

EVOLUTION OF THE ENDEMIC HAWAIIAN CERAMBYCID BEETLES¹

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Abstract: The Hawaiian cerambycid fauna presents one of the remarkable examples of great proliferation of species and form with adaptive radiation from a single ancestor. This fauna consists of over 136 species of plagithmysines (Clytini) plus 1 endemic species each of 2 somewhat widespread primitive genera (*Megopis* and *Parandra*) which breed primarily in rotten wood. There are also 17 species introduced by man. The plagithmysines undoubtedly evolved from a single immigrant ancestor species which probably came from Mexico or southern California a few million years ago. Species of the group feed in living trees and have remarkably specific host-tree food habits within a species of beetle, but have adapted to a large number of families (27) of trees for the whole group. Body form has diverged greatly from the presumed ancestral type, with the result that 7 generic names have been proposed to accommodate the species. However, these have recently been combined into a single genus, *Plagithmysus*, with 5 subgenera, following the discovery of annectant forms.

The Hawaiian Islands present a unique setting of an extremely isolated environment which has fostered remarkable examples of evolution within a limited period of time.

All of the native biota of Hawaii demonstrate very high endemism and a very unbalanced ("disharmonic") representation of groups. Many important orders or families of plants and animals are completely lacking from the indigenous and the endemic biota. Some classes are almost absent, as with the Mammalia, which are represented only by 1 marine and 1 flying species. The entire native terrestrial fauna resulted from only a few hundred successful establishments from long-distance dispersal, and the same is true for the flowering plants. Primitive plants, like algae and lichens, which are more vagile, colonized more frequently and present far lower endemism.

With an age of perhaps 25,000,000 years, and with roughly 300 each of successful introductions of fauna and flowering plants, it can be estimated that 1 animal and 1 higher plant colonized the chain every 80,000 years or so on the average. Most of these immigrants probably arrived by air currents of frontal movements from the southwest, carrying the animals or propagules partly from stepping-stone islands in the mid-Pacific. Some of these islands have since eroded away and sunk beneath the sea, suggesting that more colonizations occurred per unit time during the Miocene and early Pliocene than during late Pliocene and Pleistocene.

Among the groups which have produced spectacular evolutionary pictures within the island chain are the drepaniid birds, several families of land snails, fulgoroid leafhoppers, lygaeid and mirid plant-bugs, dolichopodid and drosophilid flies, 3 or 4 families of moths, 7 families of beetles, and 2 groups of wasps. The most conspicuous developments are in the

1. Partial results of a grant to Bishop Museum from the U.S. National Science Foundation (BG-23075); Contribution No. 65 from the Island Ecosystems Integrated Research Program, IBP.
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land snails, the drepaniid birds, and the drosophilid flies, but, following closely upon these, the plagithmysine complex presents a conspicuous example of diversification, and interesting host-plant relationships.

SETTING

GEOLOGICAL HISTORY

The Hawaiian islands were raised by vulcanism from the floor of deep ocean and have never been attached to any continent. The main islands (FIG.1) are much younger than the northwestern islands, which are now largely reduced to atolls, low reef islands, or fragmentary rocks and pinnacles. The atolls represent volcanic islands which were eroded over a long period of time until their basaltic peaks were essentially reduced to or submerged below sea level. The former fringing reef thus became an atoll. In most cases the coral growth kept pace with the sinking sea bottom or change in sea level, maintaining active growth at or near the surface of the sea. As the reef widened, sand and coral debris washed onto the top of the reef to produce atoll islets; or a single island might have developed on the sinking top of the old volcanic core. The rocks and pinnacles in the central and eastern Leeward chain represent volcanic islands in late stages of erosion, but are not as old as the

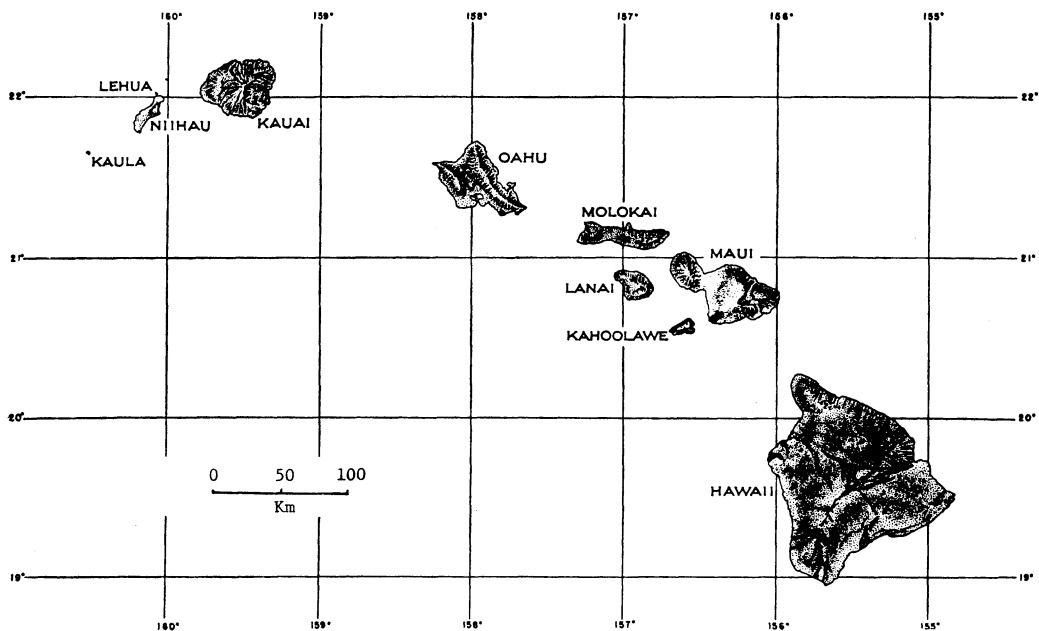


FIG. 1. The main islands of the Hawaiian chain, which support all but 1 (on Nihoa) of the plagithmysines. None are known from Kahoolawe. Remnants of 2 volcanoes each on Oahu, Molokai and Maui, and 4 on Hawaii, are shown, with fairly recent lava flows from 1 on Maui and 2 on Hawaii. (From Stearns 1946.)

atolls or flat coral islands to the west. Nihoa is the easternmost of the Leewards and is still a sizeable segment of an island, 270 m in altitude. It supports the western-most species of *Plagithmysus*.

Of the main islands, Hawaii, the youngest, farthest east, and largest island, is still growing with 2 or 3 active volcanoes. It has extruded a few cubic kilometers of lava during the past century. Kauai, the westernmost of the main group, is thought to be 5 or more million years old, with Oahu 2.2-3.4, Lanai 2, Molokai 1.3-1.8, West Maui 1.3, and East Maui 0.8 million years old. (Maui is one island now, but its 2 parts are of different age and were separate islands.)

Parts of one island may differ in age and represent separate volcanoes. This is true of the Waianae and Koolau ranges of Oahu, of western and eastern Molokai, and especially West Maui and East Maui, which were at one time definitely separate islands. Also, Molokai, Lanai, and Maui were all connected during Pleistocene ice-ages. Kohala Mt at the north-west corner of Hawaii is nearly 1 million years old, while Mauna Loa is post-Pleistocene and still active. The ages of the leeward islands have only been roughly estimated at well over 20 million years old. Their role in the evolution of the endemic Hawaiian fauna was probably significant. Some of the groups that present remarkable proliferation in Hawaii must have established first on one of the northwestern islands and begun to radiate before the main islands were formed. Zimmerman (1948) and Carson et al. (1970) summarize more fully the role of geological events in the development of Hawaii's insects.

VEGETATION

The vegetation of Hawaii provided a favorable environment for plagithmysine development. The benign climate fostered luxuriant growth and rapid speciation of plants and animals. There are about 2000 taxa of native vascular plants belonging to about 75 families. The species endemism is about 90% and the generic endemism about 16%. As with the fauna, the majority of the native flora appears to have originated from establishments resulting from long-distance, largely airborne, dispersal from the SW Pacific area.

Before the advent of man's modifications of the environment, most of the older windward slopes of the islands, up to 2200 m or so, were covered with dense rain forest. The leeward slopes probably supported more or less open dry sclerophyll forest with grassland at higher altitudes. The dry forests have suffered heavily from man, feral and domestic animals, and fire. They have largely disappeared and been replaced by plants introduced by man. The lower slopes of the damp areas are now largely in pineapple and sugarcane (Fosberg 1948, St. John 1974).

ROLE OF PLAGITHMYSINES IN FOREST

Plagithmysines are associated with about 1/3 of the native genera of Hawaiian trees. There are definite records from 36 genera of woody plants in 27 families. The majority of the known plagithmysines are associated with rain forest trees. Twenty-seven of the genera

are wet forest trees and these support 110 species of plagithmysines. Nine genera are dry forest trees or shrubs and support 22 plagithmysine species. There is the possibility that a number of species became extinct with the loss of the dry forests.

Naturally, woody plants had to have been established on the islands before cerambycids could colonize successfully. At this stage of our understanding one can only guess what might have been the host-tree adopted by the colonizing clytine progenitor of the plagithmysines. *Acacia koa* and *Metrosideros collina* would be suspect on the basis of current dominance, both in numbers of trees and in numbers of plagithmysine species hosted by them. *Metrosideros* is adapted to colonize earlier stages of lava flows than other trees. It has no doubt long been important to the plagithmysines.

Plagithmysines are associated primarily with living trees, shrubs, or vines. Often the female beetles lay their eggs in the bark of unhealthy, injured, or otherwise disadvantaged plants. It is frequently difficult to be sure whether infested branches or trunks were attacked because they were unhealthy, or whether the beetles caused the disability. However, in many cases it is clear that the beetles were attracted to branches or trunks which had fallen or become partly detached (leaning, or terminal portions on ground) as a result of wind, termites (only man-introduced species in Hawaii), or other factors.

In general, the plagithmysines play an important role in the breakdown of dead wood and possibly the elimination of genetically inferior trees. This serves to hasten the decomposition and possibly change the genetic composition of the forests. In other cases they appear to debilitate healthy trees, but this has been noticed more in disturbed environments, as with *Plagithmysus perkinsi* in *Myoporum* and *Plagithmysus greenwelli* in *Santalum* in cattle-grazing areas on Hawaii. Also, *Plagithmysus dodonaeavorus* was found in *Dodonaea* along a road in heavily goat-infested cattle-grazing land on Molokai. On the other hand, the species of the subgenera *Peleithmysus* and *Nesithmysus* bore in *Pelea* trees in undisturbed wet rain forest with the trees not always showing very clear evidence, or cause, of attack. Probably, however, attack is more severe on ridges, where occasional hikers, lightning, or strong winds have affected some of the trees.

THE HAWAIIAN CERAMBYCID FAUNA

The main group of cerambycids in Hawaii is called the plagithmysines. FIG. 2 and 3 represent examples showing varied body form.

There are 2 other lines of endemic Hawaiian Cerambycidae, but these each represent a single species (each in a different subfamily: Parandrinae and Prioninae) which have not proliferated at all. Both of these, *Parandra puncticeps* Sharp and *Megopis reflexa* (Karsch), are found on all the major islands of the chain, and individuals from the different islands do not seem to have developed any local population characteristics. Both, being large, heavy insects, may have arrived in Hawaii in floating logs, perhaps in recent times. *P. puncticeps* and *M. reflexa* belong to primitive groups, feeding only in dead wood. Species in these primitive groups have apparently evolved very slowly. Thus these two isolated endemic

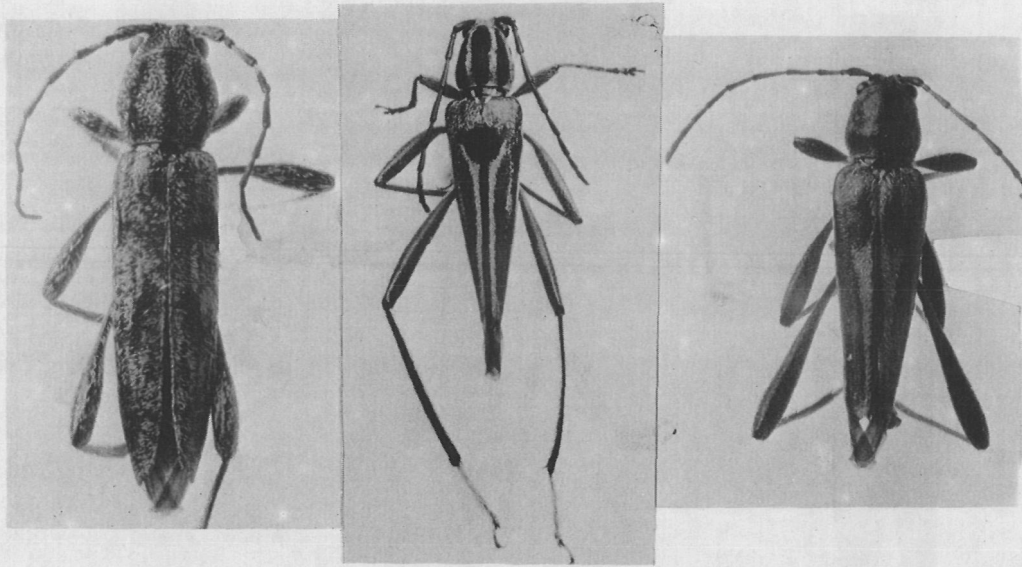


FIG. 2. Left to right: *Plagithmysus (Neoclytarlus) dodonaeavorus* Gressitt, *Dodonaea*, Molokai; *P. (s. str.) bishopi* Perkins, *Pelea*, Hawaii; *P. (s. str.) ilicis* Gr., *Ilex*, Molokai.

species could have been in Hawaii a long time without speciating. In each case the ancestral continental form could even be extinct or undiscovered. *Parandra* is a nearly cosmopolitan genus, from tropical to temperate in distribution, and some of the species are very widely distributed. The Hawaiian species probably originated from Southeast Asia or the Southwest Pacific. *Megopsis* is a tropical Old World genus, primarily continental in distribution. Both *P. puncticeps* and *M. reflexa* are nocturnal and are not often observed to fly. Both are heavy-bodied, sombre in color, and slow-moving. Their larvae bore primarily in rotting wood. These characteristics are all in contrast to those of the highly speciated group, the plagithmysines.

There are also 17 species of Cerambycidae introduced by man to the Hawaiian Islands (Gressitt & Davis 1973). These, with rather few exceptions, attack introduced trees, whereas the native species are very rarely found to breed in exotic plants.

THE PLAGITHMYSINES

The plagithmysines belong to the tribe Clytini of the subfamily Cerambycinae. The ancestor of this principal endemic group of the family Cerambycidae in Hawaii probably came from southern North America. The most closely related group on the continent appears to be the genus *Neoclytus* with many species now in North and Central America.

Now assigned to 5 subgenera of the genus *Plagithmysus*, the generic/subgeneric names used for plagithmysines are as follows:

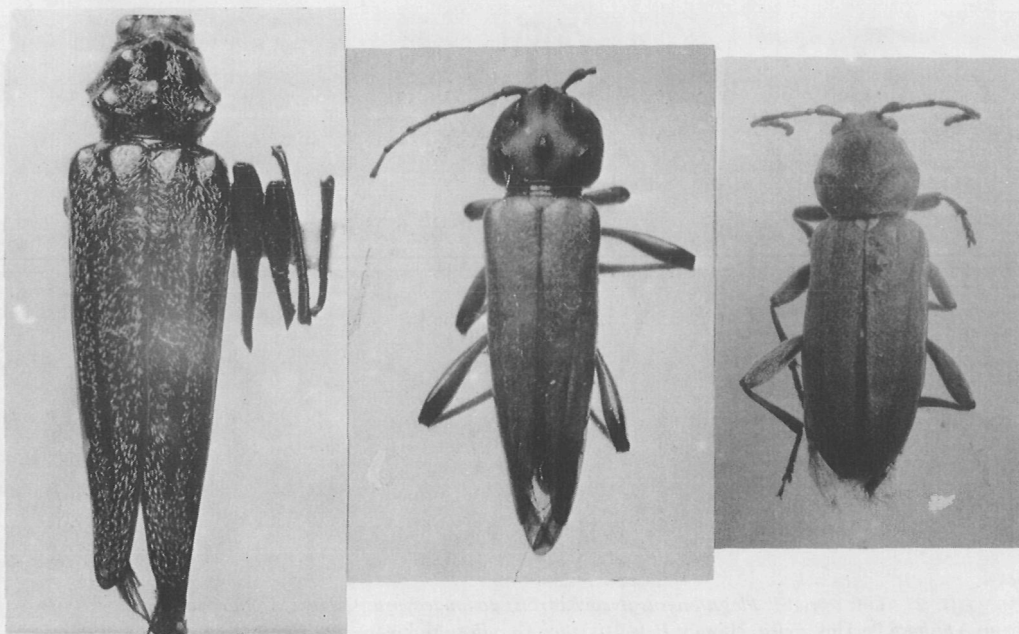


FIG. 3. Left to right: *Plagithmysus* (*Peleithmysus*) *alani* Gressitt, *Pelea*, W Maui; *P. (Nesithmysus) sylvai* Gr., *Pelea*, W Maui; *P. (Aeschrithmysus) dubautianus* Gressitt & Davis, *Dubautia*, E Maui.

Plagithmysus Motschulsky, 1845

Aeschrithmysus Perkins, 1929

Nesithmysus Perkins, 1920

Peleithmysus Gressitt, 1972

Neoclytarlus Bridwell, 1920 (*Clytarlus* Sharp, 1878)

Plagithmysus s. str.

Callithmysus Sharp, 1896 and *Paraclytarlus* Perkins, 1927 were described as distinct genera, but both of these vary only in degree of development and do not have valid distinguishing characters from *Plagithmysus* s. str. Species ascribed to *Callithmysus* have broad shoulders, greatly swollen hind femora and very hirsute hind tibiae, whereas those assigned to *Paraclytarlus* are narrow-bodied with relatively short hind legs and weakly swollen hind femora. These 2 names are used somewhat in this discussion to express opposite extremes of development.

The plagithmysines include some of the larger Hawaiian insects, though all are smaller than *Parandra* and *Megopsis* which are 2 of the very largest insects in Hawaii. Adults of the plagithmysines range in size from 5 to 27 mm long and are cylindrical to broad-shouldered and strongly narrowed posteriorly. The legs are usually long and slender and the hind pair may be conspicuously long and sometimes hairy or tufted. The prothorax is often tuberculate above, with sometimes 4 or 6 tubercles. Coloration is often quite striking, with a

tendency towards contrasted stripes, rows of spots or bands. Some of the species are extremely handsome, bearing several colors. All are strictly diurnal and sunloving, and actively run and fly. They are never attracted to light at night. As a rule, the larvae bore in living, injured, or dying portions of standing trees.

In their evolution, the plagithmysines have developed interesting patterns, not only geographically and morphologically, but also in their host-plant associations and the group provides an interesting example of insular adaptive radiation. Striking characteristics of this picture are monoisular endemism and narrow specialization of host-food habits. Monoisular endemism has apparently resulted in a different plagithmysine population for each island, though the populations of Molokai, Lanai, and Maui are very closely related and in some cases are probably conspecific. The host specialization has resulted in most species being restricted to a single genus of tree.

Directions in which the evolution has been progressing involve increase in body size with development of tubercles or other protuberances on the prothorax, decrease in body size and tendency toward very slender form related to development in slender vines (*Smilax*) or semi-woody plants (certain Compositae), and enlargement and extreme hairiness of hind femora. There is a strong tendency for the abdomen to be very small in *Plagithmysus* s. str. males and also, to some extent, females. Further directions of adaptation involve rather striking form and markings, which may be partly protective in nature.

Being active diurnal insects, these beetles are preyed upon by native forest birds. Almost never have any of them been noted to be attracted to flowers. In general the adults fly only in good weather and are very rarely seen. A conspicuous aspect of plagithmysine behavior is gregariousness, although aggregations of adults have only rarely been observed. Mating is active, rapid, and repetitive. Males attempt to mate on seeing another individual, whether male or female, and continue to follow and mount one individual or another until successful in mating.

Adults of *Aeschrithmysus*, *Nesithmysus*, and *Peleithmysus* are less active than those of *Plagithmysus* s. str. Species of *Paraclytarlus* are probably also relatively inactive, but very few specimens of this group have been collected. Individuals of species formerly assigned to *Callithmysus* are very active, as their present placement within *Plagithmysus* s. str. would imply.

Although 7 generic names had been proposed to include the plagithmysines, these have recently been reduced to 1 genus. In spite of great diversity of form, the species must be assigned to a single endemic genus, *Plagithmysus*, of 5, in part vaguely bounded, subgenera. In recent years, a number of species have been discovered (Gressitt & Davis 1969-1976; Gressitt 1972 a,b) which bridged gaps between supposed genera. As an example of the uncertainty among systematists, Perkins (1927) in proposing *Paraclytarlus*, stated that it could be considered a subgenus of either *Plagithmysus* or *Neoclytarlus*, or even of *Callithmysus*, but would probably prove to be a full genus when a thorough revision was made. Sharp (1900) remarked on the difficulty of generic separation before members of *Paraclytarlus*, *Nesithmysus*, *Aeschrithmysus*, or *Peleithmysus* had been discovered. He

pointed out similarities between the various species of *Callithmysus* and certain Oahu species of *Plagithmysus* (s. str.).

The tentative assignment of numbers of species to subgenera is presented in TABLE 1. *Paraclytarlus* is probably not a valid subgenus, but only represents some extremes of development, as did *Callithmysus*, which was untenable.

A significant point is the large number of species (50) for the Maui group of islands (Molokai, Lanai, Maui) as a whole.

The ratio of species per subgenus (TABLE 6) differs greatly between the various islands. Extremes are Molokai with 2.2 and Hawaii with 15.3, aside from Nihoa which has only 1 species and Lanai which has only 3 species.

All the members of this complex must have evolved from a single immigrant ancestor. About 135 species or subspecies of plagithmysines have been thus far named. A few of these will very likely be reduced to synonymy, or to geographical subspecies, but more remain to be discovered. Some of the young species on the island of Hawaii which are sympatric but have different host-plants are probably reproductively isolated, though they are only slightly divergent morphologically. In general, morphological variation within a species is much greater than average differences between related species. This makes the application of numerical taxonomy very difficult in this fauna. The rarity of the species and other factors make genetic studies extremely difficult. Thus, comparisons between this group and the Drosophilidae are limited in scope (see Carson et al. 1970). The intraspecies variation in the plagithmysines involves body size to a great extent, as well as leg form, especially thickening of the hind femur (sometimes more so in males), but also coloration, vestiture, pronotal tuberculation and other characters. The form of the femora has been used to separate genera (subgenera). There are sexual differences with this character, but even keying the sexes separately proves impractical. This can also be true in keying species, because of variation within 1 sex of 1 population. Often for quick identification it is simpler to separate species by species-group (also sometimes difficult to define), host, and volcano distribution, than by minor morphological or color characters. Combination of color pattern and vestiture is consistent to a fair degree in some groups, but again proves useless for certain

TABLE 1. Numbers of species of plagithmysines on different islands, by subgenus*

	<i>Aeschrith- mysus</i>	<i>Nesith- mysus</i>	<i>Peleith- mysus</i>	<i>Plagith- mysus</i>	<i>Paracly- tarlus*</i>	<i>Neocly- tarlus</i>	TOTALS
Nihoa				1			1
Kauai				14		5	19
Oahu		1	1	12	1	5	20
Molokai		1	1	4		3	9
Lanai				2		1	3
W Maui		1	1	7		1	10
E Maui	4	1	1	12	3	7	28
Hawaii				26	2	19	46
Totals	4	4	4	78	6	41	136

**Paraclytarlus*, though not considered a valid subgenus, is here used for convenience as it suggests a link between *Plagithmysus* s. str. and *Neoclytarlus*.

individuals. Secondary sexual differences are negligible in most species, and relate mostly to body and hind femur size. As an example of the degree of size variability within a species, some individual adults of *P. albertisi* Sharp are 3 times as long as others (6.6–21 mm).

Scarcity of adults has been noted by all field workers. Many entomologists long in Hawaii have never observed a plagithmysine beetle in the field. Sharp (1900) and Perkins (1896, 1921, etc.) have remarked at length on this.

HOST ASSOCIATIONS

There is a high degree of host specificity in the plagithmysines. In shifting from one island to another in the chain, or in other steps toward speciation, such as displacement by winds within one island, there has been some shifting of host-plant associations. But to a great extent closely related species on different islands have the same, or closely related, host plants.

TABLE 2. Endemic and indigenous Hawaiian woody plant genera, with numbers of associated plagithmysine beetles.*

FAMILY	GENUS	ENDEMIC	RARE	SPECIES		GEOGR. AFF.	NO. OF PLAGITH-MYSINE ASSOC. SPECIES	VOLCANOES INHABITED
				Endemic	Coloni-zations			
Palmae	Pritchardia			33	1	Indo-Pac.		
Pandanaeae	Pandanus (1 indig.)			—	1	"		
	Freycinetia			1	1	"		
Liliaceae	Smilax			2	1	"	8	8
	Dracaena			3	1	"		
Moraceae	Pseudomorus		×	1	1	Austral		
Urticaceae	Pipturus			13	1	Indo-Pac.	8	6
	Neraudia	×		6	1	"		
	Touchardia	×	×	1	1	"		
	Urera			3	2	Amer.	2	2
Santalaceae	Boehmeria			1	1	Indo-Pac.		
	Exocarpus		×	3	1	Austral		
	Santalum			7	2	"	1**	1
Polygonaceae	Rumex		×	3	1	?		
Chenopodiaceae	Chenopodium			2	1	Amer.	4	3?
Amaranthaceae	Achyranthes		×	2	1	Indo-Pac.		
	Charpentiera			3	1	Austral	2**	1
Nyctaginaceae	Nototrichium	×		3	1	"		
	Pisonia			3	2	Indo-Pac., Austral		
Phytolaccaceae	Phytolacca		×	1	1	Amer.		
Caryophyllaceae	Schiedia (+ Alsinodendron)	×		29	1	?		
	Silene			6	1	?		
Lauraceae	Cryptocarya			2	1	Indo-Pac.	1	1
Cruciferae	Lepidium		×	4	2	Indo-Pac.		
Saxifragaceae	Broussaisia			2	1	Indo-Pac.		
Pittosporaceae	Pittosporum			23	1	"	3**	3
Rosaceae	Osteomeles (1 indig.)***			—	1	"	1	1

TABLE 2 (continued).

FAMILY	GENUS	ENDEMIC	RARE	SPECIES		GEOGR. AFF.	NO. OF PLAGITH-MYSINE ASSOC. SPECIES	VOLCANOES INHABITED
				Endemic	Coloni-zations			
Leguminosae	Rubus			2	1	Amer.	2	2
	Acacia †			3	1	Indo-Pac.	23	7
	Canavalia			18	1	"		
	Cassia			1	1	"		
	Erythrina			1	1	"		
	Mezoneuron		×	1	1	"	1	1
	Mucuna			1	1	"		
	Sophora			1	1	Austral	6	4
	Sesbania		×	1	1	? Austral		
Geraniaceae	Strongyloдон			1	1	Indo-Pac.		
	Geranium			4	1	?	2	3
Rutaceae	Fagara			9	1	Indo-Pac.	1	1
	(Zanthoxylum)							
	Pelea	×		90	1	"	12	8
	Platydesma	×	×	4	1	"	1	1
Euphorbiaceae	Antidesma			2	1	Indo-Pac.		
	Claoxylon		×	2	1	"		
	Drypetes		×	1	1	"		
	Euphorbia			16	1	Indo-Pac.	4	4
Aquifoliaceae	Ilex (1 indig.)			—	1	Austral	4**	4
Celastraceae	Perrottetia			1	1	? Indo-Pac.	3**	3
Anacardiaceae	Rhus		×	1	1	Indo-Pac.		
Sapindaceae	Alectryon		×	2	1	"		
	Dodonaea			3	1	Pantropic	5**	4
	Sapindus			2	2	Indo-Pac., Amer.	3	2
Rhamnaceae	Alphitonia			1	1	Indo-Pac.	3**	1
	Colubrina		×	1	1	"		
	Gouania		×	14	1	"		
Elaeocarpaceae	Elaeocarpus			1	1	"	2**	2
Malvaceae	Abutilon		×	4	2	Amer., ?		
	Gossypium			1	1	? Amer.	?	
	Hibiscadelphus	×	×	5	1	?		
	Hibiscus			11	4	Indo-Pac., Austral., Pantropic		
Sterculiaceae	Kokia	×	×	4	1	?		
	Waltheria ††			1	1	? Amer.		
Theaceae	Eurya		×	1	1	Indo-Pac.		
Violaceae	Isodendron	×	×	14	1	? Amer.		
	Viola			8	1	?		
Thymeleaceae	Wikstroemia			28	1	Indo-Pac.		
Flacourtiaceae	Xylosma			2	1	"		
Cucurbitaceae	Sicyos			8	1	"		
Myrtaceae	Eugenia (Syzygium)			4	2	"	2**	2
	Metrosideros			1	1	Austral	10	7
Araliaceae	Cheirodendron			6	1	"		
	Reynoldsia			8	1	"		
	Tetraplasandra			10	1	Indo-Pac.		
Ericaceae	Vaccinium			6	1	Austral	2**	2
Epacridaceae	Styphelia			1	1	"		

TABLE 2 (continued).

FAMILY	GENUS	ENDEMIC	RARE	SPECIES		GEOGR. AFF.	NO. OF PLAGITH-MYSINE ASSOC. SPECIES	VOLCANOES INHABITED
				Endemic	Coloni-zations			
Primulaceae	Lysimachia			11	2	Indo-Pac., ? Austral		
Myrsinaceae	Myrsine			20	1	Indo-Pac.	2	1
Sapotaceae	Planchonella (Pouteria, Sideroxylon)			6	1	"	3	2
Ebenaceae	Diospyros			2	1	"	2**	1
Loganiaceae	Labordia	×		24	2	"		
Oleaceae	Osmanthus			1	1	"	1?	1
Apocynaceae	Alyxia			1	1	"		
	Ochrosia		×	1	1	"		
	Pteralyxia	×	×	3	1	?		
	Rauvolfia		×	7	1	?		
Convolvulaceae	Bonamia		×	1	1	?		
Labiatae	Phyllostegia			25	1	Austral		
Solanaceae	Nicotiana (introduced)						2	1
	Nothocestrum	×		5	1	Amer.		
	Solanum			4	1	?		
Myoporaceae	Myoporum			1	1	Indo-Pac.	1	1
Gesneraceae	Cyrtandra			167	1?	"		
Rubiaceae	Bobeia	×		5	1	"	3**	3
	Coprosma			18	3	Austral		
	Gardenia			3	2	Indo-Pac.		
	Hedyotis			73	1	"		
	Gouldia			3	1	"		
	Morinda		×	2	1	"		
	Psychotria (Straussia)			13	2	Indo-Pac., Amer.		
Campanulaceae	Clermontia	×		40	1	Austral		
	Cyanea	×		81	1	?	1	1
	Delissia			6	1	Indo-Pac.		
	Lobelia			23	1	"		
	Rollandia			12	1	"		
	Trematolobelia	×	×	3	1	? Indo-Pac.	?	1
Goodeniaceae	Scaevola			11	1	Indo-Pac.		
Compositae	Argyroxiphium	×		6	1	Amer.	1	1
	Wilkesia	×		2	1	"		
	Dubautia	×		9	1	"	6	2
	Artemisia			4	1	Boreal		
	Bidens			34	1	Austral	1	1
	Hesperomannia	×	×	3	1	Amer.		
	Lipochaeta	×		27	1	Indo-Pac.		
	Remya	×	×	2	1	? Amer.		
54	113			1123	126		130+ in 27 plant families	

* Partly after Fosberg (1948); modified with advice of Dr H. St. John.

** Additional species questionable or probable.

*** Native plant also attacked by exotic cerambycid (*Curtomerus*).

† Five plagithmysines reared from 2 species of exotic *Acacia*.

†† Extinct One endemic sp. extinct; 1 indig. sp. common.

With some exceptions, the more common native tree species have more plagithmysine associations. Thus koa (*Acacia koa*) and ohia (*Metrosideros collina polymorpha*) serve as hosts of more species of plagithmysines than do most other single tree species (see TABLE 2). This agrees to some extent with the comments of Southwood (1960), who pointed out that the more abundant Hawaiian tree species had more species of insects associated with them than did the less abundant trees. However, the genus *Pelea* (several spp.) hosts more plagithmysines than does *Metrosideros*. *Acacia* and *Metrosideros* do not host the most primitive species. Although *Metrosideros* is the pioneer forest element on lava flows, *Acacia koa* hosts more than twice as many species (TABLE 2). This in part may be because the plagithmysines prefer forests which are not too densely shaded, which is often the situation in old ohia forests in wet areas. Perhaps a significant factor is that ohia wood is much harder than koa wood. Many of the rarer Hawaiian endemic and indigenous tree species have no known plagithmysine associations. However, some genera of native trees with abundant species also have no known associations. It is puzzling that a number of the endemic genera

TABLE 3. Plant families with numbers of species of *Plagithmysus* associated, by subgenus.

	<i>Aeschrith-</i> <i>mysus</i>	<i>Nesith-</i> <i>mysus</i>	<i>Peleith-</i> <i>mysus</i>	<i>Plagith-</i> <i>mysus</i>	<i>Paracly-</i> <i>tarlus</i>	<i>Neocly-</i> <i>tarlus</i>
Monocotyledons						
Liliaceae				1		7
Dicotyledons						
Urticaceae					1	
Santalaceae				1*		
Chenopodiaceae						4*
Amaranthaceae				2*		
Lauraceae				1		
Pittosporaceae				3*		
Rosaceae				3		
Leguminosae				16	1	13
Geraniaceae				1		1
Rutaceae		4	4	5		
Sapindaceae				5*		3
Euphorbiaceae				1		3*
Aquifoliaceae				4*		
Celastraceae				3*		
Rhamnaceae				2*		1
Elaeocarpaceae				2*		
Myrtaceae				8*	3	1
Ericaceae				2*		
Myrsinaceae				2		
Sapotaceae				3		
Ebenaceae				1*		1
Oleaceae				1?		
Myoporaceae				1		
Rubiaceae				3*		
Campanulaceae				1		
Compositae	3*					5*

* Additional species questionable or probable. *Paraclytarlus* is not a valid subgenus but is included here for convenience.

of Hawaiian woody plants are not attacked by these beetles. Of 21 genera of woody plants endemic to Hawaii, only 6 (28.6%) are attacked. The only host genera now considered rare which are known to be attacked are *Mezoneuron* and *Platydesma*. The tendency of the plagithmysines as a group to associate with a rather large number of different host trees is perhaps partly correlated with the tendency for plant families, which in continental areas do not usually have woody members, to become woody in Hawaii. Some of the plant families concerned, such as the Violaceae, do not have proven plagithmysine associations, and those for Lobelioideae (Campanulaceae) are uncertain or only occasional. Again, however, because of the incomplete insular biota, many of the families or genera associated with North American relatives of *Plagithmysus* are lacking from the Hawaiian flora.

The native woody flora of Hawaii consists of about 1300 species of 105 genera. The 1300 species have evolved in the islands from about 119 successful establishments. The plagithmysines number about 136 known species, 1/10 the number of trees and shrubs, but over 10 times as many species per introduction. Plagithmysines probably established themselves in Hawaii long after the advent of woody plants here. At any rate, evolutionary rates are presumably different in insects and plants.

Host plants are known for 123 of the 136 taxa of plagithmysines, and it is possible to infer some of the unrecorded hosts. The 105 genera of woody plants in Hawaii belong to 52 families (TABLE 2). Twenty-seven of these families (52%), and 37 of the genera (35.2%) are attacked by plagithmysines. Thus a higher percentage of the total number of genera are attacked than is the case with the endemic genera (28.6%).

Associations of plagithmysines with their host plants are largely at the generic level. In only a few cases are different species of plagithmysines found in different species of a host genus on the same portion of the same island. (By portion of an island is meant a single major volcano or range—thus Kauai is 1 unit, Oahu is 2, Molokai 2, Lanai 1, Maui 2, and Hawaii 4.) Thus there is little or no correlation between the number of species in a genus of tree and the number of species of plagithmysines attached to the host genus. In general the distribution of a plagithmysine species is more restricted than that of its tree host, both areally and altitudinally. There are numbers of sympatric closely related species of plagithmysines with different host associations.

In spite of the introduction of many types of trees foreign to Hawaii during the past 2 centuries, very few instances have been noted of plagithmysines attacking exotic woody plants. This is probably related both to the narrow preferences of the plagithmysines and to the fact that plagithmysines are rarely found in heavily disturbed ecosystems and thus rarely occur on the fringes of native forest. Exotic plants which have been adopted by plagithmysines are *Nicotiana* (2 spp.), *Acacia decurrens* (5 spp.) and *Acacia melanoxylon* (1 sp.).

Viewing the phylogeny of the plagithmysine-associated plants (TABLE 3), only one genus of monocotyledon, *Smilax* (Liliaceae), is involved. Interestingly, the species-group of plagithmysines restricted to *Smilax* (indecens-group) is well isolated from the rest, and does not fit well in the subgenus *Neochlytarlus*, to which it has been assigned. Moreover, this is the

only species group for which species are known from all major islands (including both East and West Maui). On the other hand, a quite unrelated species, *P. giffardi*, bores in *Smilax*, but *P. giffardi* also attacks *Myrsine* (TABLE 3).

Among the dicotyledons, 26 families are attacked by plagithmysines (see TABLE 3). Fourteen of the families are attacked by members of *Plagithmysus* s. str. only, one by *Neoclytarlus* only, 7 by members of 2 subgenera, and 3 by members of 3 subgenera. The Leguminosae has the largest number of associated beetle species (30), followed by the Rutaceae (13) and Myrtaceae (11) (see TABLE 4).

In North America and Eastern Asia members of the tribe Clytini are associated with quite a number of families of plants. *Neoclytus*, assumed closest relative of *Plagithmysus*, has been associated in North America with 28 plant families, of which 12 are also *Plagithmysus*-associated. Although the number of plant families attacked by *Neoclytus* and *Plagithmysus* is similar, a significant difference is in host specificity. Many species of *Neoclytus*, which has about 30 species in North America, attack several genera of trees, and 1 species is recorded from 26 genera of about 17 families (Linsley 1962). Two plant families attacked by *Neoclytus* species which have native Hawaiian species are not attacked by *Plagithmysus*. Moreover, there are 16 host families of *Plagithmysus* which are not attacked by *Neoclytus* in North America. This relates possibly to availability of acceptable substitute foods, particularly after a considerable period of evolution in the islands but it also relates to the fact that species of *Neoclytus* attack dead wood whereas many *Plagithmysus* attack living trees. The great contrast between *Plagithmysus* and *Neoclytus* in the matter of host selection is the narrow host restriction within most individual species of *Plagithmysus*. Most (93.5%) of the 123 host-associated species of *Plagithmysus* appear restricted to a single host genus. Ex-

TABLE 4. Plant families arranged in order of numbers of plagithmysines associated per family.

FAMILY	SPECIES OF PLAG'S ASSOCIATED	SUBGENERA OF PLAG'S ASSOCIATED (PER FAMILY)	GENERA OF PLANTS INVOLVED (PER FAMILY)
Leguminosae	30	3	3
Rutaceae	13	3	3
Myrtaceae	11	3	3
Urticaceae	10	2	2
Compositae	8	2	3
Sapindaceae	8	2	2
Liliaceae	8	2	1
Euphorbiaceae	4	2	1
Chenopodiaceae, Aquifoliaceae	4	1	1
Rhamnaceae	3	2	1
Rosaceae	3	1	2
Pittosporaceae, Celastraceae, Sapotaceae, Rubiaceae	3	1	1
Geraniaceae, Ebenaceae	2	2	1
Amaranthaceae, Elaeocarpaceae, Ericaceae, Myrsinaceae	2	1	1
Santalaceae, Lauraceae, Oleaceae, Myoporaceae, Campanulaceae	1	1	1

ceptions are 1 species on Kauai recorded from 8 genera of hosts, 1 on Hawaii from 4 genera, 1 on Oahu from 3 genera, 3 from Hawaii, and a few others from 2 genera each. However, some of these may involve separate races or sibling species from the different hosts.

There is clearly host specialization on more than 1 taxonomic level of the plagithmysines. Not only are most of the beetle species limited to a single genus of host plant, but some of the subgenera of *Plagithmysus* are limited to a single genus or family of host. *Peleithmysus* and *Nesithmysus* are restricted to the genus *Pelea* (Rutaceae), and *Aeschrithmysus* is limited to 2 genera of Compositae, as far as is known. *Paraclytarlus* is limited to 3 or 4 unrelated families of plants, but it is of questionable status (TABLE 3). The 2 large subgenera, *Plagithmysus* s. str. and *Neoclytarlus*, show ample differences. The former is associated with 23 or 24 plant families, and *Neoclytarlus* is only associated with 10 families. Of the latter 10 plant families, 2 are not associated with *Plagithmysus* s. str. Moreover, of the 8 families of plants shared as hosts by *Plagithmysus* and *Neoclytarlus*, aside from the Leguminosae, Geraniaceae, and Ebenaceae, the relative numbers of species associated are quite disparate (factors on order of about 2:1 to 8:1). The heaviest concentrations of associations for *Neoclytarlus* are with the Leguminosae, Liliaceae, Compositae, and Chenopodiaceae, the latter 2 being those with which *Plagithmysus* is not associated (TABLE 3). Over 1/2 the species of *Plagithmysus* s. str. are associated with families having no *Neoclytarlus* associations.

Although the progenitor of the plagithmysines was presumably American, 32 of the associated genera of plant hosts are of Indo-Pacific or Austral derivation and only 5 are of American origin (TABLE 2). This is very likely related to availability of hosts for the beetles in terms of abundance of woody plants, and in terms of relative time-spans after establishment of the plants in the archipelago. It must be borne in mind that many of the colonists arrived in an ecological vacuum. Although many American *Neoclytus* are polytrophic, some evidence exists that the "host strains" have preferences for their ancestral host. Thus, incipient host specificity may exist in *Neoclytus*. However, N American species, so far as is known, all breed in dead wood. Although host plants of many species of *Neoclytus* are now known, all but 2 infest nonconiferous hardwoods, of which the Hawaiian archipelago has an abundance (see Linsley 1962, and pers. commun.).

The much larger number of plant genera adopted by *Plagithmysus* s. str. suggests that the latter is the more primitive form and represents the original colonist in the archipelago. Its presence on Nihoa and the generalized nature of some of its species, including the Nihoa species, is added evidence.

Most cases of *Plagithmysus* with multiple hosts (TABLE 5) are on Kauai and Hawaii. Most of those on Kauai relate to the *concolor* complex which represents 1 species with 3 sub-species, but may actually represent a single taxon or several taxa. The taxonomic problem is difficult to resolve because of variation in form.

Average number of species per host (TABLE 6) ranges from 1 (Nihoa, Molokai, Lanai, W Maui) to 2.1 (E Maui). It is striking that E Maui has by far the greatest ratio of plagithmysines to host genera. It also is the only island (volcano) with all subgenera represented. If Maui data were combined, then the ratio of species to host genera would be still greater.

TABLE 5. Species of plagithmysines per host genus, by islands.

	NIHOA	KAUAI	OAHU	MOLOKAI	LANAI	W MAUI	E MAUI	HAWAII
Liliaceae								
Smilax	-**	1	1	1	1	1	1	2
Urticaceae								
Pipturus	-	1	2	1		1	2	1
Urera	-					1		2*
Santalaceae								
Santalum	-							1
Chenopodiaceae								
Chenopodium			1					3
Amaranthaceae								
Charpentiera	-							2
Lauraceae								
Cryptocarya	-	1		-	-	-	-	-
Pittosporaceae								
Pittosporum	-	1			1	1		
Rosaceae								
Osteomeles	-							1
Rubus	-						1	1
Leguminosae								
Acacia	-	7*	3	1		1	6	7
Mezoneuron	-							1
Sophora	-						2	5
Geraniaceae								
Geranium	-						1	1*
Rutaceae								
Fagara	-							1
Pelea	-	1	2	2		2	3	2*
Platydesma	-							1
Euphorbiaceae								
Euphorbia	1	1	1					1
Aquifoliaceae								
Ilex	-		1	1		1		1
Celastraceae								
Perrottetia	-	1	1					1*
Sapindaceae								
Dodonaea	-	2*		1		1		1
Sapindus	-		2					1
Rhamnaceae								
Alphitonia	-	3*						
Elaeocarpaceae								
Elaeocarpus	-	1	1	-	-	-	-	-
Myrtaceae								
Syzygium	-	1*	1	1*			1	
Metrosideros	-	3*	2*	1	1	1	2	2
Ericaceae								
Vaccinium	-							2*
Myrsinaceae								
Myrsine	-							2*
Sapotaceae								
Planchonella	-	2*	1					
Ebenaceae								
Diospyros	-							2*
Oleaceae								
Osmanthus	-							1

TABLE 5 (continued).

	NIHOA	KAUAI	OAHU	MOLOKAI	LANAI	W MAUI	E MAUI	HAWAII
Solanaceae								
Nicotiana (introd.)	-						2	
Myoporaceae								
Myoporum	-							1
Rubiaceae								
Bobeia	-	1	1			1?		1
Campanulaceae								
Cyanea	-	1*						
Trematolobelia	-						1?	
Compositae								
Argyroxiphium	-						1	
Dubautia	-						3	3
Bidens	-			1				

* Species in part with 2 or more host genera.

** A dash indicates that host plant genus is absent.

Although Maui is 2nd in number of species of plagithmysines, it is 4th in number of host genera implicated. Because of some species on Kauai (*concolor* group) and Hawaii (*vit-tipennis* and others) having more than 1 host, the actual average number of plagithmysines per host genus on these 2 islands is greater than the ratio indicated, but still less than the ratio for E Maui.

It should be noted that almost all plagithmysines, except some on Kauai and Hawaii, are known to be associated with only 1 host genus.

SCHEMATIC EVOLUTION OF THE PLAGITHMYSINES

ANCESTRY

It is assumed that the progenitor of the plagithmysine group arrived airborne, by some erratic journey in storm winds, from southwestern North America. Possibly it used some long-eroded and sunken island as a stepping stone and reached now eroded and sea-level islets of the leeward portion of the Hawaiian Chain in the early Pliocene. This ancestor may

TABLE 6. Numbers of plagithmysine species and hosts, by islands.

ISLAND	PLAGITH-MYSINE SPECIES	PLAGITH-MYSINE SUBGENERA*	SPECIES PER SUBGENUS	HOST GENERA	AVG. PLAGITH-MYSINE SPECIES PER HOST GENUS
Nihoa	1	1	1	1	1
Kauai	19	2	9.5	16	1.2
Oahu	20	5	4	14	1.4
Molokai	9	4	2.2	9	1
Lanai	3	2	1.5	3	1
W Maui	10	4	2.5	10	1
E Maui	28	6	4.7	13	2.1
Hawaii	46	3	15.3	28	1.6

* Including *Paraclytarus*.

have been a *Neoclytus* or close relative, possibly similar in nature to *Neoclytus modestus* Fall (see Linsley 1962). The characters suggesting this species are a lack of femoral and elytral spines, narrow body, long and slender antenna, narrow prothorax, pubescent markings mostly oblique and longitudinal, as well as the male's fairly long legs and swollen femora.

Although *Neoclytus modestus* may be "typical" of *Plagithmysus* in some respects, the great variation in form of the plagithmysines as a whole goes far beyond the scope of the genus *Neoclytus* (and a coleopterist's concept of a typical mainland genus). In fact, members of the group resemble several quite different genera of Clytini, and some, like *Aeschrithmysus*, superficially suggest members of another subfamily, the Aseminae, in form, size, color, and appendages. For instance, both have the distal antennal segments shortened and thickened, as do some *Neoclytus* and members of other genera of Clytini. The plagithmysines as a group, therefore, present a very wide range of characters, much broader than would normally apply to a genus of beetles. Those who have worked on the group have repeatedly commented that generic placements are very difficult (Perkins 1929: 343). Gressitt & Davis (1969) and Gressitt (1972a, b) successively reduced the number of genera to the single genus *Plagithmysus*. If it were not for the discovery of *Plagithmysus yoshimotoi* Gressitt & Davis, *Aeschrithmysus* would still be retained as a separate genus, and but for *P. cheirodendri* Gr. & D., *Nesithmysus* might still be a separate genus. The discoveries of *P. metrosideri* Gr. & D. and *P. ukulele* Gressitt prompted the abandonment of *Paraclytarlus*. Thus, recent discoveries have demonstrated links and intermediate forms between the supposed genera. This actually demonstrates that all forms from a single ancient pair of ancestors are inevitably related, and that it is evolutionary divergence together with extinction which produces genera in the eyes of the systematist. In the favorable, relatively noncompetitive, isolated environment of Hawaii, we see examples of rapid and profuse evolution with much of the process still in evidence. The small number of phyletic lines in the Hawaiian fauna (small number of families, subfamilies, tribes, etc.) means that many potential competitors and enemies are lacking in the fauna. The introduced biota, however, is rapidly providing these, and the endemic biota appears doomed if the present rate of environmental change continues.

There presumably was speciation on the Leeward Islands among plagithmysines on trees such as *Acacia*, *Metrosideros*, *Pelea*, *Pipturus*, *Euphorbia*, *Santalum* and others probably already existing there (the last 2 still occur on these islands). There was gradual movement southeastward, as new islands developed during the Pliocene, and further as the major portion of the largest island, Hawaii, developed during the Pleistocene.

DISPERSAL

The general direction of spread was probably WNW to ESE. Species probably evolved on the older islands (WNW) and gradually spread to the younger ones. Founder events probably did not happen very often, as plagithmysines are active and not very long-lived as adult beetles and are likely vulnerable to desiccation and wind damage in air transport. From the standpoint of survival possibilities, and the known dominance of lamiine

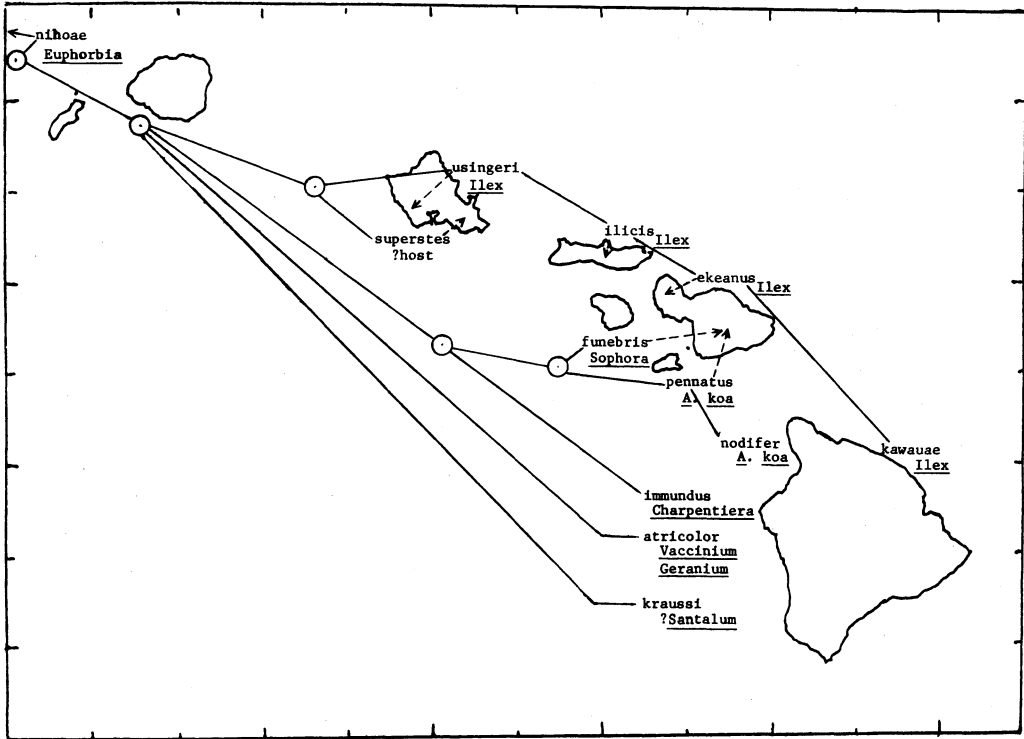


FIG. 4. Possible derivation of the most primitive living *Plagithmysus* s. str. and host-plant associations. Apparently no representative remains on Kauai. There appear to be 5 separate colonizations on the island of Hawaii.

longicorns in most of Polynesia and Micronesia, where airborne transport was also predominant, one might expect a lamiine rather than a cerambycine (subfamily) representative to have successfully colonized the Hawaiian Chain. On the other hand, many of the cerambycines, especially the clytines, are more active flyers than most lamiines, and thus are more frequently airborne. Also working against frequent founder events are the predominant trade winds, which blow from the NE, carrying airborne insects away from the island chain. Those insects, however, which are lifted high enough to enter the jet stream zone might be carried back eastward and thus have a chance to reach an island farther ESE (if they can survive temperature, desiccation, and other stress). More often the transport was probably by frontal winds from the SE which occasionally superceded the trade winds.

For the reverse trend—colonizing older islands from younger ones—the trade winds would be still less appropriate vehicles of transport for they would carry the insects too far south even if they were caught up in the jet stream. Most of the recolonizations from younger to older islands probably took place during “Kona winds”—the warmer and more humid, often stormy, winds from the south or southeast which prevail during slack trade wind periods. Kona winds are much less frequent than trade winds, but because of direction and

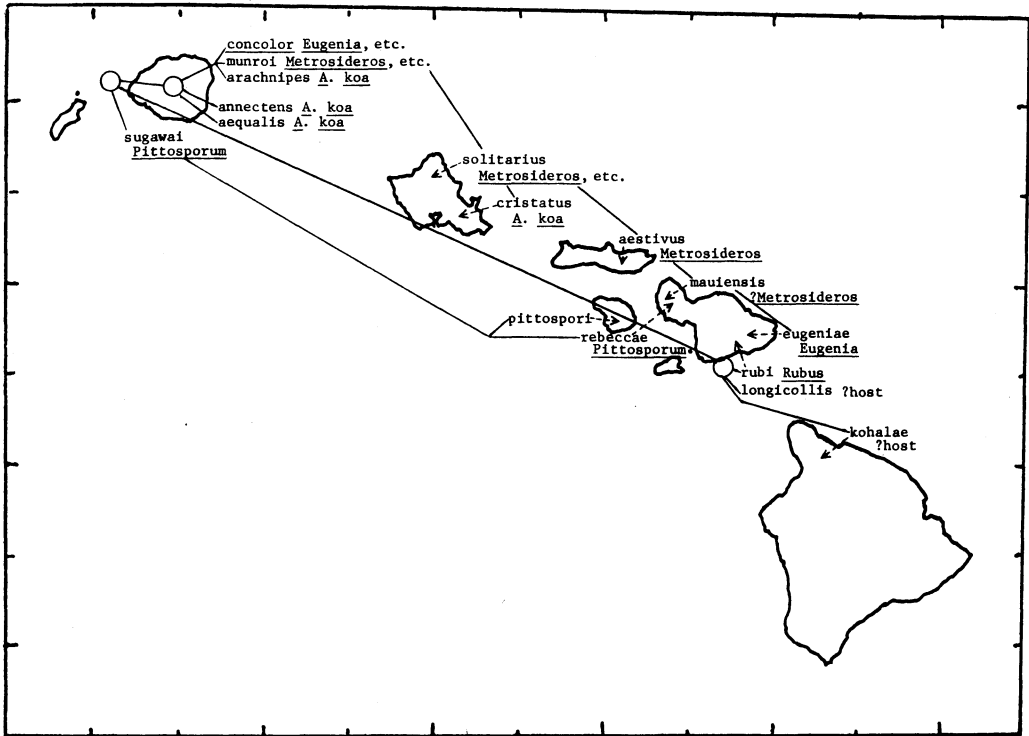


FIG. 5. Possible derivation of some of the fairly generalized groups of "typical" *Plagithmysus* s. str. — mostly very long-legged species of slender to medium build — with host-plant associations.

reduced desiccation power (due to greater humidity), Kona winds are more favorable to insect transport. For this reason, successful insect transport in both directions along the Hawaiian Chain may have occurred with about the same frequency.

Another line of evidence suggesting infrequent recolonization is the high degree of speciation. Different species or races are known on each island or major volcano for each species group. Had recolonization been frequent, the genes would have been kept close enough to the parent stock to prevent speciation.

Successful establishment would in general have been more frequent on newer islands (given sufficient host plants on the younger islands; or sufficient adaptability to available plants—see below). On older islands the competition from already established populations would have more often lead new arrivals to failure to establish, or to extinction. From the narrowness and consistency of host-plant preferences, many potential founder events would have presumably failed.

EVOLUTIONARY PATTERNS

Without the assistance of chromosomal and other data, it has been difficult to be certain of true relationships, and thoughts on this subject have been modified since publication of

the first tentative outline (Gressitt & Davis 1969: 356). The tendency has been to unite species groups into a smaller number, retaining some of the former groups as subgroups and abandoning others. Also, several groups listed before under the subgenus *Neoclytarlus* (*atricolor*, *superstes*, *pennatus*) are here shifted to *Plagithmysus* s. str., and *yoshimotoi* is united with *Aeschrithmysus*. Actually, all of these moves were suggested by questioning arrows in the above reference. However, the *indecens*-group is retained in *Neoclytarlus* as a very distinct species group. *Paraclytarlus* is tentatively considered within *Plagithmysus* s. str. or as a very weak subgenus with possible relationship to the *indecens*-group. This might suggest that the *indecens*-group would then also represent a very weak subgenus. The *chenopodii*-group has been retained in *Neoclytarlus*, but this might make the latter an unnatural subgenus. The relegation of all 3 "*Callithmysus*" to *Plagithmysus* s. str. has already been mentioned above. Since the former key characters of femoral length and femoral swelling do not uniformly separate *Plagithmysus* s. str. and *Neoclytarlus*, the main criteria used in the present study are the broad humeri of the former, being distinctly greater in width than the prothorax, and distinct narrowing posteriorly of the elytra. Thus, *Neoclytarlus* species have the prothorax about as broad as humeri and elytra hardly or

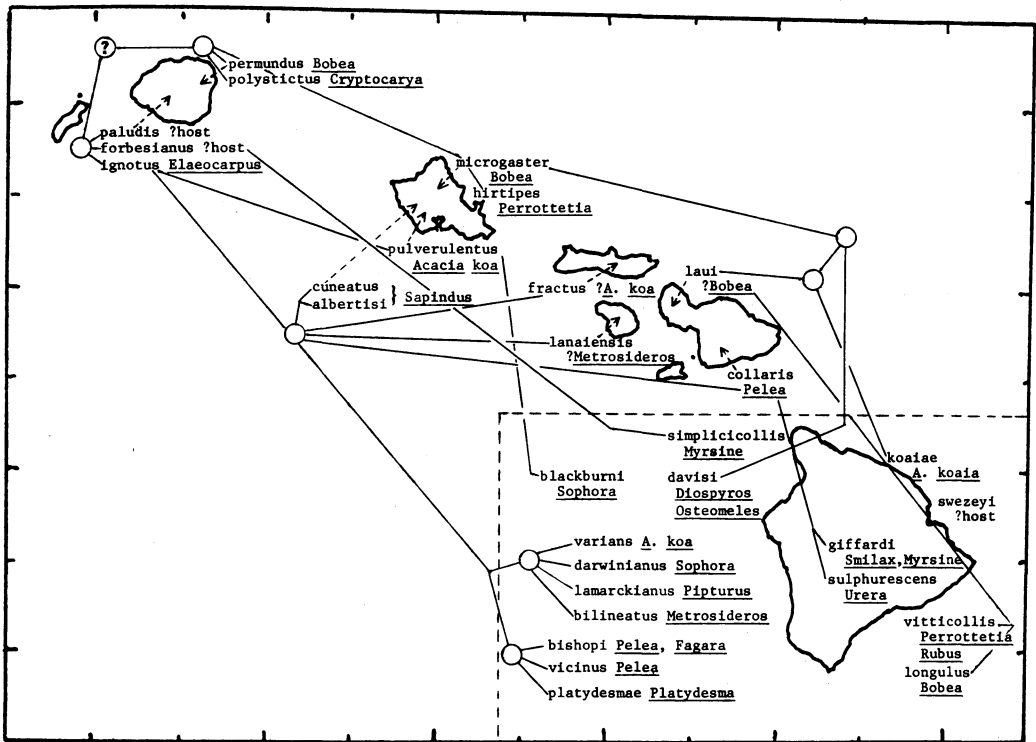


FIG. 6. Possible derivation of several subgroups of the permundus- and paludis-groups of *Plagithmysus* s. str., with host-plant associations, showing 3 probable founder events on Oahu and 8 on Hawaii, coming directly from Kauai or via Oahu or Maui.

feebly narrowed posteriorly. The chenopodii- and indecens-groups more or less conform with this division, besides having the shorter legs of most, but not all, true *Neoclytarlus*.

Plagithmysus nihoae Perkins is suggested as the most primitive or most generalized living species of the group, not merely because it is presently the westernmost occurring one, but because it appears to be a fairly common denominator without specialization of body form in any particular direction. Working on this assumption, derivations are suggested as discussed below (see FIG. 4-12). This plan offers some analogies with the interesting situations in *Nysius* (Usinger 1942), the genus *Banza* (longhorned grasshoppers) and *Drosophila* (Carson et al. 1970).

The usingeri-, funebris-, immundus-, and atricolor-groups are suggested as fairly primitive and descended from an ancestor in common with *P. nihoae* (FIG. 4). These groups are associated with *Ilex*, *Sophora*, *Acacia koa*, *Charpentiera*, and *Vaccinium*. The kraussi-group, consisting only of *P. kraussi* Gr. & D., on Hawaii, may not be so primitive and is broader-bodied, but it does not seem to be close to any other groups. Its analogies with the chenopodii-group of *Neoclytarlus* may not represent relationship, but perhaps convergence.

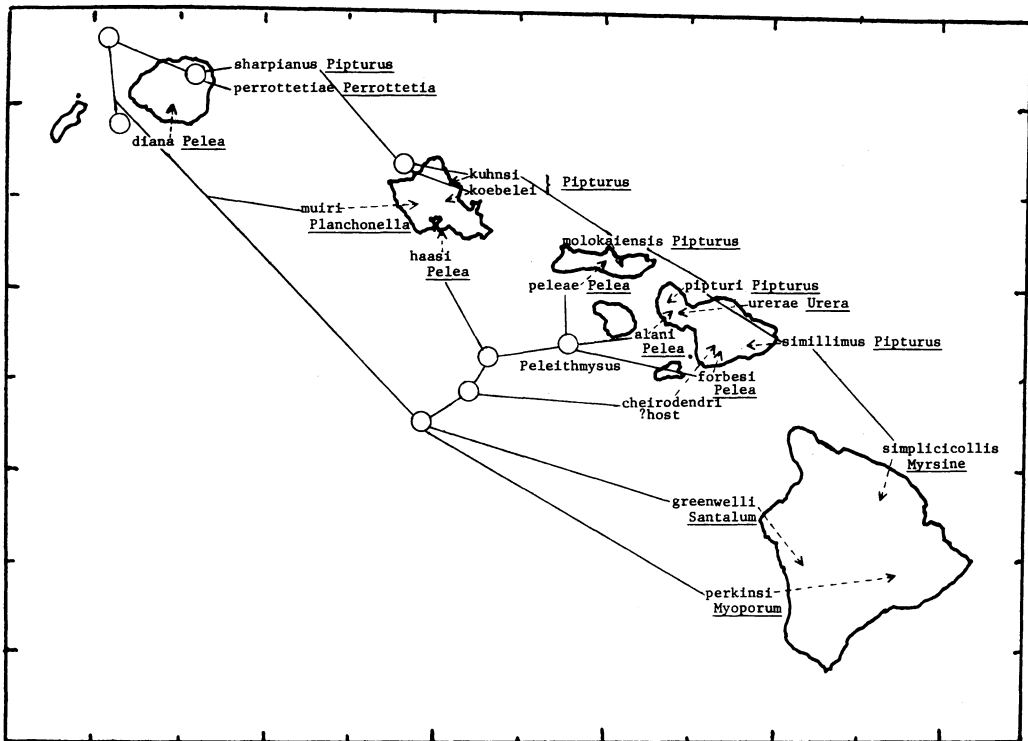


FIG. 7. Possible derivation of *Peleithmysus* and some of the specialized *Plagithmysus* s. str., with host-plant associations. Note that all but one of the sharpianus-group feed on Urticaceae, and most of the others in *Pelea* (Rutaceae). Several of the intermediate stages between the *diana* ancestor and *Peleithmysus perkinsi* are extinct.

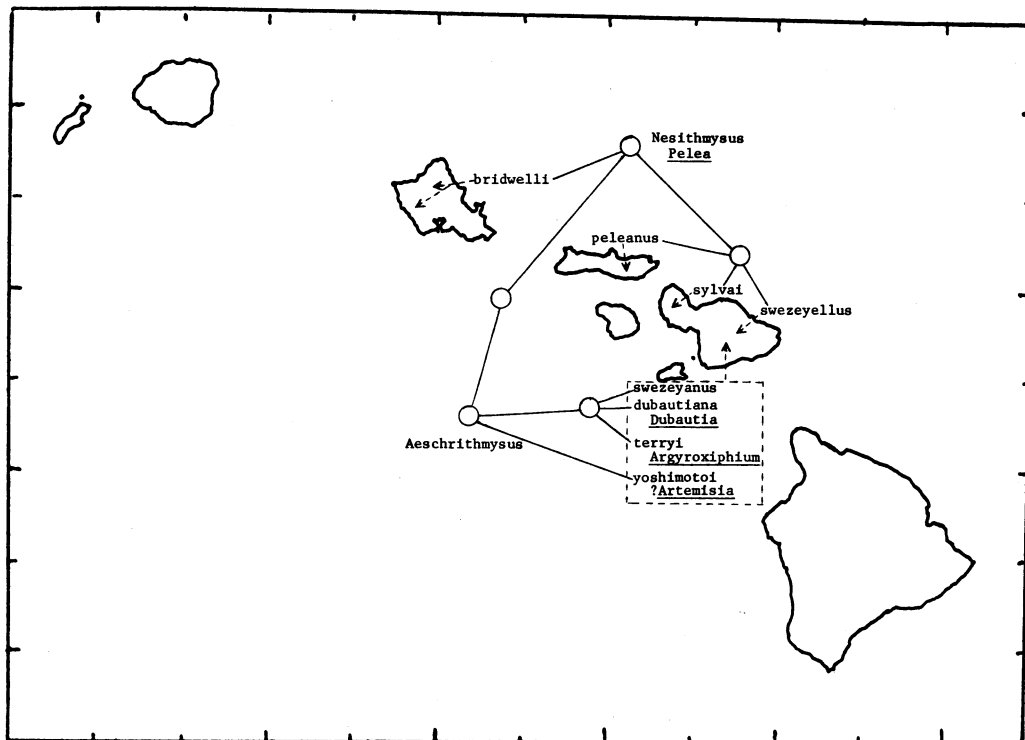


FIG. 8. Possible derivation of *Nesithmysus* and *Aeschrithmysus*. At least 2 founder events, from a possible common extinct ancestor on Kauai: *Nesithmysus* to Oahu, with later founder to Maui-Lanai-Molokai (extinct on Lanai?); *Aeschrithmysus* only to Maui, or extinct elsewhere. *Nesithmysus* all associated with *Pelea*.

It may be noted that the usingeri-group proper has retained the same host plant, *Ilex*, in moving from island to island. The above groups appear to have no representatives on Kauai. All 5 species on Hawaii represent separate colonizations.

Next (FIG. 5) are placed some groups which are very characteristic of the typical *Plagithmysus* s. str. The members are somewhat longer-bodied than those of the previous groups, but not as long as the next series of groups. Beetles of both of these groupings have very long legs and strongly tapering bodies. The large concolor-group has a number of hosts, especially the 3 species on Kauai, but most of the species are associated with *Metrosideros*, *Eugenia*, or *Acacia koa*. There is a population associated with *Eugenia* on Molokai which may be different from *P. aestivus*. The rubi-group may not be entirely natural, and too few specimens have been collected. The sugawai-group, all in *Pittosporum*, consists of closely related forms. They may be expected on other islands, as the 3 known species were all first found in the past 5 years.

The large permundus- and paludis-groups (FIG. 6) have a number of subgroups, some which developed on Oahu or Maui, but several which first appeared on Hawaii. Members of

these groups are mostly large species, quite long and tapered, with very long legs. A few, such as *P. bilineatus* Sharp and *P. platydesmae* Perkins, are somewhat broad-bodied. The species *P. microgaster* Sharp and *P. hirtipes* Sharp were among those earlier assigned to *Callithmysus*, which has been abandoned. Although *P. cuneatus* Sharp (*sapindi*) and *P. albertisi* Sharp are both from Oahu and both associated with *Sapindus*, they are very distinct species. Perhaps they evolved on the 2 separate volcanoes, and later each moved to the other as well. Some of the species on Hawaii are very closely related and have rather slight differences between populations of different hosts. On the other hand, *P. bilineatus* Sharp and *P. varians* Sharp are quite distinct. A large number of hosts are associated with this grouping, but several of the species feed in *Bobea*, *Metrosideros*, or *Acacia koa*.

Another grouping mapped (FIG. 7) includes fairly broad to quite large species of a common extinct ancestor. The members of the sharpianus-group are fairly uniform, are almost entirely associated with Urticaceae, and extend from Kauai to Hawaii. The 2 species on Kauai are closely related, but the 2 on Oahu are very distinct, and *P. koebelei* Perkins was formerly in the defunct *Callithmysus*. The groups associated with *P. diana* Sharp are rather diverse, with many gaps, but all are large-bodied and many of them, including all *Peleithmysus*, are associated with *Pelea*.

An additional grouping of stout species, the brightly colored newelli-group, is not mapped, but is related to the microgaster- and laui-subgroups of the permundus-group (FIG. 6). This group includes *P. decorus* Perkins, in *Charpentiera*, *P. elegans* Sharp and *P. nicotianae* Gr. & D., besides *P. newelli* Sharp, also from *Nicotiana*.

The subgenera *Nesithmysus* and *Aeschrithmysus* are somewhat related but the common ancestor is extinct (FIG. 8). It may have been related to the ancestor of the diana-group, *Peleithmysus* and related forms. All the *Nesithmysus* are associated with *Pelea* and occur in the central islands. *Aeschrithmysus*, the members that resemble *Plagithmysus* least in the whole complex, are known only from E Maui, and are all associated with Compositae as far as is known. The species *P. yoshimotoi* Gr. & D. is an intermediate form, and required reducing the genus to a subgenus. It might be associated with *Artemisia*, or possibly with *Dubautia* or *Argyroxiphium*. Search has failed to disclose a silversword plagithmysine on Hawaii. The members of these groups are assumed to be weak flyers, and are less active than most plagithmysines.

Most of the "true" *Neoclytarlus* species are fairly similar in body form, with flattened-cylindrical bodies and often pedunculate femora. Most of them are associated with Leguminosae and Compositae, with a few with *Dodonaea*, *Euphorbia*, *Alphitonia*, and *Geranium*. The chenopodii-group and the indecens-group are each separately rather distinct. The former are associated with *Chenopodium* and the latter all with *Smilax*. The species *P. metrosideri* Gr. & D., from Kauai, and *P. bidensae* Gr., from Molokai, are somewhat isolated groups, but perhaps related.

Although in many cases the maps or diagrams (FIG. 9-12) suggest that the flow of founders has been mainly from west to east, this has certainly not always been the case. Perhaps the Oahu representatives of *Nesithmysus* and *Peleithmysus* came to Oahu from the Maui group,

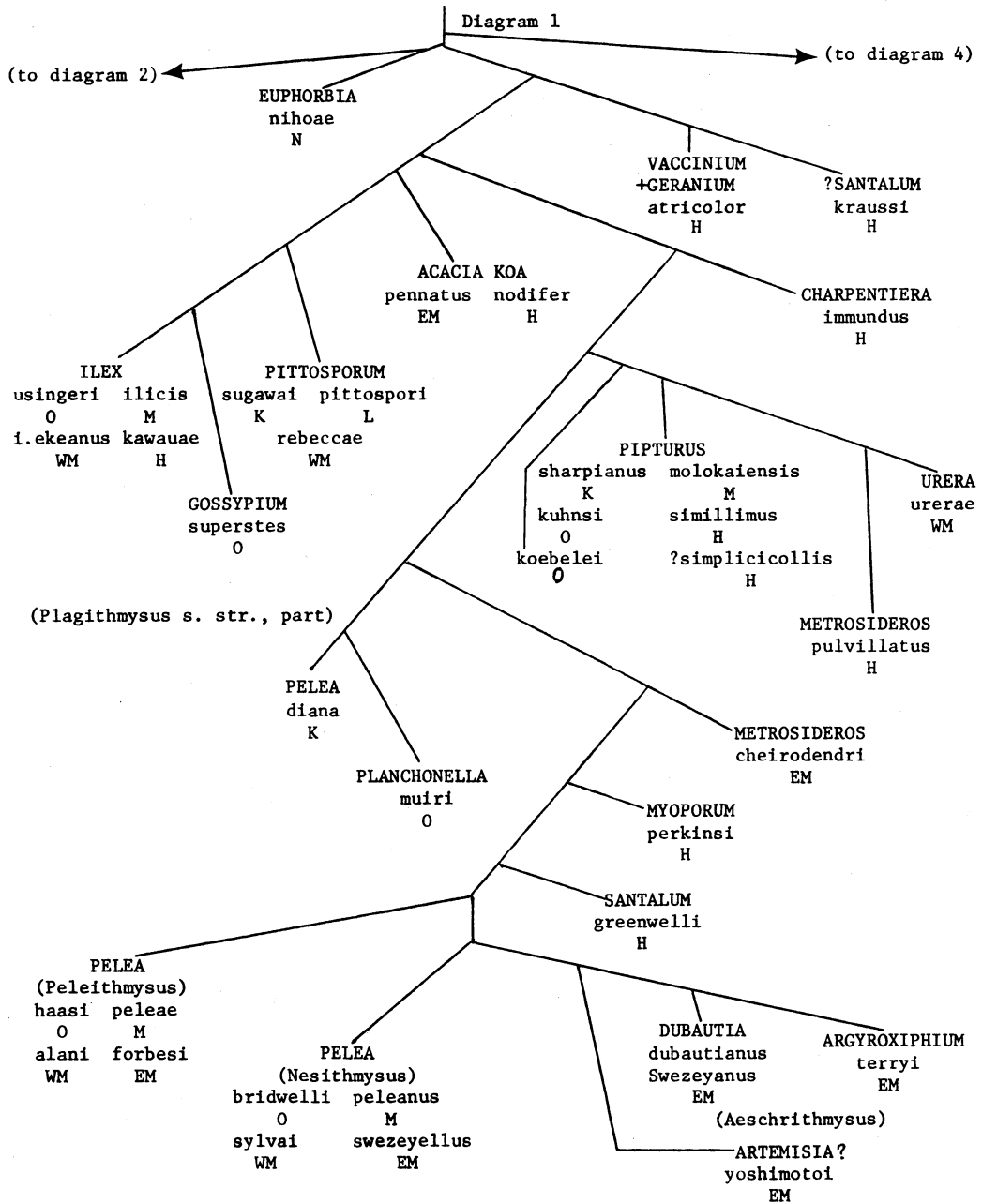


FIG. 9. Diagram showing relationships and hosts of the plagithmysines. N=Nihoa, K=Kauai, O=Oahu, M=Molokai, L=Lanai, WM=West Maui, EM=East Maui, H=Hawaii, ?=supposition of host.

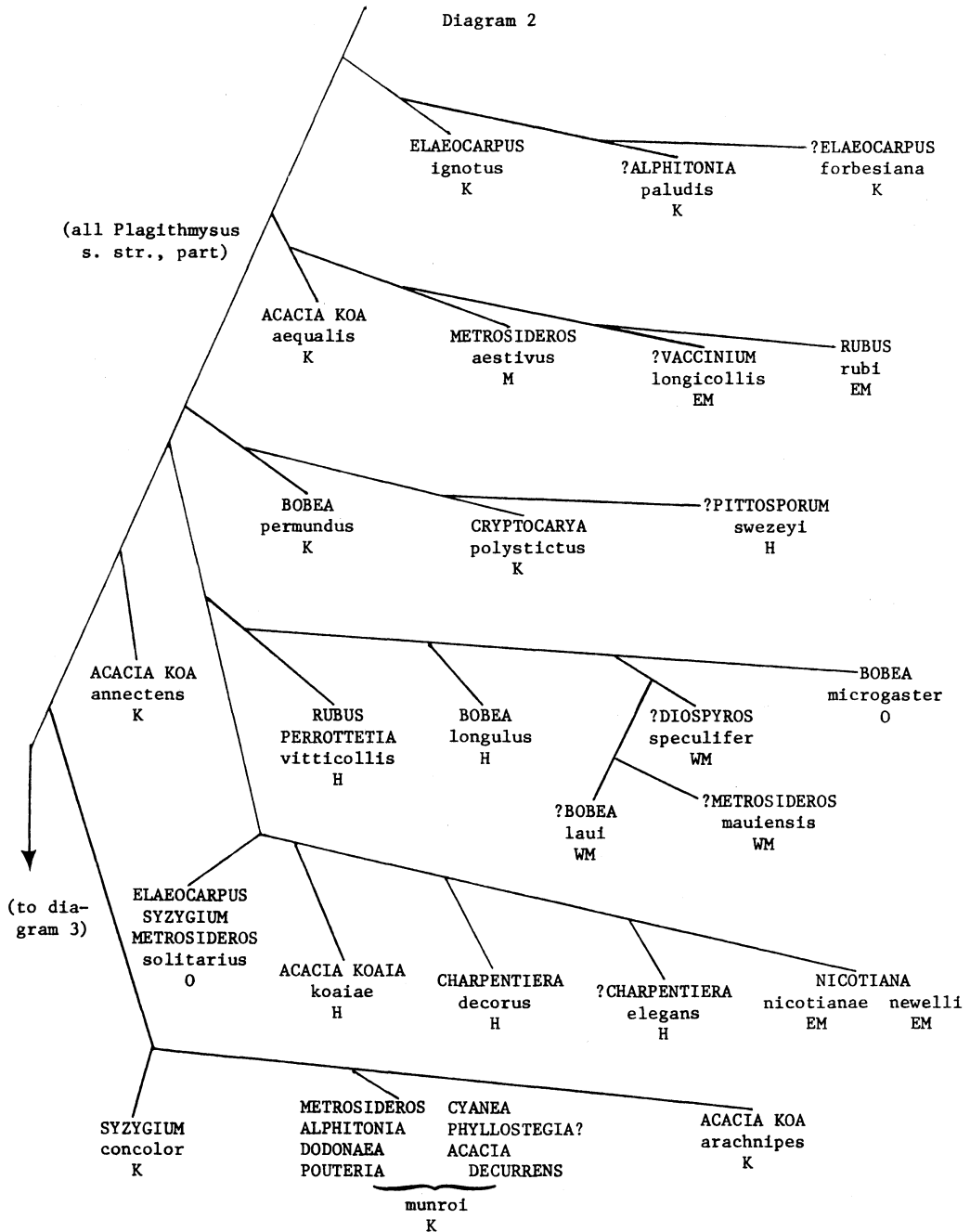


FIG. 10. Diagram showing relationships and hosts of the plagithmysines. N=Nihoa, K=Kauai, O=Oahu, M=Molokai, L=Lanai, WM=West Maui, EM=East Maui, H=Hawaii, ?=supposition of host.

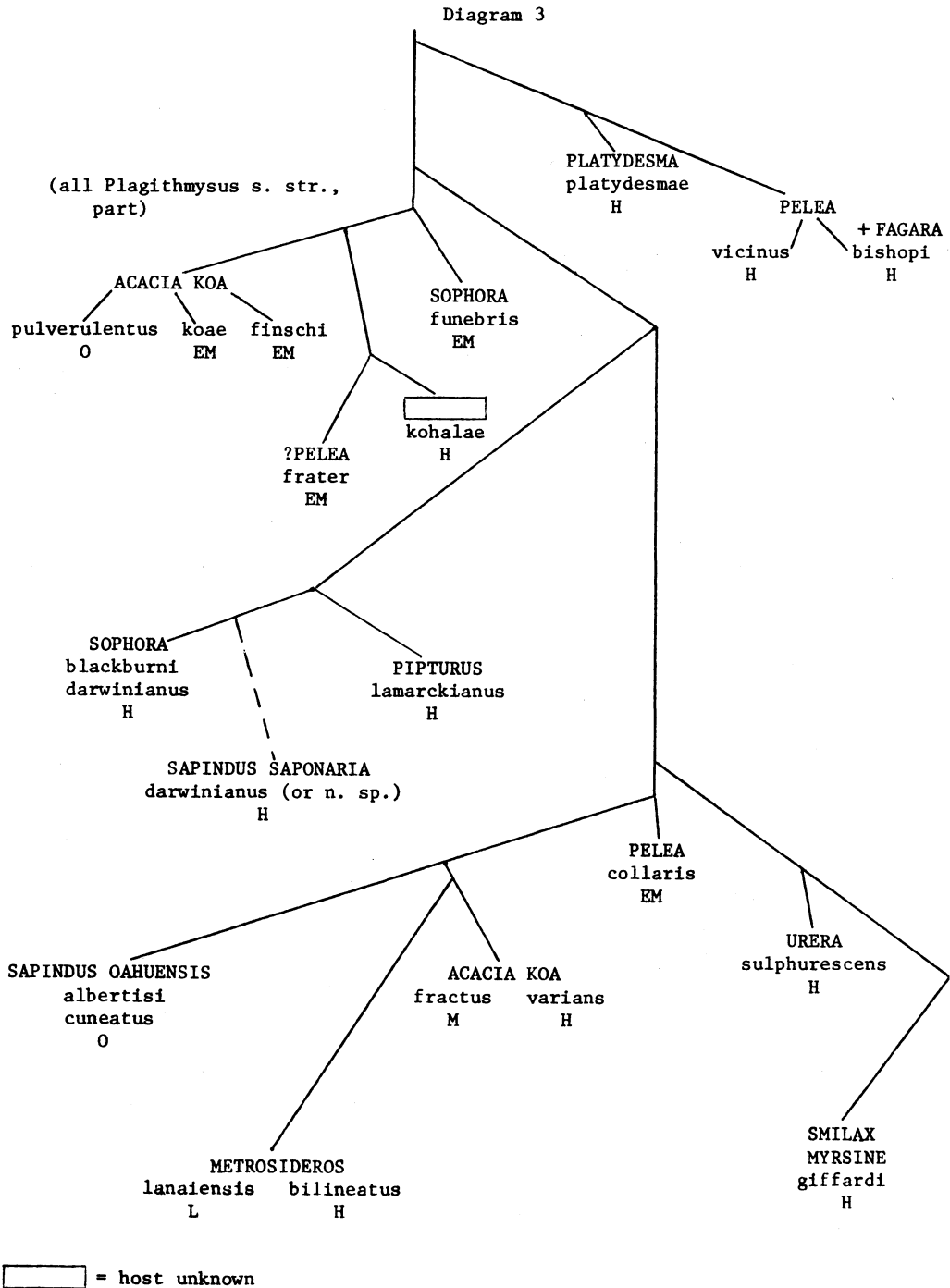


FIG. 11. Diagram showing relationships and hosts of the plagithmysines. N=Nihoa, K=Kauai, O=Oahu, M=Molokai, L=Lanai, WM=West Maui, EM=East Maui, H=Hawaii, ?=supposition of host.

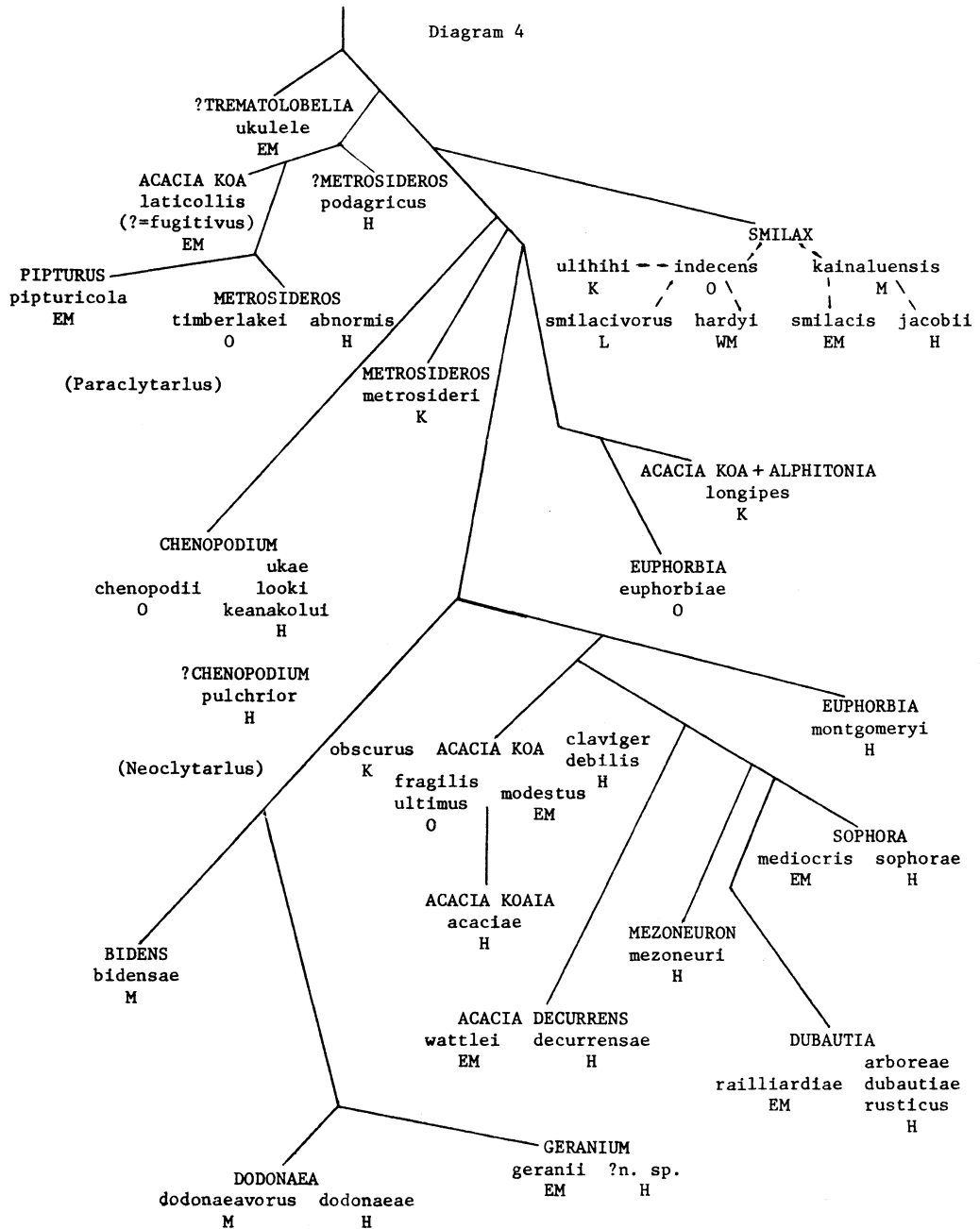


FIG. 12. Diagram showing relationships and hosts of the plagithmysines. N=Nihoa, K=Kauai, O=Oahu, M=Molokai, L=Lanai, WM=West Maui, EM=East Maui, H=Hawaii, ?=supposition of host.

and perhaps some of the Maui representatives of multi-island groups came to Maui from Hawaii. However, indications are that the majority of species groups moved down the chain towards Hawaii. Probably most founding events were inter-insular, but a number on the island of Hawaii must have been intra-insular. Some of these involved change of host-plant genus as well as island or volcano.

There are a number of parallels between the distribution-evolution pictures of the Hawaiian Cerambycidae and the picture-winged *Drosophila* (Carson, pers. commun.). The numbers of species per island are closely similar, and those in each family came from a single introduction. However, plagithmysines are not associated with some of the principal drosophilid host plants, and vice versa. Moreover, the drosophilids do not relate so conspicuously with *Acacia* and *Metrosideros* as do the plagithmysines. Twenty-seven genera of trees are used by plagithmysines but not drosophilids; 7 by drosophilids and not plagithmysines, and 11 genera are hosts to both.

SUMMARY

Except for 17 species introduced to the Hawaiian Islands by man, and 2 species (*Parandra* and a *Megopsis*) which are endemic but have not speciated, the cerambycid beetles of Hawaii belong to the single endemic genus *Plagithmysus* (subfamily Cerambycinae: tribe Clytini). *Parandra* and *Megopsis* are heavy-bodied insects and probably reached the islands in floating logs, but the single immigrant ancestor of *Plagithmysus* was an active flyer and was undoubtedly brought on air currents. Although the majority of the Hawaiian biota developed from progenitors which came from the southwest Pacific area, the *Plagithmysus* ancestor must have come from the southwest fringe of North or Central America. It probably had a common ancestor with *Neoclytus*, a genus with many species in North and Central America.

The species of *Plagithmysus* have been assigned in the past to several genera, but because of the recent discoveries of intermediate species, the group has been reduced to a single genus of 5 or 6 subgenera. At this time 136 species of the genus are known. Although a few of these may have to be relegated to synonymy or to subspecies, additional species remain to be discovered, as evidence of the existence of some of them has been noted in active tree borings, or larvae.

The plagithmysines are strikingly host-specific in their food habits. The larvae bore in living or dying wood of standing or injured trees, shrubs or vines. Hosts are known for over 90% of the species, and over 93% of these are only recorded from a single genus of host plant. This knowledge is the result of years of investigation, especially by R. C. L. Perkins, O. H. Swezey, C. J. Davis, and J. L. Gressitt. The beetles are associated with about 37 genera of plants in 27 families. Two-thirds of the species attack members of the families Leguminosae, Rutaceae, Myrtaceae, Urticaceae, Compositae, Sapindaceae, and Liliaceae, in decreasing order of recorded occurrence.

The island of Hawaii has the largest number of species of plagithmysines (46), and E Maui the next largest number (28). However, all 6 subgenera occur on E Maui, and only 3 on Hawaii. Thus Hawaii has many more species per subgenus. On the other hand, Maui has

more species of beetles per host-plant genus than does Hawaii (13 host genera on E Maui and 28 on Hawaii). There are 19 species in 2 subgenera on Kauai, and they feed in 16 genera of plants, plus some unrecorded hosts. The island of Nihoa has 1 species, which may be the most generalized one. Apparently most of the species groups moved down the chain towards Hawaii, but the ancestors of a number are lacking on Kauai and some of these groups may have developed on Oahu, Maui, or even Hawaii. A few species groups are represented on all or nearly all the islands and have 1 or more species on each island (different in E and W Maui)—all, or nearly all, feeding in the same tree genus on each island. Some species groups have changed hosts in jumping to another island. Several species groups are limited to a genus or family of hosts.

Lack of chromosome information for the plagithmysines, and great morphological variability, make precise determination of phylogeny difficult. The body form has diverged greatly in different directions to give the impression of much more than generic differences within the single genus. This is one of the most striking aspects of the evolution of this strictly Hawaiian complex.

Acknowledgments: I wish to express my indebtedness to H. L. Carson, C. J. Davis, W. Gagné, C. Higa, F. G. Howarth, J. Jacobi, R. G. and R. S. M. Lau, E. G. Linsley, S. Montgomery, D. Mueller-Dombois, T. K. Pratt, G. A. Samuelson, H. St. John, R. Sylva, and R. Taylor in connection with this study. Work leading to this report was also assisted by a grant to Bishop Museum from the U. S. Forest Service for work on borers of ohia (*Metrosideros*) and koa (*Acacia koa*).

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