

Technical Report No. 71  
EVOLUTION OF THE  
ENDEMIC HAWAIIAN CERAMBYCID-BEETLES

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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 135 species of plagithmysines (Clytini) plus one endemic species each of two somewhat widespread primitive genera (Megopis and Parandra) which breed primarily in rotten wood. There are also 17 species introduced by man. The plagithmysines evolved from a single immigrant ancestor species which probably came from Mexico or southern California a few million years ago. The group feeds in living trees and has remarkably specific host-tree food habits within a species of beetle, but has adapted to a large number of families (27) of trees for the whole group. Body form has diverged greatly, with the result that seven generic names have been proposed to accommodate the species. However, these have recently been reduced to the single genus Plagithmysus, with 5 subgenera, following the discovery of intermediate forms.

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## INTRODUCTION

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.

The entire 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 one marine and one 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 one animal and one 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, three or four families of moths, seven families of beetles, dolichopodid and drosophilid flies, and two groups of wasps. Perhaps the most conspicuous developments are in the land snails, the drepaniid birds, and the drosophilid flies. Following closely upon these, the plagithmysine complex presents a conspicuous example of diversification, and interesting host-plant relationships.

## SETTING

### Geological history

These islands were raised up by vulcanism from the floor of deep ocean and have never been attached to any continent. The main islands (Fig. 1) are much

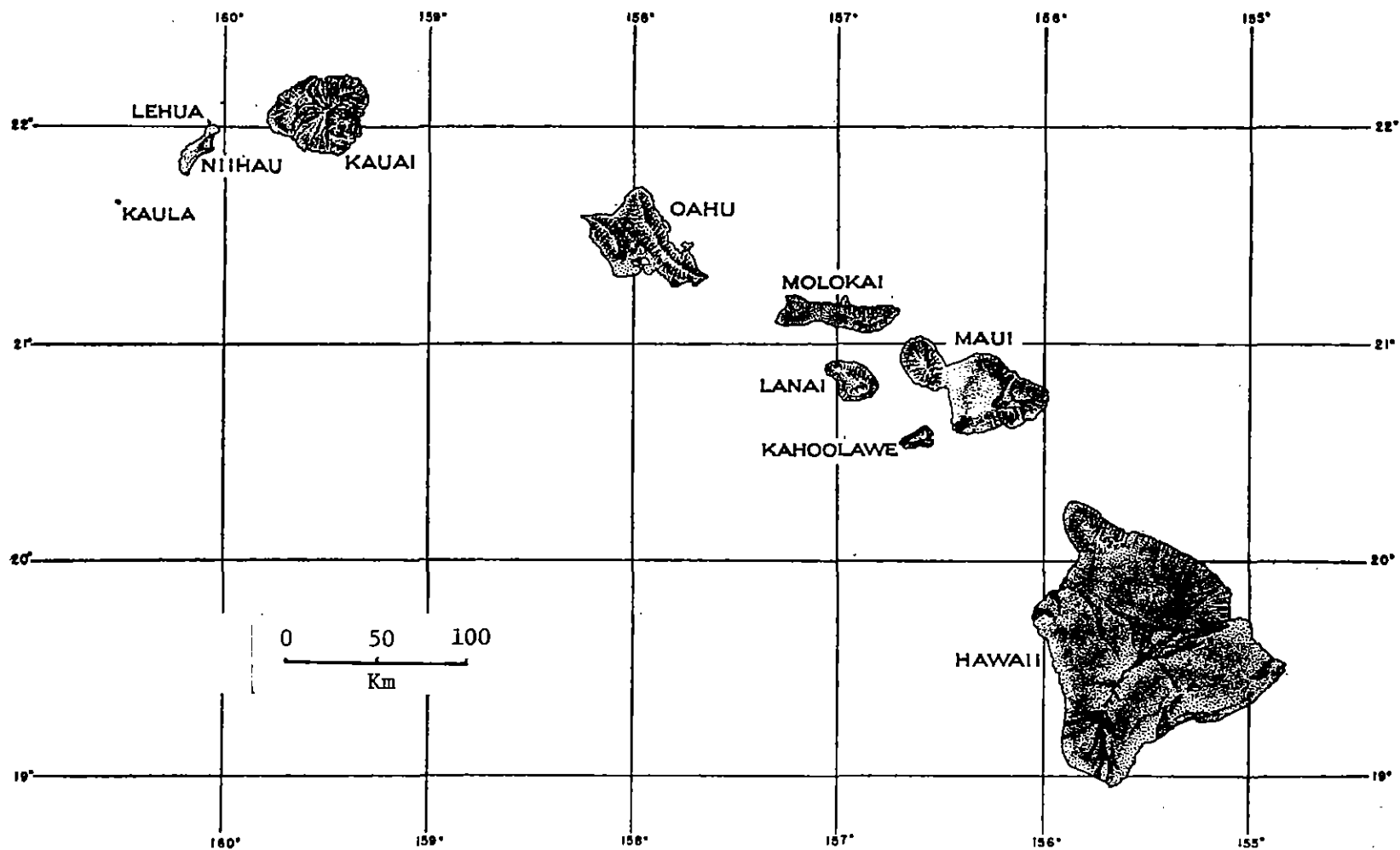


FIG. 1. The main islands of the Hawaiian chain, which support all but one (on Nihoa) of the plagithmysines. None are known from Kahoolawe. Remnants of two volcanoes each on Oahu, Molokai and Maui, and four on Hawaii, are shown, with fairly recent lava flows from one on Maui and two on Hawaii. (From Stearns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

younger than the western Leeward 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 <sup>submerged</sup> or/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 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 meters in altitude. It supports the westernmost species of Plagithmysus.

Of the main islands, Hawaii, the youngest, farthest east, and largest island, is still growing, with two or three 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.

Different parts of one island may differ in age and represent different 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 definitely separate islands. Molokai, Lanai, and Maui were also all connected during Pleistocene ice-ages. The Kohala Mt. at the northwest corner of Hawaii is nearly 1 million years old, but 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 Leewards 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 native plants belonging to about 75 families. The species endemicity 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; and St. John 1974).

#### Role of plagithmysines in forest

The majority of the known plagithmysines are associated with rain forest trees. There is the possibility that a number of species became extinct with the loss of the dry forests. Plagithmysines are associated with about one-third of the native genera of Hawaiian trees. There are definite records from 36 genera of woody plants in 27 families. Twenty-seven of the genera are wet forest trees and these support 110 species of plagithmysines, while nine genera are dry forest trees or shrubs and support 22 plagithmysine species.

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 often 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 P. greenwelli in Santalum in cattle-grazing areas on Hawaii. Also, P. 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. Figures 2 and 3 represent examples showing varied body form.

There are two 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. Parandra puncticeps and Megopis reflexa belong to primitive groups, feeding only in dead wood. These primitive groups have apparently evolved very slowly. Thus these two isolated endemic species could have been in Hawaii a long time without speciating. In each case the ancestral continental species could even be extinct or undiscovered. Parandra is a nearly cosmopolitan genus, largely tropical and subtropical in distribution. The Hawaiian species probably originated from Southeast Asia or the Southwest Pacific. Megopis is a tropical Old World genus, primarily continental in distribution. Both Parandra puncticeps Sharp and Megopis reflexa (Karsch) are nocturnal and are not often observed to fly. Both are heavy-bodied, sombre in color, and slow-moving. They bore primarily in rotting wood. These characteristics are all in contrast to those



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

the prothorax; decrease in body size and tendency toward very slender form related to boring in slender vines (Smilax) or semi-woody plants (certain Compositae); and also swelling 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 nevertheless may be partly protective in nature. Being active diurnal insects, these beetles are preyed upon by native forest birds. Rather seldom have any of them been noted to be attracted to flowers. In general the adults are very rarely seen, and fly only in good weather. A conspicuous aspect of plagithmysine behavior is that the beetles are extremely active in mating and tend to be gregarious, 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 Paraclytarus are probably also relatively inactive, but very few specimens of this grouping have been collected. Individuals of Callithmysus are very active, as their present placement within Plagithmysus s. str. would imply.

Although seven generic names had been proposed to include the plagithmysines, these have recently been reduced to one genus. In spite of great diversity of form, the species must be assigned to a single endemic genus, Plagithmysus, of five, in part vaguely bounded, subgenera. In recent years, a number of species have come to light (Gressitt & Davis 1969-1974, in press; Gressitt 1972 a,b) which bridged gaps between supposed genera. As an example of the confusion among systematists, when Perkins (1927) proposed Paraclytarus, he 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 Paraclytarus, 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 species to subgenera is presented in Table 1. Paraclytarus is probably not a valid subgenus, but only represents some

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

	Aeschrith- mysus	Nesith- mysus	Peleith- mysus	Plagith- mysus	Paracly- tarius	Neocly- tarius	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				22	1	14	37
Totals	4	4	4	74	5	36	127

extremes of development, as did Callithmysus, which was untenable. A significant point is the large number of species for the Maui group of islands (Molokai, Lanai, Maui) as a whole (50 species).

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

All the members of this complex have evolved from a single immigrant ancestor. About 135 species or subspecies of plagithmysines have been named to date. A few of these will very likely be reduced to synonymy, or to weak 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 color, vestiture, pronotal tuberculation and other characters. The femoral characters have been used to separate genera (subgenera), but even keying the sexes separately proves impractical. This can even be true in keying species, because of variation within one sex of one population. Often for quick identification it is simpler to separate species by species-group (also sometimes difficult to define), host, and volcano, 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 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 some species, some individuals of P. albertisi Sharp are three times as long as others (6.6-21 mm).

Scarcity of beetles in the adult stage has been noted by all field workers. Many entomologists long in Hawaii have never observed an adult 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 may have the same, or closely related, host plants.

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 discussions 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 may be in part because the plagithmysines prefer forests which are not too densely shady, which is often the case with 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 of Hawaiian woody plants are not attacked by these beetles. Of 21 genera of woody plants endemic to Hawaii, only six (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 Lobelioidea (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

TABLE 2. Endemic and indigenous Hawaiian woody plant genera, with numbers of associated plagithmysine beetles<sup>1</sup>.

Family	Genus	Genus		Species		Geogr. Aff.	No. of plagithmysines assoc'd	
		endemic	rare	endemic	Coloni- zations		species	Mts
Palmae	Pritchardia			2-38	1	Indo-Pac.		
Pandanaeae	Pandanus (1 indig.)			-	1	"		
	Freycinetia			1	1	"		
Liliaceae	Smilax			2	1	"	8	8
	Dracaena			2-4	1	"		
Moraceae	Pseudomorus		x	1?	1	Austral		
Urticaceae	Pipturus			13	1	Indo-Pac.	8	6
	Neraudia	x	x	9	1	"		
	Touchardia	x	x	5	1	"		
	Urera			3	2	Amer.	2	2
	Boehmeria			1	1	Indo-Pac.		
Santalaceae	Exocarpus		x	3-5	1	Austral		
	Santalum			6	2	"	1*	1
Polygonaceae	Rumex		x	2	1	?		
Chenopodiaceae	Chenopodium			1	1	Amer.	4	3?
Amaranthaceae	Achyranthes		x	2	1	Indo-Pac.		
	Charpentiera			2	1	Austral	2*	1
	Nototrichium	x		5	1	"		
Nyctaginaceae	Pisonia			3	2	Indo-Pac., Austral		

<sup>1</sup> Partly after Fosberg (1948); modified with advice of Dr. H. St. John

\* Additional species questionable or probable

TABLE 2 Continued.

Family	Genus	Genus		Species		Geogr. Aff.	No. of plagithmysines assoc'd	
		endemic	rare	endemic	Colonizations		species	Mts
Phytolaccaceae	Phytolacca		x	1	1	Amer.		
Lauraceae	Cryptocarya			2	1	Indo-Pac.	1	1
Cruciferae	Lepidium		x	4	2	Indo-Pac. +?		
Saxifragaceae	Broussaisia			2	1	Indo-Pac.		
Pittosporaceae	Pittosporum			50	1	"	3*	3
Rosaceae	Osteomeles (1 indig.) <sup>2</sup>			-	1	"	1	1
	Rubus			2	1	Amer.	2	2
Leguminosae	Acacia <sup>3</sup>			3	1	Indo-Pac.	23	7
	Cassia			1	1	"		
	Erythrina			1	1	"		
	Mezoneuron		x	1	1	"	1	1
	Sophora			1	1	Austral	6	4
	Sesbania		x	1	1	?Austral		
Geraniaceae	Geranium			6	1	?	2	3
Rutaceae	Fagara			14	1	Indo-Pac.	1	1
	Pelea	x		94	1	"	12	8
	Platydesma	x	x				1	1
Euphorbiaceae	Antidesma			6	1	Indo-Pac.		
	Claoxylon		x	8	1	"		
	Drypetes		x	1	1	"		

<sup>2</sup> Native plant also attacked by exotic cerambycid (Curtomerus)

<sup>3</sup> Five plagithmysines reared from 2 species of exotic Acacia

\* Additional species questionable or probable



TABLE 2 Continued.

Family	Genus	Genus		Species		Geogr. Aff.	No. of plagith- mysines assoc'd	
		endemic	rare	endemic	Coloni- zations		species	Mts
	Euphorbia			60	1	Indo-Pac.	4	4
Aquifoliaceae	Ilex (1 indig.)			-	1	Austral	4*	4
Celastraceae	Perrottetia			1	1	?Indo-Pac.	3*	3
Anacardiaceae	Rhus		x	1	1	Indo-Pac.		
Sapindaceae	Alectryon		x	1	1	"		
	Dodonaea			18	1	Pantropic	5*	4
	Sapindus			2	2	Indo-Pac., Amer.	3	2
Rhamnaceae	Alphitonia			1	1	Indo-Pac.	3*	1
	Colubrina		x	1	1	"		
	Gouania		x	3	1	"		
Tiliaceae	Elaeocarpus			1	1	"	2*	2
Malvaceae	Abutilon		x	2	2	Amer., ?		
	Gossypium			1	1	?Amer.	?	
	Hibiscadelphus	x	x	5	1	?		
	Hibiscus			9	4	Indo-Pac, Austral, Pantropic		
	Kokia	x	x	4	1	?		
Sterculiaceae	Waltheria <sup>4</sup>	x	*	1	1	?Amer.		
Theaceae	Eurya		x	2	1	Indo-Pac.		
Violaceae	Isodendrion	x	x	4	1	?Amer.		
	Viola			7	1	?		

<sup>4</sup> Extinct

\* Additional species questionable or probable

TABLE 2 Continued.

Family	Genus	Genus		Species		Geogr. Aff.	No. of plagith- mysines assoc'd	
		endemic	rare	endemic	Coloni- zations		species	Mts
Thymeleaceae	Wikstroemia			14	1	Indo-Pac.		
Flacourtiaceae	Xylosma			2	1	"		
Myrtaceae	Eugenia (Syzygium)			4	2	"	2*	2
	Metrosideros			1	1	Austral	10	7
Araliaceae	Cheirodendron			5	1	"		
	Reynoldsia			1	1	"		
	Tetraplasandra			10	1	Indo-Pac.		
Umbelliferae	Peucedanum		x	3	1	?		
Ericaceae	Vaccinium			8	1	Austral	2*	2
Epacridaceae	Styphelia			1	1	"		
Primulaceae	Lysimachia			12	2	Indo-Pac.;?Austral		
Myrsinaceae	Myrsine			25	1	Indo-Pac.	2	1
Sapotaceae	Planchonella (Pouteria, Sideroxylon)			6	1	"	3	2
Ebenaceae	Diospyros			7	1	"	2*	1
Loganiaceae	Labordia	x		75	2	"		
Oleaceae	Osmanthus			1	1	"	1?	1
Apocynaceae	Alyxia			1	1	"		
	Ochrosia		x	1	1	"		
	Pteralyxia	x	x	2	1	?		
	Rauwolfia		x	7	1	?		
Convolvulaceae	Breweria		x	2	1	?		

\*Additional species questionable or probable

TABLE 2 Continued.

Family	Genus	Genus		Species		Geogr. Aff.	No. of plagith- mysines assoc'd	
		endemic	rare	endemic	Coloni- zations		species	Mts
Labiatae	Phyllostegia			108	1	Austral		
Solanaceae	Nicotiana (introduced)						<2	1
	Nothocestrum	x		6	1	Amer.		
	Solanum			7	1	?		
Myoporaceae	Myoporum			1	1	Indo-Pac.	1	1
Gesneraceae	Cyrtandra			150	1?	"		
Rubiaceae	Bobea	x		4	1	"	3*	3
	Coprosma			27	3	Austral		
	Gardenia			2	2	Indo-Pac.		
	Hedyotis (Gouldia)			76	1	"		
	Morinda		x	3	1	"		
	Psychotria (Straussia)			10	2	Indo-Pac., Amer.		
Campanulaceae	Clermontia	x		42	1	Austral		
	Cyanea	x		100	1	?	1	1
	Trematolobelia	x	x	23	1	?Indo-Pac.	?	1
Goodeniaceae	Scaevola			11	1	Indo-Pac.		
Compositae	Argyroxiphium	x		3	1	Amer.	1	1
	Wilkesia	x		1	1	"		
	Dubautia	x		56	1	"	6	2
	Artemisia			5	1	Boreal		
	Bidens			60	1	Austral	1	1

\* Additional species questionable or probable

TABLE 2 Concluded.

Family	Genus	Genus		Species		Geogr. Aff.	No. of plagith- mysines assoc'd species	Mts
		endemic	rare	endemic	Coloni- zations			
	Hesperomannia	x	x	7	1	Amer.		
	Lipochaeta	x		55	1	Indo-Pac.		
	Remya	x	x	2	1	?Amer.		
	Tetramolopium			20	1	Indo-Pac.		
53 (1 extinct)	104 (1 extinct)			1260±	119			130+ in 27 plant families

genera. The 1300 species have evolved in the islands from about 119 successful establishments. The plagithmysines number about 135 known species, one-tenth 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 species 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 one unit, Oahu is two, Molokai two, Lanai one, Maui two, and Hawaii four.) 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 two centuries, very few instances have been noted of plagithmysines attacking exotic trees. This is probably related both to the narrow host 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.) and Acacia decurrens (5 spp.) and Acacia melanoxylon (1 sp.).

Viewing the phylogeny of the plagithmysine-associated plants (Table 3), only one genus of monocot, 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 Neoclytarlus, to which it has been assigned. Moreover, this is the only species group of which species are known from all major islands (including both East and West Maui). On

two 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 ten plant families, two are not associated with Plagithmysus s. str. Moreover, of the eight 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 two being those with which Plagithmysus is not associated (Table 3). Over one-half of the species of Plagithmysus s. str. are associated with families having no Neoclytarlus associations.

Although the progenitor of the plagithmysines was American, 32 of the associated genera of plant hosts are of Indo-Pacific or Austral derivation and only five 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.

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

Most of the 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 one species of 3 subspecies, 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) varies 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 the subgenera represented. If West and East Maui were combined, then the ratio of species to host genera would be still greater. Although East Maui is second in number of species of plagithmysines, it is fourth in number of host genera implicated. Because of some species on Kauai (concolor group) and Hawaii (vittipennis and others) having more than one host,

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





TABLE 5 Concluded.

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	Nihoa	Kauai	Oahu	Molokai	Lanai	W. Maui	E. Maui	Hawaii
Compositae:								
Argyroxiphium							1	
Dubautia							3	3
Bidens				1				

---

\* Species in part with 2 or more host genera

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

Island	Plagithmysine species	Plagithmysine subgenera*	Species per subgenus	Host genera	Av. Plagithmysine 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 Paraclytarlus

the actual average number of plagithmysines per host genus on these two isles is greater than the ratio indicated, but still less than the ratio for East Maui.

It should be specially noted that most plagithmysines, excluding some on Kauai and Hawaii, are known to be associated with only one 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 have been a Neoclytus or close relative, possibly similar in nature to Neoclytus modestus Fall (see Linsley 1962). The characters suggesting this species are lack of femoral and elytral spines, narrow body, long and slender antenna, narrow prothorax, pubescent markings mostly oblique and longitudinal, as well as <sup>the</sup> 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 genus). In fact, members of the group resemble several quite different genera of Clytini; and some, like Aeschrithmysus, rather closely resemble 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 were very difficult (Perkins 1929:343). Gressitt and Davis (1969) and Gressitt (1972 a,b) successively reduced the number of genera to the single genus Plagithmysus. If it were not for the discovery of P. 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 metrosideri Gr. & D. and ukulele Gressitt prompted the abandonment of Paraclytarlus. Thus, recent discoveries have demonstrated links and intermediates 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 results 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, are rapidly providing these, and the endemic biota appear 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 and others which probably already existed there. There was gradual movement southeastward, as new islands developed during the Pliocene, and further as the major portion of the large island, Hawaii, developed during the Pleistocene.

#### Spread

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 beetles, and are likely vulnerable to desiccation and wind damage in air transport. From the standpoint of survival, and the dominance of lamiine 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 supercede the trade winds.

For the reverse trend--colonizing older islands from younger ones--the

trade winds would be still less appropriate vehicles of transport. The trades 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 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 and Davis 1969:356). The tendency has been to unite species groups into a smaller number, with retention of some of the former groups as subgroups but abandonment of others. Also, several groups listed before under subgenus Neoclytarlus (atricolor, superstes, pennatus) are now 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 three "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, with the elytra distinctly narrowed posteriorly. Thus, Neoclytarlus species have the prothorax about as broad as humeri and elytra hardly or 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 diagrams 1-4, Figs. 4-8). 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 nihoae (Fig. 4). These groups are associated with Ilex, Sophora, Acacia koa, Charpentiera, and Vaccinium. The kraussi-group, consisting only of kraussi G. & D., on Hawaii, may not be so primitive, and is broader-bodied, but 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. 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 five 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. Both of these groupings have very long legs and strongly tapering bodies. The large concolor-group has a number of hosts, especially the three species on Kauai, but

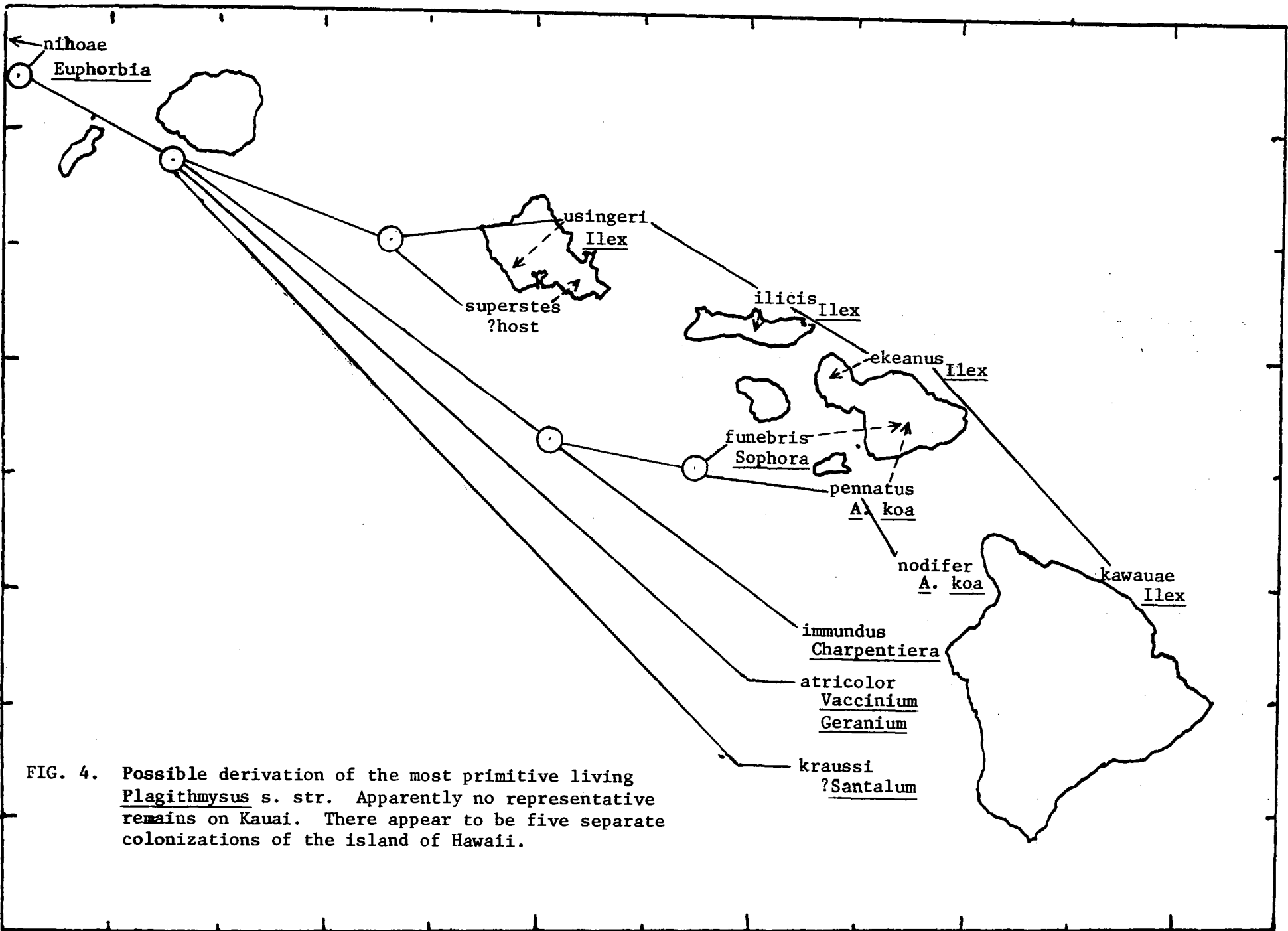


FIG. 4. Possible derivation of the most primitive living Plagithmysus s. str. Apparently no representative remains on Kauai. There appear to be five separate colonizations of the island of Hawaii.

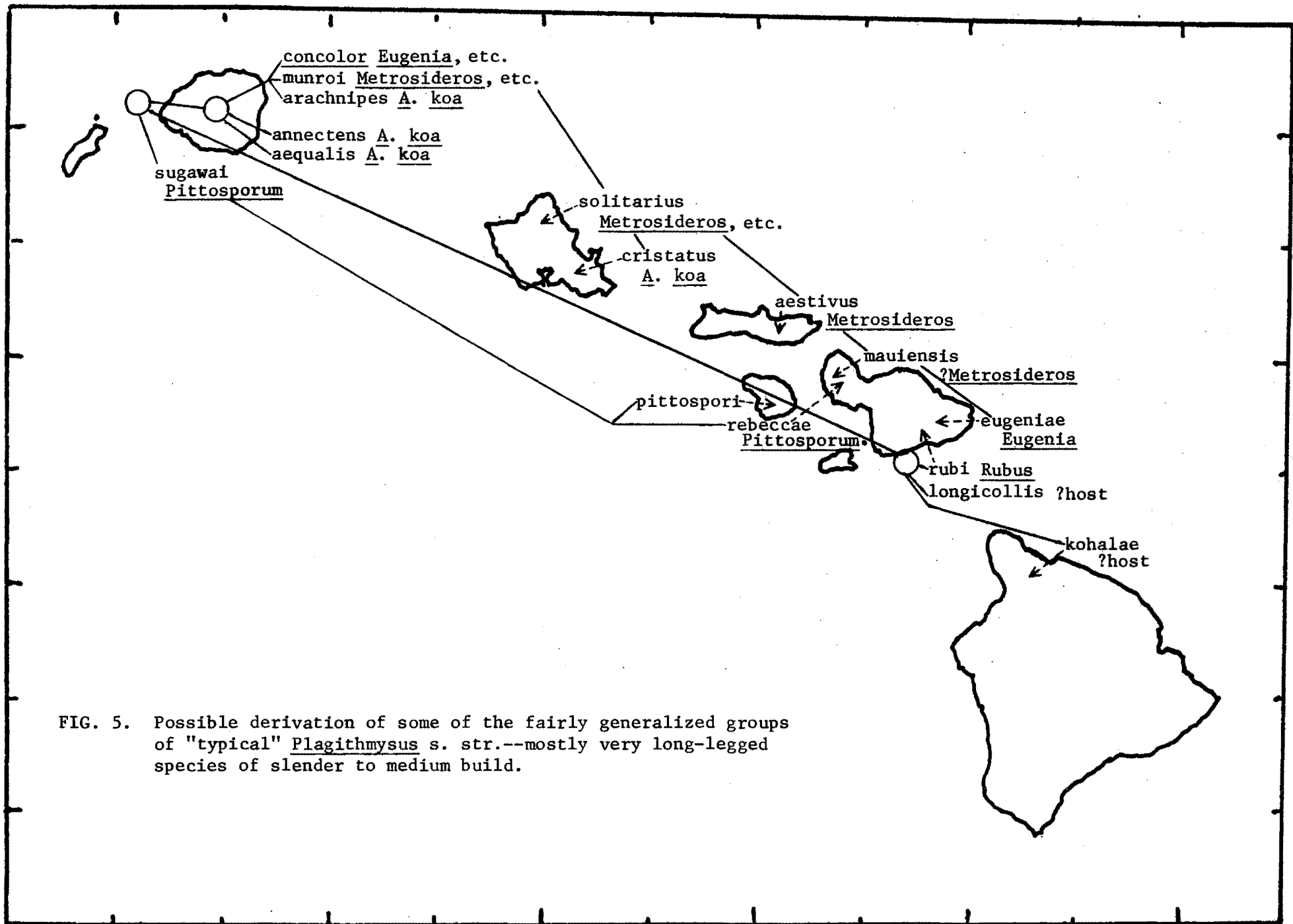


FIG. 5. Possible derivation of some of the fairly generalized groups of "typical" Plagithmysus s. str.--mostly very long-legged species of slender to medium build.



most of the species are associated with Metrosideros, Eugenia, or Acacia koa. There is a population in Eugenia on Molokai which may be different from aestivus. The rubi-group may not be entirely natural, as too few specimens have been collected. The sugawai-group, all in Pittosporum, consists of closely related forms. They may be expected on additional islands, as the three known species were all first found in the past five years.

The large permundus- and paludis-groups (Fig. 6) have a number of subgroups, some of which developed on Oahu or Maui, but several of which first appear on Hawaii. Members of these groups are mostly large species, quite long and tapered, with quite long legs. A few, such as bilineatus Sharp and platydesmae Perkins, are somewhat broad-bodied. The species microgaster Sharp and hirtipes Sharp were among those earlier assigned to Callithmysus, which has been abandoned. Although cuneatus Sharp (sapindi) and albertisi Sharp are both from Oahu and both associated with Sapindus, they are very distinct species. Perhaps they are evolved on the two 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 on different hosts. On the other hand bilineatus Sharp and 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 two species on Kauai are closely related, but the two on Oahu are very distinct, and koebelei Perkins was formerly in the defunct Callithmysus. The groups associated with diana Sharp are rather diverse, with many gaps, but all are large-bodied and many of them, including all Peleithmysus, are associated with Pelea.

Another 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 decorus Perkins, in Charpentiera, elegans Sharp and nicotianae G. & D., besides 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

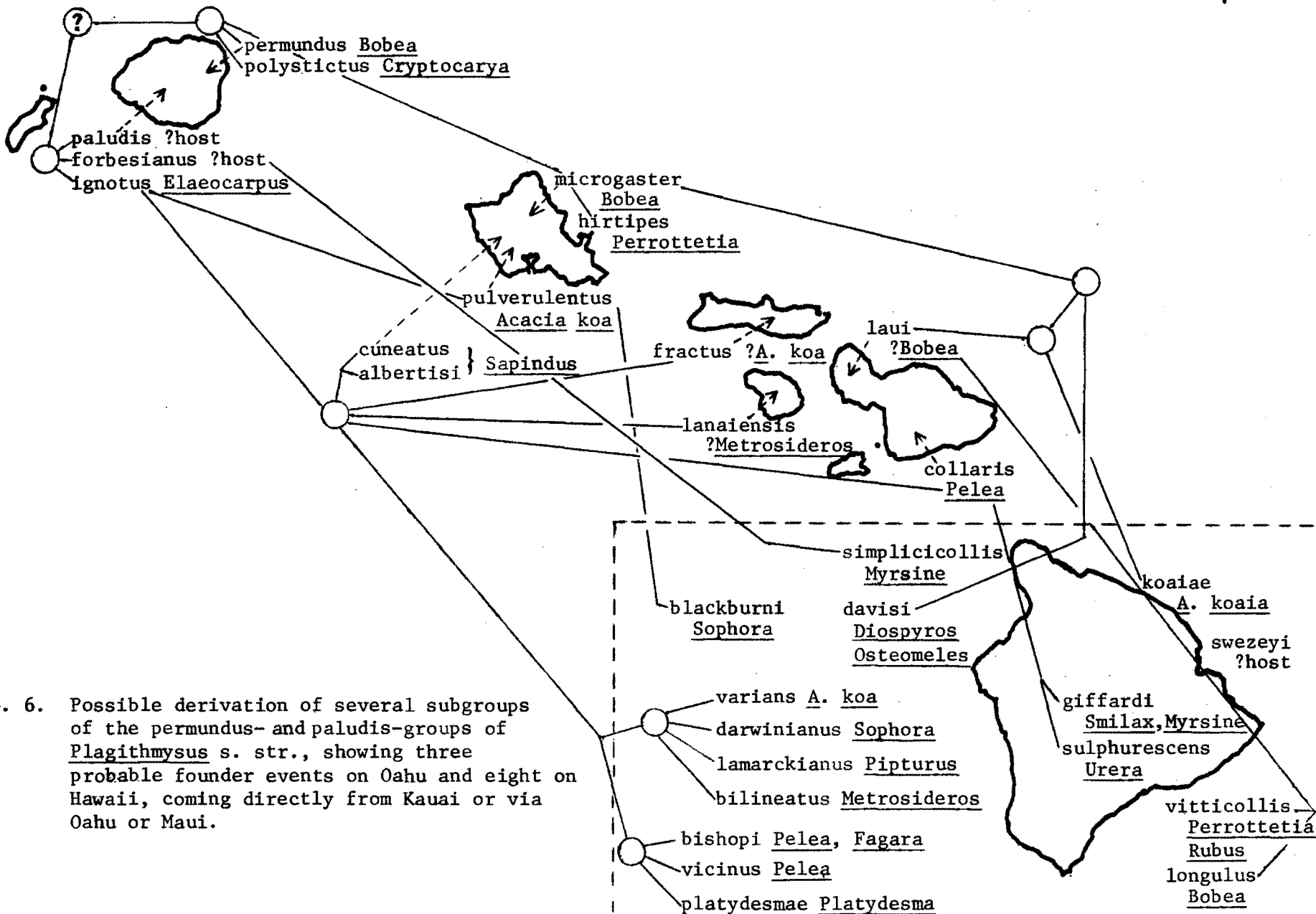


FIG. 6. Possible derivation of several subgroups of the permundus- and paludis-groups of Plagithmysus s. str., showing three probable founder events on Oahu and eight on Hawaii, coming directly from Kauai or via Oahu or Maui.

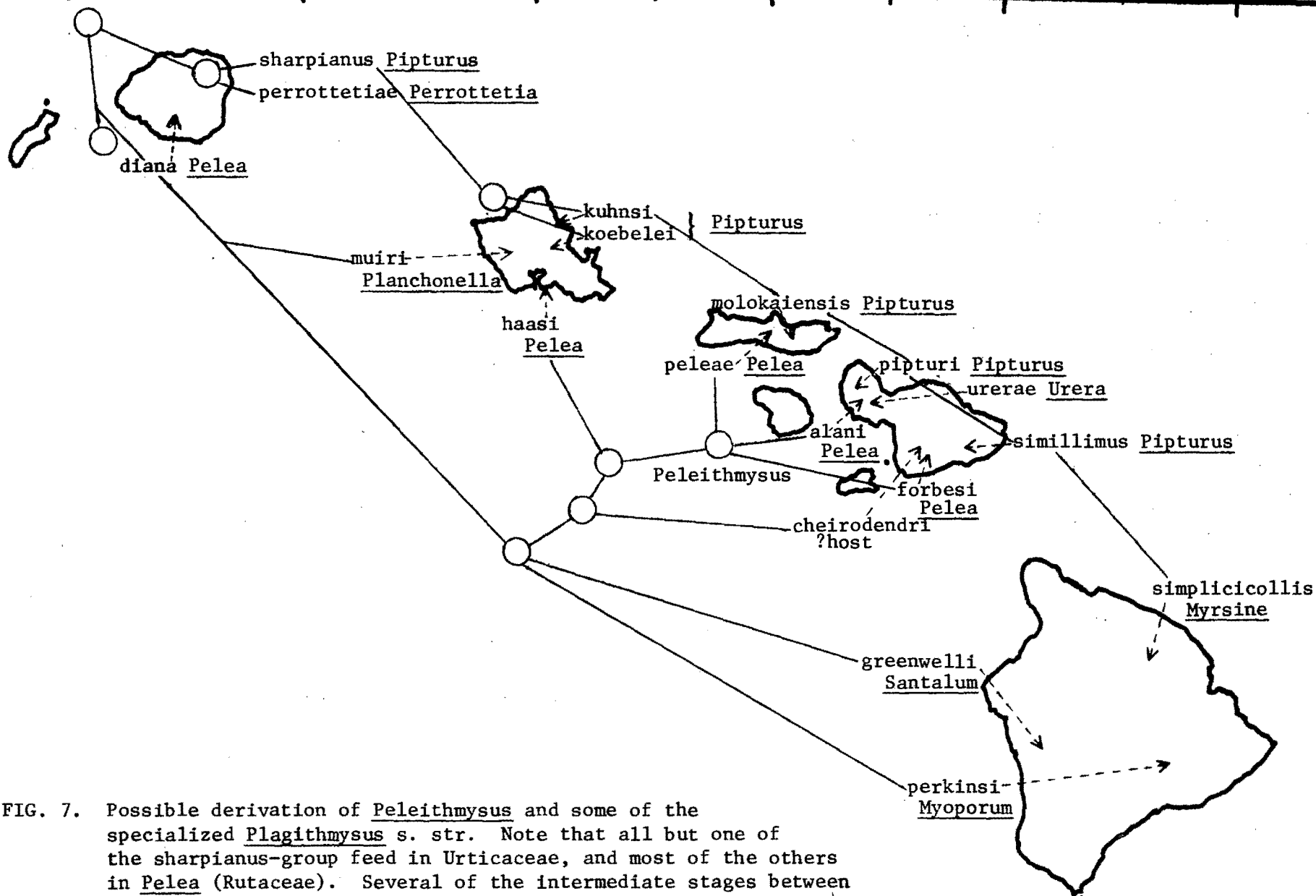


FIG. 7. Possible derivation of Peleithmysus and some of the specialized Plagithmysus s. str. Note that all but one of the sharpianus-group feed in Urticaceae, and most of the others in Pelea (Rutaceae). Several of the intermediate stages between the diana ancestor and Peleithmysus to perkinsi are extinct.

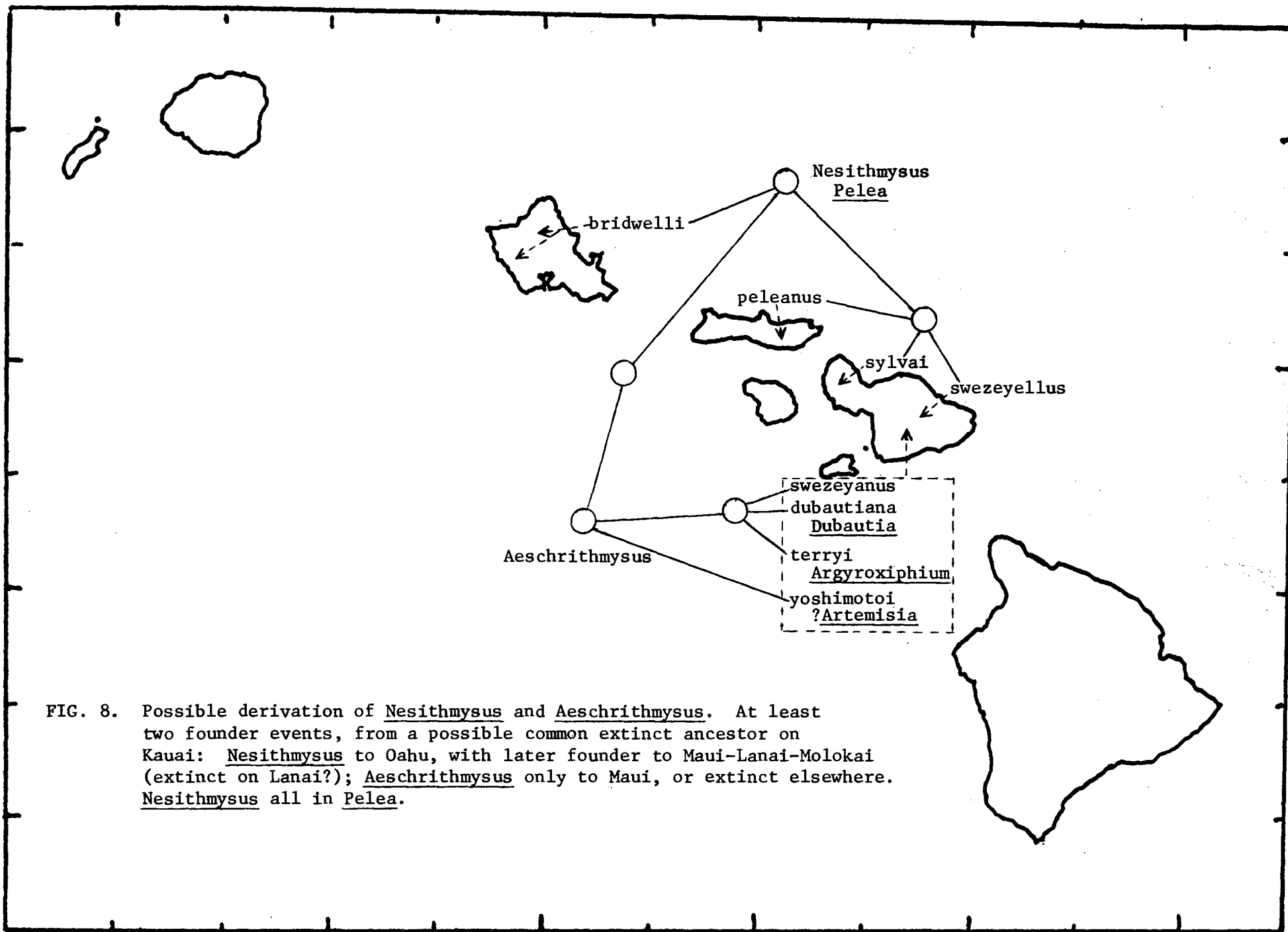


FIG. 8. Possible derivation of Nesithmysus and Aeschrithmysus. At least two founder events, from a possible common extinct ancestor on Kauai: Nesithmysus to Oahu, with later founder to Maui-Lanai-Molokai (extinct on Lanai?); Aeschrithmysus only to Maui, or extinct elsewhere. Nesithmysus all in Pelea.

associated with Pelea and occur in the central islands. Aeschrithmysus, the members that resemble Plagithmysus least in the whole complex, are known only from East Maui, and are all associated with Compositae as far as is known. The species yoshimotoi G. & D. is an intermediate form, and required reducing the genus to a subgenus. It might be associated with Artemisia, but 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 in Dodonaea, Euphorbia, Dubautia, 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 metrosideri G. & D., from Kauai, and bidensae G., from Molokai, are somewhat isolated groups, but perhaps related.

Although in many cases the maps or diagrams (see Appendix) 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. 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 volcano.

There are a number of parallels between the distribution-evolution pictures of the Hawaiian Cerambycidae and the picture-winged Drosophila (Carson, pers. comm.). 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

Besides 17 species introduced to the Hawaiian Islands by man, and two

species (Parandra and a Megopis) 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 Megopis 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 in 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 large genus common 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 five or six 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 weak 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 are associated with the families Leguminosae, Rutaceae, Myrtaceae, Urticaceae, Compositae, Sapindaceae, and Liliaceae, in decreasing order of importance.

The island of Hawaii has the largest number of species of plagithmysines (46), and East Maui the next largest number (28). However, all six subgenera occur on East Maui, and only three on Hawaii. Thus Hawaii has many more species per subgenus, but Maui has more species of beetles per host-plant genus than does Hawaii (13 host genera on East Maui and 28 on Hawaii). There are 19 species in two subgenera on Kauai, and they feed in 16 genera of plants, plus some unrecorded hosts. The island of Nihoa has one 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 one or more species on each island (different in East and West 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 host.

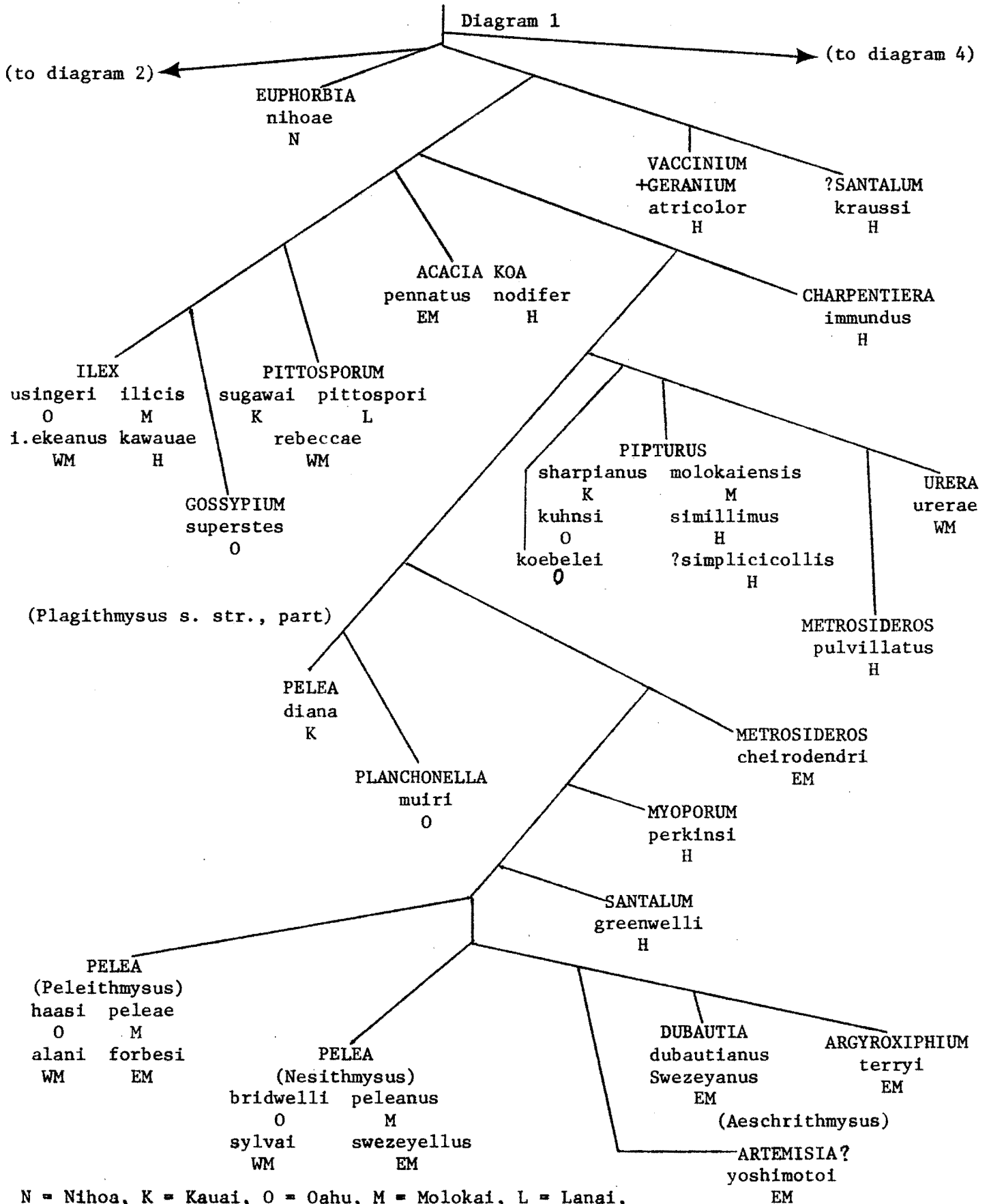
Lack of chromosome information for the plagithmysines, and great morphological variability, makes precise determination of phylogeny difficult. The body form has diverged greatly in different directions, to give the impression of much more than generic differences within the single genus. This is one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

#### ACKNOWLEDGEMENTS

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APPENDIX. Probable 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



Diagram 2

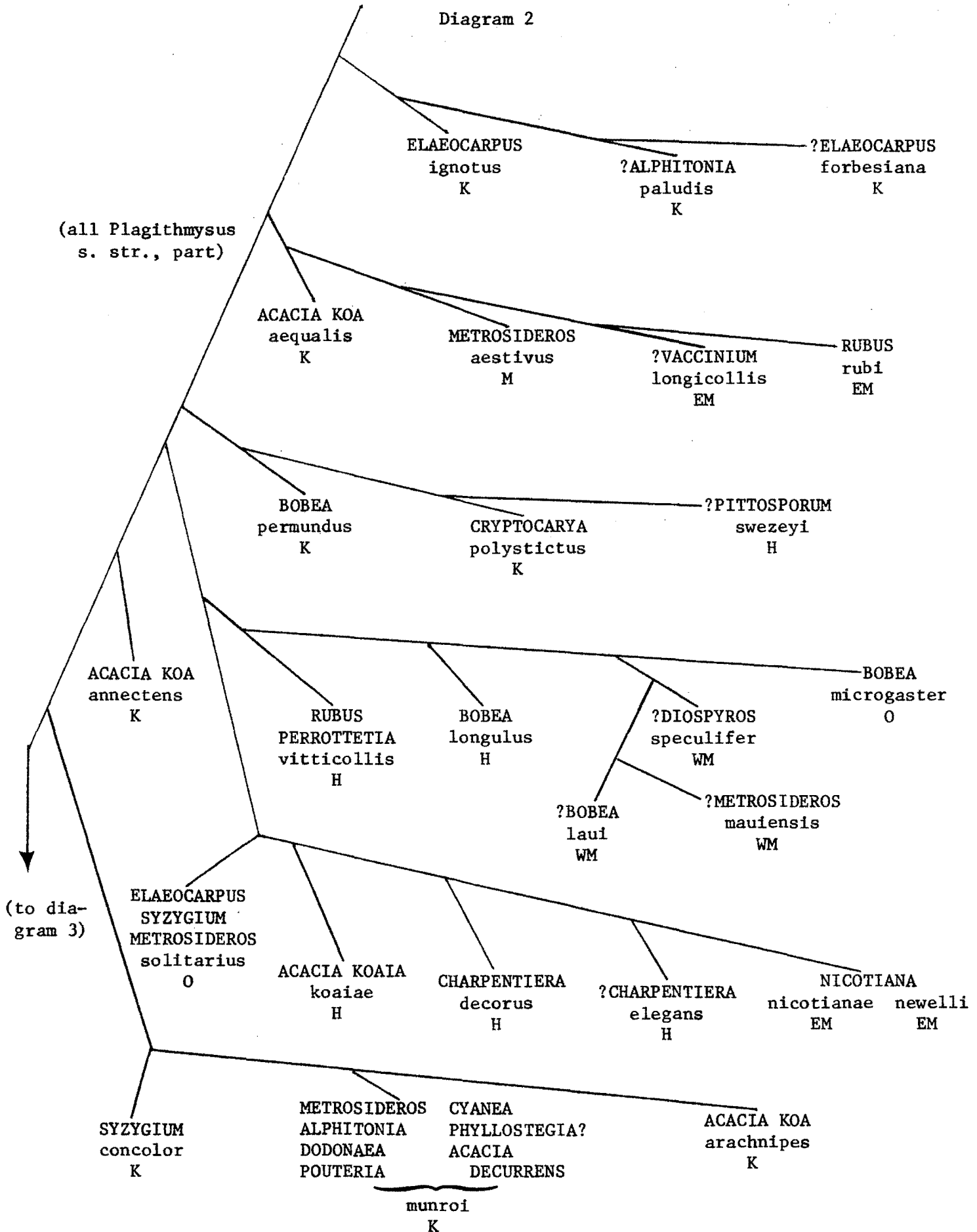
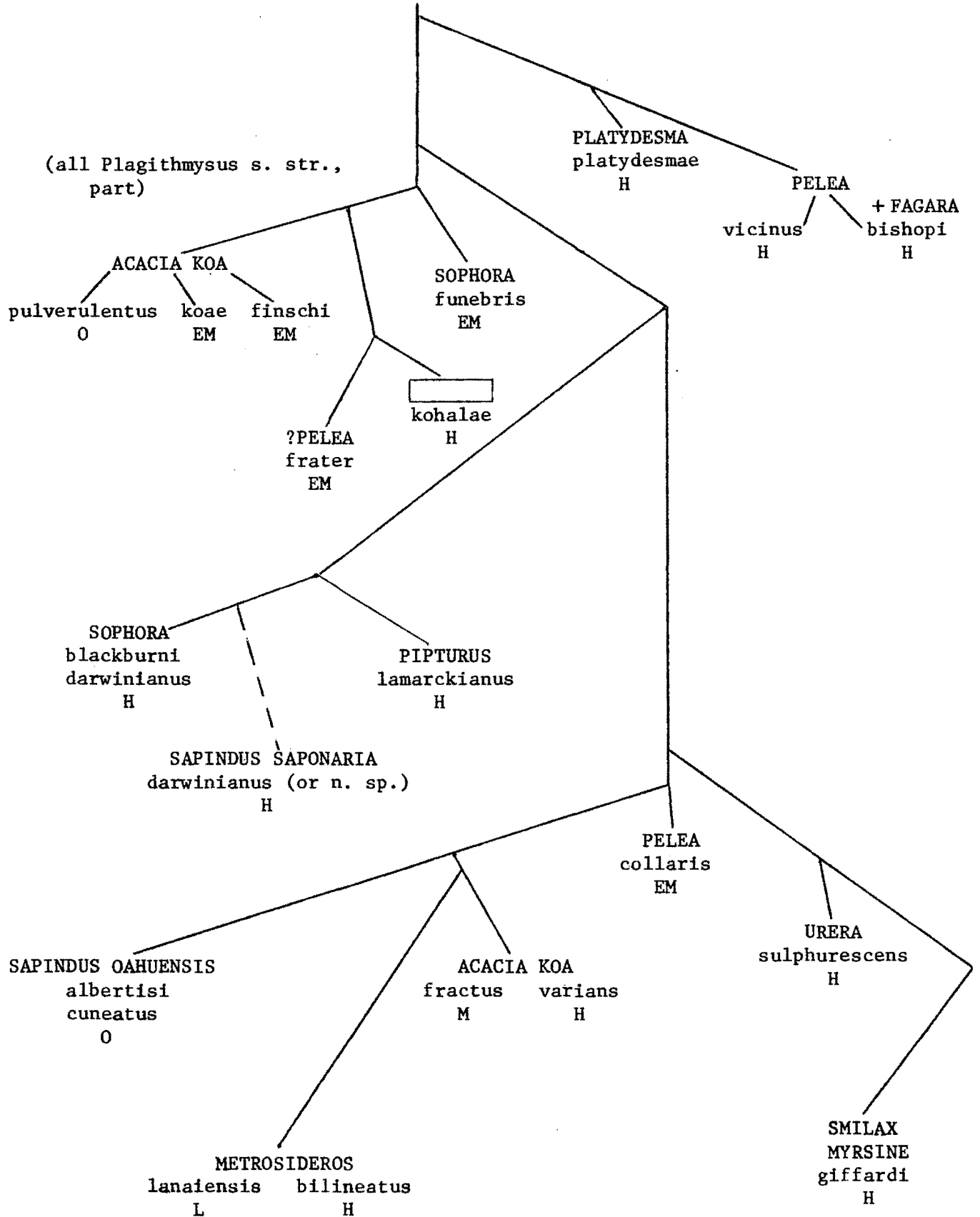
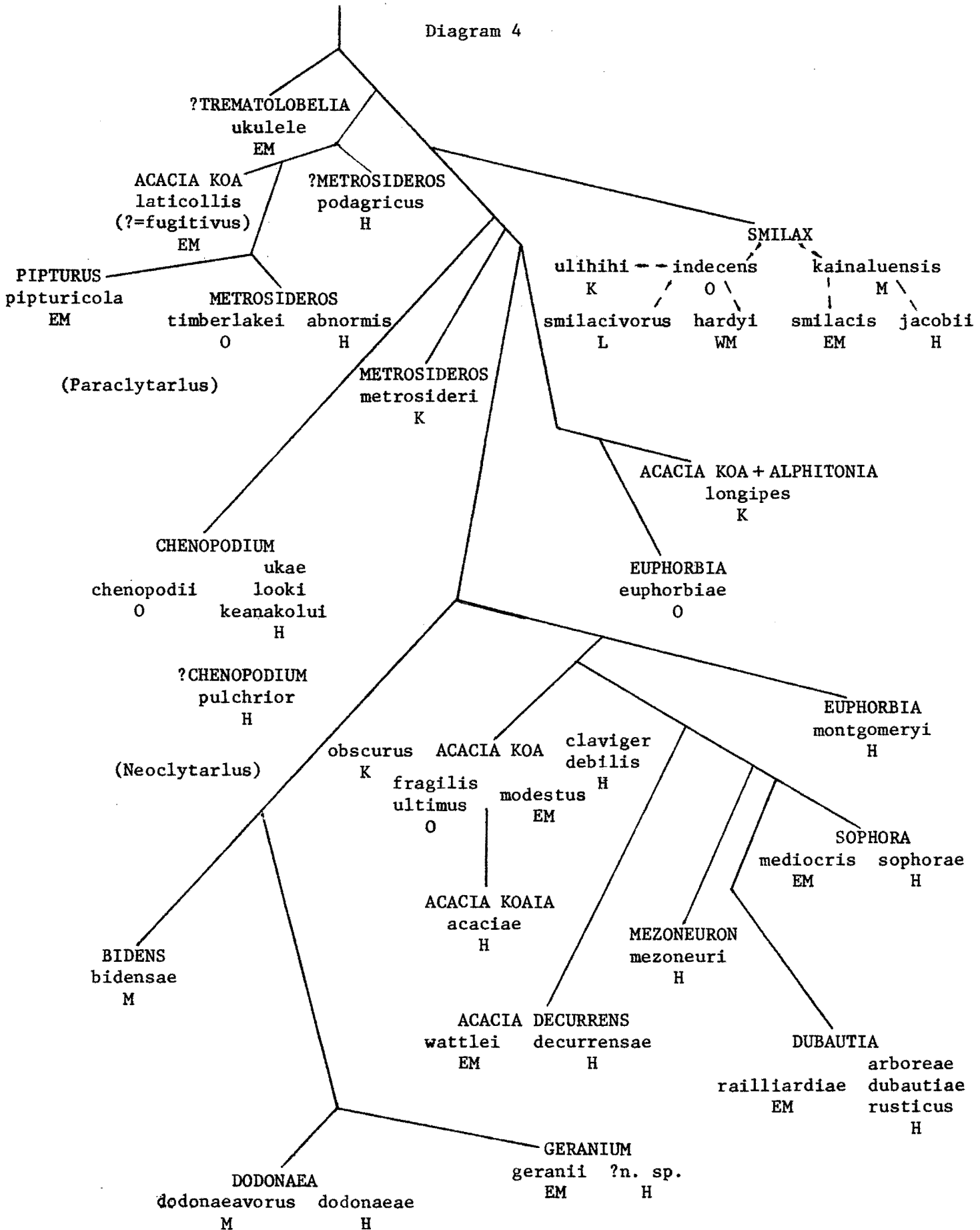


Diagram 3



[ ] = host unknown

Diagram 4



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