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A review of the endemic Hawaiian Drosophilidae and their host plants

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Abstract

The Hawaiian Drosophilidae is one of the best examples of rapid speciation in nature. Nearly 1,000 species of endemic drosophilids have evolved *in situ* in Hawaii since a single colonist arrived over 25 million years ago. A number of mechanisms, including ecological adaptation, sexual selection, and geographic isolation, have been proposed to explain the evolution of this hyperdiverse group of species. Here, we examine the known ecological associations of 326 species of endemic Hawaiian Drosophilidae in light of the phylogenetic relationships of these species. Our analysis suggests that the long-accepted belief of strict ecological specialization in this group does not hold for all taxa. While many species have a primary host plant family, females will also oviposit on non-preferred host plant taxa. Host shifting is fairly common in some groups, especially the *grimshawi* and *modified mouthparts* species groups of *Drosophila*, and the *Scaptomyza* subgenus *Elmomyza*. Associations with types of substrates (bark, leaves, flowers) are more evolutionarily conserved than associations with host plant families. These data not only give us insight into the role ecology has played in the evolution of this large group, but can help in making decisions about the management of rare and endangered host plants and the insects that rely upon them for survival.

Key words: Hawaiian, Drosophilidae, taxonomy

Introduction

The Hawaiian Drosophilidae is a large, morphologically diverse radiation, consisting of perhaps as many as 1,000 species placed in two main lineages, the Hawaiian *Drosophila* and the genus *Scaptomyza* (Kaneshiro, 1997). The Hawaiian *Drosophila* is further divided into a number of species groups: *antopocerus*, *modified tarsus*, *ciliated tarsus* (these three form a single clade, referred to here as the AMC clade), *modified mouthparts*, *picture wing*, and *haleakalae* (Figure 1, after Bonacum, 2001; O'Grady, 2002; Throckmorton, 1966). The genus *Scaptomyza*, which includes both Hawaiian and continental taxa (Bonacum, 2001) is divided into a series of 21 subgenera, ten of which (*Alloscaptomyza*, *Bunostoma*, *Celidosoma*, *Elmomyza*, *Engiscaptomyza*, *Exalloscaptomyza*, *Grimshawomyia*, *Rosenwaldia*, *Tantalia*, and *Titanochaeta*) contain Hawaiian species. The Hawaiian Drosophilidae are also ecologically diverse, utilizing 34 of the 87 families of native flowering plants (Wagner, *et al.*, 1999), as well as various ferns and fungi (Heed, 1968), as larval breeding hosts. In contrast to most continental Drosophilidae, many endemic Hawaiian species are highly host plant specific (Heed, 1968; Montgomery, 1975). Therefore, the persistence of populations or species is intimately linked to that of their breeding hosts. Although factors such as predation by alien wasps are important for some taxa, particularly the *picture wing* species (Carson, 1986; Foote & Carson, 1995), in most cases conservation of the *Drosophila* depends on maintaining sufficient host plant populations for oviposition and larval substrate.

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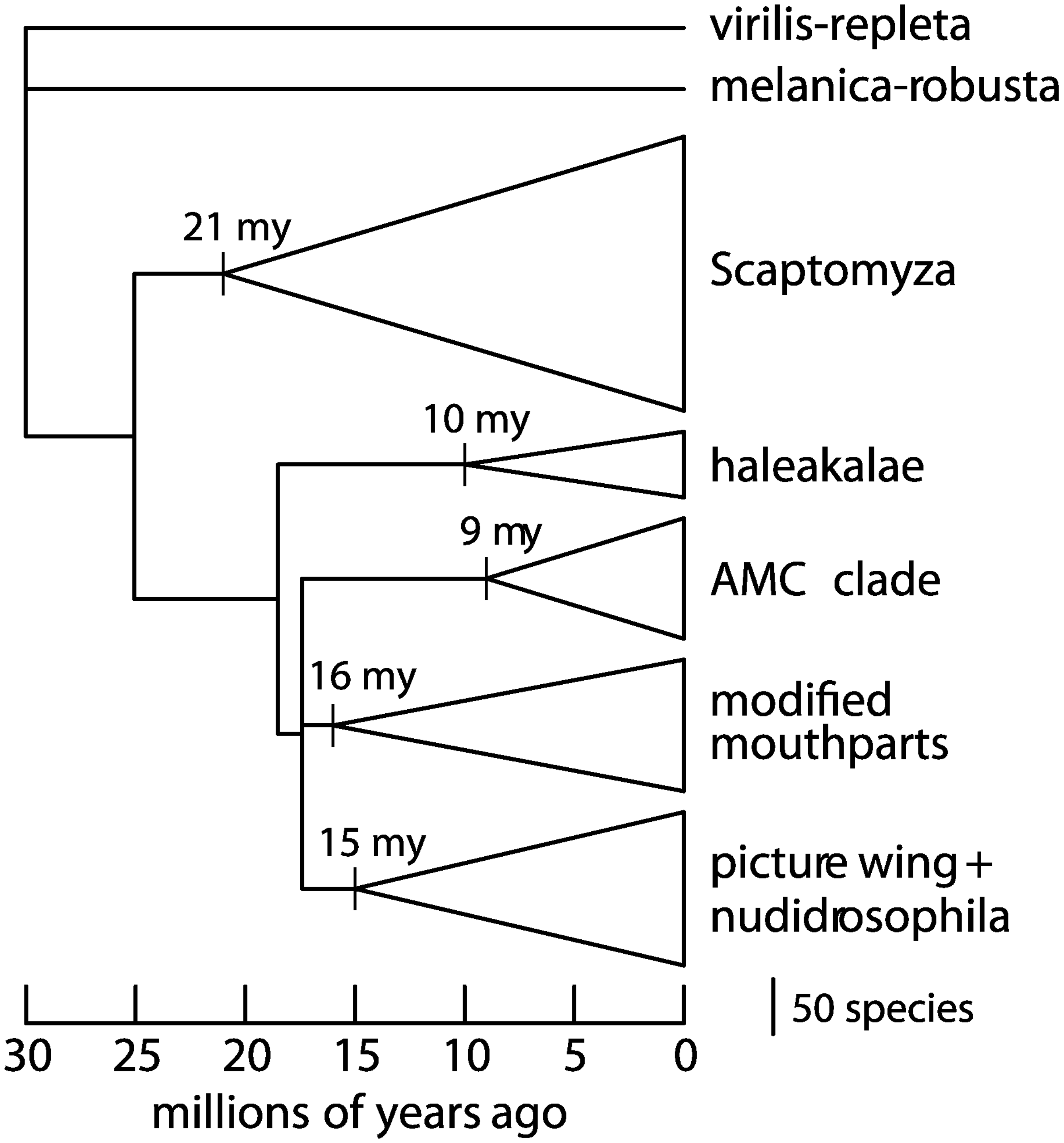

FIGURE 1. The phylogeny, age of diversification, and species diversity in the major lineages of Hawaiian Drosophilidae (O'Grady and DeSalle, in press). Vertical lines on triangles proportional to species diversity; branch lengths proportional to time. The AMC clade is composed of three commonly recognized species groups, *antopocerus*, *modified tarsus*, and *ciliated tarsus*; the latter two are probably not monophyletic. The *virilis-repleta* and *melanica-robusta* groups are continental *Drosophila* (numbers of species not shown) used as outgroups in this analysis. The phylogeny is based on analysis of nearly complete mitochondrial genomes (~10kb per taxon). The GTR+I+G model (Modeltest; Posada and Crandall, 1998) was used to perform Bayesian analyses in MrBayes (Ronquist and Huelsenbeck, 2001). Two runs, each with four chains, were performed simultaneously and sampled every 100 generations for a total of 2500000 generations. Divergence time estimates were generated using ages from Price and Clague (2002) and a penalized likelihood algorithm in r8s (Sanderson 2003).

Research into the breeding site ecology of Hawaiian drosophilids has been episodic. A few species had been reared out by Bryan and others in the first half of the 20th century, but in the first comprehensive study of the group Hardy (1965:25) said, “I suspect that many of our native species live in leaf mold, mosses, in rotting bark, and other such environments although the many attempts which have been made to obtain specimens by rearing them from such media brought in from the field have not been too successful.” Prior to the publication of Hardy's monograph in 1965, the ecological associations of only 7 species were known. Hardy (1965) added 11 more, bringing the total to 18. Surprisingly, many of the species with association data at this time were also those with the most unusual habits: *Drosophila apicipuncta* and *D. sadleria* mining fern rachises, *D. asketostoma* and *Scaptomyza latitergum* from subalpine *Argyroxiphium* flower heads, *S. cyrtandrae* from the surface of living *Cyrtandra* leaves, and *S. (Titanochaeta)* spp. from spider egg masses (Heed, 1968). Only 6 species had been reared from what might be considered "typical" larval substrates: rotting bark, fruit, and leaves of wet and mesic forest trees and shrubs.

The initiation of the Hawaiian *Drosophila* project in 1963 and publication of Hardy's (1965) monograph describing 300 new species sparked a period of intense research into all aspects of Hawaiian drosophilid biology (Spieth, 1980). William Heed began a large-scale rearing program that spanned the entire Hawaiian Drosophilidae, including the genus *Scaptomyza* and all major groups of Hawaiian *Drosophila*. The product of this work (Heed, 1968) has given us important insight into the breadth of host plant and substrate diversity in this clade. Montgomery (1975) followed up on this work, focusing specifically on the *picture wing* group and obtaining rearing records for over two-thirds of the known *picture wing* species. Although additional records have been reported since, these two studies together still account for nearly three-quarters of current drosophilid rearing records.

Here we present the first comprehensive summary of all rearing records across the Hawaiian Drosophilidae as a whole since Heed's study in 1968 (Appendix 1). This work spans over 40 years of the Hawaiian *Drosophila* project, as well as earlier work dating back to the 1930's, and is the result of the efforts of many scientists. A total of over 1,100 records for 326 drosophilid species are reported, including 83 new species records and 203 new host associations. These data are presented and analyzed in a phylogenetic context in order to examine the patterns and evolution of host usage in the Hawaiian Drosophilidae.

Materials and Methods

All species reported here were reared directly from rotting substrates collected in the field and brought into the laboratory. Rearing methods used are summarized in Heed (1968) and Montgomery (1975). Rearing data were obtained from the literature, specimen labels, and recent collections made by KM and DF on the island of Hawai‘i. Substrate types (i.e., plant parts) are reported in Appendix 1 as written in the original papers or specimen labels. In the past, branches of semi-woody (e.g. *Charpentiera*, *Clermontia*) and woody (*Cheirodendron*, *Urera*) trees have been referred to as both "bark" and "stems". However, a distinction between them is not warranted with respect to drosophilid ecology. Species that utilize the unlayered stems of *Freycinetia* and *Pleomele* do not appear to be more likely to use other plants with stems or layered wood, such as *Charpentiera*, as alternate hosts than plants with cambium-type bark such as *Cheirodendron*. The terms may be considered interchangeable here.

Specificity is considered at the host family level, although low host diversity means that often only one species of most families is available to a particular drosophilid species. Table 1 distinguishes between "monophagous" species which may utilize both primary and incidental hosts, and oligophagous or polyphagous species. The number of families for which records exist cannot be used as an absolute guide, since many species are capable of breeding on alternate hosts despite having a clear preference for a single host family. We define "monophagous" species as those with a single host family accounting for 2/3 or more of the rearing records, with no other host accounting for more than 1/4. Most species that do not meet this criterion are considered "oligophagous". There is no clear distinction between oligophagous and polyphagous. Only *D. crucigera*, with 20 native host family records, is considered highly polyphagous; no other species is recorded from more than 10 families. Incidental hosts for monophagous species are considered to be those comprising 1/4 or less of rearing records; records from exotic plants are considered incidental by definition. Host switching will be referred to as complete (i.e. monophagous on the new host) or partial (as part of an oligophagous diet).

Table 1. Summary of rearing records for all drosophilid species (new species records are marked with an asterisk next to the species name). For details, see Appendix 1.

			Substrates[a]							Major Hosts										Minor Hosts									
Species Group/Subgenus **Species Subgroup** Species Complex	Records	Individuals	Bark/Stem/Rachis	Leaf	Fruit	Flower	Sap Flux	Fungal Body	Spider Egg Mass	Agavaceae	Amaranthaceae	Aquifoliaceae	Araliaceae	Campanulaceae	Fabaceae	Nyctaginaceae	Pandanaceae	Sapindaceae	Urticaceae	Asteraceae	Convolvulaceae	Euphorbiaceae	Myoporaceae	Myrsinaceae	Oleaceae	Pittosporaceae	Rutaceae	Thymelaeaceae	Other Hosts[b]
species records			166	121	42	27	24	23	6	17	25	17	99	68	19	37	21	11	36	9	4	9	6	9	8	5	10	3	58
monophagous			132	90	12	10	16	17	6	10	9	12	75	36	4	15	14	7	16	6	4	3	4	2	1	2	4	3	10
Drosophila **haleakalae**																													
bipolita	1	13						●																					
chicae	1	14						●																					
curtitarsis	1	9						●																					
demipolita	1	6						●																					
denotata	1	14						●																					
fungiperda	1	40						●																					
iki	1	1						●																					
illusiopolita	1	1						●																					
luteola	2	many						●																					
macrochaetae	1	10						●																					
melanoloma	1	5						●																					
nigella	1	120						●																					
ochropleura	3	8						●																					
polita	1	45						●																					
antopocerus–modified tarsus–ciliated tarsus **antopocerus**																													
adunca	10	32		●									●																
arcuata	1	3		●									●																
cognata	8	38		●								◉	◉																
curvata	1			●									●																
diamphidiopoda	8	18		●									●																
entrichocnemia	1	1		●								●																	

Species Group/Subgenus **Species Subgroup** Species Complex			Substrates							Major Hosts										Minor Hosts									Other
	Rec	Ind	bk	lf	fr	fl	sf	fg	sp	Ag	Am	Aq	Ar	Ca	Fa	Ny	Pa	Sa	Ur	As	Co	Eu	Mp	Mr	Ol	Pi	Ru	Th	Hosts
longiseta	1	1		●									●																
orthoptera	4	4		●									●																
tanythrix	11	1014		●									●																
yooni	2	24		●									●																
J41	1	2		●									●																
J99	1	5		●									●																
bristle tarsus																													
basimacula	3	29		●									●																
bicondyla	1	1		●								●																	
brunneisetae	1	2		●								●																	
expansa	4	16		●									●																
perissopoda	4	37		●									⊙						⊙										22
petalopeza	4	14		●									●																
prodita	3	15		●																				●					
quasiexpansa	7	87		●																							●		
redunca	1	4		●									●																
seclusa	5	11		●									●																
spicula	1	5		●								●																	
torula	1	1		●								●																	
trichaetosa	14	279		●									●																
G33	1	3		●								●																	
HH15	1	2		●									●																
J7a	1	2		●									●																
J8	1	3		●									●																
K17,N77	2	12		●																			●						
ciliated tarsus																													
carnosa	1	7		●									●																
fusticula	4	18		●										●															
imparisetae	7	72	○	⊙	⊙								⊙					⊙						⊙					
* *kraussi*[c]	1	4	●																	●									
latigena	15	41	●										●																
medialis	10	48	●										●																
* *melanopedis*	1	3	●										●																

Species Group/Subgenus **Species Subgroup**			Substrates							Major Hosts										Minor Hosts									Other Hosts
Species Complex	Rec	Ind	bk	lf	fr	fl	sf	fg	sp	Ag	Am	Aq	Ar	Ca	Fa	Ny	Pa	Sa	Ur	As	Co	Eu	Mp	Mr	Ol	Pi	Ru	Th	
orestes	4	14	◉	◉	◉*									●															
paucula	1	11		●									●																
setipalpus	4	12		●									◉	◉													◉		
williamsi	1	29		●									●																
12.iii.1965	1	100+		●									●																
20.vii.1964	1	2		●									●																
G41b, G59b	2	3		●																						●			
* R90	1	7		●																●									
* sp. 3	5	11	●									◉	◉																
split tarsus																													
ancyla	2	31		●									●																
attenuata	2	3	◉	◉									●																
chaetocephala	2	16	◉	◉										●															
* *clavata*	2	16		●									●																
cnecopleura	2	2		●									●																
cornutitarsus	1	16		●									●																
cracens	1	1		●									●																
dicropeza	1	24		●																							●		
fundita	4	5		●									●														○		
pectinitarsus	1	4		●											●														
spiethi	5	70		●									●		○														
systenopeza	1	1		●																							●		
variabilis	2	9		●									●																
K14a	1	1		●									●																
K19	1	4		●									●																
spoon tarsus																													
conformis	6	27		●								●																	
dasycnemia	9	43		●									●																
mimiconformis	4	9		●								○	●																
neutralis	11	40	○	●									●																
percnosoma	16	292		●									●	○															
septuosa	7	32		●									●																
sordidapex	7	53		●								●	○																

Species Group/Subgenus **Species Subgroup**			Substrates							Major Hosts										Minor Hosts									Other Hosts
Species Complex	Rec	Ind	bk	lf	fr	fl	sf	fg	sp	Ag	Am	Aq	Ar	Ca	Fa	Ny	Pa	Sa	Ur	As	Co	Eu	Mp	Mr	Ol	Pi	Ru	Th	
waddingtoni	33	819	○	●									●	○										○		○			
G30,34,51,80a,J98	6	66		●										●															
G41a,45,59a	3	49		●									⊙													⊙			
G80b	1	4		●									●																
G87a	1	1		●									●																
G87b	1	2		⊙*	⊙*	⊙*								●															
* sp. 1	4	7		●									●																
unplaced																													
achyla	2	26		●																						●			
fastigata	1	1		●									●																
mimiconfutata	2	9		●								●																	
unicula	3	12		●								●																	
G87	1	2	●									●																	
G89	1	4	●									●																	
J12	1	1	●																										9
modified mouthpart																													
adventitia																													
* *adventitia*	2	5	●								●																		
bridwelli																													
apicipuncta	1	1	●																										4
sadleria	1	1	●																										3
ceratostoma																													
ceratostoma	1	5						●																					
humeralis	4	9	⊙		⊙									●															
dissita																													
amydrospilota	4	14	⊙	⊙*										●		○													
* *brevissima*	2	5	●											⊙		⊙													
dissita	10	37	●								⊙		⊙	⊙		⊙		⊙	⊙										
* *dissita* (Maui)	3	24	●											⊙		⊙			⊙										
* *dissita* (Molokai)	2	6	●													⊙			⊙										
* *dissita* (Oahu)	5	29	●	○						⊙	⊙								⊙	⊙									
dissita (Kauai)	2	19			⊙			⊙																					22
dracaenae	1	5								●																			

Species Group/Subgenus Species Subgroup			Substrates							Major Hosts										Minor Hosts									
Species Complex	Rec	Ind	bk	lf	fr	fl	sf	fg	sp	Ag	Am	Aq	Ar	Ca	Fa	Ny	Pa	Sa	Ur	As	Co	Eu	Mp	Mr	Ol	Pi	Ru	Th	Other Hosts
* *eumecothrix*	4	10	●											○		○			○										
* *larifuga*	3	24	○		○											○						○							10
G87,J20	3	9	●										●																
* J6G	1	1	●														●												
* P59A	2	11	●																●										
* P59B	2	4	●											○					○										
* P72,P77A	3	30	●																○			○							
* P77B	1	1	●																			●							
* P85	1	1	●										●																
* Q20A	1	2	●													●													
* Q88	5	60	●											○					○										
* R33	2	11		○	○												●												
* sp. 18	4	10	●														●												
* sp. 20	2	3	●										●																
* sp. 25	11	30	●										●																
freycinetiae																													
asketostoma	1	23				●														●									
* *freycinetiae*	1	1		●													●												
* *nalomano*	1	1	●																									●	
* *prominens*	1	2	●																●										
* 11.iv.1970	1	1	●																●										
* 11.iii.1973	1	1		●													●												
* 25.vii.1979	1	2		●																									11
fuscoamoeba																													
* *aquila*	2	2	●																										13, 20
* *araiotrichia*	1	2	●																										20
* *fuscoamoeba*	3	7	●								○								○										“fern”
hirtitarsus																													
goureaui	1	5						●																					
* *hirtitarsus*	2	3					●																		●				
10.ix.1964	1	38						●																					
mimica																													
conjectura																													

Species Group/Subgenus **Species Subgroup** Species Complex	Rec	Ind	Substrates							Major Hosts										Minor Hosts									Other Hosts
			bk	lf	fr	fl	sf	fg	sp	Ag	Am	Aq	Ar	Ca	Fa	Ny	Pa	Sa	Ur	As	Co	Eu	Mp	Mr	Ol	Pi	Ru	Th	
conjectura	1	76		●												●													
kambysellisi	10	134	○	●										○		●													17, 26
reschae	1			●												●													
flavibasis																													
chimera	1	1		●										●															
flavibasis	2	13		●												●													22
xenophaga	5	61		●							●																		19, 26
infuscata																													
infuscata	11	40	●											◉			◉								◉				
maemae	1	8	●														●												
involuta																													
involuta	3	3			◉	◉								◉	◉														
kauluai																													
chaetopeza	2	10	◉		◉									●															
kauluai	3	25			●																								1, 18
mimica																													
antecedens	1	6		●																									22
gagne	1	2			●													●											
mimica	9	121	○	○	●			○										●											15
soonae																													
lobatopalpus	1	1					●											●											
nanella																													
* *dolomata*	3	12	◉	◉	◉						◉				◉	◉													
* *nanella*	3	34		●												●													
quadrisetae																													
* *ischnotrix*	7	20	◉	◉	◉						◉				◉		◉		◉										12
quadrisetae	5	41	◉	◉	◉	◉*								●															22
* *residua*	1	14	●											●															
tendomentum	12	82	◉	◉	◉	○		◉						◉					◉										6, 16, 20, 26, 28
G41	2	7	◉*	◉*										◉					◉										
J17, J28	12	71	◉	◉		○					◉			◉					◉										11, 26
* P84B	1	5	●											●															

Species Group/Subgenus **Species Subgroup** Species Complex	Rec	Ind	Substrates							Major Hosts										Minor Hosts									Other Hosts
			bk	lf	fr	fl	sf	fg	sp	Ag	Am	Aq	Ar	Ca	Fa	Ny	Pa	Sa	Ur	As	Co	Eu	Mp	Mr	Ol	Pi	Ru	Th	
* R84	1	2	●																●										
scolostoma																													
* *deltaneuron*	2	3			●																								2
semifuscata																													
* *acanthostoma*	3	16					●																		○				14
* *anoplostoma*	6	37					●								○								○		○				14
* Q12	4	14					●								○									○	○				
setiger																													
* *desallei*	1	1	●													●													
* *imitator*	1	1	●																●										
unplaced																													
* *barbata*	7	37	●											○		○	○		○										
* *lelolua*	1	1		●													●												
* *omnivora*	3	26	○		○										○				○										“fern”
* *toxacantha*	3	10	●										●																
* *umiumi*	1	4	●											○		○	○		○										
ateledrosophila																													
* *papala*	5	68	●								○					○													
nudidrosophila																													
hirtitibia																													
* *hirtitibia*	1	2	●																●										
* *konaensis*	3	10	●								○					○													
* *mawaena*	2	6	●													●													
kahania																													
* *kahania*	1	1	●																●										
nudidrosophila																													
* *aenicta*	2	7	●																○			○							
* *amita*	2	17	●								○											○							
* *canavalia*	2	12	●								○				○														
* *eximia*	3	24	●													○	○		○										
* *gemmula*	3	4	●																●										
* *lepidobregma*	1	15	●															●											
* *mahui*	1	5	●																			●							

Species Group/Subgenus **Species Subgroup** Species Complex			Substrates							Major Hosts										Minor Hosts									Other Hosts
	Rec	Ind	bk	lf	fr	fl	sf	fg	sp	Ag	Am	Aq	Ar	Ca	Fa	Ny	Pa	Sa	Ur	As	Co	Eu	Mp	Mr	Ol	Pi	Ru	Th	
* *poonia*	1	3	●								●																		
J6	1	8	●														●												
* P29 (nr. *aenicta*)	1	1	●																●										
okala																													
* *akoko*	1	50	●																			●							
* *kuhao*	1	1	●																										12
okala	5	24	●										◉	◉				◉											
velata																													
* *halapepe*	1	3	●							●																			
* *kauaiensis*	2	18	●							●																			
* *lauoho*	4	23	●							●																			
* *milolii*	1	2	●								●																		
picture wing																													
adiastola																													
adiastola	24	211	●	○	○	○								●															
cilifera	2	4	◉			◉								●															
clavisetae	8	27	●											●															
neogrimshawi	1	3	●											●															
ochrobasis	3	19	◉	◉										◉										◉					13
ornata	2	11	●											●															
paenehamifera	1	2	●											●															
peniculipedis	3	24	●																●										
setosimentum	16	18+	●	○*	○*	○*							○	●															5
touchardiae	1	12	●																●										
toxochaeta	1	2	●																●										
R13	1	1	●																●										
grimshawi																													
crucigera																													
balioptera	1	1		●													●												
bostrycha	1	2	●														●												
craddockae	4	16	●																									●	
crucigera	55	384	◉		◉		○	○		◉	◉	◉	◉	◉	◉	◉	◉	◉	◉	◉		◉		◉		◉			1, 2, 10, 12, 18, 22, 23, 24

Species Group/Subgenus **Species Subgroup**			Substrates							Major Hosts										Minor Hosts									Other
Species Complex	Rec	Ind	bk	lf	fr	fl	sf	fg	sp	Ag	Am	Aq	Ar	Ca	Fa	Ny	Pa	Sa	Ur	As	Co	Eu	Mp	Mr	Ol	Pi	Ru	Th	Hosts
disjuncta	5	17	●		○									⊙		⊙	⊙												
grimshawi	29	196	●		○			○		⊙	⊙		⊙	⊙		⊙	⊙		⊙										27, 28
pullipes	1	30	●																									●	
R85	1	1	●														●												
discreta																													
pilimana	1	1	●										●																
distinguenda																													
inedita	6	35	●								⊙					⊙													
hawaiiensis																													
flexipes	2	8					●											●											
gradata	9	16	○				●					⊙	⊙		⊙										⊙				24
gymnobasis	1	3					●																●						
hawaiiensis	7	32	○				●						⊙		⊙								⊙	⊙	⊙				
heedi	7	214					●																●						
musaphilia	1	35					●								●														
recticilia	1	40					●								●														
silvarentis	47	575					●								○								●		○				
turbata	5	79					●								●														
odontophallus																													
gymnophallus	1	4	●							●																			
liophallus	4	42	●							●																			
odontophallus	3	58	●							●																			
psilophallus	2	3	●							●																			
orphnopeza																													
atrimentum	2	23	●										●																
ciliaticrus	5	24	●				○			⊙			⊙																
engyochracea	1	38	●															●											
limitata	5	7	●							⊙				⊙															
murphyi	10	29	●	○									●	○													○		
obatai	5	29	●							●																			
ochracea	2	2	●														●												
orphnopeza	3	13	●										●																
orthofascia	5	83	⊙				⊙						●																

Species Group/Subgenus **Species Subgroup** Species Complex			Substrates							Major Hosts										Minor Hosts									Other Hosts
	Rec	Ind	bk	lf	fr	fl	sf	fg	sp	Ag	Am	Aq	Ar	Ca	Fa	Ny	Pa	Sa	Ur	As	Co	Eu	Mp	Mr	Ol	Pi	Ru	Th	
reynoldsiae	8	132	●				○						●																
sejuncta	1	1	●													●													
sobrina	8	124	⊙				⊙						●																
sodomae	1	1	●							●																			
sproati	4	57	●										●																
villosipedis	10	57	●				○			⊙			⊙	⊙	⊙							⊙							
P50, Q10	4	15	⊙				⊙						●																
Q94	1	24	●										●																
punalua																													
ocellata	1	1	●													●													
paucicilia	2	7					●											●											
paucipuncta	3	21	●								⊙		⊙			⊙													
prolaticilia	1	1	●														●												
punalua	10	58	⊙	⊙		○				○			○				●												
vesciseta																													
aglaia	1	1	●																●										
ambochila	3	10	●													●													
assita	1	2	●																●										
digressa	2	44	●								●																		
hexachaetae	4	7	●								●					○													
macrothrix	4	38	●								●					○													
montgomeryi	2	3	●																●										
oreas	1	2	●													●													
pisonia	2	4	●								⊙					⊙													
tarphytrichia	2	3	●								●																		
virgulata	2	75	●								●																		
planitibia																													
cyrtoloma																													
cyrtoloma	2	3	●										●																
melancephala	2	14	●										●																
oahuensis	8	68	●	○									●																
neopicta																													
neopicta	3	17	●										●																

Species Group/Subgenus **Species Subgroup** Species Complex	Rec	Ind	Substrates							Major Hosts										Minor Hosts									Other Hosts
			bk	lf	fr	fl	sf	fg	sp	Ag	Am	Aq	Ar	Ca	Fa	Ny	Pa	Sa	Ur	As	Co	Eu	Mp	Mr	Ol	Pi	Ru	Th	
nigribasis	6	10	●										●																
substenoptera	3	39	●										●																
picticornis																													
picticornis	4	17					●								⊙														14
setosifrons	4	7	●										●																
planitibia																													
differens	1	1	●											●															
hemipeza	3	14	●											⊙					⊙										
heteroneura	13	55	●										○	●															
planitibia	10	40	●											●															
silvestris	13	119	●				○						⊙	⊙	○														13
primaeva																													
primaeva	2	14	●										●																
quasianomalipes																													
quasianomalipes	3	10	●										●																
Scaptomyza																													
Bunostoma																													
palmae	2	4				●																							2, 12
xanthopleura	1	2						⊙																					
Elmomyza																													
affinicuspidata	1	many												●															
* *apiciguttula*	2	2	⊙		⊙								⊙																4
* *argentifrons*	2	44		⊙	⊙											⊙													7
cryptoloba	2	15+		●							⊙			⊙															
cuspidata	1												●																
cyrtandrae	2			●																									8
exigua	16	122+	⊙	⊙	⊙	⊙								●															16
hackmani	10	18+	⊙	⊙	⊙	⊙							⊙	⊙													⊙		16
* *inaequalis*	3	6	⊙	⊙										●															
intricata	7	50+	⊙*	⊙	⊙	⊙								●						○									
latitergum	3	18				●														●									
longipecten *griseonigra*	1	4				●														●									

Species Group/Subgenus **Species Subgroup**			Substrates							Major Hosts										Minor Hosts									Other Hosts
Species Complex	Rec	Ind	bk	lf	fr	fl	sf	fg	sp	Ag	Am	Aq	Ar	Ca	Fa	Ny	Pa	Sa	Ur	As	Co	Eu	Mp	Mr	Ol	Pi	Ru	Th	
mediana	1	4				●														●									
platyrhina	2	30			◉*	◉*								●															
scoloplichas	3	13	●											●															
tumidula	5	7+		◉	◉	◉								●															16
varia	2	49			◉	◉								●															
G56	1	6		●										●															
G80	1	many				●								●															
G87, G90	2	85		○	●	○								●															
G90	1	4		●										●															
N23	1	5			●																						●		
* sp. 1	13	79	◉	◉	◉*	◉								●															
* sp. A	1				●											●													
* sp. B	1				●											●													
* sp. C	1				●											●													
* sp. D	1			●																									8
* sp. E	1				●																								16
Exalloscaptomyza																													
caliginosa	5	250				●															●								
mauiensis	3	9				●															●								
oahuensis	4	100				●															●								
throckmortoni	1	37				●															●								
Tantalia																													
flavida	2	3		●										◉										◉					
gilvivirilia	4	9		●									◉	◉		◉											◉		
* *nigrosignata*	3	5		◉	◉								◉	◉															20
varipicta	2	4		◉	◉									◉													◉		
G90	1	1			●																			●					
* nr. *nigrosignata*	1	2			●									●															
Titanochaeta																													
bryani	1	2							●																				
chauliodon	2	3							●																				
ichneumon	3								●																				
neoevexa	1	5							●																				

Species Group/Subgenus **Species Subgroup** Species Complex	Rec	Ind	Substrates bk	lf	fr	fl	sf	fg	sp	Major Hosts Ag	Am	Aq	Ar	Ca	Fa	Ny	Pa	Sa	Ur	Minor Hosts As	Co	Eu	Mp	Mr	Ol	Pi	Ru	Th	Other Hosts
setosiscutellum	1	6							●																				
swezeyi	3	6							●																				
unplaced taxa																													
vinnula	1	4		●									●																
alien Drosophilidae																													
Chymomyza																													
procnemis	1	2	◉*				◉*								◉														
Dettopsomyia																													
formosa	1	2			◉																	◉							
nigrovittata	2	6		◉												◉													
Drosophila (Dorsilopha)																													
busckii	5	10+	◉	◉				◉			◉			◉		◉													
Drosophila (Drosophila)																													
hydei	1					◉																							25
immigrans	30	3186	◉	◉	◉	◉	◉						◉	◉	◉	◉	◉	◉	◉			◉							1, 15, 21, 23, 26, 27, 29
mercatorum	4	26+			◉	◉	◉								◉				◉										25, 28
sulfurigaster	2	1+			◉																								25, 29
Sophophora																													
simulans	5	21+	◉			◉	◉							◉	◉		◉												17, 29
suzukii	1	75			◉																								16
Parascaptomyza																													
pallida	4	9+		◉		◉	◉	◉								◉		◉		◉									

[a] Solid circles indicate the species is monophagous for that plant family or substrate (including species with only a single record), thick rings indicate oligophagy/polyphagy, thin rings indicate records believed to be incidental. For definitions of terms, see Methods. Asterisk indicates record comes from a single sample with multiple substrates (e.g., a branch tip that contains both bark and leaves).

[b] Other native families: 1) Apocynaceae, 2) Arecaceae, 3) Blechnaceae, 4) Cucurbitaceae, 5) Dicksoniaceae, 6) Dryopteridaceae, 7) Elaeocarpaceae, 8) Gesneriaceae, 9) Gunneraceae, 10) Lauraceae, 11) Liliaceae, 12) Malvaceae, 13) Marattiaceae, 14) Myrtaceae, 15) Piperaceae (*Peperomia*), 16) Rosaceae, 17) Rubiaceae, 18) Sapotaceae, 19) Solanaceae (*Nothocestrum*), 20) Woodsiaceae. Alien hosts: 21) Aristolochiaceae, 22) Corynocarpaceae, 23) Euphorbiaceae (*Aleurites*), 24) Moraceae, 25) Musaceae, 26) Passifloraceae, 27) Piperaceae (*Piper*), 28) Solanaceae (*Solanum*), 29) Zingiberaceae. Note that Euphorbiaceae, Piperaceae, and Solanaceae are listed twice, as they have both native and alien hosts represented.

Undescribed species collected by Heed (1968), Montgomery (1975), and other researchers are referred to by their collection number (e.g., “G56”) or collection date (e.g., “11.iv.1970”); those obtained during KM and DF’s rearing on Hawai‘i are designated as “sp. N”. Use of manuscript names from forthcoming revisions of the *nudidrosophila* group (Magnacca & O’Grady, in press) and parts of the *modified mouthparts* group (Magnacca and O’Grady, submitted) should not be considered as valid descriptions (ICZN, 1999). However, for the purpose of numerical comparison they are included in counts of described species. Manuscript names in other groups are not statistically included among described species.

Our ecological analysis of *Drosophila* species group host associations is based upon the molecular phylogeny reconstructions of Hawaiian Drosophilidae found in Bonacum (2001) and O’Grady (2002) and summarized in Markow and O’Grady (2006).

Results

Rearing records

Table 1 summarizes all known data for each species, from rearing records of 279 endemic species of *Drosophila* and 47 *Scaptomyza*, as well as Hawai‘i records for 11 exotic species. These come from 1,237 host records and hundreds of collections of plant material, which produced over 10,000 drosophilid specimens. Although the four largest groups of Hawaiian Drosophilidae are of similar size (*antopocerus* + *modified tarsus* + *ciliated tarsus* [AMC]: 95 spp.; *modified mouthparts*: 101 spp.; *picture wing*: 110 spp.; *Scaptomyza (Elmomyza)*: 86 spp.), they are not evenly represented here (Table 2; Figure 2). The *picture wing* species are the most extensively studied, largely due to the efforts of Montgomery (1975). The *Scaptomyza* subgenus *Elmomyza* is poorly known, and the other two are intermediate. In addition to raw species representation, 42% of those with rearing data are known from only a single record, and therefore cannot provide information on host or substrate specificity. Most of the non-*picture wing* rearing records are based on just two surveys, Heed (1968) and the much more limited recent work on Hawai‘i (included here), neither of which was intended to be comprehensive. Although many non-*picture wing* species were also obtained during Montgomery’s (1975) study (data first presented here), it was largely limited to substrates favored by *picture wing* species. Ecological studies in these underrepresented groups suffer from several difficulties including the availability of recent taxonomic revisions, variability in islands and species groups sampled, amount of effort expended on potential host plants, and differences in relative abundance.

Availability of a comprehensive, recent taxonomic revision has a large impact on our knowledge of rearing records. The *picture wing* group, for example, has been the focus of much Hawaiian *Drosophila* research. They are conspicuous in the forest, readily attracted to baits, and relatively easy to collect. Most known species have been described and the ecological associations of this group are very well known. The taxonomy of the non-*picture wing* groups, however, is much more poorly understood, although revisions of some groups have been done (notably Hardy, 1977; Hardy & Kaneshiro, 1979; Hardy, *et al.*, 2001; O’Grady, *et al.*, 2003). Because many non-*picture wing* species are small, inconspicuous, and often not attracted to baits, they are only rarely collected in numbers sufficient for descriptive work. This creates a situation where rearing records of undescribed species remain unpublished awaiting the description of the species.

Rearing effort is also highly biased in favor of certain islands, largely due to the degree of accessibility of diverse habitats. Figure 2 shows the proportion of the various species groups with rearing records from each island. We counted widespread (multi-island) species as having data for each island even if the records were from a single island, making it a liberal estimate. It is likely that when these “species” are examined further, many will be found to be composed of several island endemics (O’Grady, *et al.*, 2003) which may or may not have a different host plant association. Forty years ago Heed (1968) stated that more rearing and collecting work needed to be done on Moloka‘i and Kaua‘i, and little has changed since that time, with only about 30% of described species from these islands having a known host association (Figure 2). Overall, Hawai‘i is the best sampled island; over half of species have at least one rearing record. The non-*picture wing* taxa have been poorly sampled throughout the islands, especially on Molokai, Oahu, and Kauai where less than 30% of these species are associated with a host plant. *Scaptomyza* species are also poorly known from all islands, both in terms of taxonomy and rearing records. Records from only 21% of described species are available, a figure that drops to 16% when the highly specialized taxa *Exalloscaptomyza* and *Titanochaeta* are excluded.

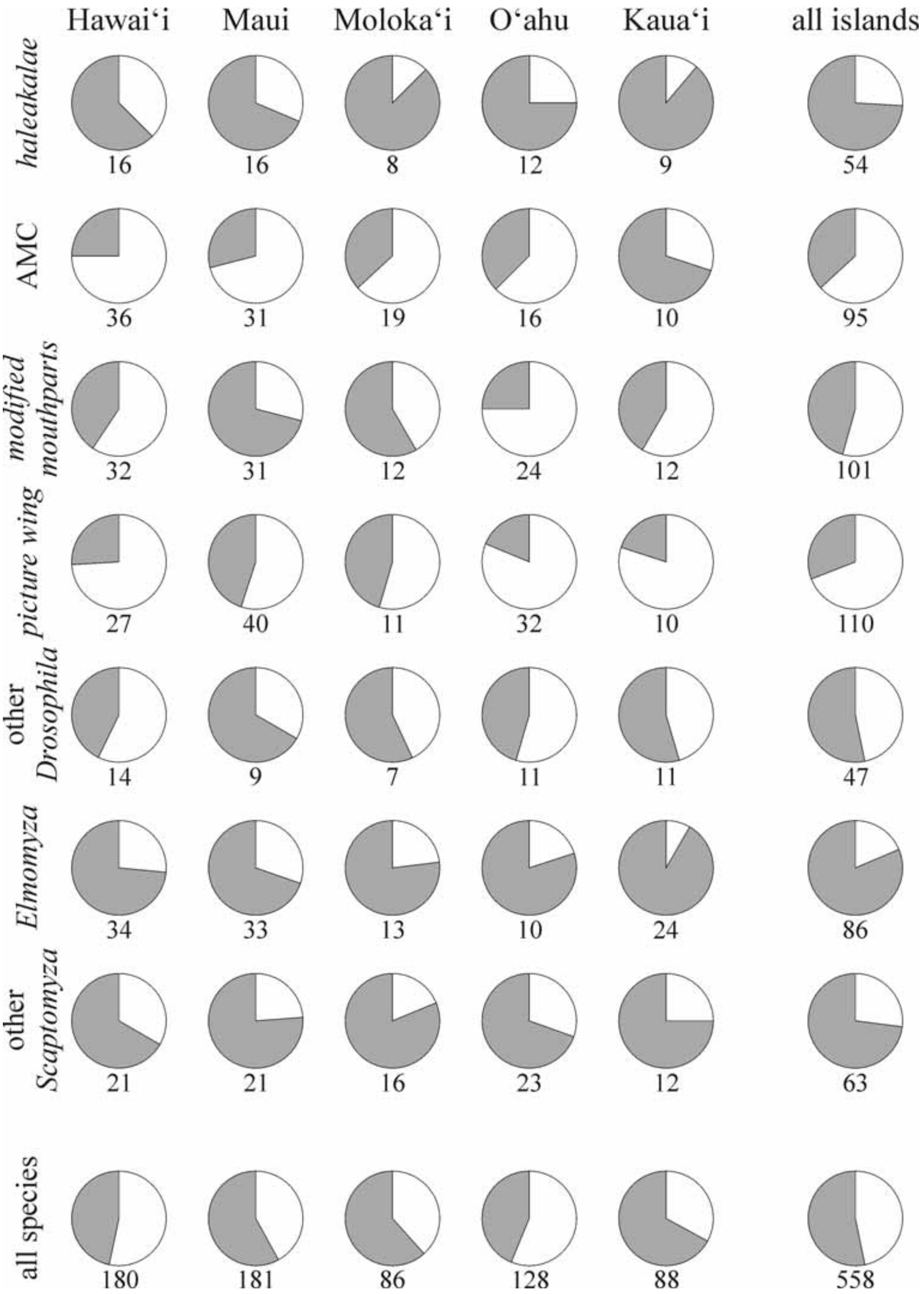

FIGURE 2. Species group coverage for breeding host data by island. White portions indicate the proportion of species with at least one rearing record, gray the proportion with no records. Numbers under the pies are the number of species for that group present on the island. Numbers under each island do not add up to the "all islands" total due to the existence of multi-island species. Note that proportion of species with records refers to the number of species inhabiting the island that have data from anywhere; thus a species inhabiting both Maui and Moloka‘i will be counted as having rearing data under both columns even if data only come from Maui. Data for Lâna‘i is not shown because it had so few rearing records (23 records for 17 species), and is poorly collected in general. All figures are for described species only.

TABLE 2. Coverage of major Hawaiian drosophilid groups.

clade	described species	with rearing data		% of descr.	% of total	known from 1 sample	
		described	undescribed				
haleakalae	54	14	0	25.9%	25.9%	12	85.7%
AMC	95	60	23	63.2%	70.3%	33	44.6%
modified mouthparts	101[a]	50	26	49.5%	59.8%	32	42.1%
nudidrosophila	29[b]	19	2	65.5%	67.7%	11	52.4%
picture wing	110	76	5	69.1%	70.4%	24	29.6%
Elmomyza	86	16	9	18.6%	26.3%	13	52.0%

[a] Includes 18 new species from Magnacca and O'Grady (submitted).

[b] Includes 22 new species from Magnacca and O'Grady (in press).

Broad-scale patterns of host plant use

The main ecological theme that unites the Hawaiian Drosophilidae is flexible larval specialization. This is true for both host plant family and substrate type (plant part). By our definition, 67% of the species with more than one rearing record are host monophagous and 79% are substrate monophagous, but many of these were also reared from alternate or incidental hosts. Several species groups are highly specific with respect to host use (Figure 3), and even more are for substrate type (Figure 4). The *haleakalae* species group, for example, appears to be entirely mycophagous. The AMC clade is composed primarily of leaf-breeders; over 80% of the species are monophagous on leaves, primarily *Cheirodendron*. The *picture wing* and *nudidrosophila* groups are variable in host plant, but largely restricted to bark and stems as a substrate. The *modified mouthparts* group may be "specialized" for oligophagy; it is the only one where a majority of species with more than one record are not host monophagous, and shows a relatively high rate of substrate oligophagy as well.

The placement of species into these host usage categories is important for the purposes of comparison, but is subject to sampling bias. Figure 5 illustrates this, comparing the proportion of species considered oligophagous, monophagous with incidental records, and monophagous from only a single plant family. As the number of samples increases, the likelihood of obtaining records from more than one plant family increases, but the proportion of species rated as monophagous increases slightly as the host preference becomes apparent. Thus, many of the species currently listed as "oligophagous" with only a few records may in fact be monophagous. For example, *D. ochrobasis* has one record each from Campanulaceae, Myrsinaceae, and Marattiaceae; but it is a member of the *adiastola* clade, which otherwise breed almost entirely on Campanulaceae or Urticaceae. More records would likely show it to have a preference for Campanulaceae.

Nearly all of the plant genera utilized as breeding hosts are not particularly diverse themselves, a pattern also seen with the *Hylaeus* bees (Daly & Magnacca, 2003). This suggests that the long-term cospeciation driven by host plant diversification observed in other insect groups (Becerra, 2003) has not taken place in Hawaiian *Drosophila*. Although the lobelioids (Campanulaceae) form the largest plant clade in Hawai‘i, all other major hosts belong to radiations of six or fewer species (Table 3). The other diverse Hawaiian plant groups are represented only by incidental records or a small number of specialist drosophilid species, or are completely absent among rearing records (Table 4). This may be due to the fact that these groups either decay in a manner that is unsuitable for drosophilid breeding, or live in arid habitats where conditions suitable for rotting seldom occur. For example, the bark of many woody Hawaiian plants is very thin and susceptible to rapid drying, rather than the wet fermentation required by drosophilids. Rarity of host plants may also play a role, as some plants might be so rare and highly dispersed that specialized *Drosophila* species cannot maintain a sufficiently large population on them. Finally, certain plants may be unsuitable as hosts because they contain compounds that are toxic or prevent larval development in Hawaiian drosophilids. The last appears to be the case in the cactophilic *Drosophila* endemic to the Sonoran Desert where only *D. pachea* and *D. mettleri* can tolerate the high levels of alkaloids produced by senita cactus (*Lophocereus schottii* Engelm.) (Fogleman, *et al.*, 1982; Kircher, *et al.*, 1967). Hawaiian plants have not been intensively investigated for their chemicals, but *Melicope* is known to contain large quantities of essential oils, as well as alkaloids in at least some species (Scheuer, 1955; Scheuer & Hudgins, 1964). *Melicope* appears to be suitable for at least leaf-breeders, but is only used by a few species.

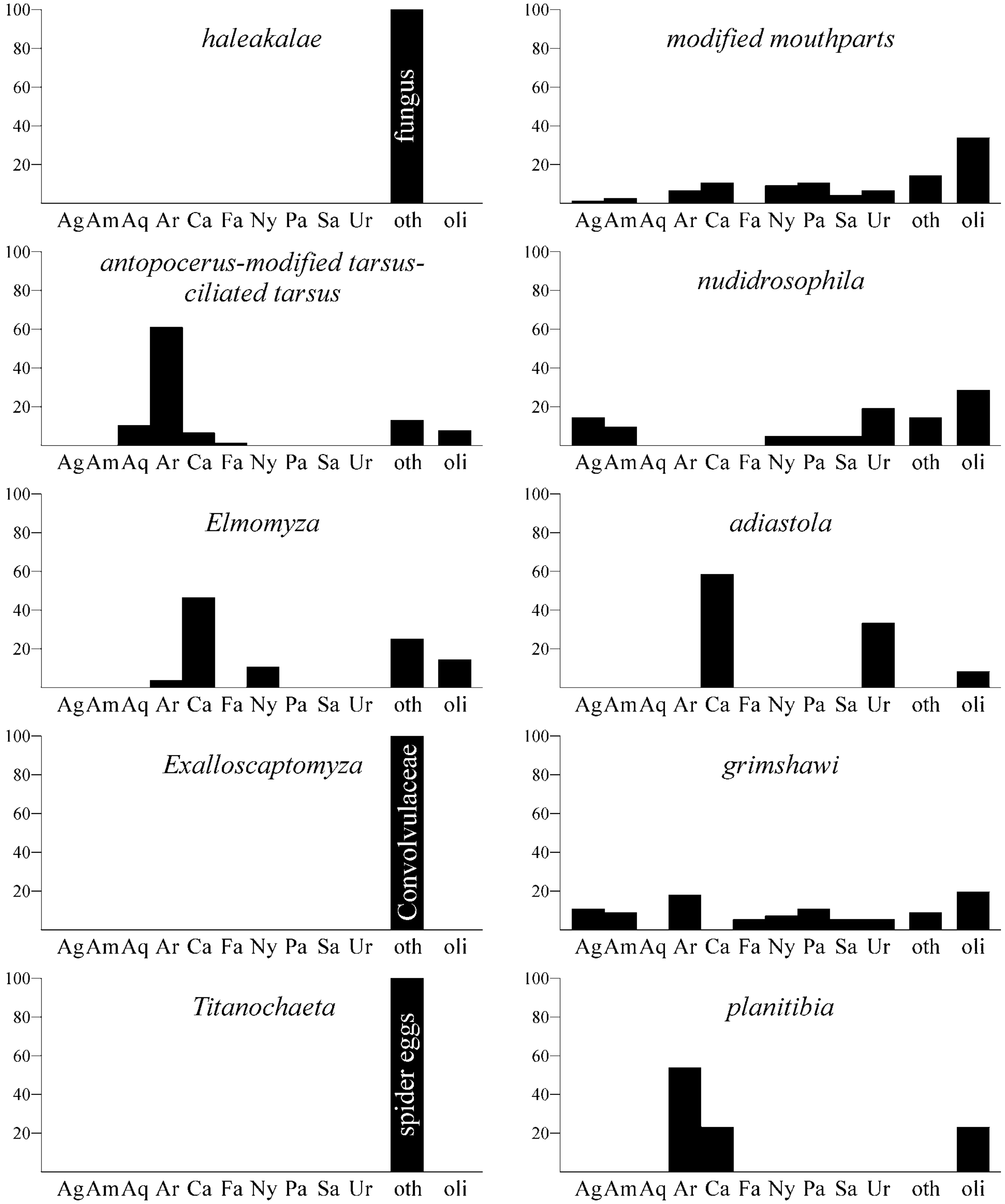

FIGURE 3. Distribution of monophagous species on important plant families in major clades and species groups of *Drosophila*, and subgenera of *Scaptomyza*. Columns represent (left to right) Agavaceae (Ag), Amaranthaceae (Am), Aquifoliaceae (Aq), Araliaceae (Ar), Campanulaceae (Ca), Fabaceae (Fa), Nyctaginaceae (Ny), Pandanaceae (Pa), Sapindaceae (Sa), Urticaceae (Ur), other host families (oth), and oligophagous (oli).

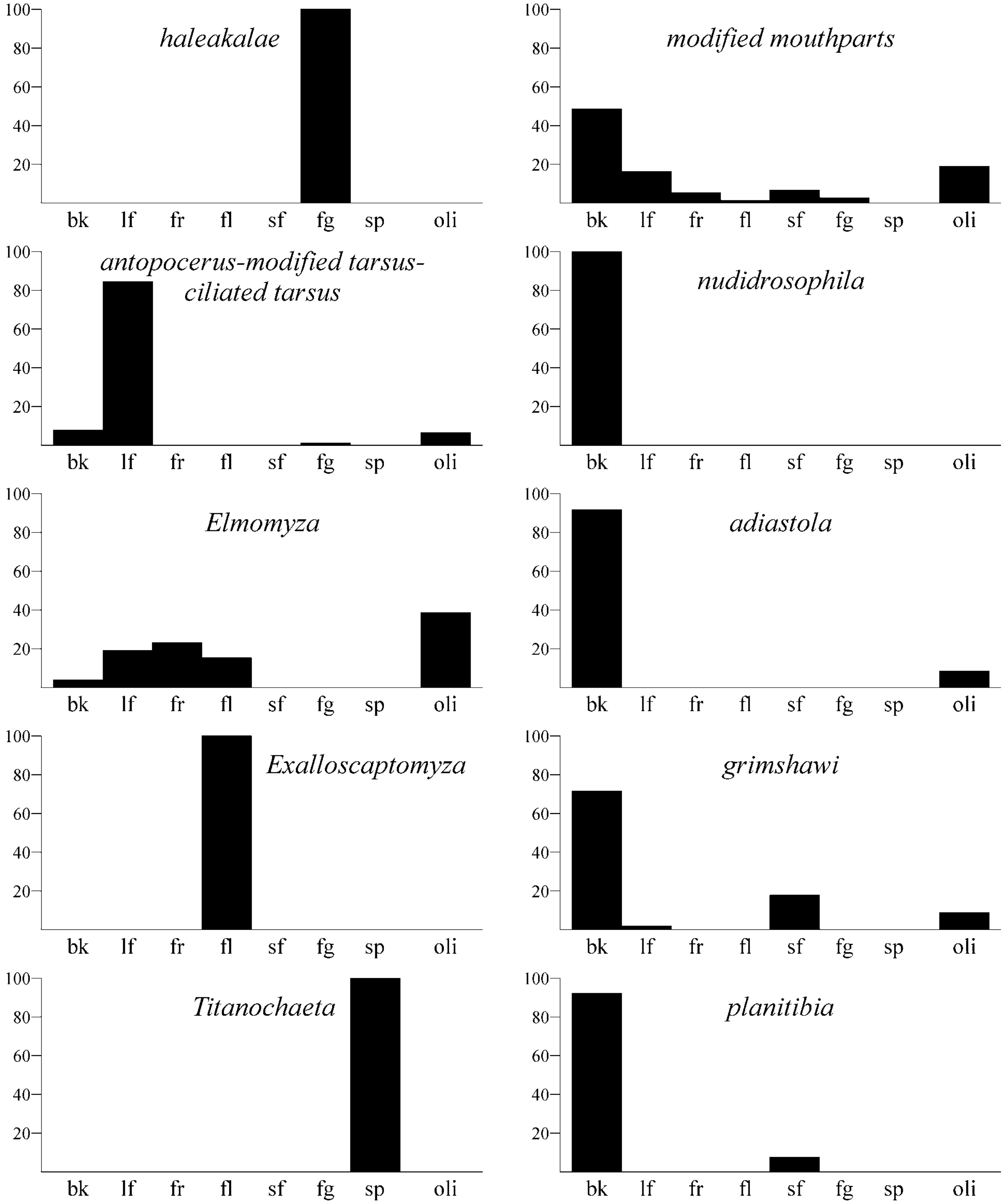

FIGURE 4. Distribution of monophagous species on host substrates for major clades and species groups of *Drosophila*, and subgenera of *Scaptomyza*. Columns (left to right) are bark/stem/rachis (bk), leaf (lf), fruit (fr), flower (fl), sap flux (sf), fungus (fg), spider eggs (sp), and oligophagous (oli).

TABLE 3. Major drosophilid host families and genera, with the number of species in each genus and the number from which native Drosophilidae have been reared.

Family	Genus/Genera	Species	Reared from[a]
Agavaceae	*Pleomele*	6	5
Amaranthaceae	*Charpentiera*	5	1
Aquifoliaceae	*Ilex*	1	1
Araliaceae	*Cheirodendron*	5	2
	Reynoldsia	1	1
	Tetraplasandra	6	3
Campanulaceae	*Clermontia*	22	6
	Cyanea	63	4
	Lobelia	13	3
Fabaceae	*Acacia*	2	1
Nyctaginaceae	*Pisonia*	5	3
Pandanaceae	*Freycinetia*	1	1
Sapindaceae	*Sapindus*	2	2
Urticaceae	*Touchardia*	1	1
	Urera	2	2

[a] In many records the host species is not specified, so figures in the Reared from column are minimums. This is especially true for *Clermontia* and *Cyanea*, which typically have multiple sympatric species, and probably *Charpentiera* as well, where the species are difficult to tell apart.

Because usage of both host plant and substrate type are highly correlated with phylogenetic relationship, we will discuss each major clade individually.

Antopocerus-modified tarsus-ciliated tarsus (AMC) clade

The AMC clade (Figure 1) is based on recent molecular work by Bonacum (2001) which suggests that the *ciliated tarsus* species group is a paraphyletic assemblage most closely related to the *antopocerus*, *bristle tarsus*, *split tarsus*, and *spoon tarsus* species groups. Previous workers (Throckmorton, 1966) had considered the *ciliated tarsus* group to be basal, in part because of its wider host and substrate range (Heed, 1971). The paraphyly of the *ciliated tarsus* group is not surprising as it lacks the modifications found in the *modified tarsus* and *antopocerus* groups, and is instead characterized by having long cilia on the forelegs of males, a character present in several other groups. Taken together, the AMC clade consists of 95 described species, 60 of which have been reared from a variety of substrates, primarily leaves of Araliaceae (*Cheirodendron* and *Tetraplasandra*). Heed (1968) also obtained 20 undescribed species, and three more emerged from recent collections.

Recent collections have shown that, contrary to the data presented by Heed (1968), the *split tarsus* and *spoon tarsus* species are not exclusively leaf breeders. Although leaves are the preferred substrate type for most species in the AMC clade, at least bark is also acceptable for oviposition and larval development. Such alternate substrates appear to be incidental in both the *spoon* and *split tarsus* subgroups and probably do not play a large role in the ecology or evolution of either group. However, five *ciliated tarsus* species have been reared only from bark. Three of these, *D. latigena*, *D. medialis*, and *D.* sp. 3, have been found in numbers that indicate bark is the preferred, if not exclusive, substrate. Although it is not possible to tell the ancestral host plant of the AMC clade based on Bonacum's (2001) phylogenetic study, there seem to have been multiple switches from leaves to bark as an oviposition and larval development substrate. Additional taxon sampling within the AMC clade will be required to confidently address this issue.

TABLE 4. Largest Hawaiian plant radiations and genera (excluding Campanulaceae).

Family	Genus/Genera	Species[a]	Drosophilid species[b]	Total records	Plant part
Arecaceae	*Pritchardia*	19	3(1)	4	
Asteraceae	*Bidens*	19	0	0	
	Dubautia-Argyroxiphium-Wilkesia	28	7(5)	9	bark, leaf, flower
	Lipochaeta	20	0	0	
Caryophyllaceae	*Schidea-Alsinodendron*	26	0	0	
Cucurbitaceae	*Sicyos*	14	1	1	fruit
Euphorbiaceae	*Chamaesyce*	15	6(3)	6	bark
Gesneriaceae	*Cyrtandra*	53	1(1)	2	leaf
Lamiaceae	*Phyllostegia-Stenogyne-Haplostachys*	52	0	0	
Loganiaceae	*Labordia*	15	0	0	
Myrsinaceae	*Myrsine*	20	9(2)	13	leaf, fruit, flux
Piperaceae	*Peperomia*	23	2	2	leaf
Pittosporaceae	*Pittosporum*	10	5(1)	8	leaf
Rubiaceae	*Coprosma*	12	0	0	
	Hedyotis	20	0	0	
	Psychotria	11	1	1	leaf
Rutaceae	*Melicope*	47	7(3)	11	leaf
Thymelaeaceae	*Wikstroemia*	12	3(3)	6	bark

[a] Some genera, such as *Cyrtandra* and *Lipochaeta*, may actually be derived from multiple smaller, independent radiations (Wagner, *et al.*, 1999).

[b] Number in parentheses is possible specialists (including species with only one rearing record).

Although they are infrequent, some host family changes have also occurred within the AMC clade. The most prevalent shift in this clade seems to be from Araliaceae to Aquifoliaceae or Campanulaceae. This transition has occurred independantly several times and includes both partial and complete shifts (as well as incidental records). Members of the *antopocerus* group have only been recorded from Aquifoliaceae as an alternate host, while members of the *bristle*, *ciliated*, *split*, and *spoon tarsus* subgroups have been reared from both. Host switching appears to be correlated with morphology in the *bristle tarsus* subgroup, where most species breeding on Aquifoliaceae lack the strong, composite bristle found in the others. A few isolated shifts to other families (Blechnaceae, Myrsinaceae, Nyctaginaceae, Sapindaceae) have also taken place, but in most cases the number of records is too low to determine if they are complete, partial, or merely incidental.

It is interesting to note several partial or possibly complete shifts to Rutaceae, a family for which there are very few records outside the AMC clade. *Drosophila quasiexpansa* is monophagous on the family, with 6 rearing records and 86 individuals (an additional record from *Myoporum* in Heed [1968], from Hawai‘i rather than Maui, is probably an undescribed species). Four other AMC species – *D. setipalpus* in the *ciliated tarsus* subgroup and *D. dicropeza*, *D. fundita*, and *D. systenopeza* in the *split tarsus* subgroup – have been reared from Rutaceae, for a total of 10 records and 113 individuals (Table 1, Appendix 1). In comparison, a total of only 3 incidental records with 8 individuals (*D. murphyi*, *S. gilvivirilia*, and *S. hackmani*, all species found more abundantly in other hosts) are known for non-AMC species. This suggests that the AMC taxa have been able to exploit Rutaceae as a host plant more effectively than have other groups of Hawaiian Drosophilidae.

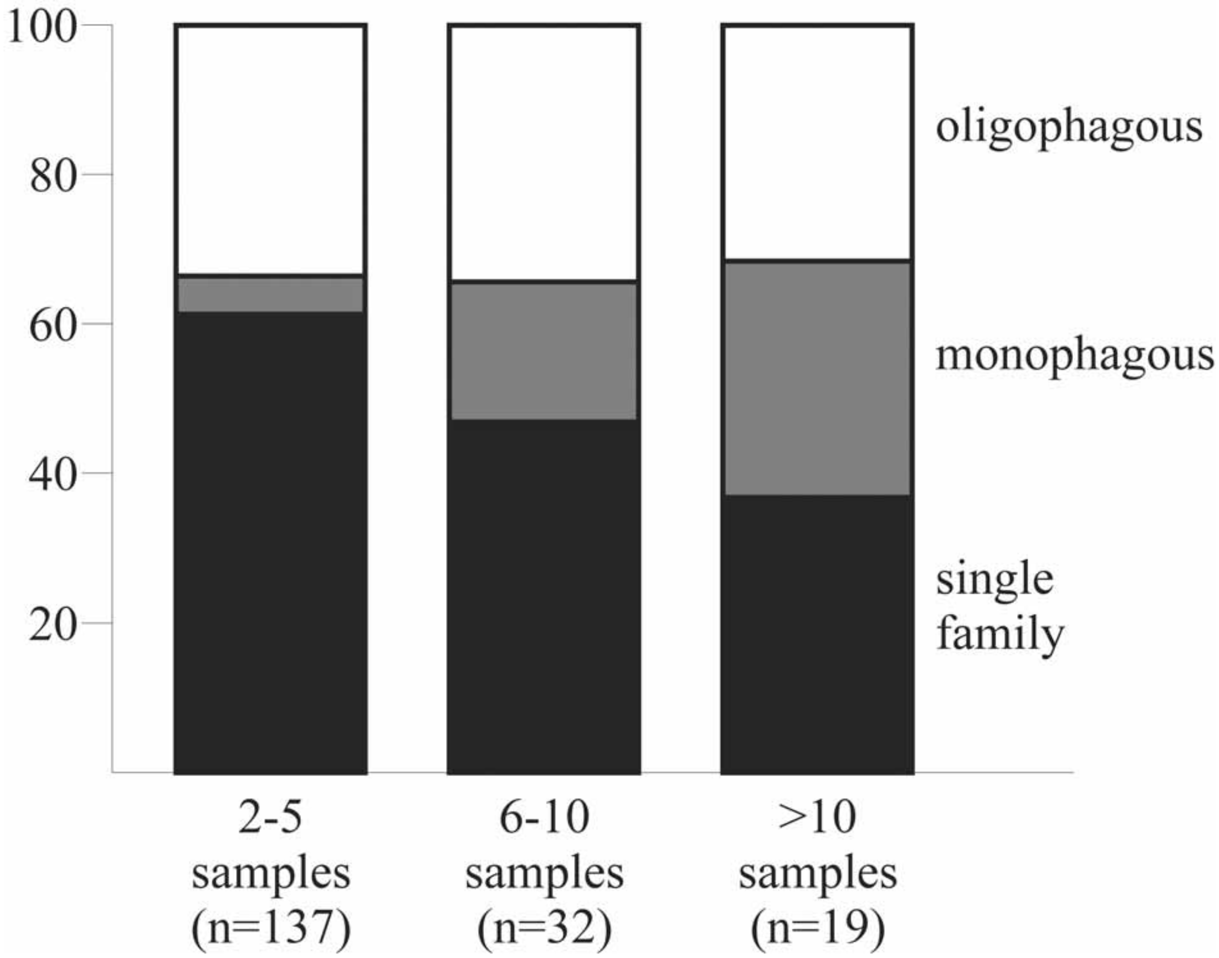

FIGURE 5. Effect of sampling on determinations of host family monophagy.

Modified mouthparts group

This is the most ecologically diverse group of Hawaiian drosophilids, in terms of both breeding host and substrate type. Five families, Araliaceae, Campanulaceae, Nyctaginaceae, Pandanaceae, and Urticaceae, account for 139 of 229 rearing records and 33 of 49 monophagous species. However, the breadth in host plant family in the *modified mouthparts* group far exceeds that of the other groups of Hawaiian *Drosophila,* encompassing 30 native families as well as various fungi. Some species have even been reared from introduced plants, including *Corynocarpus* (New Zealand laurel, Corynocarpaceae) and *Passiflora* (passionfruit, Passifloraceae). Unlike other groups of Hawaiian *Drosophila*, a variety of substrate types are also used (Figure 4). At the species level, however, about 70% are still substrate specific. Bark/stem is most prevalent, followed by leaves, fruit, and occasionally flowers; most of the undescribed species have been reared from bark. It is interesting to note that 6 undescribed species, but no described ones, have been reared from bark of Araliaceae, suggesting that this substrate type has been overlooked as a potential source of *modified mouthparts* species diversity.

The broad host range and low sample numbers for many species make generalizations difficult to make, but some patterns do emerge. The group is divided into subgroups based largely on mouthpart morphology (Magnacca & O'Grady, 2007), and some of these correspond to ecological habits (Table 1). The *conjectura* and *flavibasis* complexes of the *mimica* subgroup are specialists on leaves, while the *mimica* complex is probably adapted to *Sapindus* fruits (the only record for *D. antecedens* is for the exotic *Corynocarpus*, so its native host remains unknown). Some members of the *quadrisetae* subgroup have an unusually eclectic substrate as well as host range, but in general they appear to prefer Campanulaceae and Urticaceae. Finally, the large *dissita* subgroup primarily utilizes bark but is found on a wide variety of hosts, similar to the *grimshawi* clade of the *picture wings*.

Even more so than in other groups, analysis of ecology in the *modified mouthparts* group is complicated by the very large number of undescribed species. Many have been obtained only through rearing (Table 2), suggesting that these species are rare and/or highly specific to their host plant. For those species with rearing data, over 40% are known from a single rearing record. When more complete data are available it is likely that many species will be shown to be oligophagous or polyphagous, rather than monophagous as they appear now. Only 41% of the species with more than one rearing record are monophagous, a much lower proportion than for other groups.

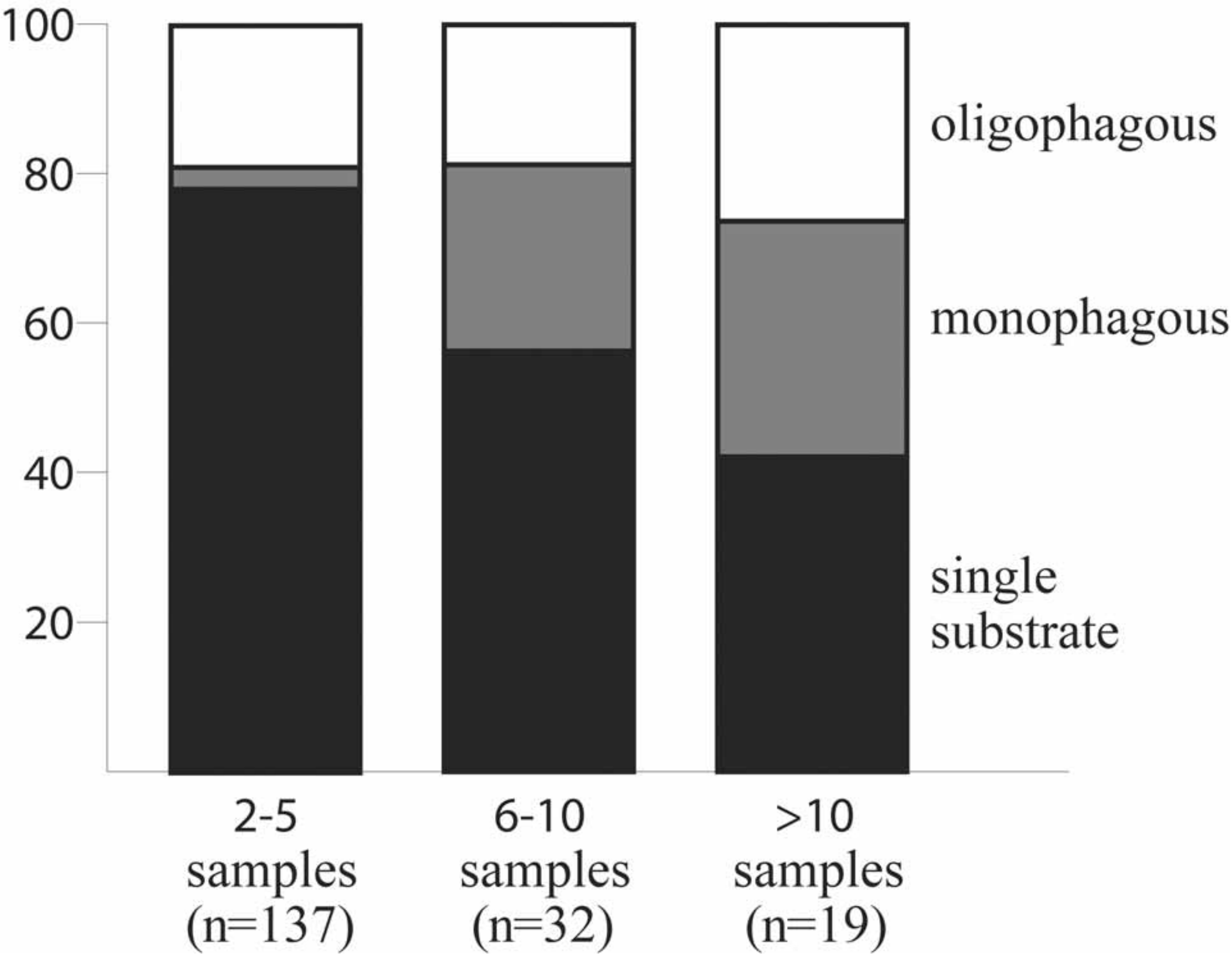

FIGURE 6. Effect of sampling on determinations of host substrate monophagy.

nudidrosophila and ateledrosophila groups

Ecological data for these two closely-related groups have been almost completely absent. We present here the first rearing records for an *ateledrosophila* species, and a greatly expanded data set for *nudidrosophila*. Because they breed in similar habitats, many *nudidrosophila* species were obtained during Montgomery's (1975) study of the *picture wing* group, but they were left unsorted. Twenty of the 31 described species now have records, although 9 are still known from only a single record. In general *nudidrosophila* appears to have a broad host range, with records from 11 plant families in only 39 rearing samples. It is concentrated on plants characteristic of mesic forest – *Charpentiera*, *Pisonia*, *Pleomele*, *Sapindus*, and *Urera* – though they may extend into wet areas as well. The only evolutionarily significant example of host specialization is that of three closely related members of the *velata* subgroup that are known only from *Pleomele* (Agavaceae).

Bonacum's (2001) phylogenetic study, which included two representative *nudidrosophila* species, suggested that this group may be nested within the *picture wing* group. While this might seem strange given their very different appearance, some characters of the male genitalia and ovipositor are suggestive of a close relationship between *nudidrosophila–ateledrosophila* and the *grimshawi* and *planitibia* clades, to the exclusion of the *adiastola* clade (Bonacum, 2001; Kaneshiro, 1976). Although *ateledrosophila* was not represented in Bonacum's (2001) or any other phylogenetic analysis, the male genitalia and ovipositor also appear to show close affinities with the *grimshawi* and *planitibia* clades (Kaneshiro, 1976). The *ateledrosophila*, *nudidrosophila*, and *grimshawi* groups all breed primarily in bark or stems of mesic forest plants. Relationships among these groups need to be clarified and more host data obtained before any definitive statements can be made regarding their role in breeding habit evolution.

picture wing group

This group has been by far the best-studied of the Hawaiian drosophilids thanks mainly to a major study by Montgomery (1975). Breeding records exist for 76 of the 110 described and 5 undescribed species. Compared to other groups of Hawaiian Drosophilidae the *picture wing* clade has relatively few undescribed species remaining, probably owing to their large size, ease of collection, and charismatic appearance. These same factors probably also contribute to their vulnerability to predation by the alien yellowjacket wasp *Vespula pensylvanica*, which has led to a decline in both species diversity and population size of many picture wing species (Carson, 1986; Foote & Carson, 1995).

The only consistent factor in *picture wing* breeding ecology is their almost exclusive use of bark and stems as a substrate; the only commonly-used alternative is sap flux, which is sometimes difficult to distinguish from rotting bark (Montgomery, 1975). This is partially due to the large size of most *picture wing* species, a characteristic which generally precludes use of small ephemeral substrates like leaves or flowers. The fact that few Hawaiian plant species have large, fleshy fruits probably also contributed to the reliance on bark as a larval development substrate among Hawaiian *Drosophila* species. Although some *Clermontia* and *Cyanea* (Campanulaceae) species have large fruits, only the outer layer (pericarp) appears to provide a suitable substrate for drosophilids; the remainder of the fruit is spongy placental tissue (Lammers, 1991) that does not ferment as the pericarp does, or does so much more slowly (pers. obs.).

The three major clades – *adiastola*, *grimshawi*, and *planitibia* – have very different breeding host preferences and will be discussed separately. As noted above, the monophyly of the *picture wing* group is not fully established, and it may be paraphyletic with respect to the *nudidrosophila* and *ateledrosophila* groups.

adiastola clade

The *adiastola* clade contains 16 species, 11 of which have rearing records. The primary host plants are species of Campanulaceae, specifically the bark of *Clermontia*. One species, *D. ochrobasis*, seems to be oligophagous, although additional rearing efforts might show these records to be incidental. It is clear that at least one host plant shift has taken place in this group: three species, *D. peniculipedis*, *D. touchardiae*, and *D. toxochaeta*, have only been reared from *Touchardia latifolia* (Urticaceae). Use of plant parts other than bark (leaves, fruit, and even flowers) seems to be more common in this group than other *picture wing* species, which are rarely found on alternate substrates other than sap flux. This may be related to the less specialized ovipositor of *adiastola* clade species compared to the long, narrow ovipositor of the *grimshawi* and *planitibia* subgroups.

planitibia clade

Another relatively small group, with 17 species (13 with host records), the *planitibia* clade is also similar to the *adiastola* clade in its restricted use of host plants. The group can be divided into the *picticornis*, *cyrtoloma*, *neopicta*, and *planitibia* subgroups. The *picticornis* group is basal and contains two species, *D. picticor-*

nis and *D. setosifrons*, that lack the extra crossvein that is characteristic of the remaining species. These taxa are widely divergent and may be relics of a larger clade (Bonacum, *et al.*, 2005). The sap breeding ecology of *D. picticornis* is unique in the *planitibia* clade. It is also the only *picture wing* to be reared from *Metrosideros polymorpha* (Myrtaceae), the most abundant tree in Hawaiʻi, but one that some suggest is very recently introduced to the islands (Wright, *et al.*, 2001). *Drosophila setosifrons* is a more typical *planitibia* species and breeds in Araliaceae bark, making the reconstruction of ancestral host plant for this group uncertain. The hosts of the remaining species are correlated with the subgroups: the *cyrtoloma* and *neopicta* subgroups are strictly on Araliaceae, while the *planitibia* subgroup is primarily on Campanulaceae. Due to their large size, the latter tend to be associated with the larger, arborescent species of *Clermontia* and *Cyanea* rather than the shrubbier species, such as *Cl. parviflora*, that are often more common. In many areas the larger lobelioid species have declined due to damage from feral ungulates and rats (Pratt & Abbott, 1997).

grimshawi clade

With 77 species, the *grimshawi* clade accounts for the bulk of *picture wing* species. It is also the most diverse in host usage, comparable to the *modified mouthparts* clade. On a finer scale, however, more specificity emerges. Within each species subgroup, a relatively small number of host shifts appears to have taken place (Table 5; to avoid confusion with the larger clade, their "*grimshawi* subgroup" is referred to here as the *crucigera* subgroup). For example, 12 of the 17 *orphnopeza* subgroup species are from either Agavaceae or Araliaceae, including one oligophagous species that uses both; species of the *vesciseta* subgroup use only Amaranthaceae, Nyctaginaceae, or Urticaceae; the *odontophallus* subgroup is exclusively on Agavaceae; and monophagous species of the *crucigera* subgroup use only Pandanaceae or Thymelaeaceae. The low overlap in host families between subgroups implies that specialization on a host plant may have played a major role in the early diversification of the *picture wing* clade. This is in contrast to the AMC clade, where little host-switching has taken place across the whole group, and the *modified mouthparts* group, where the *dissita* and *quadrisetae* subgroups show no clear pattern of host usage. The lack of a detailed species-level phylogeny such as exists for the *planitibia* group (Bonacum, *et al.*, 2005), and numerous confounding shifts to rarer hosts such as Nyctaginaceae and Sapindaceae, preclude further speculation on evolution of host usage among the *grimshawi* subgroups.

TABLE 5. Distribution of host family usage among subgroups of the *grimshawi* clade, *picture wing* group.

species complex[a]	species with ecological data												
	y	n	Agavaceae	Amaranthaceae	Araliaceae	Fabaceae	Myoporaceae	Nyctaginaceae	Pandanaceae	Sapindaceae	Thymelaeaceae	Urticaceae	oligophagous/ polyphagous
crucigera	8	1							3		2		3
hawaiiensis	9	5				3	3			1			2
odontophallus	4		4										
orphnopeza	17	2	2		9			1	1	1			3
punalua	5	3						1	2	1			1
vesciseta	11	5		5				2				3	1

[a] The *discreta* and *distinguenda* subgroups are not shown since rearing data is only available for one species from each.

Despite the wide diversity of host families used by the *grimshawi* clade, the only substrate shift has been from stems and bark proper to sap flux in the *hawaiiensis* subgroup. The latter is a similar habitat that is sometimes used by other *picture wing* species, particularly in the *orphnopeza* subgroup. Only two species commonly use other substrate types: *D. punalua* will sometimes use the fruit and leaves of *Freycinetia* in addition to the stems, and *D. crucigera*, a highly polyphagous species, will also use fruit.

The most striking aspect of the breeding records for the *grimshawi* clade is not so much the variety of host families that are used, as one that is not: Campanulaceae. This is considered one of the most important hosts for Hawaiian drosophilids in general, but especially for the other clades (*adiastola* and *planitibia*) in the *picture wing* group. Yet there are almost no records for the family in the *grimshawi* clade; in addition to four polyphagous species (*D. crucigera*, *D. disjuncta*, *D. grimshawi*, and *D. villosipedis*), there are only 4 records from 2 species (*D. limitata* and *D. murphyi*), and even these may be incidental. The near-absence of such a significant host from this large, highly host-variable group is remarkable, and warrants further investigation.

Araliaceae, particularly the genus *Cheirodendron*, is another very common host plant for Hawaiian Drosophilidae. While there are several records of *grimshawi* clade species using Araliaceae, nearly all are confined to the *orphnopeza* subgroup, the same 4 polyphagous species mentioned above, and scattered incidental records. Of those species that do use Araliaceae, 80% have been reared from either *Tetraplasandra* or *Reynoldsia* (see Appendix 1), often in lowland and/or relatively dry habitats. In contrast, none of the 240 Araliaceae records from the AMC and *modified mouthparts* clades are from *Reynoldsia* and only 22 (9%) are from *Tetraplasandra*, and all but one are from montane wet locations.

In general, the species of the *grimshawi* clade tend to favor more mesic to dry forest plants: *Acacia*, *Charpentiera*, *Myoporum*, *Pisonia*, *Pleomele*, *Reynoldsia*, *Sapindus*, *Tetraplasandra*, *Urera*, and *Wikstroemia*. Although many of these live in wet forest as well, it appears likely that the *grimshawi* clade evolved as a mesic assemblage, perhaps as sister to the *nudidrosophila* and *ateledrosophila* groups. It is perhaps not so surprising then that the characteristic plants of the wet forest – *Cheirodendron*, *Clermontia*, and *Cyanea* – are lacking from their diet, especially when these plants are already heavily utilized by other *picture wings*.

Elmomyza

This is by far the largest subgenus of *Scaptomyza* in the world, with 86 described and at least 30 undescribed species. Unfortunately its breeding habits are poorly known: there are rearing records for only 26 species, ten of which are undescribed. The majority of these are associated with Campanulaceae, and most species with large numbers of records have been found breeding in all parts of the plant. Because their body size is significantly smaller than that of the Hawaiian *Drosophila*, they are often the predominant native drosophilids to emerge from smaller, more ephemeral substrates such as rotting fruit and flowers. A number of species have made unusual host shifts coupled with substrate specialization: larvae of *S. cyrtandrae* and a related undescribed species live on the pubescent surface of living *Cyrtandra* (Gesneriaceae) leaves; three taxa have been reared from, or are closely associated with, various composite (Asteraceae) flowers; and a complex of undescribed species live on the sticky fruits of *Pisonia* (Nyctaginaceae), preying on insects stuck on to them. Such unusual records suggest that other species might be obtained by looking at similarly unconventional hosts.

other Scaptomyza

Only a few of the remaining *Scaptomyza* subgenera have rearing records. The subgenus *Exalloscaptomyza* is highly specialized on the ephemeral flowers of morning glory (*Ipomoea*, Convolvulaceae). This is a habitat utilized by other continental drosophilids, including *D. floricola* which has been introduced to Hawaiʻi. *Exalloscaptomyza* females are unusual in laying a single, well-developed egg or first instar larva (Kambysellis & Heed, 1971) and have among the shortest development times of all Hawaiian Drosophilidae (Heed, 1968), both adaptations to a short-lived substrate.

Titanochaeta has taken an unusual path as a predator of spider egg sacs. The pointed, sclerotized ovipositor they use to pierce the sac is characteristic of the group. Although a fair number of them have been reared, including 6 of the 11 species, little is known of their habits and they are uncommon in collections. Predation is also found in other drosophilid groups, especially the Steganinae, but rarely in *Drosophila* or *Scaptomyza* (Ashburner, 1981), although the *Pisona*–breeding *Elmomyza* are also predators.

The only other *Scaptomyza* subgenus with a moderate number of rearing records is *Tantalia*, which breed largely on leaves but do not appear to be host-specific, even within a species. *Bunostoma* has too few rearing records to draw even preliminary conclusions, and only one of the 8 unplaced species originally described as *Drosophila* but probably belonging to *Scaptomyza* (*D. vinnula*) has been reared. The other Hawaiian *Scaptomyza* subgenera – *Alloscaptomyza*, *Celidosoma*, *Engiscaptomyza*, *Grimshawomyia*, and *Rosenwaldia* – lack any data at all.

alien Drosophilidae

Although they are often the most abundant species on bait sponges, alien drosophilids – primarily *D. immigrans*, *D. simulans*, and *D. suzukii* – were relatively uncommonly reared from native substrates. The large populations of most aliens are maintained primarily by the abundant fleshy fruits of exotic plants, especially *Psidium* spp. (guava, Myrtaceae), *Passiflora tarminiana* (banana poka, Passifloraceae), and *Rubus* spp. (brambleberries, Rosaceae), rather than native plants. The only species reared in large numbers was *D. immigrans*, which could be found in bark, leaves, flowers, and fruit, especially of *Clermontia* (Campanulaceae). This species was present in high enough numbers that it could potentially exert competition pressure on Hawaiian drosophilids in their native host plants. *Drosophila suzukii* was also found breeding in the fruit of native *Rubus*, but relatively few natives (mostly *Elmomyza*) utilize it, apparently as a secondary host.

Discussion

Evolution of host usage

The data compiled here show an emerging picture of host plant usage in Hawaiian Drosophilidae that is quite different from that published in the past (Heed, 1968; Montgomery, 1975; Kambysellis 1995). In contrast to the highly host plant specific view of the Hawaiian drosophilid radiation, these data suggest the importance of secondary host plants in the evolution of this group. While a majority of species have a strong preference for a single host family, many also use secondary or incidental hosts. The frequency with which alternate host use occurs suggests that many of the Hawaiian drosophilids may not be as specialized on their primary hosts as previously thought. Such alternates can play a significant role in the diversification of the drosophilids through exposure to novel chemical, physical, and microbial habitats. Use of secondary hosts may therefore be a stepping stone to host switching, even in cases where the non-preferred host is toxic. For example, Kircher *et al.* (1967) found that even non-adapted species could produce adults, albeit sterile ones, on toxic hosts such as the senita cactus, (*Lophocereus schottii*) from southern Arizona. In such a case, a mutation allowing a relatively slight increase in tolerance for the toxin would allow exploitation of a large unused niche, followed by rapid selection for greatly increased tolerance. In Hawaii, this process may be what has allowed *D. quasiexpansa* and other leaf-breeding species to shift to *Melicope* (Rutaceae), the leaves of which are structurally similar to *Cheirodendron* but contain large quantities of essential oils (Scheuer, 1955; Scheuer & Hudgins, 1964).

The biological mechanisms behind specialization in Hawaiian drosophilids are largely unstudied and are potentially highly productive subjects for research. Kircher (1969) and Kircher and Heed (1970) investigated the sterols and fatty acids present in *Cheirodendron* leaves and found nothing distinctive about them, concluding that the leaves were more significant for their physical than their chemical properties. Although the failure of Hawaiian species to develop on standard *Drosophila* medium indicates that they do have some special nutritional needs, many species can be reared on Wheeler-Clayton or "yeastless" media (Spieth, 1980). This is in contrast to the North American cactophilic species *D. pachea*, which must obtain certain sterols from its senita cactus host (Kircher & Heed, 1970). Some members of the continental *quinaria* species group exhibit a much looser type of specialization where flies will readily oviposit and develop on other hosts in the lab, even in preference to their wild host, yet almost never do so in the field (James, *et al.*, 1988; Kibota & Courtney, 1991). The Hawaiian drosophilids appear to be intermediate between these two cases: the ability of many species to breed on non-preferred hosts and artificial media suggests most do not exhibit strict nutritional dependency, but females will usually not oviposit unless presented with a piece of their host plant. Ovipositor, ovary, and egg morphology is at least partly related to host substrate, with leaf-breeders in the AMC clade possessing fewer ovarioles and mature eggs than bark-breeders in the *picture wing* clade (Kambysellis & Heed, 1971; Kambysellis, *et al.*, 1995). However, species that have shifted substrates (e.g., bark-breeding *ciliated tarsus* or leaf-breeding *modified mouthparts* species), and those utilizing multiple plant parts, have not been investigated.

The ability to switch hosts and substrates, or at least the evolutionary value of doing so, clearly varies considerably between groups. This can be seen in a comparison of leaf breeding in the AMC and *modified mouthparts* groups. In the former, 3/4 of the species are restricted to Araliaceae or Aquifoliaceae, or both; most of the remainder are on a variety of "unusual" hosts such as Myoporaceae, Myrsinaceae, Pittosporaceae, and Rutaceae. Leaf breeders among the latter do not have a preferred host as a group, but are never found in the families listed above. The only place of overlap between the two *Drosophila* groups is in Campanulaceae, where *modified mouthparts* species are commonly found, AMC species occasionally so. This suggests that adaptations required to breed in Araliaceae and similar leaves are different from those required for the bark and leaves of other plants that the *modified mouthparts* species use, and that such adaptations may restrict the ability to breed in other hosts.

While monophagy of individual species may be lower than previously thought, the data do show that host plant and substrate range is indeed a relatively good marker for phylogenetic relationship (O'Grady, *et al.*, 2001). This is true for both specialization within a group, and broad oligophagy; the latter is found only in the *modified mouthparts* and *nudidrosophila* groups, the *grimshawi* clade, and *Elmomyza*, and only the first and the last use a range of substrates. Even within the *grimshawi* clade, each subgroup only uses a restricted number of host families (Table 5). The implication of this is that diversification in host plant usage has played a major role in the separation of the major lineages and their subgroups.

Reconstruction of ancestral breeding hosts has been a common topic of Hawaiian *Drosophila* researchers (Bonacum, 2001; Heed, 1971; Kambysellis, *et al.*, 1995), but thus far has not produced viable results. The conclusion (Kambysellis, *et al.*, 1995) that the first Hawaiian drosophilids were specialists on Araliaceae leaves is based on the basal position of an *antopocerus* species in a tree with only two other non-*picture wing* species. Montgomery's (1975) conclusion that Araliaceae were the primitive host of the *picture wing* clade was based on the number of species reared from the family; the ability of some "specialist" species (e.g., *D. setosimentum* and *D. silvestris*) to use Araliaceae as an incidental host; and rearing records of the putatively basal *D. primaeva* and *D. quasianomalipes* from the family. However, araliad monophagy is largely restricted to the *orphnopeza* subgroup of the *grimshawi* clade and the *cyrtoloma* subgroup of the *planitibia* clade. In addition, the predominance of *Tetraplasandra* and *Reynoldsia* among the former, rather than *Cheirodendron* (derived from a separate introduction) as in the latter and virtually all other araliad breeders, suggests an independent shift to the family.

An alternate possibility, again based largely on anecdotal evidence, is Campanulaceae. Multiple lines of evidence place the *Drosophila*-*Scaptomyza* split at 25–30 million years ago (Figure 1; Beverley & Wilson, 1985; DeSalle, 1992; Russo, *et al.*, 1995; Thomas & Hunt, 1993), not long after the last period during which there were no subaerial islands in the Hawaiian chain, about 30 Mya (Clague, 1996). Diversification of the extant lineages of Hawaiian *Drosophila*, on the other hand, occurred between 16 and 9 Mya (Figure 1;

O'Grady and DeSalle, submitted), a time roughly corresponding to the peak area and elevation of Gardner island (Price & Clague, 2002). The hypothesized arrival date of the Hawaiian lobelioids (which include the common hosts *Clermontia* and *Cyanea*) is also about 15 Mya (Givnish, *et al.*, 1996), which could be used to argue Campanulaceae as the ancestral host of the current major *Drosophila* lineages, and possibly the cause of the rapid explosion of diversity. The family is also used as at least an incidental host by all major lineages except the *haleakalae* group, as well as many *Scaptomyza*. However, we know virtually nothing of the other flora of this period; only a few plant taxa have been dated, and of those only the lobelioids predate Kaua‘i (Price & Clague, 2002).

Several factors make ancestral host inferences extremely uncertain. The most important of these is the likelihood of many wholly extinct lineages, both among drosophilids and host plants. The two "bottleneck" periods of low and/or distant volcanoes between Kure (30 Mya) and Lisianski (23 Mya), and Necker (11 Mya) and Kaua‘i (5.1 Mya), likely produced a significant reduction in diversity of the native biota (Price & Clague, 2002). With each step along the way, failure of a lineage to disperse from an older to a younger island would result in extinction as the island subsided, eroded, and became a dry atoll. Even in the more optimal dispersal conditions that have existed in the past 5 million years, the relatively high proportion of extant plant groups that have failed to disperse beyond Kaua‘i or O‘ahu indicates that subsidence of any island will take some lineages with it. It is possible that the ancestral hosts for even many of the currently extant drosophilid groups are extinct in Hawai‘i. Indeed, much of the evolutionary history of Drosophilidae in Hawai‘i may have been spent on islands possessing little or no wet forest, similar to Lāna‘i or Kaho‘olawe, with bursts of diversification during periods of extensive wet forest and diverse flora as in the last 5 million years.

A related issue is that the ancestors of today's *Drosophila* and *Scaptomyza* species probably bore little resemblance to any that exist today. For example, it is tempting to consider the *modified mouthparts* group to be primitive, given its flexibility in host plant and substrate usage (Heed, 1971). However, the *haleakalae* and AMC clades may have split off prior to the *modified mouthparts* group (Bonacum, 2001), and the courtship behavior of the latter is highly developed (Spieth, 1966). All of the current major clades and species groups are defined by their secondary sexual characters related to courtship or their breeding adaptations (often both), and therefore are all specialized offshoots from the ancestral trunk. As a result, there is no way to determine whether an attribute such as the ability to switch among many hosts is a holdover from an ancestral state or a derived one; and if the latter, what the original state was.

Ecology and conservation

Investigation of Hawaiian drosophilid ecology is especially critical for conservation. Twelve *picture wing* species were recently listed as Endangered or Threatened species (U.S. Fish and Wildlife Service, 2006). The population sizes of many more species have declined drastically (Carson, 1986), especially those restricted to rare plants such as *Urera* (U.S. Fish and Wildlife Service, 2006). Others have suffered severe declines in spite of abundant hosts, such as *D. murphyi* in ‘Ōla‘a (Foote & Carson, 1995), demonstrating a need to look for other causes.

It is also possible that inferred rarity in some Hawaiian drosophilid species may be a reflection of our ignorance of their host plant association or ecological niche, rather than that they are truly rare or should be considered endangered. For example, Hardy (1965: 493) states that *S. undulata* is "Known only from the type (female) taken in 1896, and from one male specimen taken…[in] 1903". This species was only taken infrequently in the past fifty years, in spite of intense collection effort. Recently, however, large numbers of individuals have been collected in pan traps, a method that has not traditionally been used when collecting Hawaiian Drosophilidae, in the same areas where Hawaiian *Drosophila* Project workers did much of their collecting. This demonstrates that conservation manangement decisions should not be made in the absence of comprehensive biological surveys and at least basic ecological data, including information concerning oviposition and larval development substrate.

Species reliant on a particular host are vulnerable to extinction if the host becomes too rare or scattered, even if the host does not itself become extinct. Many of the most important hosts of drosophilids – *Charpentiera* (Amaranthaceae), *Reynoldsia* and *Tetraplasandra* (Araliaceae), the lobelioids *Clermontia* and *Cyanea* (Campanulaceae), *Urera* (Urticaceae), and *Pleomele* (Agavaceae) – are also among the most susceptible to damage from alien ungulates such as pigs and goats, especially when combined with competition from invasive plants. Bark-breeding species are particularly sensitive to bottlenecks in host populations due to their dependence on older, senescent or dying plants. Microclimate alteration, such as opening of the canopy or understory, may also adversely affect the flies, either directly through increased desiccation or by causing host plants to dry more rapidly and rot differently. Even when conservation measures are implemented (e.g., fencing out feral ungulates from sections of native forest or controlling alien weeds), there may be a gap between the death of older trees that had long been unable to reproduce, and the maturation of new seedlings to the point where they are able to provide sufficient resources for drosophilid populations to survive. Other species that are dependent on more readily renewable substrates, such as those breeding in leaves, have been shown to persist for years at a single tree (Heed, 1968) and may not be subject to the same bottleneck pressures that impact bark-specific taxa.

Breeding information such as presented here, combined with a comprehensive phylogenetic classification, can be extremely important for conservation by allowing prediction of the host for a missing species. For example, *D. basisetae* is the second most-common *picture wing* in ʻŌlaʻa Forest (Foote & Carson, 1995), yet its breeding host is unknown. It is a member of the *punalua* subgroup, whose members are known from Nyctaginaceae, Sapindaceae, and Pandanaceae (Table 5). Since the first is highly restricted, the second absent, and the last abundant in this area, it can be concluded that it probably breeds in *Freycinetia*, a plant that has only a few rearing records from this area. Such predictions are important in cases where information on a particular species is needed quickly, and the predictions can be rapidly tested.

Interspecies competition at breeding sites is a largely unknown factor. Although *Cheirodendron* leaf-breeders of the AMC clade have been examined (Mangan, 1978), competition among the other groups, and between native and non-native species, remains unstudied. It is difficult to assess for several reasons, including the difficulty of locating larvae without disturbance and the many potential micro-niches available. Sciaridae and Psychodidae, both native and alien, emerge in large numbers from rotting branches and occasionally leaves, but may be feeding in the wood since they can continue to emerge long after the cambium layer (where the drosophilids are usually found) appears to be completely gone. Despite their extreme abundance in many areas, exotic *Drosophila* do not seem to be a major source of competition, as they are relatively uncommon in the substrates such as bark and leaves that most native drosophilids use. They may have a greater effect on fruit and flower breeding *Scaptomyza*. However, in recent years an alien crane fly, *Libnotes* sp. (Diptera: Limoniidae), has become extremely abundant in *Cheirodendron* bark (unpublished data). It is quite large (late-instar larvae may be over 30 mm long and 2-3 mm wide), and may occur in large numbers. It is not uncommon to bring a *Cheirodendron* branch into the lab to rear drosophilids, only to find that three weeks later all that remains between the outer bark and wood is limoniid frass. This level of resource depletion must have a serious effect on the drosophilid larvae in the same bark.

Future directions for Hawaiian Drosophilidae ecology studies

The biggest impediment to studies of the evolution of host use and ecology of Hawaiian drosophilids is our incomplete knowledge of their taxonomy. The large number of undescribed species obtained only from rearing studies underscores the importance of this technique for collecting the full set of species. Recent survey work in both rearing (presented here) and baiting with mushroom and banana bait (unpublished data) in ʻŌlaʻa Forest (Hawaiʻi Volcanoes National Park) on Hawaiʻi provides a striking example of the need for both methods in drosophilid research. During weekly baiting to survey *picture wing* populations, other species were collected *en masse* about every other week for nearly a year. Of the 32 *Drosophila* species (and several hundred individuals) collected, 21 were from the AMC clade, 6 from the *haleakalae* clade, and only 5 *modified mouthparts*. Of the last, only *mitchelli* subgroup members *D. mitchelli* and *D. nigrocirrus* (breeding hosts unknown) were collected in numbers, suggesting that most *modified mouthparts* species are not attracted to typical *Drosophila* baits. At the same time, leaves and bark of *Charpentiera* (Amaranthaceae), *Ilex* (Aquifoliaceae), *Cheirodendron*, *Tetraplasandra* (both Araliaceae), *Clermontia*, *Cyanea* (both Campanulaceae), *Pisonia* (Nyctaginaceae), *Freycinetia* (Pandanaceae), *Touchardia*, and *Urera* (both Urticaceae) were collected for rearing. Twelve *modified mouthparts* species, eight of them undescribed, were reared, as well as one *ateledrosophila* and three *nudidrosophila*; only two of the seven undescribed AMC species collected at sponges were reared. The contrast between the species sets collected by different methods is a clear demonstration that rearing is necessary not only for learning about the species we know, but to discover the possibly hundreds of undescribed species that are not attracted to the standard baits.

In addition to taxonomy, an understanding of phylogenetic relationships among Hawaiian *Drosophila* species, as well as among host plants, is key if we are to understand the evolution of host preference in this radiation. It is clear from the data collected thus far that host usage is highly correlated with phylogeny, yet our understanding of the latter remains incomplete. This is especially true for the internal relationships of the *modified mouthparts* and *picture wing* groups, which are the most interesting due to their high degree of variability in host and substrate usage. Many subgroups of the former have few representatives among rearing records. In addition, a number of smaller species groups such as *ateledrosophila*, *rustica*, *Alloscaptomyza*, *Celidosoma*, and *Rosenwaldia* appear to occupy important positions in the evolutionary history of the Hawaiian drosophilids, but are rarely collected and we lack any solid data on either their phylogenetic relationships or ecological associations.

In spite of the large amount of data on ecological affiliations of Hawaiian Drosophilidae, it is clear that additional rearing studies must be done targeting both known host plants and those plant species that historically have not been considered important as host substrates. The persistent failure to obtain many species in rearing from familiar hosts (the “major primary hosts” of Table 1) shows that other plants need to be explored. Among the major groups, the greatest deficiencies are among the *modified mouthparts* group and *Elmomyza*. The first is highly flexible in host usage, while the second is already known from unusual hosts such as *Cyrtandra* and Asteraceae. The fact that the host plants for many common species remain unknown indicates the need to look to “non-traditional” hosts for the breeding sites of many species. This is especially true for *Scaptomyza*, most of which remain uncommon in rearing, baiting, and sweeping. The observation by Heed (1968) that *Elmomyza* tend to use fresher substrates than *Drosophila* suggests that it may be necessary to examine plant parts in a very early stage of decay, such as leaves that are still attached to a plant, rather than after they have undergone a significant amount of decomposition.

Even among those plants that are well-known as hosts for drosophilids, much remains to be learned. Sampling has been uneven; *Clermontia* and *Cheirodendron* have acquired reputations for being good host plants and have been intensively reared from, though many new records continue to be found from them. On the other hand, 11 of the 24 non-*picture wing* rearing records for *Charpentiera* (Amaranthaceae), and 6 of 35 from *Pisonia* (Nyctaginaceae), have come from the relatively limited recent work done on Hawaiʻi, suggesting that these plants will continue to produce many new records with greater attention. Like many Hawaiian plants, both are woody descendents of non-woody ancestors (Carlquist, 1980). The trunk consists of wood interlayered with soft tissue (anomalous secondary growth; Eliasson, 2004; Wagner, *et al.*, 1999), and decay of the latter makes a large volume available for drosophilid breeding. Geographic bias is also present; the easily-accessible forests of Oʻahu and Hawaiʻi are much better represented than those of Kauaʻi, Molokaʻi, and especially Lānaʻi (Figure 2). The last has only 23 rearing records (1.9% of the total).

Drosophilid larvae feed primarily on microbes, and the different flora found on various plant species and substrates may play a major role in the evolution of host preference. For example, most members of the *modified mouthparts* group are not attracted to the standard banana/mushroom baits used for *picture wing* flies;

whether this basic difference in adult feeding preferences translates into a difference in breeding substrate usage is unknown, but may be related to the microbial flora. This area is little studied in Hawai‘i, and is a fertile ground for research. No survey of yeasts on decaying Hawaiian plants has been published except for *Ipomoea* flowers associated with *Exalloscaptomyza* (Lachance, *et al.*, 1989). However, a grouping of yeast floras by physiological similarity placed those of *Pisonia* and *Cheirodendron* bark close together and distinct from those of *Clermontia* bark, *Myoporum* sap flux, or *Cheirodendron* leaves (Starmer, 1981). Yeasts are generally thought of as the most important part of the *Drosophila* diet; however, the better development of many Hawaiian *Drosophila* on yeastless medium suggests that yeasts are not necessary for them. The only Hawaiian *Drosophila* species whose larval gut contents have been examined, the *Cheirodendron* leaf breeder *D. waddingtoni*, was found to contain almost entirely bacteria (Robertson, *et al.*, 1968). Whether the bacteria are being consumed or are symbiotic by breaking down plant material (or both) has not been determined.

Discovering the genetic determinants of ecological specialization and how they are distributed in natural populations has been the goal of ecological genetics since this field was conceived (e.g. Barker, *et al.*, 1990; Carson & Kaneshiro, 1976; Ford, 1964; Hollocher & Templeton, 1994). Recent studies by Jones (1998; 2001) on the evolution of host plant specificity in *Drosophila sechellia* suggests the potential to use this species as a model to correlate ecological affinity with the expression of genes encoding olfactory and gustatory receptor neurons. This is an exciting new line of research that could easily be extended to other species in the genus *Drosophila* via the 12 newly sequenced genomes and microarray studies of differential gene expression. It is possible that, with the genome sequence of *Drosophila grimshawi*, we can begin to understand the basic genetics underlying host plant choice in nearly 1000 species that have adapted to an amazing diversity of host plants.

A synergistic relationship exists among knowledge of ecology, behavior, evolution, and phylogenetics of the Hawaiian Drosophilidae. Although work on systematics, mating behavior, and chromosomal evolution of this extraordinary radiation has been ongoing, little has been added to our understanding of their ecology in the past 30 years. The data we have compiled and analyzed here is the result of a great deal of work by many people, but it is still far from complete. It is our hope that these data can be augmented by additional ecological studies and used to better understand host plant associations in Hawaiian Drosophilidae. Recent advances in genomics and the need for basic information about the biology of many species make synthetic studies such as this of critical importance (Markow & O’Grady, 2005). Meanwhile, the alarming decline of many species, and increasing awareness of insect conservation, makes further ecological study an imperative. We hope that this paper will inspire more interest in the ecology of these remarkable insects.

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Appendix. Rearing Records of the Hawaiian Drosophilidae

Records of the same substrate type and plant species are grouped. Where a record lists two (or more) substrate types, the sample contained both. Rec=records, Ind=individuals, Ref=references. References: 1. Swezey (1929); 2. Swezey (1934); 3. Bryan (1934); 4. Bryan (1938); 5. Swezey (1952); 6. Wirth (1952);7. Carson (1965); 8. Hardy (1965); 9. Carson (1966); 10. Hardy (1966); 11. Spieth (1966); 12. Heed (1968); 13. Kaneshiro *et al.* (1973); 14. Hardy and Kaneshiro (1975); 15. Montgomery (1975); 16. Hardy (1977); 17. Kam (1978); 18. Mangan (1978); 19. Hardy & Kaneshiro (1979); 20. Perreira & Kaneshiro (1990); 21. Hardy *et al.* (2001); 22. O'Grady *et al.* (2003); 23. Magnacca and O'Grady (in press); 24. this paper. Islands: H (Hawai'i), M (Maui), L (Lāna'i), Mo (Moloka'i), O (O'ahu), and K (Kaua'i). Unless otherwise stated, notes saying "listed as... refer to reference 12 or 15.

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref	
Drosophila								
haleakalae								
bipolita	Basidiomycetes	gill fungus	fungus	1	13	O	12	
chicae	Basidiomycetes	fungus	fungus	1	14	H	21	
curtitarsis	Basidiomycetes	mushroom	fungus	1	9	K	21	
demipolita	Basidiomycetes	gill fungus	fungus	1	6	H	10	
denotata	Basidiomycetes	fleshy fungus	fungus	1	14	O	8	
fungiperda	Basidiomycetes	*Polyporus sulphureus*	fungus	1	40	H	11	
iki	Basidiomycetes	gill fungus	fungus	1	1	H	12	
illusiopolita	Basidiomycetes	gill fungus	fungus	1	1	H	12	
luteola	Basidiomycetes	gill fungus	fungus	2	many	O	12	
macrochaetae	Basidiomycetes	soft-shell fungus	fungus	1	10	M	8	
melanoloma	Basidiomycetes	*Agaricus* sp.	fungus	1	5	Mo	12	
nigella	Basidiomycetes	*Polyporus sulphureus*	fungus	1	120	M	12	
ochropleura	Basidiomycetes	gill fungus	fungus	3	8	H	12,21	listed as *D. luteola* in ref. 12
polita	Basidiomycetes	gill fungus	fungus	1	45	H	21	
antopocerus-modified tarsus-ciliated tarsus								
antopocerus								
adunca	Araliaceae	*Cheirodendron trigynum*	leaf	10	32	M	12	
arcuata	Araliaceae	*Cheirodendron* sp.	leaf	1	3	O	12	
cognata	Aquifoliaceae	*Ilex anomala*	leaf	5	32	H	12	
	Araliaceae	*Cheirodendron trigynum*	leaf	3	6	H	12	
curvata	Araliaceae	*Tetraplasandra* sp.	leaf	1	x		24	
diamphidiopoda	Araliaceae	*Cheirodendron trigynum*	leaf	8	18	M,Mo	12	
entrichocnemia	Aquifoliaceae	*Ilex anomala*	leaf	1	1	M	12	
longiseta	Araliaceae	*Cheirodendron trigynum*	leaf	1	1	Mo	12	
orthoptera	Araliaceae	*Cheirodendron trigynum*	leaf	4	4	M	12	
tanythrix	Araliaceae	*Cheirodendron trigynum*	leaf	10	1013	H	12,18	
		Tetraplasandra sp.	leaf	1	1	H	12	

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref	
yooni	Araliaceae	*Cheirodendron trigynum*	leaf	2	24	H	12,16,18	
J41	Araliaceae	*Cheirodendron trigynum*	leaf	1	2	Mo	12	
J99	Araliaceae	*Cheirodendron trigynum*	leaf	1	5	M	12	
bristle tarsus								
basimacula	Araliaceae	*Cheirodendron platyphyllum*	leaf	1	3	K	12	
		Cheirodendron sp.	leaf	2	26	K	12	
bicondyla	Aquifoliaceae	*Ilex anomala*	leaf	1	1	H	12	
brunneisetae	Aquifoliaceae	*Ilex anomala*	leaf	1	2	M	12	
expansa	Araliaceae	*Cheirodendron trigynum*	leaf	3	15	H,M	12,18	
		Tetraplasandra sp.	leaf	1	1	M	12	
fusticula	Campanulaceae	*Clermontia arborescens*	leaf	4	18	M	12	
perissopoda	Araliaceae	*Cheirodendron trigynum*	leaf	1	2	K	12	
		Tetraplasandra sp.	leaf	1	2	K	12	
	Corynocarpaceae	*Corynocarpus laevigatus*	leaf	1	3	K	24	
	Urticaceae	*Pipturus* sp.	leaf	1	30	K	24	
petalopeza	Araliaceae	*Cheirodendron trigynum*	leaf	4	14	M	12	
prodita	Myrsinaceae	*Myrsine lessertiana*	leaf	3	15	H,M	12	
quasiexpansa	Rutaceae	*Melicope* sp.	leaf	5	74	M	12	
		Platydesma campanulata	leaf	2	13	M	12	
redunca	Araliaceae	*Cheirodendron trigynum*	leaf	1	4	M	12	
seclusa	Araliaceae	*Cheirodendron trigynum*	leaf	5	11	M	12	
spicula	Aquifoliaceae	*Ilex anomala*	leaf	1	5	H	12	
torula	Aquifoliaceae	*Ilex anomala*	leaf	1	1	M	12	
trichaetosa	Araliaceae	*Cheirodendron trigynum*	leaf	14	279	H	12,18	
G33	Aquifoliaceae	*Ilex anomala*	leaf	1	3	L	12	"n. sp. also with bristle tarsi" in 12
HH15	Araliaceae	*Cheirodendron trigynum*	leaf	1	2	M	12	"n. sp. rel. *petalopeza*" in 12
J7a	Araliaceae	*Tetraplasandra* sp.	leaf	1	2	K	12	"n. sp. rel. *perissopoda*" in 12
J8	Araliaceae	*Cheirodendron platyphyllum*	leaf	1	3	K	12	"n. sp. rel. *perissopoda*" in 12
K17,N77	Myoporaceae	*Myoporum sandwicense*	leaf	2	12	H	12,24	listed as part of *D. quasiexpansa* in 12, probably n. sp.
ciliated tarsus								
carnosa	Araliaceae	*Cheirodendron* sp.	leaf	1	7	O	12	
imparisetae	Araliaceae	*Cheirodendron trigynum*	bark	2	3	H	24	
		Cheirodendron trigynum	leaf	1	1	H	12	
	Myrsinaceae	*Myrsine lessertiana*	fruit	2	30	H	12	
	Sapindaceae	*Sapindus saponaria*	fruit	2	38	H	12	
kraussi	Asteraceae	*Dubautia* sp.	bark	1	4	O	24	identification uncertain
latigena	Araliaceae	*Cheirodendron trigynum*	stem,	15	41	H	12,24	

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref	
			branch, root					
medialis	Araliaceae	*Cheirodendron trigynum*	branch, stem, root	10	48	H	12,24	
melanopedis	Araliaceae	*Cheirodendron trigynum*	bark, stem, root	1	3	H	24	
orestes	Campanulaceae	*Clermontia* sp.	fruit, leaf	1	3	H	12	
		Clermontia sp.	stem	1	1	H	12	
		Cyanea stictophylla	leaf	1	1	H	24	
		Cyanea tritomantha	leaf	1	9	H	24	
paucula	Araliaceae	*Cheirodendron* sp.	leaf	1	11	O	12	
sadleria	Blechnaceae	*Sadleria* sp.	rachis	1	1	O	4	
setipalpus	Araliaceae	*Tetraplasandra* sp.	leaf	2	7	M	12	
	Campanulaceae	*Lobelia* sp.	leaf	1	4	M	12	
	Rutaceae	*Melicope* sp.	leaf	1	1	M	12	
williamsi	Araliaceae	*Cheirodendron* sp.	leaf	1	29	O	12	
12.iii.1965	Araliaceae	*Tetraplasandra* sp.	leaf	1	100+	O	12	"n. sp. rel. *paucula*" in 12
20.vii.1964	Araliaceae	*Cheirodendron trigynum*	leaf	1	2	Mo	12	"n. sp. rel. *kraussi*" in 12
G41b, G59b	Pittosporaceae	*Pittosporum* sp.	leaf	2	3	M	12	"n. sp. rel. *orestes*" in 12
R90	Asteraceae	*Argyroxiphium caliginis*	leaf	1	7	M	24	
sp. 3	Aquifoliaceae	*Ilex anomala*	bark	3	7	H	24	
	Araliaceae	*Cheirodendron trigynum*	bark	2	4	H	24	
split tarsus								
ancyla	Araliaceae	*Cheirodendron trigynum*	leaf	2	31	M	12	
attenuata	Araliaceae	*Cheirodendron trigynum*	bark	1	2	H	24	
		Cheirodendron trigynum	leaf	1	1	H	12	
chaetocephala	Campanulaceae	*Clermontia* sp.	leaf	1	14	O	19	
		Cyanea sp.	bark	1	2	O	24	
clavata	Araliaceae	*Tetraplasandra* sp.	leaf	2	16	O	24	
cnecopleura	Araliaceae	*Cheirodendron trigynum*	leaf	2	2	H	12,18	
cornutitarsus	Araliaceae	*Tetraplasandra* sp.	leaf	1	16	M	19	
cracens	Araliaceae	*Cheirodendron trigynum*	leaf	1	1	M	12	
dicropeza	Rutaceae	*Melicope* sp.	leaf	1	24	H	19	
fundita	Araliaceae	*Cheirodendron trigynum*	leaf	3	4	M,L	12	
	Rutaceae	*Melicope* sp.	leaf	1	1	M	12	
pectinitarsus	Fabaceae	*Sophora chrysophylla*	leaf	1	4	H	12	
spiethi	Araliaceae	*Cheirodendron trigynum*	leaf	4	65	H	12,18	
	Fabaceae	*Sophora chrysophylla*	leaf	1	5	H	12	

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref	
systenopeza	Rutaceae	*Melicope* sp.	leaf	1	1	M	12,19	"n. sp. #2 nr. *variabilis*" in 12
variabilis	Araliaceae	*Cheirodendron trigynum*	leaf	2	9	M,Mo	12	
K14a	Araliaceae	*Cheirodendron trigynum*	leaf	1	1	H	12	"n. sp. #4 nr. *cracens*" in 12
K19	Araliaceae	*Cheirodendron trigynum*	leaf	1	4	H	12	"n. sp. #3 nr. *cracens*" in 12
spoon tarsus								
conformis	Aquifoliaceae	*Ilex anomala*	leaf	6	27	H	12	
dasycnemia	Araliaceae	*Cheirodendron trigynum*	leaf	9	43	H	12,18	
mimiconformis	Aquifoliaceae	*Ilex anomala*	leaf	1	1	M	12	
	Araliaceae	*Cheirodendron trigynum*	leaf	2	6	M,Mo	12	
		Tetraplasandra sp.	leaf	1	2	Mo	12	
neutralis	Araliaceae	*Cheirodendron trigynum*	bark	2	3	H	24	
		Cheirodendron trigynum	leaf	8	35	H	12,18	
		Tetraplasandra oahuensis	bark	1	2	H	24	
percnosoma	Araliaceae	*Cheirodendron trigynum*	leaf	15	291	H	12,18	
	Campanulaceae	*Clermontia* sp.	leaf	1	1	M	12	
septuosa	Araliaceae	*Cheirodendron trigynum*	leaf	3	10	H	12	
		Tetraplasandra oahuensis	leaf	4	22	H	24	
sordidapex	Aquifoliaceae	*Ilex anomala*	leaf	6	50	H	12	
	Araliaceae	*Cheirodendron trigynum*	leaf	1	3	H	12	
waddingtoni	Araliaceae	*Cheirodendron trigynum*	leaf	28	812	H,M, Mo,L	12,18	
		Tetraplasandra sp.	leaf	1	1	M	12	
	Campanulaceae	*Clermontia* sp.	leaf	1	1	H	12	
		Clermontia sp.	stem	1	1	L	12	
	Myrsinaceae	*Myrsine lessertiana*	leaf	1	2	M	12	
	Pittosporaceae	*Pittosporum* sp.	leaf	1	2	M	12	
G30,34,51,80a,J98	Campanulaceae	*Clermontia* sp.	leaf	5	57	M	12	"n. sp. #5 nr. *mimiconformis*" in 12
G41a,45,59a	Araliaceae	*Tetraplasandra* sp.	leaf	1	3	L	12	"n. sp. #3 nr. *mimiconformis*" in 12
	Pittosporaceae	*Pittosporum* sp.	leaf	2	46	M	12	"n. sp. #3 nr. *mimiconformis*" in 12
G80b	Araliaceae	*Tetraplasandra* sp.	leaf	1	4	M	12	"n. sp. rel. *mimiconformis*" in 12
G87a	Araliaceae	*Cheirodendron trigynum*	leaf	1	1	H	12	"n. sp. #1 nr. *neutralis*" in 12
G87b	Campanulaceae	*Clermontia* sp.	leaf, fruit, flower	1	2	H	12	"n. sp. nr. *neutralis*" in 12
sp. 1	Araliaceae	*Tetraplasandra oahuensis*	leaf	4	7	H	24	
unplaced								
achyla	Pittosporaceae	*Pittosporum* sp.	leaf	2	26	M	12	
fastigata	Araliaceae	*Cheirodendron platyphyllum*	leaf	1	1	O	12	
mimiconfutata	Aquifoliaceae	*Ilex anomala*	leaf	2	9	O	12	

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref	
unicula	Aquifoliaceae	*Ilex anomala*	leaf	3	12	H	12	
G87	Aquifoliaceae	*Ilex anomala*	fruit	1	2	H	12	"n. sp. *fusticula* type" in 12
G89	Aquifoliaceae	*Ilex anomala*	stem	1	4	H	12	"n. sp. nr. *confutata*" in 12
J12	Gunneraceae	*Gunnera petaloidea*	petiole	1	1	M	12	"n. sp. nr. *confutata*" in 12
modified mouthpart								
adventitia								
adventitia	Amaranthaceae	*Charpentiera* sp.	stem	2	5	K	24	
bridwelli								
apicipuncta	Blechnaceae	*Sadleria* sp.	rachis	1	1	H	4	
ceratostoma								
ceratostoma	Basidiomycetes	bracket fungus	fungus	1	5	H	10	label has "reared from" crossed out and "feeding on" handwritten in
humeralis	Campanulaceae	*Clermontia* sp.	stem	3	7	K	12,24	"n. sp. pattern wing, thorax" in 12
		Clermontia sp.	fruit	1	2	K	12	
dissita								
amydrospilota	Campanulaceae	*Clermontia arborescens*	stem, leaf	2	11	M	12	
brevissima	Campanulaceae	*Clermontia* sp.	stem	1	3	M	24	
	Nyctaginaceae	*Pisonia* sp.	stem	1	2	Mo	24	
dissita	Amaranthaceae	*Charpentiera obovata*	bark	2	13	H	24	
	Araliaceae	*Cheirodendron trigynum*	bark	1	5	H	24	
	Campanulaceae	*Clermontia* sp.	bark	1	1	H	24	
	Nyctaginaceae	*Pisonia brunoniana*	bark	2	5	H	24	
	Sapindaceae	*Sapindus saponaria*	bark	1	1	H	24	
		Sapindus saponaria	fruit	1	1	H	24	
	Urticaceae	*Urera glabra*	stem	2	11	H	12,24	
dissita (Maui)	Campanulaceae	*Clermontia* sp.	bark	1	12	M	24	
	Nyctaginaceae	*Pisonia* sp.	stem	1	6	M	24	
	Urticaceae	*Touchardia latifolia*	bark	1	6	M	24	
dissita (Molokai)	Nyctaginaceae	*Pisonia* sp.	stem	1	1	M	24	
	Urticaceae	*Touchardia latifolia*	bark	1	5	M	24	
dissita (Oahu)	Agavaceae	*Pleomele* sp.	leaf	1	1	O	24	
	Amaranthaceae	*Charpentiera* sp.	stem	1	19	O	24	
	Asteraceae	*Dubautia* sp.	bark	1	2	O	24	
	Urticaceae	*Urera* sp.	stem	2	7	O	24	
dissita (Kauai)	Basidiomycetes	bait mushroom	fungus	1	1	K	24	
	Corynocarpaceae	*Corynocarpus laevigatus*	fruit	1	18	K	12	grouped with *D. dissita* in 12 (as J7G)
dracaenae	Agavaceae	*Pleomele aurea*		1	5	K	8	substrate not recorded

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref	
eumecothrix	Campanulaceae	*Lobelia* sp.	stem	1	1	M	24	
	Nyctaginaceae	*Pisonia* sp.	stem	1	2	L	24	
	Urticaceae	*Touchardia latifolia*	bark	1	3	M	24	
		Urera glabra	bark	1	4	Mo	24	
larifuga	Euphorbiaceae	*Chamaesyce* sp.	bark	1	1	O	24	
	Lauraceae	*Cryptocarya oahuensis*	fruit	1	19	O	24	
	Nyctaginaceae	*Pisonia* sp.	stem	1	4	O	24	
vicaria	Campanulaceae	*Clermontia* sp.	fruit	1	2	M	12	
	Nyctaginaceae	*Pisonia* sp.	stem	1	1	Mo	24	
G87,J20	Araliaceae	*Cheirodendron trigynum*	stem	3	9	H	12,24	"n. sp. nr. *ischnotrix*" in 12
J6G	Pandanaceae	*Freycinetia arborea*	stem	1	1	H	24	
P59A	Urticaceae	*Touchardia latifolia*	bark	1	2	K	24	
		Urera glabra	stem	1	1	K	24	
P59B	Campanulaceae	*Cyanea* sp.	stem	1	2	K	24	
	Urticaceae	*Touchardia latifolia*	bark	1	2	K	24	
P72,P77A	Euphorbiaceae	*Chamaesyce* sp.	bark	1	8	O	24	
	Urticaceae	*Urera kaalae*	bark	2	22	O	24	
P77B	Euphorbiaceae	*Chamaesyce* sp.	bark	1	1	O	24	
P85	Araliaceae	*Tetraplasandra* sp.	bark	1	1	M	24	
Q20A	Nyctaginaceae	*Pisonia* sp.	stem	1	2	L	24	
Q88	Campanulaceae	*Clermontia clermontioides*	bark	2	5	H	24	
	Urticaceae	*Urera glabra*	bark	2	51	H	24	
R33	Pandanaceae	*Freycinetia arborea*	fruit	1	6	M	24	
		Freycinetia arborea	leaf axil	1	5	M	24	
sp. 18	Pandanaceae	*Freycinetia arborea*	stem	3	6	H	24	
sp. 20	Araliaceae	*Cheirodendron trigynum*	bark	2	3	H	24	
sp. 25	Araliaceae	*Cheirodendron trigynum*	bark	11	30	H	24	
freycinetiae								
asketostoma	Asteraceae	*Argyroxiphium sandwicense*	flower	1	23	M	8	collected on flowers, not reared
freycinetiae	Pandanaceae	*Freycinetia arborea*	leaf base	1	1	O	24	
nalomano	Thymelaeaceae	*Wikstroemia* sp.	bark	1	2	O	24	
prominens	Urticaceae	*Touchardia latifolia*	stem?	1	2	K	24	substrate not recorded
11.iv.1970	Urticaceae	*Touchardia latifolia*	stem	1	1	O	24	
11.iii.1973	Pandanaceae	*Freycinetia arborea*	leaf axil	1	1	L	24	
25.vii.1979	Liliaceae	*Astelia menziesiana*	leaf	1	2	Mo	24	
fuscoamoeba								
aquila	Marattiaceae	*Marattia douglasii*	rachis	1	1	H	24	

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref	
	Woodsiaceae	*Athyrium microphyllum*	rachis	1	1	H	24	
araiotrichia	Woodsiaceae	*Athyrium microphyllum*	rachis	1	2	Mo	24	
fuscoamoeba	Amaranthaceae	*Charpentiera* sp.	stem	1	1	O	24	
	Urticaceae	*Urera* sp.	stem	1	1	O	24	
	fern		rachis	1	5	O	24	
hirtitarsus								
goureaui	Basidiomycetes	bracket fungus	leaf	1	5	O	8	
hirtitarsus	Oleaceae	*Nestegis sandwicensis*	sap flux	2	3	Mo,L	24	
10.ix.1964	Basidiomycetes	gill fungus	fungus	1	38	H	10	"n. sp. rel. *hirtitarsus*" in 12
mimica								
antecedens	Corynocarpaceae	*Corynocarpus laevigatus*	leaf	1	6	K	12,22	
chaetopeza	Campanulaceae	*Clermontia clermontioides*	bark	1	8	H	24	
		Clermontia sp.	fruit	1	2	H	12	
chimera	Campanulaceae	*Clermontia* sp.	leaf	1	1	O	22	
conjectura	Nyctaginaceae	*Pisonia umbellifera*	leaf	1	76	L	22	
flavibasis	Corynocarpaceae	*Corynocarpus laevigatus*	leaf	1		K	17	
	Nyctaginaceae	*Pisonia umbellifera*	leaf	1	13	K	22	
gagne	Sapindaceae	*Sapindus oahuensis*	fruit	1	2	O	22	
infuscata	Campanulaceae	*Clermontia* sp.	stem, bark	3	22	H	12	
	Oleaceae	*Nestegis sandwicensis*	stem, bark	1	1	H	8	
	Pandanaceae	*Freycinetia arborea*	stem, bark	7	17	H	12,22,24	
involuta	Campanulaceae	*Clermontia* sp.	flower	1	1	H	24	
		Clermontia sp.	fruit	1	1	H	12,22	G90 in 12
	Fabaceae	*Canavalia* sp.	flower	1	1	H	22	
kambysellisi	Campanulaceae	*Clermontia* sp.	leaf	1	2	H	17	
	Nyctaginaceae	*Pisonia brunoniana*	bark	1	1	H	24	
		Pisonia brunoniana	leaf	6	128	H	11,12,22	
	Passifloraceae	*Passiflora* sp.	leaf	1		H	17	
	Rubiaceae	*Psychotria* sp.	leaf	1	3	H	22	
kauluai	Apocynaceae	*Pteralyxia* sp.	fruit	1	1	O	22	
	Sapotaceae	*Pouteria sandwicensis*	fruit	2	24	O	3,22	
lobatopalpus	Sapindaceae	*Sapindus oahuensis*	flux, soil	1	1	O	22	
maemae	Pandanaceae	*Freycinetia arborea*	stem, bark	1	8	M	22	
mimica	Basidiomycetes	bracket fungus	fungi	1	1	H	12	
	Piperaceae	*Peperomia* sp.	leaf	1	1	H	12	
	Sapindaceae	*Sapindus saponaria*	fruits	6	116	H	12,22	
reschae	Nyctaginaceae	*Pisonia* sp.	leaf	1		O	14	

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref	
xenophaga	Amaranthaceae	*Charpentiera obovata*	leaf	2	3	H	24	
		Charpentiera sp.	leaf	1	1	H	22	
	Passifloraceae	*Passiflora* sp.	leaf	1	54	H	12,22	
	Solanaceae	*Nothocestrum longifolium*	leaf	1	3	H	24	
nanella								
dolomata	Amaranthaceae	*Charpentiera* sp.	stem	1	1	O	24	
	Fabaceae	*Strongylodon lucida*	fruit	1	1	O	24	
	Nyctaginaceae	*Pisonia* sp.	leaf	1	10	O	24	
nanella	Nyctaginaceae	*Pisonia* sp.	leaf	3	31	K	24	
quadrisetae								
ischnotrix	Amaranthaceae	*Charpentiera* sp.	stem	2	12	O	24	
	Fabaceae	*Strongylodon lucida*	fruit	1	1	O	24	
	Malvaceae	*Hibiscus* sp.	bark	1	1	O	24	
	Pandanaceae	*Freycinetia arborea*	leaf	1	1	O	24	
	Urticaceae	*Touchardia latifolia*	leaf	2	5	O	24	
quadrisetae	Campanulaceae	*Clermontia* sp.	branch	1	1	K	12	
		Clermontia sp.	fruit, flower	2	27	K	12	
		Clermontia sp.	leaf	1	11	K	12	
	Corynocarpaceae	*Corynocarpus laevigatus*	fruit	1	2	K	12	
residua	Campanulaceae	*Clermontia lindseyana*	bark	1	14	H	24	
tendomentum	Basidiomycetes	bracket & gill fungus	fungus	1	24	H	11,12	
	Campanulaceae	*Clermontia* sp.	fruit	1	6	H	12	
		Clermontia sp.	leaf	1	2	H	12	
		Clermontia sp.	stem	2	17	H	12	
	Dryopteridaceae	*Dryopteris* sp.	rachis	1	1	H	24	
	Liliaceae	*Astelia menziesii*	flower	1	4	H	24	
	Passifloraceae	*Passiflora pulchella*	flower	1	1	H	12	
	Rosaceae	*Rubus* sp.	fruit	1	1	H	12	
		Rubus sp.	leaf	1	21	H	12	
	Solanaceae	*Solanum pseudocapsicum*	fruit	1	3	H	24	
	Urticaceae	*Urera glaba*	fruit, stem, leaf	1	2	H	24	
	Woodsiaceae	*Athyrium microphyllum*	rachis	1	4	H	24	
G41	Campanulaceae	*Clermontia* sp.	leaf, stem	1	2	M	12	"n. sp. nr. *laciniosa*" in 12
	Urticaceae	*Touchardia latifolia*	bark	1	5	M	24	
J17, J28	Amaranthaceae	*Charpentiera obovata*	leaf	2	3	H	24	
	Campanulaceae	*Clermontia clermontioides*	bark	1	1	H	24	

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref	
		Clermontia parviflora	bark	2	24	H	24	
		Clermontia sp.	leaf, stem	2	6	H	12,24	"n. sp. rel. *biseriata*" in 12
		Cyanea tritomantha	leaf	1	24	H	24	
	Liliaceae	*Astelia menziesii*	leaf	1	2	H	24	
	Passifloraceae	*Passiflora* sp.	leaf	1	6	H	12	"n. sp. rel. *dissita*" in 12
	Urticaceae	*Urera glabra*	bark	1	1	H	24	
P84B	Campanulaceae	*Lobelia* sp.	stem	1	5	M	24	
R84	Urticaceae	*Touchardia latifolia*	bark	1	2	Mo	24	
scolostoma								
deltaneuron	Arecaceae	*Pritchardia* sp.	fruit	2	3	O	24	
semifuscata								
acanthostoma	Myrtaceae	*Metrosideros polymorpha*	sap flux	2	11	H	24	
	Oleaceae	*Nestegis sandwicensis*	sap flux	1	5	H	24	
anoplostoma	Fabaceae	*Acacia koa*	sap flux	1	9	M	24	
	Myoporaceae	*Myoporum sandwicense*	sap flux	1	9	M	24	
	Myrtaceae	*Metrosideros polymorpha*	sap flux	1	1		24	
	Oleaceae	*Nestegis sandwicensis*	sap flux	3	18	M,L	24	
Q12	Fabaceae	*Acacia koa*	sap flux	1	4	O	24	
	Myrsinaceae	*Myrsine* sp.	sap flux	1	1	O	24	
	Oleaceae	*Nestegis sandwicensis*	sap flux	2	9	O	24	
setiger								
desallei	Nyctaginaceae	*Pisonia brunoniana*	stem	1	1	H	24	
imitator	Urticaceae	*Touchardia latifolia*	stem	1	1	O	24	
unplaced								
barbata	Campanulaceae	*Clermontia* sp.	bark	4	13	H	24	
	Nyctaginaceae	*Pisonia brunoniana*	bark	1	1	H	24	
	Pandanaceae	*Freycinetia arborea*	stem	1	3	H	24	
	Urticaceae	*Urera glabra*	bark	1	20	H	24	
lelolua	Pandanaceae	*Freycinetia arborea*	live leaf	1	1	L	24	
omnivora	Fabaceae	*Strongylodon lucida*	fruit	1	8	O	24	
	Urticaceae	*Touchardia latifolia*	rachis	1	9	O	24	
	fern		rachis	1	9	O	24	
toxacantha	Araliaceae	*Cheirodendron trigynum*	bark	3	10	H	12,24	"n. sp. nr. *latigena*" in 12
umiumi	Campanulaceae	*Clermontia* sp.	bark	1	4	H	24	
ateledrosophila								
papala	Amaranthaceae	*Charpentiera obovata*	bark	3	64	H	24	
	Nyctaginaceae	*Pisonia brunoniana*	bark	2	4	H	24	

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref	
nudidrosophila								
hirtitibia								
hirtitibia	Urticaceae	*Urera* sp.	stem	1	9	O	23	
konaensis	Amaranthaceae	*Charpentiera obovata*	bark	2	8	H	23	
	Nyctaginaceae	*Pisonia* sp.	stem	1	2	H	23	
mawaena	Nyctaginaceae	*Pisonia* sp.	stem	1	2	L	23	females only
kahania								
kahania	Urticaceae	*Urera* sp.	stem	1	1	O	23	
nudidrosophila								
aenicta	Euphorbiaceae	*Chamaesyce* sp.	bark	1	5	O	23	
amita	Amaranthaceae	*Charpentiera obovata*	bark	1	6	H	23	
	Euphorbiaceae	*Claoxylon sandwicense*	bark	1	11	H	23	
canavalia	Amaranthaceae	*Charpentiera obovata*	bark	1	8	H	23	
	Fabaceae	*Canavalia* sp.	bark	1	4	H	23	
eximia	Nyctaginaceae	*Pisonia* sp.	stem	1	7	Mo	23	
	Pandanaceae	*Freycinetia arborea*	stem	1	1	Mo	23	
	Urticaceae	*Urera glabra*	stem	1	16	L	23	
gemmula	Urticaceae	*Urera* sp.	stem	2	2	O	23	
lepidobregma	Sapindaceae	*Sapindus saponaria*	bark	1	14	H	23	
mahui	Euphorbiaceae	*Claoxylon sandwicense*	bark	1	5	H	23	
poonia	Amaranthaceae	*Charpentiera* sp.	stem	1	2	K	23	
J6	Pandanaceae	*Freycinetia arborea*	stem	1	8	H	12	"n. sp. near *amita*" in 12
P29	Urticaceae	*Urera glabra*	stem	1	1	H	23	
okala								
akoko	Euphorbiaceae	*Chamaesyce* sp.	bark	1	50	O	23	
kuhao	Malvaceae	*Hibiscus* sp.	bark	1	1	O	23	
okala	Araliaceae	*Cheirodendron trigynum*	bark	3	4	H	12,23	"n. sp. marked wings" in 12
	Campanulaceae	*Clermontia* sp.	stem	1	19	H	23	
	Sapindaceae	*Sapindus saponaria*	bark	1	1	H	23	
velata								
halapepe	Agavaceae	*Pleomele hawaiiensis*	stem	1	3	H	23	
kauaiensis	Agavaceae	*Pleomele aurea*	stem	1	17	K	23	
lauoho	Agavaceae	*Pleomele auwahiensis*	stem	4	23	M,Mo	23	
milolii	Amaranthaceae	*Charpentiera* sp.	stem	1	2	K	23	
picture wing								
adiastola								
adiastola	Campanulaceae	*Clermontia* sp.	fruit	1	6	M	12	

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref	
		Clermontia sp.	leaf	2	6	M	12	
		Clermontia sp.	stem, bark, root	16	172	M,L	12,15	
		Cyanea sp.	flower	1	1	M	12	
		Cyanea sp.	fruit	1	3	M	12	
		Cyanea sp.	stems	2	19	M	15	
		Lobelia grayanum	stems	1	4	M	15	
cilifera	Campanulaceae	*Clermontia* sp.	branch	1	2	Mo	12	
		Cyanea sp.	flower	1	2	Mo	12	
clavisetae	Campanulaceae	*Clermontia arborescens*	stem	8	27	M	12	
neogrimshawi	Campanulaceae	*Clermontia* sp.	bark	1	3	O	15	
ochrobasis	Campanulaceae	*Clermontia* sp.	root	1	15	H	15	
	Marattiaceae	*Marattia douglasii*	rachis	1	3	H	15	
	Myrsinaceae	*Myrsine lessertiana*	leaf	1	1	H	12	
ornata	Campanulaceae	*Cyanea* sp.	stem	2	11	K	15	
paenehamifera	Campanulaceae	*Cyanea* sp.	stem	1	2	M	15	
peniculipedis	Urticaceae	*Touchardia latifolia*	bark	3	24	M	15	
setosimentum	Araliaceae	*Cheirodendron trigynum*	bark	1	2	H	15	
		Cheirodendron trigynum	bark	2	3	H	15,24	
		Tetraplasandra oahuensis	bark	1	1	H	24	
	Campanulaceae	*Clermontia parviflora*	bark	3	3	H	24	
		Clermontia sp.	leaf, fruit, flower	2	2	H	12	
		Clermontia sp.	stem, bark	6	6+	H	12,15	
	Dicksoniaceae	*Cibotium* sp.	frond	1	1	H	15	
touchardiae	Urticaceae	*Touchardia latifolia*	bark	1	12	O	15	
toxochaeta	Urticaceae	*Touchardia latifolia*	bark	1	2	Mo	15,20	"sp. nr. *touchardiae*" in 15
R13	Urticaceae	*Touchardia latifolia*	bark	1	1	H	15	"sp. nr. *peniculipedis*" in 15
grimshawi								
aglaia	Urticaceae	*Urera glabra*	bark	1	1	O	15	
ambochila	Nyctaginaceae	*Pisonia* sp.	stem	3	10	O	15	
assita	Urticaceae	*Urera glabra*	stem	1	2	H	15	
atrimentum	Araliaceae	*Tetraplasandra oahuensis*	bark	1	14	O	15	
		Tetraplasandra sp.	bark	1	9	O	15	
balioptera	Pandanaceae	*Freycinetia arborea*	leaf axil	1	1	M	15	
bostrycha	Pandanaceae	*Freycinetia arborea*	bark	1	2	Mo	15	
ciliaticrus	Agavaceae	*Pleomele hawaiiensis*	stem, bark	2	17	H	15	
	Araliaceae	*Reynoldsia sandwicensis*	stem, bark,	2	4	H	15	

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref
			sap flux				
		Tetraplasandra hawaiensis	stem	1	3	H	15
craddockae	Thymelaeaceae	*Wikstroemia* sp.	bark	4	16	O,K	15
crucigera	Agavaceae	*Pleomele* sp.	bark	4	70	O	15
		Pleomele sp.	leaf	1	15	O	15
	Amaranthaceae	*Charpentiera* sp.	stem	4	21	O	15
	Apocynaceae	*Pteralyxia* sp.	fruit	1	14	O	15
	Aquifoliaceae	*Ilex anomala*	bark	2	3	O	15
	Araliaceae	*Reynoldsia sandwicensis*	bark	1	13	O	15
		Reynoldsia sandwicensis	sap flux	2	7	O	15
		Tetraplasandra oahuensis	bark	3	18	O	15
	Arecaceae	*Pritchardia* sp.	fruit	1	14	O	15
	Asteraceae	*Dubautia plantaginea*	bark	1	9	O	15
	Basidiomycetes	mushroom	fungus	1	6	O	9
	Campanulaceae	*Clermontia* sp.	bark	1	3	O	15
		Cyanea sp.	stem	1	1	O	15
	Corynocarpaceae	*Corynocarpus laevigatus*	fruit	1	2	K	12
	Euphorbiaceae	*Aleurites moluccana*	fruit	2	4	O	12,15
		Chamaesyce sp.	bark	1	3	O	15
	Fabaceae	*Acacia koa*	flux	3	8	O	9,15
		Erythrina sp.	bark	1	1	O	15
		Strongylodon lucidus	pod	1	8	O	15
	Lauraceae	*Cryptocarya oahuensis*	fruit	1	65	O	15
	Malvaceae	*Hibiscus arnottianus*	bark	2	8	O	15
	Moraceae	*Broussonetia papyrifera*	slime flux	1	8	O	12
	Myrsinaceae	*Myrsine lessertiana*	sap flux	1	1	O	15
	Nyctaginaceae	*Pisonia* sp.	bark, stem	6	50	O	15
		Pisonia sp.	leaf	1	1	O	15
	Pandanaceae	*Freycinetia arborea*	shoot	1	1	O	9
	Pittosporaceae	*Pittosporum* sp.	sap flux	1	2	O	15
	Sapindaceae	*Alectryon macrococcus*	fruit	1	1	O	3,5
	Sapotaceae	*Pouteria sandwicensis*	fruit	1	3	O	15
	Urticaceae	*Pipturus* sp.	bark	2	6	O	15
		Touchardia latifolia	not recorded	1	3	O	15
		Urera glabra	bark, stem	3	12	O	15
		Urera kaalae	bark	1	3	O	15
digressa	Amaranthaceae	*Charpentiera obovata*	stem	2	44	H	15

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref	
disjuncta	Campanulaceae	*Clermontia* sp.	bark	1	5	M	15	
	Nyctaginaceae	*Pisonia* sp.	stem	1	3	M	15	
	Pandanaceae	*Freycinetia arborea*	fruit	1	2	M	15	
		Freycinetia arborea	stem, bark, fruit	2	7	M	15	
engyochracea	Sapindaceae	*Sapindus saponaria*	bark	1	38	H	15	
flexipes	Sapindaceae	*Sapindus oahuensis*	sap flux	2	8	O	15	
gradata	Aquifoliaceae	*Ilex anomala*	bark with flux	1	1	O	15	
	Araliaceae	*Reynoldsia sandwicensis*	bark with flux	1	2	O	15	
		Reynoldsia sandwicensis	stems	1	5	O	15	
		Tetraplasandra oahuensis	sap flux, bark	2	3	O	15	
	Fabaceae	*Acacia koa*	sap flux	2	2	O	15	
	Moraceae	*Broussonetia papyrifera*	slime flux	1	1	O	12	
	Oleaceae	*Nestegis sandwicensis*	sap flux	1	2	O	15	
grimshawi	Agavaceae	*Pleomele auwahiensis*	stem	4	58	M,Mo	15	
		Pleomele fernaldii	stem	1	2	L	15	
	Amaranthaceae	*Charpentiera* sp.	stem	3	10	M,Mo, L	15	
	Araliaceae	*Reynoldsia sandwicensis*	bark, stem	1	4	Mo	15	
		Tetraplasandra kavaiensis	bark	1	2	M	15	
		Tetraplasandra sp.	bark	1	1	L	15	
	Basidiomycetes	*jelly-like fungus*	fungus	1	6	L	12	
	Campanulaceae	*Clermontia* sp.	stem, bark	4	9	M	12,15	
	Nyctaginaceae	*Pisonia* sp.	stem	5	19	M,Mo, L	15	
	Pandanaceae	*Freycinetia arborea*	bark	3	14	M,Mo, L	15	
		Freycinetia arborea	leaf	1	1	M	15	
	Piperaceae	*Piper methysticum*	stem	1	2	Mo	15	
	Solanaceae	*Solanum linnaeanum*	fruit	1	1	M	12	
	Urticaceae	*Touchardia latifolia*	bark	1	2	Mo	15	
		Urera glabra	stem	1	65	L	15	
gymnobasis	Myoporaceae	*Myoporum sandwicense*	sap flux	1	3	M	15	
gymnophallus	Agavaceae	*Pleomele* sp.	bark	1	4	O	15	"sp. nr. *liophallus*" in 15
hawaiiensis	Araliaceae	*Reynoldsia sandwicensis*	stem	1	7	H	15	

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref
	Fabaceae	*Acacia koa*	sap flux	2	15	H	15
	Myoporaceae	*Myoporum sandwicense*	sap flux	1	2	H	15
	Myrsinaceae	*Myrsine lessertiana*	sap flux	2	2	H	15
	Oleaceae	*Nestegis sandwicensis*	sap flux	1	6	H	15
heedi	Myoporaceae	*Myoporum sandwicense*	soil wet by flux	7	214	H	13
hexachaetae	Amaranthaceae	*Charpentiera* sp.	stem	3	4	O	15
	Nyctaginaceae	*Pisonia* sp.	stem	1	3	O	15
inedita	Amaranthaceae	*Charpentiera* sp.	bark, stem	2	4	O	15
	Nyctaginaceae	*Pisonia* sp.	bark, stem	4	31	O	15
limitata	Agavaceae	*Pleomele auwahiensis*	stem	2	3	Mo	15
		Pleomele fernaldii	stem	1	2	L	15
	Campanulaceae	*Clermontia* sp.	stem	2	2	M	15
liophallus	Agavaceae	*Pleomele auwahiensis*	stem	4	42	M,Mo	15
macrothrix	Amaranthaceae	*Charpentiera obovata*	stem	1	30	H	15
	Nyctaginaceae	*Pisonia brunoniana*	stem	3	8	H	15,24
montgomeryi	Urticaceae	*Urera kaalae*	stem	2	3	O	15
murphyi	Araliaceae	*Cheirodendron trigynum*	bark	6	22	H	15,24
		Tetraplasandra oahuensis	bark	1	1	H	15
	Campanulaceae	*Clermontia clermontioides*	bark	1	4	H	24
		Clermontia sp.	bark	1	1	H	15
	Rutaceae	*Melicope* sp.	leaf	1	1	H	15
musaphilia	Fabaceae	*Acacia koa*	sap flux	1	35	K	15
obatai	Agavaceae	*Pleomele* sp.	bark, stem	5	29	O	15
ocellata	Nyctaginaceae	*Pisonia* sp.	stem	1	1	K	15
ochracea	Pandanaceae	*Freycinetia arborea*	stem, bark	2	2	H	12,15
odontophallus	Agavaceae	*Pleomele auwahiensis*	stem	3	58	H	15
oreas	Nyctaginaceae	*Pisonia* sp.	stem	1	2	M	15
orphnopeza	Araliaceae	*Tetraplasandra kavaiensis*	bark	1	1	M	15
		Tetraplasandra oahuensis	bark	2	12	M	15
orthofascia	Araliaceae	*Cheirodendron trigynum*	bark	1	1	M	15
		Tetraplasandra hawaiensis	stem, bark, flux	3	79	M,L	15
		Tetraplasandra oahuensis	stem	1	3	M	15
paucicilia	Sapindaceae	*Sapindus oahuensis*	sap flux	2	7	O	15
paucipuncta	Amaranthaceae	*Charpentiera obovata*	bark	1	1	H	24
	Araliaceae	*Cheirodendron trigynum*	stem	1	19	H	15
	Nyctaginaceae	*Pisonia brunoniana*	bark	1	1	H	24

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref	
pilimana	Araliaceae	*Cheirodendron* sp.	bark	1	1	O	15	
pisonia	Amaranthaceae	*Charpentiera* sp.	stem	1	2	H	15	
	Nyctaginaceae	*Pisonia* sp.	stem	1	2	H	15	
prolaticilia	Pandanaceae	*Freycinetia arborea*	bark	1	1	H	15	
psilophallus	Agavaceae	*Pleomele* sp.	bark, stems	2	3	O	15	
pullipes	Thymelaeaceae	*Wikstroemia* sp.	bark	1	30	H	15	
punalua	Agavaceae	*Pleomele* sp.	bark	2	3	O	15	
	Araliaceae	*Tetraplasandra oahuensis*	bark	1	1	O	15	
	Pandanaceae	*Freycinetia arborea*	bark	3	26	O	15	
		Freycinetia arborea	flower	1	7	O	12	
		Freycinetia arborea	leaf	3	21	O	12,15	
recticilia	Fabaceae	*Acacia koa*	sap flux	1	40	M	15	
reynoldsiae	Araliaceae	*Reynoldsia sandwicensis*	bark, stem	7	131	O	15	
		Reynoldsia sandwicensis	bark/flux	1	1	O	15	
sejuncta	Nyctaginaceae	*Pisonia* sp.	wood, bark	1	1	K	15	
silvarentis	Fabaceae	*Acacia koa*	sap flux	1	22	H	15	
	Myoporaceae	*Myoporum sandwicense*	sap flux	45	550	H	15	
	Oleaceae	*Nestegis sandwicensis*	sap flux	1	3	H	15	
sobrina	Araliaceae	*Reynoldsia sandwicensis*	bark, flux	4	36	O	15	
		Tetraplasandra oahuensis	bark	1	45	O	15	
		Tetraplasandra oahuensis	sap flux	2	41	O	15	
		Tetraplasandra sp.	sap flux	1	2	O	15	
sodomae	Agavaceae	*Pleomele auwahiensis*	stem	1	1	Mo	15	
sproati	Araliaceae	*Cheirodendron trigynum*	bark	4	57	H	15,24	
tarphytrichia	Amaranthaceae	*Charpentiera* sp.	stem	2	3	O	15	
turbata	Fabaceae	*Acacia koa*	sap flux	5	79	O	15	
villosipedis	Agavaceae	*Pleomele aurea*	bark, stem	6	30	K	15	
	Araliaceae	*Tetraplasandra* sp.	bark	1	2	K	15	
	Campanulaceae	*Cyanea* sp.	stem	1	10	K	15	
	Euphorbiaceae	*Euphorbia haeleeleana*	bark	1	14	K	15	
	Fabaceae	*Acacia koa*	sap flux	1	1	K	15	
virgulata	Amaranthaceae	*Charpentiera* sp.	stem	2	75	M	15	
P50, Q10	Araliaceae	*Tetraplasandra hawaiensis*	bark, flux	4	15	H	15	"sp. nr. *sobrina*" in 15
Q94	Araliaceae	*Reynoldsia sandwicensis*	bark	1	24	Mo	15	"sp. nr. *reynoldsiae*" in 15
R85	Pandanaceae	*Freycinetia arborea*	stem	1	1	Mo	15	"sp. nr. *balioptera*" in 15
planitibia								
cyrtoloma	Araliaceae	*Cheirodendron trigynum*	bark	1	1	M	15	

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref	
		Tetraplasandra oahuensis	bark	1	2	M	15	
differens	Campanulaceae	*Clermontia* sp.	stem	1	1	Mo	14,15	"sp. nr. *planitibia*" in 15
hemipeza	Campanulaceae	*Cyanea angustifolia*	bark	1	5	O	15	
		Lobelia yuccoides	stem	1	3	O	15	
	Urticaceae	*Urera kaalae*	bark	1	6	O	15	
heteroneura	Araliaceae	*Cheirodendron trigynum*	stem	1	4	H	15	
	Campanulaceae	*Clermontia clermontioides*	bark	7	27	H	24	
		Clermontia sp.	branch	4	21	H	12,15	
		Delissea undulata	stem	1	3	H	15	
melancephala	Araliaceae	*Tetraplasandra oahuensis*	bark	2	14	M	15	
neopicta	Araliaceae	*Cheirodendron trigynum*	bark	1	1	Mo	15	
		Tetraplasandra kavaiensis	stem	1	14	M	15	
		Tetraplasandra oahuensis	bark	1	2	M	15	
nigribasis	Araliaceae	*Cheirodendron platyphyllum*	stem, bark	3	6	O	15	
		Cheirodendron sp.	bark	1	1	O	15	
		Tetraplasandra sp.	bark	2	3	O	15	
oahuensis	Araliaceae	*Cheirodendron platyphyllum*	bark	1	1	O	15	
		Cheirodendron sp.	bark	1	51	O	15	
		Tetraplasandra oahuensis	bark	3	11	O	15	
		Tetraplasandra sp.	bark	2	4	O	15	
		Tetraplasandra sp.	leaf	1	1	O	15	
picticornis	Fabaceae	*Acacia koa*	sap flux	2	11	K	15	
	Myrtaceae	*Metrosideros polymorpha*	sap flux	2	6	K	12,15	
planitibia	Campanulaceae	*Clermontia* sp.	branch	8	30	M	12,15	
		Cyanea sp.	stem	1	2	M	15	
		Lobelia grayanum	stem	1	8	M	15	
setosifrons	Araliaceae	*Cheirodendron trigynum*	bark	2	3	H	15	
		Tetraplasandra hawaiensis	bark	2	4	H	15	
silvestris	Araliaceae	*Cheirodendron trigynum*	bark	3	10	H	15,24	
	Campanulaceae	*Clermontia clermontioides*	bark	4	5	H	24	
		Clermontia sp.	bark	3	101	H	15	
		Cyanea sp.	stems	1	1	H	15	
	Fabaceae	*Acacia koa*	flux	1	1	H	15	
	Marattiaceae	*Marattia douglasii*	rachis	1	1	H	15	
substenoptera	Araliaceae	*Cheirodendron platyphyllum*	bark	1	3	O	15	
		Cheirodendron sp.	bark	1	34	O	15	
		Tetraplasandra sp.	bark	1	2	O	15	

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref	
primaeva								
primaeva	Araliaceae	*Cheirodendron* sp.	bark	1	5	K	15	
		Tetraplasandra sp.	bark	1	9	K	15	
quasianomalipes								
quasianomalipes	Araliaceae	*Cheirodendron* sp.	bark	2	9	K	15	
		Tetraplasandra sp.	bark	1	1	K	15	
Scaptomyza								
Bunostoma								
palmae	Arecaceae	from palm species		1	2	H	8	
	Malvaceae	*Hibiscadelphus giffardianus*	flower	1	2	H	24	
xanthopleura	Basidiomycetes	bracket fungus	fungus	1	2	O	8	
Elmomyza								
affinicuspidata	Campanulaceae	*Lobelia gloria-montis*		1	many	M	12	substrate not recorded
apiciguttula	Araliaceae	*Cheirodendron trigynum*	bark	1	1	H	24	
	Cucurbitaceae	*Sicyos macrophyllus*	fruit	1	1	H	24	
argentifrons	Elaeocarpaceae	*Elaeocarpus bifidus*	fruit	1	43	O	24	
	Nyctaginaceae	*Pisonia* sp.	leaf	1	1	O	24	
cryptoloba	Amaranthaceae	*Charpentiera* sp.	leaf/frass	1	x	O	8	
	Campanulaceae	*Clermontia* sp.	leaf	1	15	H	24	
cuspidata	Araliaceae	*Cheirodendron trigynum*	leaf	1	x	M	12	
cyrtandrae	Gesneriaceae	*Cyrtandra platyphylla*	leaf	2	x	H	8	
exigua	Campanulaceae	*Clermontia clermontioides*	flower	2	12	H	24	
		Clermontia clermontioides	leaf	1	1	H	24	
		Clermontia hawaiiensis	fruit, flower	1	1	H	24	
		Clermontia lindseyana	bark	1	13	H	24	
		Clermontia lindseyana	leaf	3	5	H	24	
		Clermontia montis-loa	bark	1	8	H	24	
		Clermontia parviflora	bark	4	63	H	24	
		Clermontia sp.	bark	1	10	H	24	
		Clermontia sp.	leaf	1	9	H	24	
	Rosaceae	*Rubus* sp.	fruit	1	many	H	12	
hackmani	Araliaceae	*Cheirodendron trigynum*	leaf	2	2	M,H	12	
	Campanulaceae	*Clermontia clermontioides*	flower	1	1	H	24	
		Clermontia lindseyana	leaf	2	4	H	24	
		Clermontia parviflora	bark	1	1	H	24	

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref	
		Clermontia sp.	leaf	2	6	H	12,24	
	Rosaceae	*Rubus* sp.	fruit	1	x	H	12	
	Rutaceae	*Melicope* sp.	leaf	1	4	H	12	
inaequalis	Campanulaceae	*Clermontia clermontioides*	bark	2	2	H	24	
		Clermontia sp.	leaf	1	4	H	24	
intricata	Asteraceae	*Senecio* sp.	flower	1	12	M	12	
	Campanulaceae	*Clermontia* sp.	flower	1	8	M	12	
		Clermontia sp.	fruit	2	23	M	12	
		Clermontia sp.	leaf	1	many	M	12	
		Clermontia sp.	leaf & stem	2	7	M	12	
latitergum	Asteraceae	*Argyroxiphium sandwicense*	flower	3	18	M	8	
longipecten	Asteraceae	*Dubautia* sp.	flower	1	4	M	12	
griseonigra								
mediana	Asteraceae	*Senecio* sp.	flower	1	4	M	12	
platyrhina	Campanulaceae	*Clermontia* sp.	fruit, flower	2	30	K	12	
scoloplichas	Campanulaceae	*Clermontia parviflora*	bark	2	4	H	24	
		Clermontia sp.	stem	1	9	H	12	
tumidula	Campanulaceae	*Clermontia clermontioides*	flower	2	4	H	24	
		Clermontia clermontioides	leaf, fruit	1	1	H	24	
		Cyanea marksii	leaf	1	2	H	24	
	Rosaceae	*Rubus* sp.	fruit	1	many	H	12	
varia	Campanulaceae	*Clermontia* sp.	fruit	1	15	K	12	
		Lobelia sp.	flower	1	34	K	12	
G56	Campanulaceae	*Clermontia* sp.	leaf	1	6	O	12	"n. sp. close to *affinicuspidata*" in 12
G80	Campanulaceae	*Lobelia gloria-montis*	flower	1	many	M	12	"n. sp. rel. *exigua*" in 12
G87, G90	Campanulaceae	*Clermontia* sp.	fruit	2	85	H	12	"n. sp. nr. *exigua*" in 12; 2 from a sample which also had flowers and leaves
G90	Campanulaceae	*Clermontia* sp.	leaf	1	4	H	12	"n. sp. rel. *intricata*" in 12
sp. 1	Campanulaceae	*Clermontia clermontioides*	flower	2	35	H	24	
		Clermontia clermontioides	leaf, fruit	3	7	H	24	
		Clermontia hawaiiensis	fruit, flower	2	10	H	24	
		Clermontia lindseyana	bark	1	1	H	24	
		Clermontia montis-loa	bark	1	14	H	24	

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref	
		Clermontia parviflora	bark	2	7	H	24	
		Clermontia sp.	leaf	1	4	H	24	
		Cyanea marksii	leaf	1	1	H	24	
sp. A	Nyctaginaceae	*Pisonia* sp.	fruit	1		K	24	
sp. B	Nyctaginaceae	*Pisonia* sp.	fruit	1		O	24	
sp. C	Nyctaginaceae	*Pisonia* sp.	fruit	1		H	24	
sp. D	Gesneriaceae	*Cyrtandra* sp.	leaf	1		M	24	
sp. E	Rosaceae	*Rubus hawaiensis*	fruit	1		H	24	
Exalloscaptomyza								
caliginosa	Convolvulaceae	*Ipomoea* sp.	flower	5	250	H	10	collected on flowers, not reared
mauiensis	Convolvulaceae	*Ipomoea alba*	flower	1	2	M	12	
		Ipomoea sp.	flower	2	7	M	10,12	
oahuensis	Convolvulaceae	*Ipomoea* sp.	flower	4	100	O	10,12	collected on flowers, not reared
throckmortoni	Convolvulaceae	*Ipomoea* sp.	flower	1	37	K	10	collected on flowers, not reared
Tantalia								
flavida	Campanulaceae	*Clermontia* sp.	leaf	1	1	H	12	
	Myrsinaceae	*Myrsine* sp.	leaf	1	2	H	12	
gilvivirilia	Araliaceae	*Cheirodendron trigynum*	leaf	1	2	M	12	
	Campanulaceae	*Clermontia arborescens*	leaf	1	2	M	12	
	Nyctaginaceae	*Pisonia* sp.	leaf	1	2	H	12	
	Rutaceae	*Platydesma spathulata*	leaf	1	3	M	12	
nigrosignata	Araliaceae	*Tetraplasandra oahuensis*	leaf	1	1	H	24	
	Campanulaceae	*Cyanea tritomantha*	leaf	1	3	H	24	
	Woodsiaceae	*Athyrium microphyllum*	rachis	1	1	H	24	
varipicta	Campanulaceae	*Clermontia* sp.	leaf	1	1	K	12	
G90	Myrsinaceae	*Myrsine* sp.	fruit	1	1	H	12	"n. sp. *Tantalia* arista" in 12
nr. nigrosignata	Campanulaceae	*Clermontia oblongifolia*	fruit	1	1	O	24	
Titanochaeta								
bryani		spider egg mass		1	2	O	6,8	
chauliodon	Thomisidae	spider egg mass		2	3	M,Mo	12	
ichneumon		spider egg mass		3	x	H	1,8	
neoevexa	Thomisidae	spider egg mass		1	5	Mo	12	
setosiscutellum	Thomisidae	spider egg mass		1	6	Mo	12	
swezeyi		spider egg mass		3	6	M,O	6,8	
unplaced								
vinnula	Araliaceae	*Cheirodendron* sp.	leaf	1	4	O	12	

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref
alien Drosophilidae							
Chymomyza							
procnemis	Fabaceae	*Acacia koa*	bark, sap	1	2	O	15
Dettopsomyia							
formosa	Euphorbiaceae	*Aleurites moluccana*	fruit	1	2	M	15
nigrovittata	Nyctaginaceae	*Pisonia brunoniana*	leaf	2	6	H	24
Drosophila (Dorsilopha)							
busckii	Amaranthaceae	*Charpentiera obovata*	bark	1	4	H	24
	Basidiomycetes	bracket fungus	fungus	2	4+	H,M	12
	Campanulaceae	*Clermontia parviflora*	bark	1	1	H	24
	Nyctaginaceae	*Pisonia brunoniana*	leaf	1	1	H	24
Drosophila (Drosophila)							
hydei	Musaceae	*Heliconia* sp.	flower	1	x	O	5
immigrans	Apocynaceae	*Pteralyxia* sp.	fruit	1	24	O	15
	Araliaceae	*Tetraplasandra oahuensis*	bark	1	1	H	24
	Aristolochiaceae	*Aristolochia gigas*	flower	1	2800	O	2
	Campanulaceae	*Clermontia clermontioides*	flower	1	15	H	24
		Clermontia hawaiiensis	fruit, flower	3	14	H	24
		Clermontia parviflora	bark	3	69	H	24
		Clermontia sp.	bark	2	8	M,L	15
		Clermontia sp.	leaf	1	2	O	12
		Clermontia sp.	fruit	1	15	K	12
		Clermontia sp.	flower	1	1	L	12
		Cyanea tritomantha	leaf	1	19	H	24
	Euphorbiaceae	*Aleurites moluccana*	fruit	2	46	O,M	12,15
	Fabaceae	*Acacia koa*	sap flux	2	13	H	7,12
		Erythrina sp.	bark	1	6	O	15
	Nyctaginaceae	*Pisonia brunoniana*	bark	1	13	H	24
	Pandanaceae	*Freycinetia arborea*	fruit	1	12	O	15
	Passifloraceae	*Passiflora* sp.	fruit	1	28	H	12
	Piperaceae	*Piper methysticum*	stem	1	34	Mo	15
	Sapindaceae	*Sapindus oahuensis*	flux	1	7	O	15
		Sapindus oahuensis	fruit	1	14	O	24
		Sapindus saponaria	fruit	1	9	H	12
	Urticaceae	*Pipturus albidus*	fruit	1	3	H	12
	Zingiberaceae	*Hedychium* sp.	flower	1	33	O	12

Species	Host Family	Host Species	Substrate	Rec.	Ind.	Island	Ref
mercatorum	Fabaceae	*Acacia koa*	flux	1	11	O	7
	Musaceae	*Heliconia* sp.	flower	1	x	O	5
	Solanaceae	*Solanum linnaeanum*	fruit	1	14	Mo	12
	Urticaceae	*Touchardia latifolia*	bark	1	1	O	15
nasuta	Musaceae	*Heliconia* sp.	flower	1	x	O	5
	Zingiberaceae	*Hedychium* sp.	flower	1	1	O	12
Drosophila (Sophophora)							
simulans	Campanulaceae	*Clermontia parviflora*	bark	1	4	H	24
	Fabaceae	*Acacia koa*	flux	1	12	H	12
	Pandanaceae	*Freycinetia arborea*	Lepidoptera frass	1	2	O	12
	Rubiaceae	*Hedyotis terminalis*	sap flux	1	3	Mo	15
	Zingiberaceae	*Hedychium coronarium*	flower	1	x	O	7
suzukii	Rosaceae	*Rubus hawaiensis*	fruit	1	75	H	24
Scaptomyza (Parascaptomyza)							
pallida	Asteraceae	*Senecio* sp.	flower	1	2	M	12
	Basidiomycetes	gill fungus	fungus	1	1	O	12
	Nyctaginaceae	*Pisonia brunoniana*	leaf	1	6	H	12
	Sapindaceae	*Sapindus saponaria*	flux	1	many	H	7