Maui (Haleakala)	<i>Sophora</i>
<i>Cydia plicata</i> (Walsingham, 1907)	124.06	Maui (Haleakala)	<i>Sophora</i>
<i>Cydia plicata</i> (Walsingham, 1907)	133.21	Maui (Haleakala)	<i>Sophora</i>
<i>Cydia plicata</i> (Walsingham, 1907)	135.02	Hawaii (Mauna Kea)	<i>Sophora</i>

Table 1. (Continued)

<i>Cydia plicata</i> (Walsingham, 1907)	136.09	Hawaii (Mauna Kea)	<i>Sophora</i>
<i>Cydia plicata</i> (Walsingham, 1907)	157.08	Hawaii (Mauna Loa)	<i>Sophora</i>
<i>Cydia plicata</i> (Walsingham, 1907)	157.10	Hawaii (Mauna Loa)	<i>Sophora</i>
<i>Cydia plicata</i> (Walsingham, 1907)	278.22	Hawaii (Mauna Loa)	<i>Sophora</i>
<i>Cydia plicata</i> (Walsingham, 1907)	303.07	Hawaii (Mauna Kea)	<i>Sophora</i>
<i>Cydia plicata</i> (Walsingham, 1907)	536.01	Maui (Haleakala)	<i>Sophora</i>
<i>Cydia plicata</i> (Walsingham, 1907)	593.01	Hawaii (Hualalai)	<i>Sophora</i>
<i>Cydia plicata</i> (Walsingham, 1907)	594.04	Hawaii (Hualalai)	<i>Sophora</i>
<i>Cydia pomonella</i> (Linnaeus, 1758)	448.04	California	<i>Malus</i>
<i>Cydia prosperana</i> (Kearfott, 1907)	608.01	California	<i>Pseudotsuga</i> <sup>1</sup>
<i>Cydia pseudomalesana</i> Clarke, 1986	650.09	Marquesas Islands	<i>Dodonaea</i>
<i>Cydia rufipennis</i> (Butler, 1881)	512.01	Kauai (Kokee)	<i>Acacia</i> <sup>1</sup>
<i>Cydia rufipennis</i> (Butler, 1881)	515.01	Kauai (Kokee)	<i>Acacia</i> <sup>1</sup>
<i>Cydia rufipennis</i> (Butler, 1881)	515.02	Kauai (Kokee)	<i>Acacia</i> <sup>1</sup>
<i>Cydia succedana</i> (Denis & Schiffermüller, 1775)	599.02	Portugal	<i>Ulex</i>
<i>Cydia trasias</i> (Meyrick, 1928)	600.01	Japan	<i>Sophora</i>
<i>Cydia undosa</i> (Diakonoff, 1957)	449.05	Reunion Island	<i>Sophora</i>
<i>Cydia walsinghamii</i> (Butler, 1882)	054.01	Hawaii (Hualalai)	<i>Acacia</i>
<i>Cydia walsinghamii</i> (Butler, 1882)	201.03	Molokai (Kamiloloa)	<i>Acacia</i>
<i>Cydia walsinghamii</i> (Butler, 1882)	226.04	Hawaii (Mauna Kea)	<i>Acacia</i>
<i>Cydia walsinghamii</i> (Butler, 1882)	268.01	Oahu (Koolau Mtns.)	<i>Acacia</i>
<i>Cydia walsinghamii</i> (Butler, 1882)	470.17	Kauai (Kokee)	<i>Acacia</i>
<i>Cydia walsinghamii</i> (Butler, 1882)	509.03	Kauai (Kokee)	<i>Acacia</i>
<i>Cydia walsinghamii</i> (Butler, 1882)	529.04	Maui (Haleakala)	<i>Acacia</i>
<i>Cydia walsinghamii</i> (Butler, 1882)	560.02	Oahu (Waianae Mts)	<i>Acacia</i>
<i>Cydia walsinghamii</i> (Butler, 1882)	560.04	Oahu (Waianae Mts)	<i>Acacia</i>
<i>Cydia walsinghamii</i> (Butler, 1882)	570.01	Hawaii (Kilauea)	<i>Acacia</i>
<i>Cydia koaiae</i> Oboyski, 2011	323.02	Hawaii (Kohala)	<i>Acacia</i>
<i>Cydia hawaiiensis</i> Oboyski, 2011	218.02	Hawaii (Mauna Loa)	<i>Acacia</i> <sup>1</sup>
<i>Cydia hawaiiensis</i> Oboyski, 2011	238.08	Hawaii (Kilauea)	<i>Acacia</i> <sup>1</sup>
<i>Cydia hawaiiensis</i> Oboyski, 2011	280.04	Hawaii (Mauna Loa)	<i>Acacia</i> <sup>1</sup>
<i>Cydia haleakalaensis</i> Oboyski, 2011	521.01	Maui (Haleakala)	<i>Sophora</i> <sup>1</sup>
<i>Cydia anomolosa</i> Oboyski, 2011	129.08	Maui (Haleakala)	<i>Acacia</i> <sup>1</sup>
<i>Cydia anomolosa</i> Oboyski, 2011	513.04	Kauai (Mt. Kahili)	<i>Acacia</i> <sup>1</sup>
<i>Cydia anomolosa</i> Oboyski, 2011	513.08	Kauai (Mt. Kahili)	<i>Acacia</i> <sup>1</sup>
<i>Cydia mauiensis</i> Oboyski, 2011	544.07	Maui (East Shore)	<i>Canavalia</i> <sup>1</sup>
<i>Cydia mauiensis</i> Oboyski, 2011	544.08	Maui (East Shore)	<i>Canavalia</i> <sup>1</sup>
<i>Cydia acaciavora</i> Oboyski, 2011	095.20	Maui (Haleakala)	<i>Acacia</i> <sup>1</sup>
<i>Cydia acaciavora</i> Oboyski, 2011	149.01	Hawaii (Kohala)	<i>Acacia</i> <sup>1</sup>
<i>Cydia acaciavora</i> Oboyski, 2011	343.05	Maui (Haleakala)	<i>Acacia</i> <sup>1</sup>
<i>Cydia makai</i> Oboyski, 2011	153.01	Hawaii (Kohala)	<i>Sophora</i>
<i>Cydia makai</i> Oboyski, 2011	154.04	Hawaii (Kilauea)	<i>Sophora</i>
<i>Cydia makai</i> Oboyski, 2011	154.05	Hawaii (Kilauea)	<i>Sophora</i>
<i>Cydia makai</i> Oboyski, 2011	197.05	Molokai (Kamakou)	<i>Sophora</i>
<i>Cydia makai</i> Oboyski, 2011	197.28	Molokai (Kamakou)	<i>Sophora</i>
<i>Cydia makai</i> Oboyski, 2011	277.01	Hawaii (Mauna Kea)	<i>Sophora</i>
<i>Cydia makai</i> Oboyski, 2011	464.03	Kauai (Kokee)	<i>Sophora</i> <sup>1</sup>
<i>Cydia makai</i> Oboyski, 2011	466.06	Kauai (Kokee)	<i>Sophora</i>
<i>Cydia velocilimitata</i> Oboyski, 2011	519.01	Kauai (North Shore)	<i>Canavalia</i> <sup>1</sup>
<i>Cydia velocilimitata</i> Oboyski, 2011	519.03	Kauai (North Shore)	<i>Canavalia</i> <sup>1</sup>
<i>Ecdytolopha mana</i> (Kearfott, 1907)	605.06	Mississippi	at light

Table 2. *Cydia* host-plant relationships by island. The epithet of each Hawaiian *Cydia* species is given for each of three host plant genera on each of the main Hawaiian Islands. Note that moth species may be found on more than one island, but are only listed for one host plant genus <sup>a</sup> (specimens of *C. parapteryx* have also been reared from *Strongylodon ruber*, and *C. falsifalcella* from *Vicia menziessii*). <sup>b</sup> indicates seed-feeding in herbarium specimens, <sup>c</sup> indicates questionable/uncertain distribution status, and <sup>d</sup> indicates the species may require synonymization with another. The five species with unknown host plants are known from one to three individuals each collected 1896-1909.

Island / Host	<i>Canavalia</i>	<i>Sophora</i>	<i>Acacia</i>	Host Unknown	Total # spp.
<b>Kauai</b>	<i>C. velocilimitata</i>	<i>C. makai</i>	<i>C. conspicua</i> <i>C. anomalosa</i> <i>C. rufipennis</i> <i>C. walsinghami</i>	---	<b>6</b>
<b>Oahu</b>	<i>C. parapteryx</i> <sup>a</sup>	<sup>b, c</sup>	<i>C. conspicua</i> <i>C. rufipennis</i> <i>C. walsinghami</i>	<i>C. chlorostola</i> <i>C. gypsograpt</i>	<b>6</b>
<b>Molokai</b>	<sup>b, c</sup>	<i>makai</i>	<i>C. walsinghami</i>	---	<b>2</b>
<b>Lanai</b>	<sup>c</sup>	<sup>b, c</sup>	<sup>c</sup>	---	<sup>c</sup>
<b>Kahoolawe</b>	---	---	---	---	---
<b>Maui</b>	<i>C. mauiensis</i>	<i>C. latifemoris</i> <i>C. plicata</i> <i>C. haleakalaensis</i>	<i>C. acaciavora</i> <i>C. conspicua</i> <i>C. montana</i> <i>C. anomalosa</i> <i>C. walsinghami</i>	<i>C. storeella</i> <sup>d</sup>	<b>10</b>
<b>Hawaii</b>	<i>C. falsifalcella</i> <sup>a</sup>	<i>C. latifemoris</i> <sup>c</sup> <i>C. makai</i> <i>C. plicata</i>	<i>C. hawaiiensis</i> <i>C. koaiae</i> <i>C. montana</i> <i>C. walsinghami</i>	<i>C. crassicornis</i> <i>C. obliqua</i> <sup>d</sup>	<b>10</b>
<b>Total # spp.</b>	<b>4</b>	<b>4</b>	<b>8</b>	<b>5</b>	<b>21</b>

Table 3. Five gene fragments and associated primers.

Region	# bp	Primer	Primer sequence (5' → 3')	Reference
COI	658	LCO1490	GGT CAA CAA ATC ATA AAG ATA TTG G	<i>Folmer et al.</i> (1994)
		HCO2198	TAA ACT TCA GGG TGA CCA AAA AAT CA	
COII	477	Eva	GAG ACC ATT ACT TGC TTT CAG TCA TCT	Caterino & Sperling (1999)
		Strom	TAA TTT GAA CTA TYT TAC CNG CA	
28S	520	28Sa	GAC CCG TCT TGA AGC ACG	
		S8Sr5d2	CCA CAG CGC CAG TTC TGC TTA	
EF1 $\alpha$	518	M13-rcM4	TGT AAA ACG ACG GCC AGT ACA GCV ACK GTY TGY CTC ATR TC	T. Gilligan (tortricid.net)
		M13REV_M51.9tort	CAG GAA ACA GCT ATG ACC CAR GAY GTN TAC AAA ATC GG	
WG	400	LepWG1	GARTGYAARTGYCAYGGYATGTCTGG	Brower & DeSalle (1998)
		LepWG2a	ACTICGCARCACCARTGGAATGTRCA	



Table 4. PCR Reactions (volume and concentration of reagents) for five gene fragments.

<b>Gene Region</b>	<b>COI, COII, 28S</b>		<b>LepWG, EF1<math>\alpha</math></b>	
Reagents	$\mu\text{L}$	[rxn]	$\mu\text{L}$	[rxn]
dH <sub>2</sub> O	8.8	-	5.9	-
10x buffer*	3	-	3	-
MgCl <sub>2</sub> (25 mM)	2	2.5 mM	2.5	3.125 mM
BSA (0.1 x)	1	0.1 x	1	0.05
Betaine (1 x)	-	-	3	0.15 x
dNTPs (8 $\mu\text{M}$ )	1	0.4 $\mu\text{M}$	1	0.4 $\mu\text{M}$
F primer (10 $\mu\text{M}$ )	1	0.5 $\mu\text{M}$	0.75	0.375 $\mu\text{M}$
R primer (10 $\mu\text{M}$ )	1	0.5 $\mu\text{M}$	0.75	0.375 $\mu\text{M}$
Taq (5 U)	0.2	0.05 U	0.2	0.05 U
DNA template	2		2	
Total volume	20		20	

\*500 mM KCL, 100 mM Tris-HCL at pH 8.3, 15 mM

Table 5. Patterns of genetic variation. Basepair (bp) frequencies for all 89 Tortricidae (All) and 68 Hawaiian *Cydia* (Hawaii) specimens, for five genes (COI, COII, 28S, WG, EF1 $\alpha$ ). Numbers indicate number of loci, numbers in parentheses indicate percentage. The percentage of parsimony-informative loci (Inform.) is out of the total number of loci. Note that Variable (Var) and Constant (Const.) loci sum to “Total”; synonymous (Syn) and Non-synonymous (Non.) substitutions do not always sum to “Var” because some loci had both synonymous and non-synonymous substitutions; and 1<sup>st</sup>, 2<sup>nd</sup>, and 3<sup>rd</sup> codon positions sum to either “Syn” or “Non” for each column. Ambiguous or polymorphic loci for WG and EF1 $\alpha$  were treated as synonymous if one of the possible bases would result in a synonymous substitution.

	COI		COII		28S		WG		EF1 $\alpha$		Total	
	All	Hawaii	All	Hawaii	All	Hawaii	All	Hawaii	All	Hawaii	All	Hawaii
Total	658 bp	658 bp	480 bp	477 bp	520 bp	520 bp	403	400 bp	518 bp	518 bp	2579 bp	2573 bp
Inform.	181 (28)	90 (14)	142 (30)	70 (15)	22 (4)	2 (0.4)	111 (28)	18 (5)	74 (14)	14 (3)	530 (21)	194 (8)
Const.	437 (66)	538 (82)	290 (60)	391 (82)	480 (92)	515 (99)	247 (61)	341 (85)	383 (74)	461 (89)	1837 (71)	2246 (87)
Var.	221 (34)	120 (18)	187 (40)	86 (18)	40 (8)	5 (1)	156 (39)	59 (15)	135 (26)	57 (11)	739 (29)	327 (13)
Syn.	203	116	143	70			114	59	130	56	590	301
1 <sup>st</sup>	28	14	12	6			7	3	3	4	50	27
2 <sup>nd</sup>	0	0	0	0			0	0	5	4	5	4
3 <sup>rd</sup>	175	102	131	64			107	56	122	48	535	270
Non.	13	4	44	16			42	0	5	1	84	21
1 <sup>st</sup>	7	2	29	10			18	0	2	0	56	12
2 <sup>nd</sup>	4	2	12	5			14	0	1	1	31	8
3 <sup>rd</sup>	2	0	3	1			10	0	2	0	17	1
A	(30)	(30)	(36)	(36)	(25)	(25)	(21)	(21)	(23)	(23)	(27)	(27)
C	(16)	(16)	(13)	(13)	(22)	(22)	(31)	(31)	(32)	(32)	(22)	(22)
G	(14)	(14)	(11)	(11)	(30)	(30)	(33)	(33)	(25)	(25)	(22)	(22)
T	(40)	(40)	(40)	(40)	(23)	(23)	(15)	(15)	(20)	(20)	(29)	(29)
A/T	(70)	(70)	(76)	(76)	(48)	(48)	(36)	(36)	(43)	(43)	(56)	(56)
C/G	(30)	(30)	(24)	(24)	(52)	(52)	(64)	(64)	(57)	(57)	(44)	(44)

Table 6. Genetic variation (percent difference) within and among Hawaiian *Cydia* species. Within and among species genetic distance (uncorrected P x 100) for Hawaiian *Cydia* for five gene fragments separately and combined (all).

	<b>Within Species of Hawaiian <i>Cydia</i></b>				<b>Among Species of Hawaiian <i>Cydia</i></b>			
	Range	Mode	Median	Mean ± SE	Range	Mode	Median	Mean ± SE
<b>COI</b>	0.00 – 1.98	0.91	0.91	0.84 ± 0.03	1.37 – 6.38	2.89	3.19	3.34 ± 0.02
<b>COII</b>	0.00 – 1.89	0.63	0.63	0.59 ± 0.03	0.42 – 6.29	3.35	3.35	3.51 ± 0.02
<b>28S</b>	0.00 – 0.58	0.00	0.00	0.03 ± 0.01	0.00 – 0.77	0.19	0.19	0.14 ± 0.00
<b>WG</b>	0.00 – 0.51	0.00	0.00	0.12 ± 0.01	0.00 – 2.50	0.50	0.51	0.79 ± 0.01
<b>EF1α</b>	0.00 – 0.97	0.00	0.00	0.16 ± 0.02	0.00 – 1.37	0.58	0.58	0.47 ± 0.01
<b>All</b>	0.00 – 1.47	0.61	0.55	0.54 ± 0.01	0.73 – 4.45	2.09	2.41	2.46 ± 0.01

Table 7. Models tested using Bayes factors. Comparison of alternative models using Bayes factors. The log likelihood functions ( $\log_e f(X|M)$ ) are given for a null model ( $M_0$  – an unconstrained consensus tree) and an alternative model ( $M_1$  – phylogeny constrained by host or distribution). “Three host clades” forced monophyly for species feeding on each of three host plant genera. “Three host grades” constrained the topology to a progression of host plant feeding from *Canavalia* to *Sophora* to *Acacia*. “Younger islands nested” constrained Maui and Hawaii Island-limited species to a clade (*i.e.* Nested within the older islands). \*  $2\log_e B_{10} < 2$  indicates the two models being compared are indistinguishable;  $2\log_e B_{10} > 10$  is a “very strong” indication that the model with the higher likelihood function (*i.e.* less negative) is a better fit (see Kass and Raftery 1995, Nylander et al. 2004).

Model comparison ( $M_1/M_0$ )	$\log_e f(X M_1)$	$\log_e f(X M_0)$	$\log_e B_{10}$	$2\log_e B_{10}$
Three host clades / unconstrained	<b>-6818.18</b>	-6816.19	1.99	3.98
Three host grades / unconstrained	<b>-6816.76</b>	-6816.19	0.57	1.14*
Younger islands nested / unconstrained	-6922.97	<b>-6816.19</b>	107	214

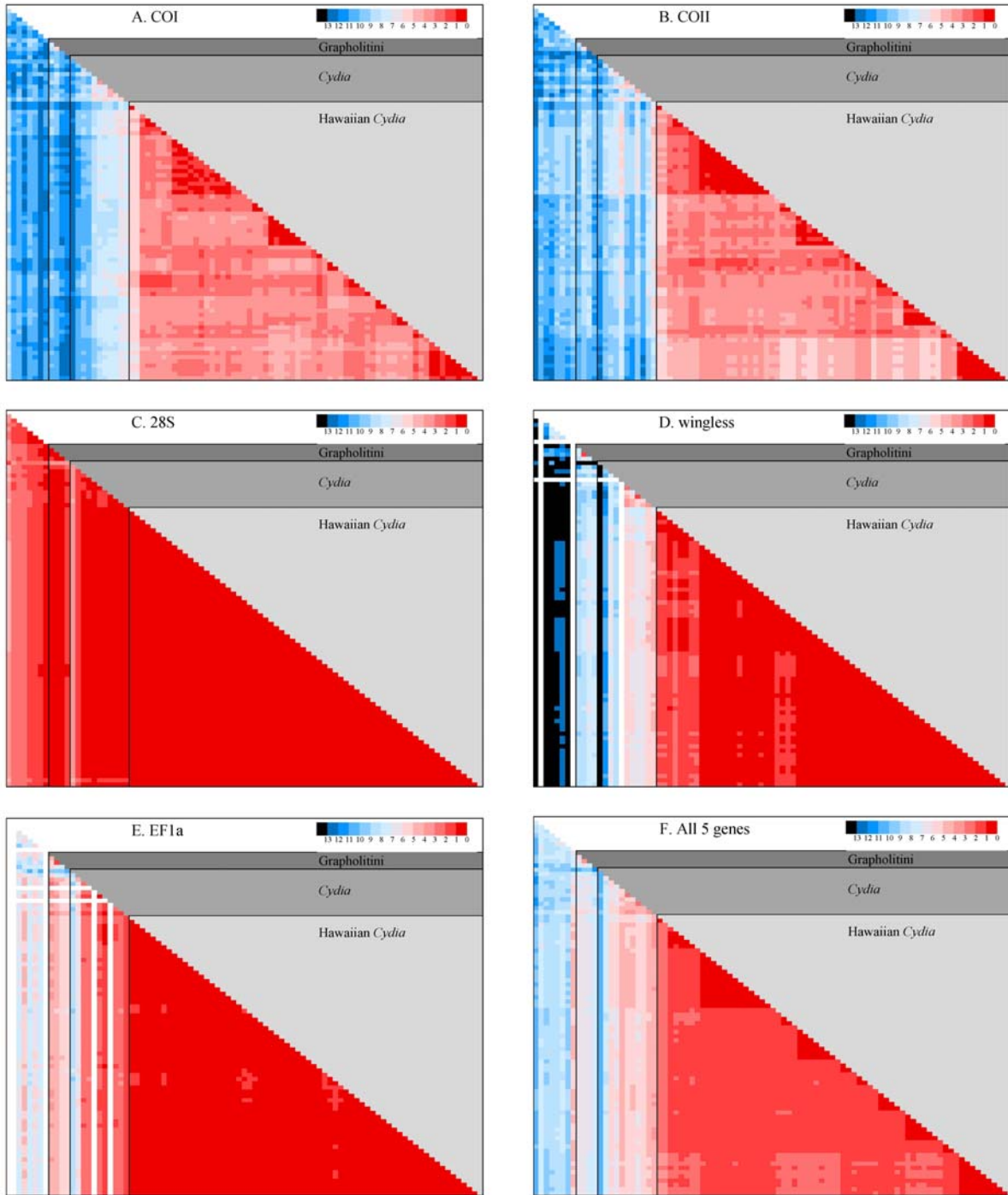


Figure 2. Heat maps – genetic distances between tortracid species. Visual depiction of genetic distance to illustrate the range of genetic variation at different taxonomic scales for five genes separately (A-E) and all genes combined (F). Color scale = uncorrected p distance x 100, with deep red indicating virtually identical genotypes to black indicating maximum genetic distance (>13% difference, missing data in white). Note that the combined map (F) “smooths” the erratic variation of the individual genes and distinguishes genetic outliers for each taxonomic group (*i.e.* conspicuously different heat color than neighboring species). Order of taxa along the left and bottom axes follows the order of specimens in Figure 8, except *Cydia deshaisiana* is in the first *Cydia* position. The diagonal (*i.e.* each specimen compared to itself) is not displayed.

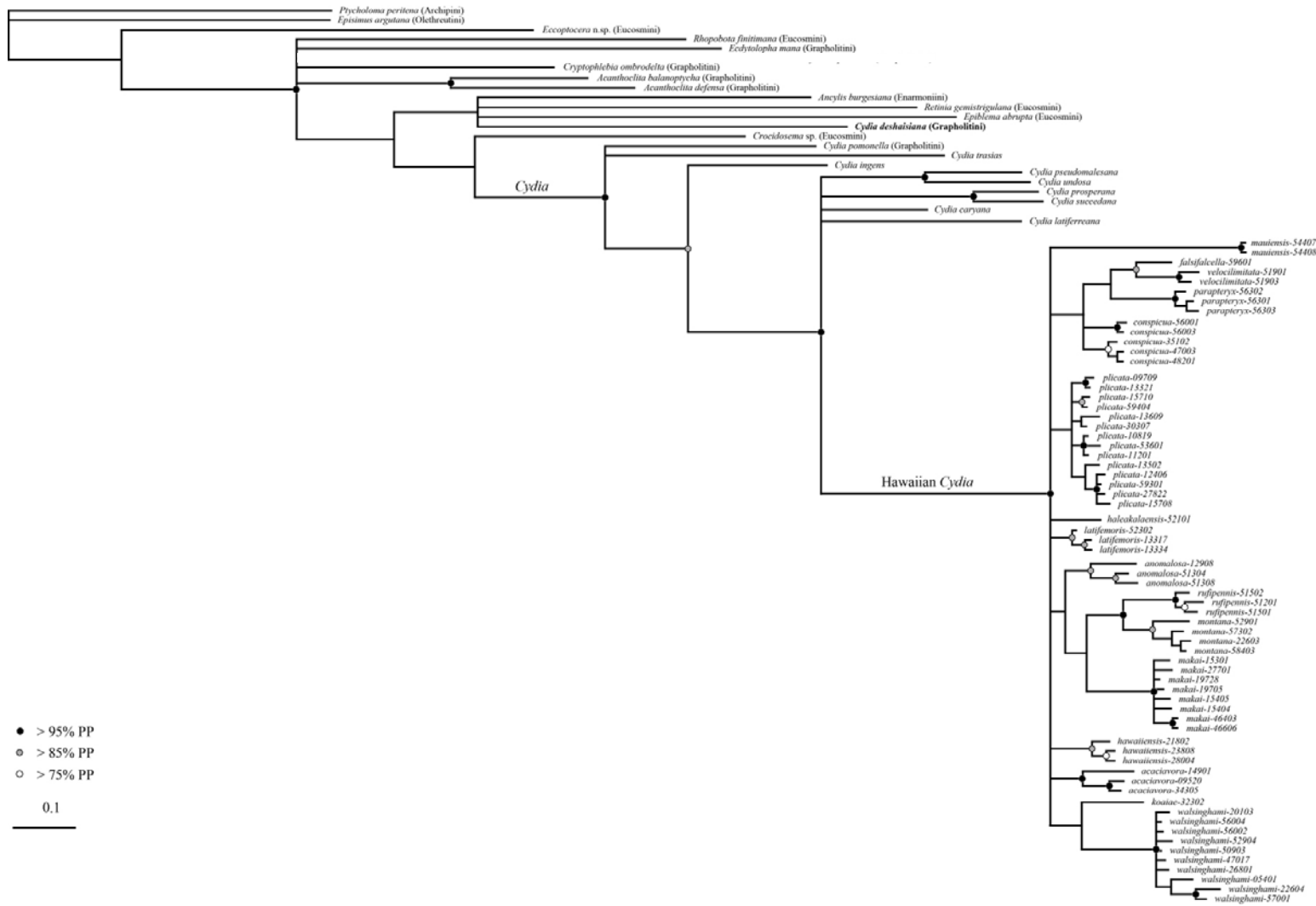


Figure 3. Gene tree for COI. Bayesian partitioned analysis (GTR model, nst=6, rates=invgamma) allowing each codon position to vary independently. Branch length scale bar indicates expected number of basepair changes. Black, gray, and white circles indicate node support. Nodes without circles have less than 75% posterior probability support.

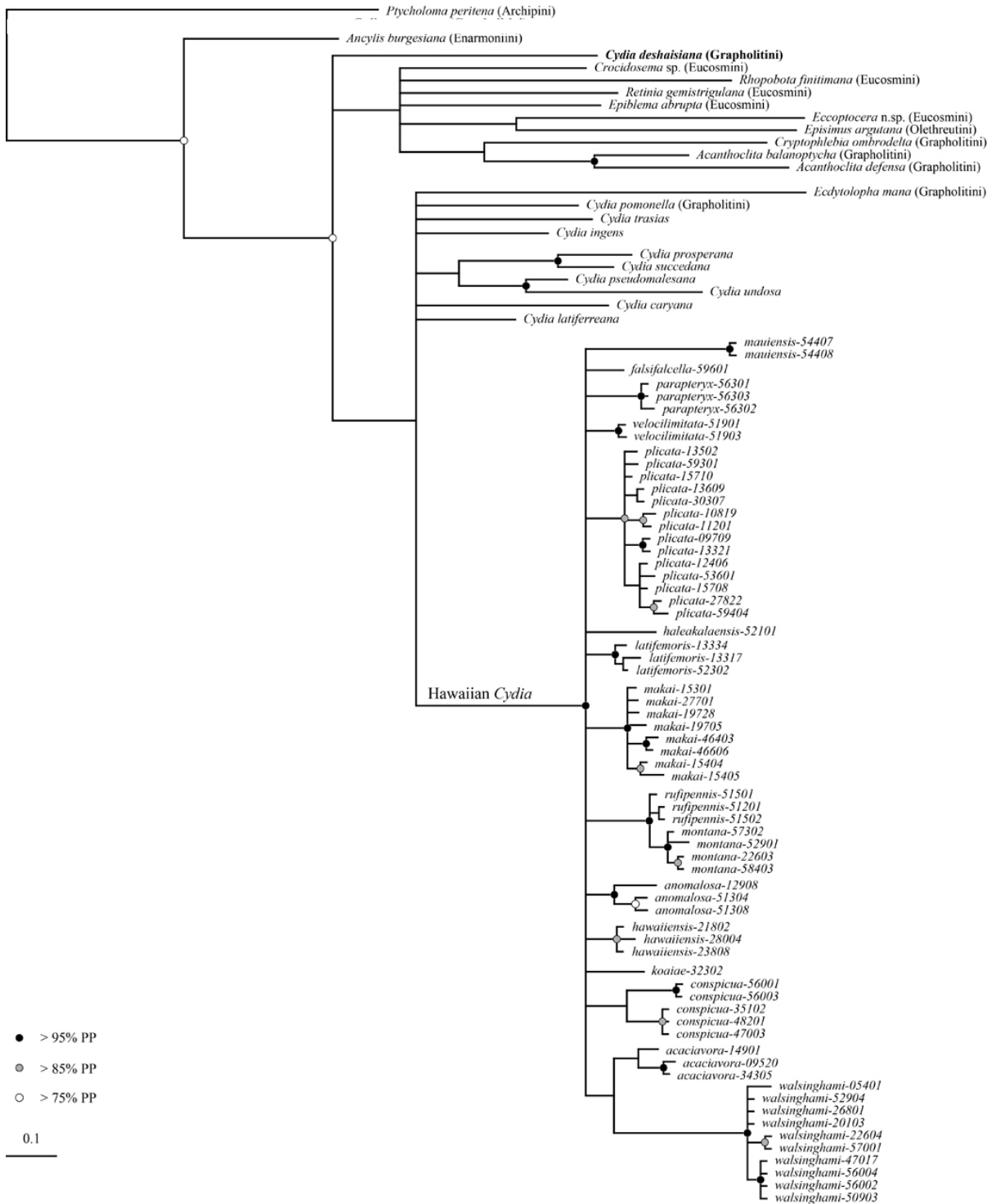


Figure 4. Gene tree for COII. Bayesian partitioned analysis (GTR model, nst=6, rates=invgamma) allowing each codon position to vary independently. Branch length scale bar indicates expected number of basepair changes. Black, gray, and white circles indicate node support. Nodes without circles have less than 75% posterior probability support.



Figure 5. Gene tree for 28S. Bayesian partitioned analysis (nst=6, rates=propinv) with no partitions. Branch length scale bar indicates expected number of basepair changes. Black, gray, and white circles indicate node support. Nodes without circles have less than 75% posterior probability support.



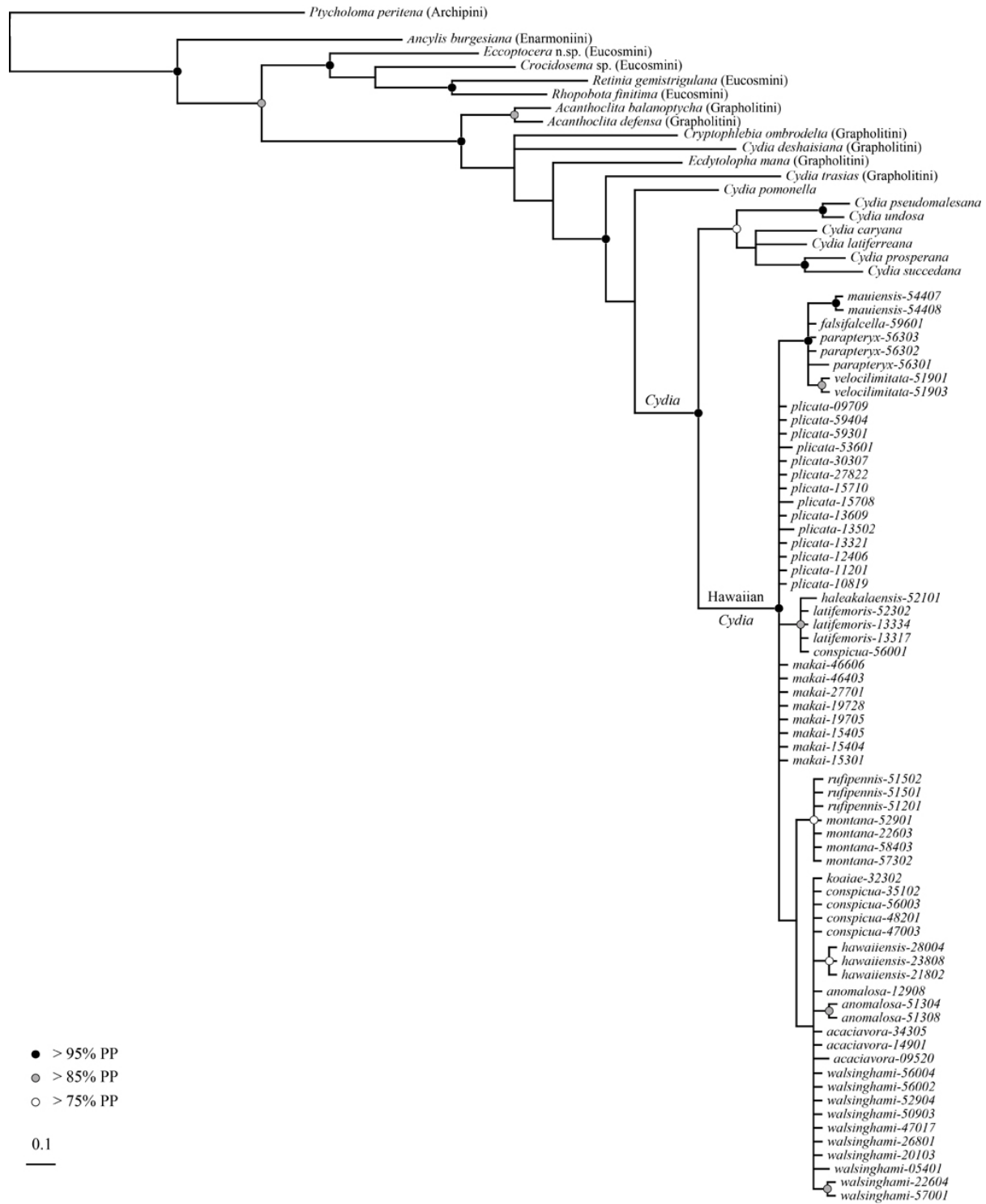


Figure 6. Gene tree for wingless (WG). Bayesian partitioned analysis (GTR model, nst=6, rates=invgamma) allowing each codon position to vary independently. Branch length scale bar indicates expected number of basepair changes. Black, gray, and white circles indicate node support. Nodes without circles have less than 75% posterior probability support.

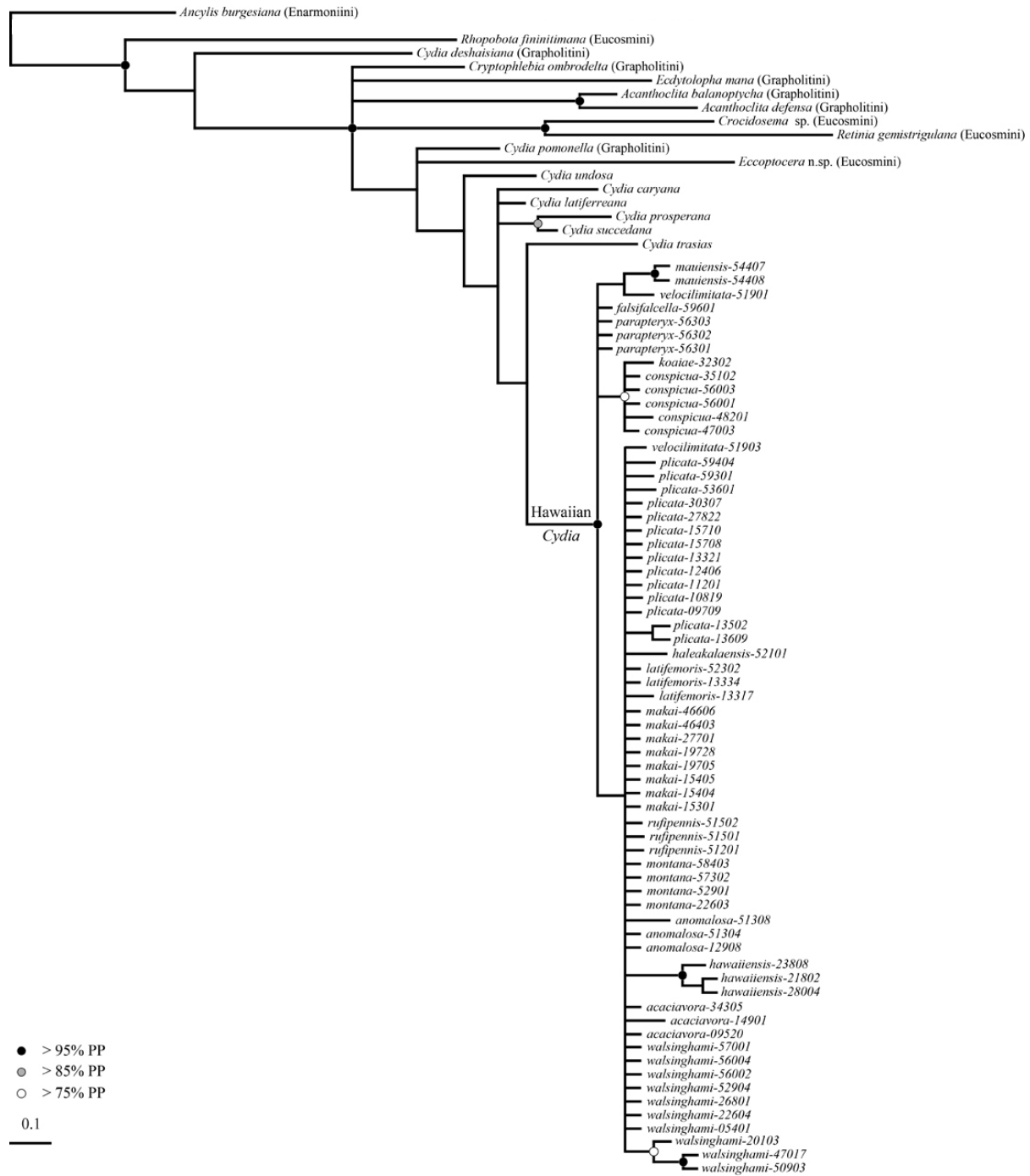


Figure 7. Gene tree for Elongation Factor 1  $\alpha$  (EF1 $\alpha$ ). Bayesian partitioned analysis (GTR model, nst=6, rates=invgamma) allowing each codon position to vary independently. Branch length scale bar indicates expected number of basepair changes. Black, gray, and white circles indicate node support. Nodes without circles have less than 75% posterior probability support.

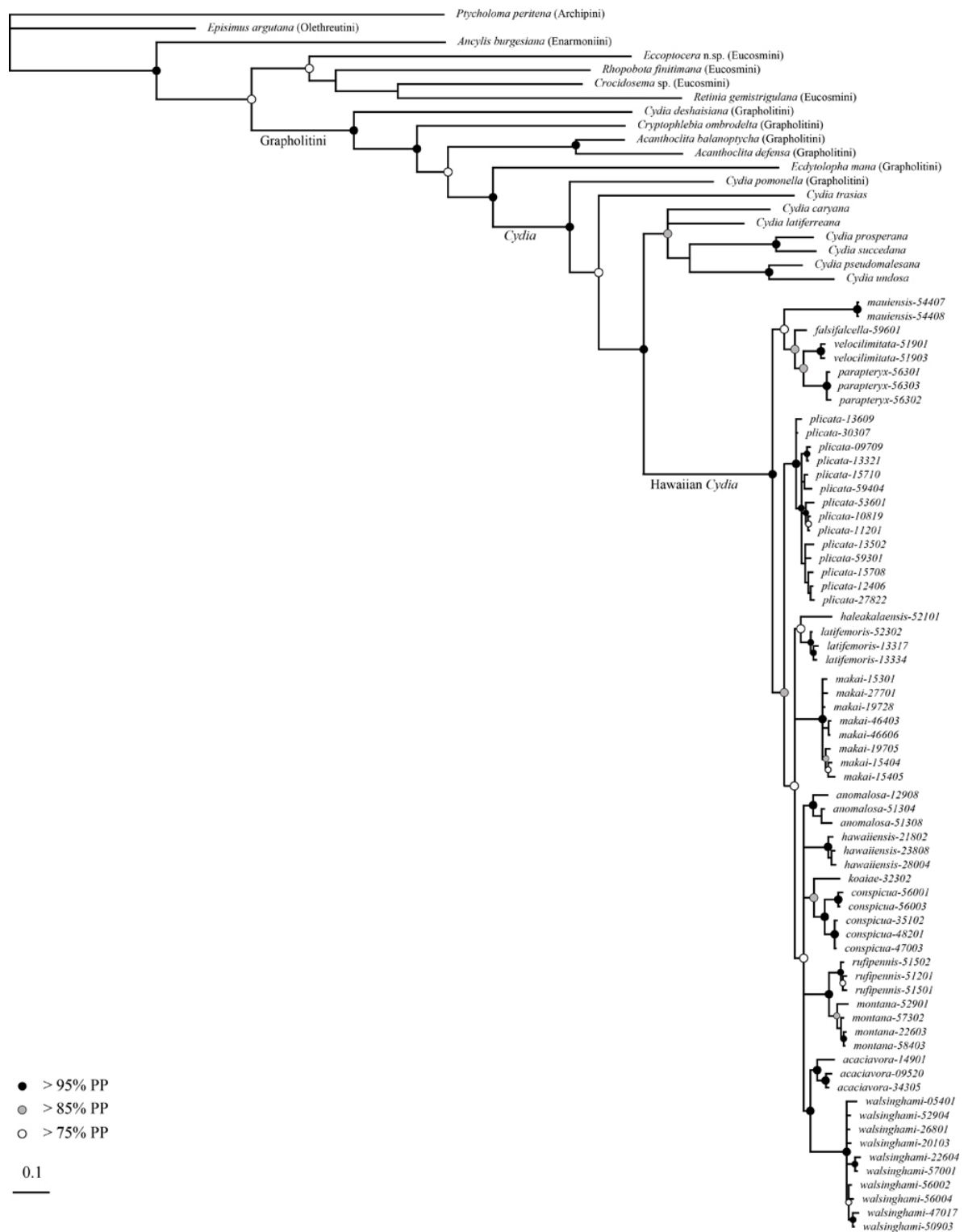


Figure 8. Phylogeny using five genes combined (COI, COII, 28S, WG, EF1 $\alpha$ ). Bayesian partitioned analysis (GTR model, nst=6, rates=invgamma) allowing each codon position to vary independently for mtDNA and nDNA; and (nst=6, rates=propinv) with no partitions for 28S. Branch length scale bar indicates expected number of basepair changes. Black, gray, and white circles indicate node support. Nodes without circles have less than 75% posterior probability support.

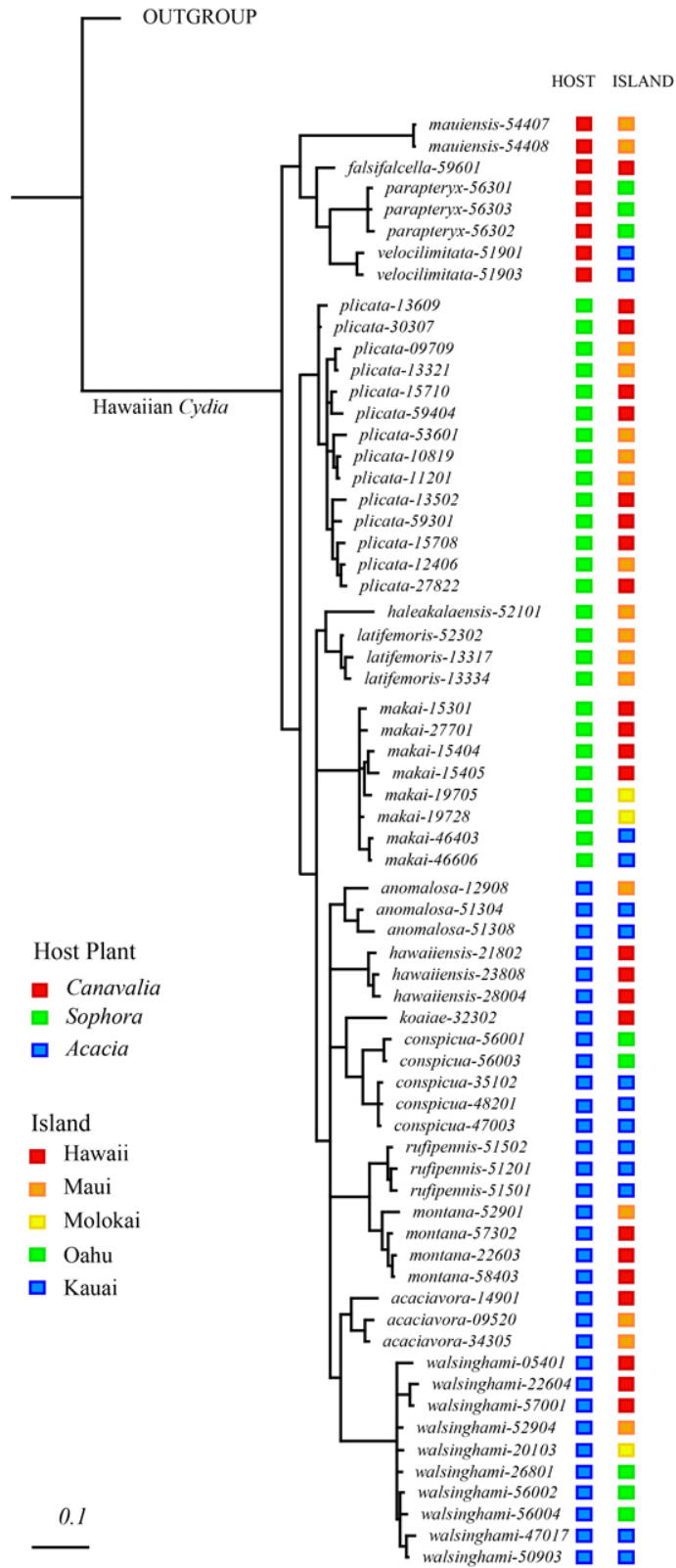


Figure 9. Phylogeny, host-plant affinities, and distribution for Hawaiian *Cydia*. Bayesian reconstruction using five gene fragments (see previous figure) with outgroups collapsed to a single branch, and each specimen color coded for host-plant and island origin. Scale bar indicates expected number of basepair changes.

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