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PSOCOPTERA OF THE HAWAIIAN ISLANDS

Part III. The endemic *Ptycta* complex (Psocidae): systematics, distribution, and evolution

Ian W. B. Thornton[1]

Abstract. A complex of 51 psocopteran species of the genus *Ptycta* is reported as endemic to the Hawaiian Islands. Thirty-nine species are newly described and redescriptions provided for 12 others. Eleven species groups are recognized and characterized, and a key to species groups is provided. A cladogram based on apomorphies of species groups is constructed, and their archipelago distribution is related to this. Analysis of the distribution of the complex shows that the Kauai-Oahu strait has been the greatest barrier to distribution of *Ptycta* species in the island group, 2 species groups being confined to Kauai. It is suggested that a section of the genus with a strong synapomorphy, containing 21 species in 5 species groups, arose in recent geological time on the Maui complex of islands; that it derived from a Kauai source; and that it has not been able to reinvade Kauai. Isolating factors for these insects in the present high Hawaiian Islands are reviewed, the geological history of the whole Hawaiian-Emperor chain is discussed, and it is concluded that the *Ptycta* complex may represent the end results of evolutionary processes acting over a period well in excess of the 5 million years since Kauai, the oldest of the present high islands, arose.

This is the 3rd part of a series treating the Psocoptera of the volcanic, oceanic Hawaiian Islands. The fauna is remarkable, comprising some 42 nonendemic species in 20 genera (Thornton 1981c) and over 200 species in 3 endemic complexes: 2 of elipsoid genera (*Kilauella* Enderlein and *Palistreptus* Enderlein) and 1 of the genus *Ptycta* Enderlein (family Psocidae), with which this paper is concerned. Thus, the fauna is of interest not only to specialist entomologists but also to biogeographers, island biologists, and students of island and archipelagic evolution.

Some psocopterans (or psocids) are domestic and stored products insects, and some others occur in nature in leaf litter and on the surfaces of dead leaves, rocks, timber and straw, for example, which support the microepiphytes on which they feed. Most, however, and all the Hawaiian endemic species, are found on trees and shrubs.

I made preliminary collections on Oahu and Hawaii in 1961, collected extensively on Kauai, Oahu, Molokai, Lanai, Maui and Hawaii (Fig. 1) throughout 1963, and made small collections on Oahu, Molokai and Maui in 1982. I have also had at my

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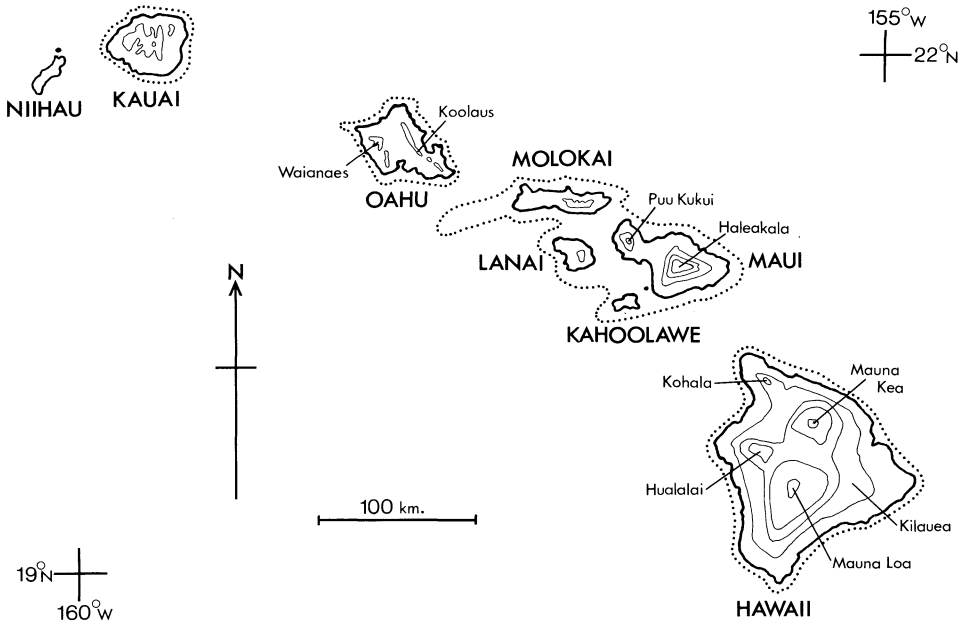

FIG. 1. Hawaiian Is (main or windward group), to show main volcanoes. Contours at 300 m below sea level (dotted), 500 m, 1600 m, 2000 m, and 4000 m elevation.

disposal the considerable collections of other workers (see Thornton 1981c for details). The islands of Niihau and Kahoolawe were not visited and no psocopterans are recorded from them. They are privately owned, relatively low and dry, and now support little native vegetation. The former is largely agricultural and the latter has been a bombing range for several decades. On the remaining islands of the main or windward group, collections were made in the lowlands as well as in the highlands of all volcanic massifs. That on West Molokai (Mauna Loa) is relatively low (400 m), dry, and has little native forest. Lanai is largely cultivated, but a remnant of native vegetation persists on its single ridge, which reaches a height of 1027 m. The other islands are less disturbed, but the destruction of lowland forests as a result of agricultural activities and urbanization is almost complete, and the introduction of exotic and domestic (in some cases feral) mammals and plants, together with exotic birds, insects (notably ants), and molluscs has had a great impact on the endemic biota of the islands, including some upland areas. As a result, in some groups one cannot expect to encounter the endemic biota below 350–500 m elevation.

The low Northwestern Hawaiian Islands, or leeward chain, have not been visited by psocopteran specialists. These rocks, atolls, reefs, and shoals extend for some 2000 km almost in line WNW from Nihoa, W of Kauai, to Kure Atoll (Fig. 336). Collections made from some of these islands by other workers have been studied, and although

no endemic species have been discovered, 6 nonendemic species that also occur on the main group have been reported (Thornton 1981c).

In temperate areas, psocopterans are often common and sometimes abundant in the forests, although with relatively few species represented. The reverse is often the case in the tropics but here, too, they may be locally common. In Hawaii they do not usually reach the densities encountered, for example, in England; they nevertheless make up an important component of the insect fauna, and Zimmerman (1957) regarded them as "among the most numerous of all insects in our forests."

Gagné & Howarth (1981) have recently reported on a survey of canopy arthropods of the dominant trees (*Metrosideros collina* and *Acacia koa*) in the montane tropical rain forest of the Kilauea area (1200–1800 m) on the slopes of Mauna Loa on the island of Hawaii (Fig. 1). They found Psocoptera present on every tree sampled. Moreover, in a transect of Mauna Loa extending from the shore to the *Metrosideros* tree line at 2440 m, Psocoptera occurred at all sampling sites, outranked in absolute numbers all other taxa at most sites above 750 m, and at mid- and high elevations (1200–2440 m) usually outranked all other taxa combined in absolute numbers per sample (Gagné 1979). The sampling method excluded dead branches; this probably precluded the recording of several psocid species (see below).

Gagné & Howarth (1981) categorize Psocoptera as saprophages, and they are labelled detritivores by Gagné (1979). They are also important primary consumers; although many feed largely on lichens and some take the spores of honeydew molds and sooty molds on the surfaces of leaves and bark, many others feed predominantly on unicellular protococcal algae. Temperate psocids, at least, appear to have diversified into lichen feeders on the one hand and *Protococcus* and fungal spore feeders on the other (Broadhead & Thornton 1954, Broadhead & Wapshere 1966, Broadhead 1958). In their studies of tropical psocids, Broadhead & Richards (1980) concluded that 2 of 14 species of East African psocopterans were lichenophilous, while the rest were more generalized feeders; 4 species of *Ptycta* were included in their study, and none was found to feed on lichen, the main components of their gut contents being fungal spores and *Protococcus*, along with pollen grains, and, infrequently, bryophyte rhizomes and a multicellular alga.

Zimmerman (1948a, 1948b) states that in Hawaii ants, green and brown lacewings, dolichopodid flies, and emesine and reduviid bugs are known to prey on psocopterans, and he believes that psocopterans probably were the principal food source of predators such as the lacewings before aphids arrived in the Hawaiian Is. The carnivorous caterpillars of several endemic Hawaiian species of the geometrid genus *Eupithecia* Curtis have been observed catching and feeding on psocids at night (Montgomery 1982).

Baldwin (1953) found that psocids were an important prey item for 3 species of drepanidids (endemic Hawaiian honeycreepers) which, as well as feeding on nectar, feed selectively on insects and spiders. On examining crop and some gizzard contents of 63 specimens of *Loxops virens* (the amakahi), 63 *Himatione sanguinea* (the apapane),

and 32 *Vestiaria coccinea* (the iiwi) collected in the Kilauea area of Hawaii I from 1938 to 1949, Baldwin found psocopteran occurrences in the samples at frequencies of 10%, 41%, and 43%, respectively. S.L. Montgomery (pers. commun.) examined gizzard contents of 11, 41, and 3 individuals, respectively, of the same drepanidid species collected recently in the same area. He found psocopteran remains in 2 *Loxops* and 7 *Himatione* gizzards. I have examined these samples and found all identifiable psocopterans to be endemic species. *Kilauella* species were found in gizzards of both honeycreepers; one of the *Himatione* gizzards contained the remains of at least 6 individuals of 2 species. *Ptycta* remains were identified in samples from *Loxops* (*Ptycta sylvestris* (Perkins) or a species of the *oahuensis* or *haleakalae* groups), and *Himatione* (*Ptycta hawaiiensis* Thornton).

Thus, psocopterans are among the most frequent and numerous arthropods on Hawaiian forest trees and are of considerable ecological importance in being part of a number of food chains. Moreover, the endemic complexes are evidently relatively old components of the biota and are likely to have been of importance in the evolution of Hawaiian forest ecosystems.

The genus *Ptycta* is well represented outside Hawaii, particularly in the tropics and subtropics. In Hawaii, the *Ptycta* complex of species exemplifies the characteristics of endemism noted by Zimmerman (1948a): the species are largely confined to native forests, are usually restricted to single islands, often have very local distributions, and the complex consists of a large number of related forms.

Perkins (1899) assigned the 14 species of Psocidae that he described from the main group to the genus *Psocus* Fabricius; they were later transferred by Enderlein (1913) to *Clematostigma* Enderlein, 2 of them being reduced to varieties of a single species. Later, Enderlein (1920) returned them to *Psocus* but reduced them to 2 species, one with 5, the other with 3 varieties (6 of Perkins' original species were reduced to synonyms). Five years later, Enderlein (1925) erected the genus *Ptycta*, with the Hawaiian species *P. haleakalae* (Perkins) as the type-species, and placed the other Hawaiian species within it along with a species from Java. In his treatment of Hawaiian Psocoptera, Zimmerman (1948b) preferred to retain Perkins' original species of Psocidae and referred them to the genus *Psocus*.

Enderlein's diagnosis of *Ptycta* rested solely on venational characters; in the light of the present examination of the known 51 Hawaiian species, all clearly related to one another and including the type-species, I provide a diagnosis additional to that of Enderlein.

Further diagnosis of Ptycta *Enderlein*

Ventral valve of ♀ gonapophyses at least ½ length dorsal valve; dorsal valve with subapical lobe, or with blunt apex abruptly narrowing subapically, or gradually tapering; outer valve with distal lobe. Distal process of ♀ subgenital plate lacking lateral longitudinal sclerotization near each edge. Median tongue of hypandrium bearing teeth at least along each lateral margin, with or without median basal boss. Phallosome closed anteriorly, symmetrical, narrowing and rounded or angular anteriorly, narrowing posteriorly to apical tine which may be bifid. Epiproct

of ♂ with median basal sclerotized rugose lobe. Paraproct of ♂ with rounded conical process, sometimes rugose, basad of trichobothrial field; process usually not 2× as high as diameter of its base.

Chui & Thornton (1972) assigned 50 recognizable taxa of Hawaiian *Ptycta* to 10 species groups on the basis of multivariate analysis of a large number of characters, and 11 taxa were unassigned. The groups derived from that study have now been examined and characterized, and the unassigned taxa have been related to groups. In this process, a few taxa have been transferred from one group to another on the basis of taxonomically important characters, and 11 groups result.

SPECIES GROUPS OF HAWAIIAN *PTYCTA*

In this section the species groups are characterized, alterations to the groups set out in Table 10 of Chui & Thornton (1972) are noted in parentheses, and taxa previously unassigned to groups by Chui & Thornton are identified by an asterisk, with reasons for their present assignment.

Most of the names used in Chui & Thornton (1972) are *nomina nuda* that are being validated in this present work. The following list correlates the code numbers used for the Hawaiian taxa by Chui & Thornton (1972) in their Table 1 with the validated names for species treated herein: 1, *zimmermani,* n. sp.; 2, *apicantha,* n. sp.; 3, *aaroni mauiensis,* n. subsp.; 4, *peleae,* n. sp.; 5, *aaroni aaroni,* n. sp.; 6, *apicanthoides apicanthoides,* n. sp.; 7, *apicanthoides palligena,* n. subsp.; 8, *diacantha,* n. sp.; 9, *diadela,* n. sp.; 10, *diastema,* n. sp.; 11, *disclera,* n. sp.; 12, *iaoensis,* n. sp.; 13, *dicrosa,* n. sp.; 14, *distinguenda* (Perkins); 15, *drepana drepana,* n. sp., n. subsp.; 16, *drepana drepanoides,* n. subsp.; 17, *episcia,* n. sp.; 18, *frogneri,* n. sp.; 19, *giffardi,* n. sp.; 20, *gynegonia,* n. sp.; 21, *haleakalae haleakalae* (Perkins); 22, *haleakalae hualalai* (Perkins) (see also 50); 23, *hardyi,* n. sp.; 24, *heterogamias* (Perkins), n. comb.; 25, *kaala,* n. sp.; 26, *kauaiensis* (Perkins), n. comb.; 27, *lanaiensis lanaiensis* (Perkins), n. status; 28, *lanaiensis fusca,* n. subsp.; 29, *lanaiensis halawa,* n. subsp.; 30, *lanaiensis persclera,* n. subsp.; 31, *leurothorax,* n. sp.; 32, *lobophora,* n. sp.; 33, *maculifrons,* n. sp.; 34, *microctena,* n. sp.; 35, *microglena,* n. sp.; 36, *molokaiensis* (Perkins), n. comb.; 37, *monticola* (Perkins), n. comb.; 38, *oahuensis* (Perkins), n. comb.; 39, *oligocantha,* n. sp.; 40, *pardena,* n. sp.; 41, *pedina,* n. sp.; 42, *perkinsi,* n. sp.; 43, *persimilis,* n. sp.; 44, *pikeloi,* n. sp.; 45, *placophora,* n. sp.; 46, *pupukea,* n. sp.; 47, *rhina rhina,* n. sp., new subsp. (see also 57); 48, *schisma,* n. sp.; 49, *simulator simulator* (Perkins) (see also 52); 50, *haleakalae konae* (Perkins), n. comb.; 51, *palikea,* n. sp.; 52, *simulator kilauea,* n. subsp.; 53, *stena,* n. sp.; 54, *stenomedia,* n. sp.; 55, *swezeyi,* n. sp.; 56, *sylvestris* (Perkins), n. comb.; 57, *rhina symmetrica,* n. subsp.; 58, *telma,* n. sp.; 59, *unica* (Perkins); 60, *hawaiiensis,* n. sp.; 61, *vittipennis* (Perkins), n. comb.

The placement of a few species into groups is doubtful; for example, *sylvestris* in the *lanaiensis* rather than the *disclera* group, *kaala* in the *schisma* rather than the *lanaiensis* group, and *dicrosa* in the *schisma* rather than the *disclera* group. These placements have been made on the balance of characters. Such cases are few, and

TABLE 1. Distribution of 51 species (61 taxa) of 11 species groups of *Ptycta* in the Hawaiian Is (no. of species in parentheses). See *Discussion* for explanation of Sections A and B. Code numbers next to taxa are those used in Table 1 of Chui & Thornton (1972) for the same taxa (see under *Species Groups of Hawaiian* Ptycta). Taxa named by Perkins are indicated (P.); all other taxa are described for the first time in this paper.

	KAUAI	OAHU	MOLOKAI	LANAI	MAUI	HAWAII
Section A (30) (all islands)						
apicantha group (6) (all islands)						
2 *apicantha*						x
6 *apicanthoides apicanthoides*			x			
7 *apicanthoides palligena*					x	
33 *maculifrons*						x
5 *aaroni aaroni*		x		x		
3 *aaroni mauiensis*					x	
41 *pedina*	x					
4 *peleae*			x			
diacantha group (1) (Oahu)						
8 *diacantha*		x				
haleakalae group (9) (all but Kauai)						
21 *haleakalae haleakalae* (P.)		x	x		x	
22 *haleakalae hualalai* (P.)						x
50 *haleakalae konae* (P.)						x
60 *hawaiiensis*						x
34 *microctena*					x	
35 *microglena*		x		x		
51 *palikea*		x				
49 *simulator simulator* (P.)					x	
52 *simulator kilauea*						x
53 *stena*		x	x			
54 *stenomedia*						x
59 *unica* (P.)					x	
kauaienses group (8) (Kauai)						
26 *kauaiensis* (P.)	x					
10 *diastema*	x					
20 *gynegonia*	x					
37 *monticola* (P.)	x					
43 *persimilis*	x					
45 *placophora*	x					
58 *telma*	x					
1 *zimmermani*	x					
oahuensis group (5) (all islands)						
38 *oahuensis* (P.)		x				
14 *distinguenda* (P.)			x	x	x	x
31 *leurothorax*	x					
32 *lobophora*						x
36 *molokaiensis* (P.)			x		x	
vittipennis group (1) (Kauai)						
61 *vittipennis* (P.)	x					
Section B (21) (all but Kauai)						
disclera group (4) (Molokai, Maui, Hawaii)						
11 *disclera*			x		x	
12 *iaoensis*					x	
40 *pardena*						x
55 *swezeyi*					x	
diadela group (3) (Oahu, Molokai)						

TABLE 1. Continued.

	KAUAI	OAHU	MOLOKAI	LANAI	MAUI	HAWAII
9 *diadela*		x				
17 *episcia*		x				
44 *pikeloi*			x			
frogneri group (5) (Molokai, Lanai, Maui, Hawaii)						
18 *frogneri*					x	
15 *drepana drepana*			x		x	
16 *drepana drepanoides*				x		
19 *giffardi*			x	x		
23 *hardyi*						x
42 *perkinsi*					x	
lanaiensis group (3) (all but Kauai)						
27 *lanaiensis lanaiensis* (P.)				x		
28 *lanaiensis fusca*			x			
29 *lanaiensis halawa*			x			
30 *lanaiensis persclera*					x	
24 *heterogamias* (P.)		x				
56 *sylvestris* (P.)						x
schisma group (6) (Oahu, Molokai, Maui)						
48 *schisma*		x				
13 *dicrosa*			x			
25 *kaala*		x				
39 *oligocantha*		x				
46 *pupukea*		x				
47 *rhina rhina*		x				
57 *rhina symmetrica*					x	

the alternative placements would not affect the general points made in this work. The species criterion is explained in the Discussion. All taxa treated in this work are listed in Table 1, which also shows their distributions in the Hawaiian Is.

apicantha group (6 species)

Phallosome tine single; hypandrial tongue symmetrical, teeth confined to margins, with median basal prong; ♂ epiproct lobe single or double; dorsal valve of ♀ gonapophyses distally narrow, tapering; outer valve lobe rather longer than thickness of transverse part of valve; distal process of ♀ subgenital plate short, broad, usually a pair of setae centrally at base; thoracic terga dull; transverse pigmented fascia on ♀ fore wing angled, sometimes broken up, never including basal angle of discoidal cell.

Distribution: KAUAI, OAHU, MOLOKAI, LANAI, MAUI, HAWAII.

Species: apicantha, apicanthoides, maculifrons (from *disclera* group on single phallosome tine), *aaroni, pedina** (character combinations), *peleae.*

diacantha group (1 species)

As *apicantha* group except hypandrium with pair of stout spines at base of tongue, no median basal prong; distal process of ♀ subgenital plate very broad, trapezoid; transverse fascia of ♀ fore wing broad, continuous, includes basal angle of discoidal cell.

Distribution: OAHU.
Species: *diacantha.*

haleakalae group (9 species)

As *apicantha* group except hypandrial tongue long, narrow, asymmetrical, marginal teeth on one side pointed, on other fused, smooth or less sharply pointed, no median basal prong; ♂ epiproct lobe single; outer valve lobe much shorter than thickness of transverse part of valve; ♀ fore wing with small, discrete, rounded pigment patch on vein *m* distal to *rs-m* junction.

Distribution: OAHU, MOLOKAI, LANAI, MAUI, HAWAII.
Species: *haleakalae, hawaiiensis, microctena, microglena, palikea* (from *oahuensis* group on hypandrium, thoracic terga), *simulator, stena, stenomedia, unica.*

kauaiensis group (8 species)

As *apicantha* group except hypandrial teeth in basal ½ of tongue fused, reflected mesad to form pair of lateral carinae; ♂ epiproct lobe double or incipiently so; ♀ fore wing fascia sometimes includes basal angle of discoidal cell.

Distribution: KAUAI.
Species: *kauaiensis, diastema, gynegonia* (♀ only, from *diacantha* group on fore wing), *monticola** (on hypandrium), *persimilis, placophora* (from *diacantha* group on hypandrium), *telma, zimmermani** (on hypandrium).

oahuensis group (5 species)

As *apicantha* group except tip of phallosome tine notched or slightly bulging subapically; no median basal prong on hypandrial tongue, tongue often slightly asymmetrical, ♂ epiproct lobe single; dorsal valve of ♀ gonapophyses with large subapical lobe or narrowing abruptly subapically; outer valve lobe very long, longer than thickness of transverse part of valve; distal process of ♀ subgenital plate very long, usually 1½× as long as broad, no prominent pair of long setae at base; thoracic terga usually glossy; ♀ fore wing transverse fascia usually well marked, continuous, rather more transverse, not including basal angle of discoidal cell, vein *m* with discrete rounded pigment patch distal to *rs-m* junction.

Distribution: KAUAI, OAHU, MOLOKAI, LANAI, MAUI, HAWAII.
Species: *oahuensis, distinguenda, leurothorax, lobophora, molokaiensis* [*distinguenda* group of Chui & Thornton (1972) now merged].

vittipennis group (1 species)

As *apicantha* group except hypandrial tongue asymmetrical, teeth on left and right margins different shape, no median basal prong; ♂ epiproct lobe single; thoracic terga glossy; ♀ fore wing with marginal cloud in apical ½.

Distribution: KAUAI.
Species: *vittipennis** (new group).

disclera group (4 species)

Phallosome tine bifid; hypandrial tongue as broad as long, symmetrical, teeth confined to margins, median basal prong; ♂ epiproct lobe high, narrow, single; dorsal valve of ♀ gonapophyses tapering, unlobed; outer valve lobe no longer than thickness of transverse part of valve; distal process of ♀ subgenital plate about as long as breadth at midlength, trapezoid, a pair of long setae medially at base; thoracic terga dull; ♀ fore wing with transverse fascia.

Distribution: MOLOKAI, MAUI, HAWAII.
Species: *disclera, iaoensis, pardena, swezeyi** (character combinations).

diadela group (3 species)

As *disclera* group except hypandrial tongue long, asymmetrical, teeth of left and right margins differ; dorsal valve of ♀ gonapophyses massive, very abruptly pointed apically, not tapering gradually; outer valve lobe longer than thickness of transverse part of valve; ♀ subgenital plate apical process about 2× as long as broad, parallel-sided; no transverse fascia in ♀ fore wing.

Distribution: OAHU, MOLOKAI.
Species: *diadela, episcia** (on hypandrium), *pikeloi** (character combinations).

frogneri group (5 species)

As *disclera* group except hypandrial tongue long, with or without medial basal prong; ♂ epiproct lobe double; dorsal valve of ♀ gonapophyses narrowing subapically; outer valve lobe usually longer than thickness of transverse part of valve; no transverse fascia in ♀ fore wing.

Distribution: MOLOKAI, LANAI, MAUI, HAWAII.
Species: *frogneri, drepana, giffardi* (from *schisma* group, on ♂ epiproct and hypandrium), *hardyi, perkinsi** (on ♀ genitalia and ♂ epiproct).

lanaiensis group (3 species)

As *disclera* group except hypandrium asymmetrical, teeth on left and right margins different; outer valve of ♀ gonapophyses with lobe about ⅔ as long as thickness of transverse part of valve; distal process of ♀ subgenital plate usually with central small sclerotized flap basally or plate sclerotized at that position; ♀ fore wing transverse fascia acutely angled, broken, pigment streak along basal section vein *m+cu* posteriorly.

Distribution: OAHU, MOLOKAI, LANAI, MAUI, HAWAII.
Species: *lanaiensis, heterogamias** (on subgenital plate), *sylvestris.*

schisma group (6 species)

As *disclera* group except hypandrial tongue often with teeth on surface as well as margins, no medial basal prong; ♀ fore wing transverse fascia acutely angled.

Distribution: OAHU, MOLOKAI, MAUI.
Species: *schisma, dicrosa, kaala** (on hypandrium), *oligocantha, pupukea, rhina.*

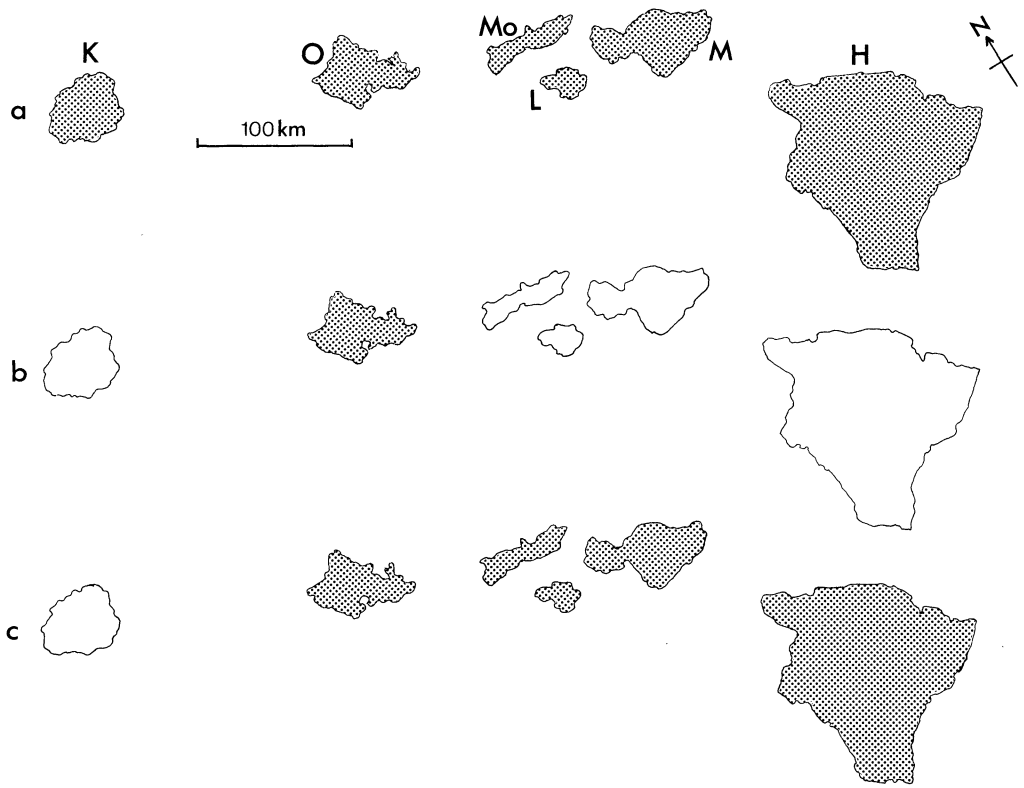

FIG. 2. Archipelago distributions of species groups of *Ptycta*: **a,** *apicantha* (6 species); **b,** *diacantha* (1); **c,** *haleakalae* (9).

KEY TO SPECIES GROUPS OF *Ptycta* IN HAWAII

1. Phallosome apical tine simple 2
   Phallosome apical tine bifid or forked 7
2. Basal marginal teeth of hypandrial tongue reflected mesad and often fused to form carinae ..... **kauaiensis group**
   Basal marginal teeth of hypandrial tongue not reflected mesad, no carinae 3
3. Apical ½ of ♀ fore wing posteriorly with broad fuscous cloud over medial cells ... . **vittipennis group**
   Female fore wing hyaline posteriorly in apical ½ 4
4. Thoracic terga glossy (except *molokaiensis*); dorsal valve of ♀ gonapophyses with subapical lobe or abruptly narrowing subapically ..... **oahuensis group**
   Thoracic terga dull; dorsal valve smoothly tapering distally 5
5. Female fore wing with small, discrete rounded pigment patch on vein *m* distal to *rs-m* junction; marginal teeth on left of hypandrial tongue differ from those on right ..... **haleakalae group**

Female fore wing without discrete pigment patch on vein *m* distal to *rs-m* junction; hypandrial tongue teeth symmetrical 6

6. Transverse fascia of ♀ fore wing broad, includes basal angle of discoidal cell; cubital cell with large distal pigment patch; hypandrial tongue with large isolated spines each side basally ..... **diacantha group**

Transverse fascia of ♀ fore wing variable, never includes basal angle of discoidal cell; cubital cell with separate distal and subdistal patches of pigment; hypandrial tongue lacks large, isolated spines basally ..... **apicantha group**

7. Hypandrial tongue symmetrical 8

Teeth on left and right margins of hypandrial tongue differ 10

8. Cubital cell of ♀ fore wing with separate distal and subdistal pigment patches; hypandrial tongue short, broad, teeth often on surface as well as margins; outer valve of ♀ gonapophyses lobe shorter than ½ thickness of transverse part of valve ... . **schisma group**

Cubital cell of ♀ fore wing with single pigment patch in distal angle; teeth on hypandrial tongue confined to margins; outer valve lobe longer than ⅔ thickness of transverse part of valve 9

9. Fore wing of ♀ with transverse fascia; ♂ epiproct lobe high, single; dorsal valve of ♀ gonapophyses tapering smoothly to apex; outer valve lobe shorter than thickness of transverse part of valve ..... **disclera group**

Fore wing of ♀ lacking transverse fascia; ♂ epiproct lobe double; dorsal valve abruptly narrowing subapically; outer valve lobe longer than thickness of transverse part of valve ..... **frogneri group**

10. Fore wing of ♀ with angled transverse fascia; distal process of ♀ subgenital plate usually with median basal small sclerotized flap, short, broad, trapezoid; dorsal valve of ♀ gonapophyses gradually tapering, slender; hypandrial tongue short, broad .... **lanaiensis group**

Fore wing of ♀ without transverse fascia; distal process of ♀ subgenital plate without flap, long, parallel-sided; dorsal valve massive, abruptly narrowing apically; hypandrial tongue longer than wide ..... **diadela group**

DESCRIPTIONS OF HAWAIIAN SPECIES OF *PTYCTA*

In the following section, collectors' initials are given only on first mention. Where no collector is mentioned, specimens were collected by the author. Under "distribution" the name HAWAII refers to the island of Hawaii. Holotypes and allotypes are placed in the B.P. Bishop Museum, Honolulu (BPBM), paratypes in the Australian Museum, Sydney. The I.O.:D. ratio is the relationship between the interocular distance and the eye diameter as measured by Pearman and explained in Ball (1943).

In the figures accompanying the species descriptions, the scale lines for the fore wings are 1.0 mm, those for the epiproct lobes, phallosome apices and hypandria are 0.05 mm, and those for the subgenital plates, phallosomes and gonapophyses are 0.1 mm, unless otherwise indicated.

apicantha group

This group of 6 fairly plesiomorphic species is represented on all the major islands (Fig. 2) and may be regarded as the closest to the probable ancestral Hawaiian population of *Ptycta*.

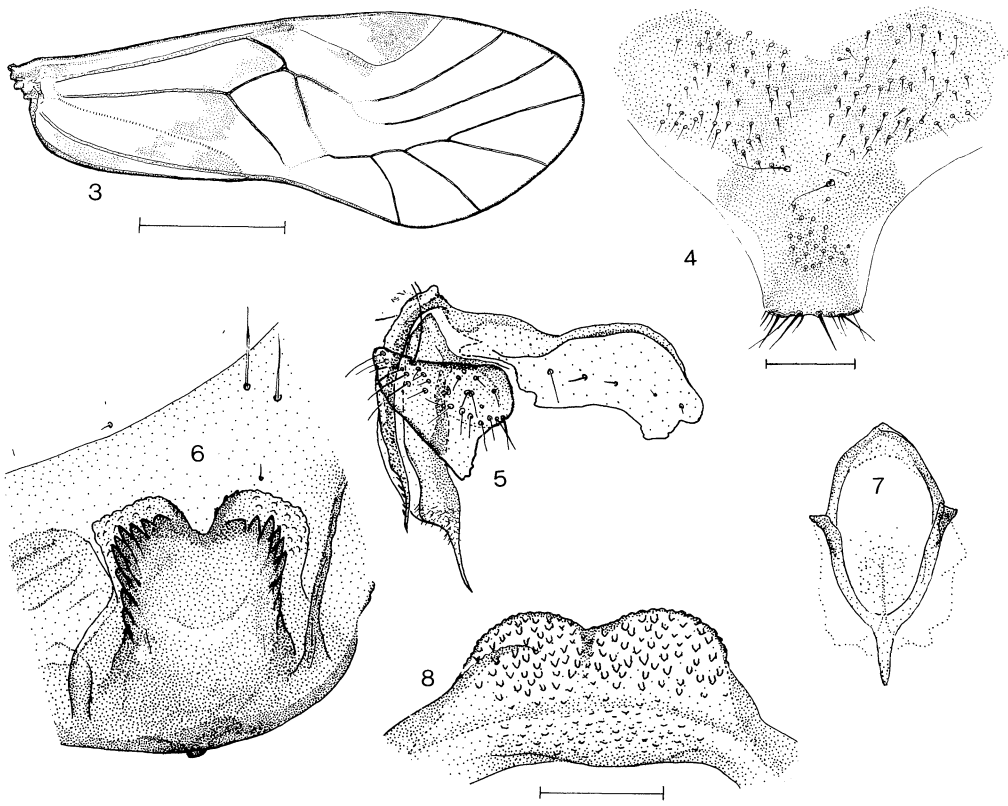

FIG. 3–8. *Ptycta apicantha:* **3,** ♀ fore wing; **4,** subgenital plate; **5,** gonapophyses; **6,** hypandrium; **7,** phallosome; **8,** ♂ epiproct lobe. Fig. 4, 5, 7 and Fig. 6, 8 to common scales.

Ptycta apicantha Thornton, **new species** Fig. 3–8

♀. *Coloration* (freshly killed, in alcohol). Head generally whitish cream, usual vertex markings brown. Gray-brown mark each side of ocellar protuberance, continued as line along frons-vertex suture. Frons with gray-brown median stirrup mark each side and sometimes touching this a dark gray-brown mark along anterior frontal suture. Clypeus with brown parallel striae merging medially in anterior ½, clypeus laterally in anterior ½ without striae. Genae with brown band from orbit to antennal socket; below this a complicated dark gray mark. Eyes black. Maxillary palpi brown, apical segment darker. Antennae brown. Thoracic terga brown, dorsal lobes with cream margins, a cream arrow-shaped mark on mesothoracic antedorsum posteriorly, cream median band between dorsal lobes of meso- and metathorax, scutella cream. Pleura brown. Legs: coxa brown, pale whitish-buff apically; trochanter and femur pale buff, femur pale brown apically; tibia pale brown, darker apically; tarsus brown. Fore wing (Fig. 3) with transverse fascia angled, somewhat interrupted, 2 brown patches in anal cell; area within pterostigma white by reflected light, a brown patch distally, not reaching vertex; vague brown infuscation for a short distance along *rs* and *m* after their point of departure; veins bordering basal ½ of areola postica unpigmented. Hind wing hyaline, very faintly brown in anal cell. Abdomen with dark gray transverse bands along terga, these broader on basal 3 terga and

sometimes fusing in midline and dorsolaterally to produce 3 narrow longitudinal lines. *Morphology.* I.O.:D. = 2.6. Hind wing with 8–11 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 20–21; 2+1. Subgenital plate (Fig. 4) with broad arms and broad distal process, 2 longer setae at base of process. Gonapophyses (Fig. 5): dorsal valve narrowing fairly gradually to apical spine; outer valve with large smoothly tapering lobe. Gonopore plate not well sclerotized, not bilobed anteriorly. A field of 22–25 trichobothria on each paraproct.

♂. *Coloration* (freshly killed, in alcohol). As ♀, except lateral frons marks discrete, not transversely elongate; fore wing transverse fascia lacking, pterostigma brown pigment more extensive, occupying more than ½ pterostigma and reaching vertex. *Morphology.* Eyes large, I.O.: D. = 0.8–1.3. Hind wing with 6–8 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 21–23; 2+1. Hypandrium (Fig. 6) symmetrical, with 6–9 pointed marginal teeth each side of apical tongue, these progressively longer apically; V-shaped hyaline area formed by sclerotized areas at base of tooth-rows, a small smooth median prong at base of tongue. Phallosome tine simple, pointed (Fig. 7). Epiproct anterior lobe fairly high, bilobed, tuberculate (Fig. 8). Paraproct with prominent sclerotized basal boss, a field of 23–25 trichobothria.

Nymph. Recognizable by frontal, clypeal, and genal patterns.

Distribution. HAWAII, common.

Holotype ♂, HAWAII: Kilauea, Kipuka Puaulu (Bird Park), 1210 m, *Sophora,* 24.VI.1963 (I.W.B. Thornton) (BPBM 12,965). Allotype ♀, same data as holotype. 2♂,6♀ paratypes, same data as holotype.

P. apicantha has been taken in January and June 1963, from 450 to 2100 m. It occurs on *Acacia koa, Pipturus, Metrosideros, Myoporum sandwicense, Sophora chrysophylla, Charpentiera obovata, Urea sandwicensis, Juniperus, Datura, Acacia koaea,* mango, *Macadamia, Dodonoeia,* and *Diospyros* and has been taken in the Kilauea area, on the saddle between Mauna Kea and Mauna Loa, in the Kamuela area, at Kawaihai Uka, Halepula, Kona, and Puuwaawaa, and at 2000 m on the SE slope of Mauna Loa. It is one of the commonest species of the genus on the island of Hawaii.

This species is superficially similar, in head and wing markings, to *Ptycta diacantha,* n. sp., but differences in male terminalia are diagnostic and unmistakable.

Ptycta apicanthoides apicanthoides Thornton, **new species** Fig. 9–13

♀. *Coloration* (freshly killed, in alcohol). Differs from *P. apicantha* in the following respects: frons with lateral marks as discrete small rounded patches, not contiguous with anterior suture, gena with gray-brown band about ½ way down; areola postica veins of fore wing (Fig. 9) extensively pigmented, *rs* and *m* after bifurcation without infuscation. *Morphology.* As *P. apicantha.*

♂. *Coloration.* As ♀ but only small vestiges of fore wing transverse fascia [Fig. 10 (from paratype)]. *Morphology.* As *P. apicantha* with following exceptions: eyes relatively small, I.O.: D. = 2.1–2.5; 8 hypandrial marginal teeth (Fig. 11); phallosome and ♂ epiproct as Fig. 12, 13.

Distribution. MOLOKAI, occasional.

Holotype ♂, MOLOKAI: 730 m above Kamiloloa, *Diospyros* in gully, 19.VII.1963 (I.W.B. Thornton) (BPBM 12,966). Allotype ♀, same data as holotype. 3♂ paratypes, MOLOKAI, Kainalu, 27.VII.1927 (E.H. Bryan, Jr); 4♂,1♀ paratypes, same data as holotype.

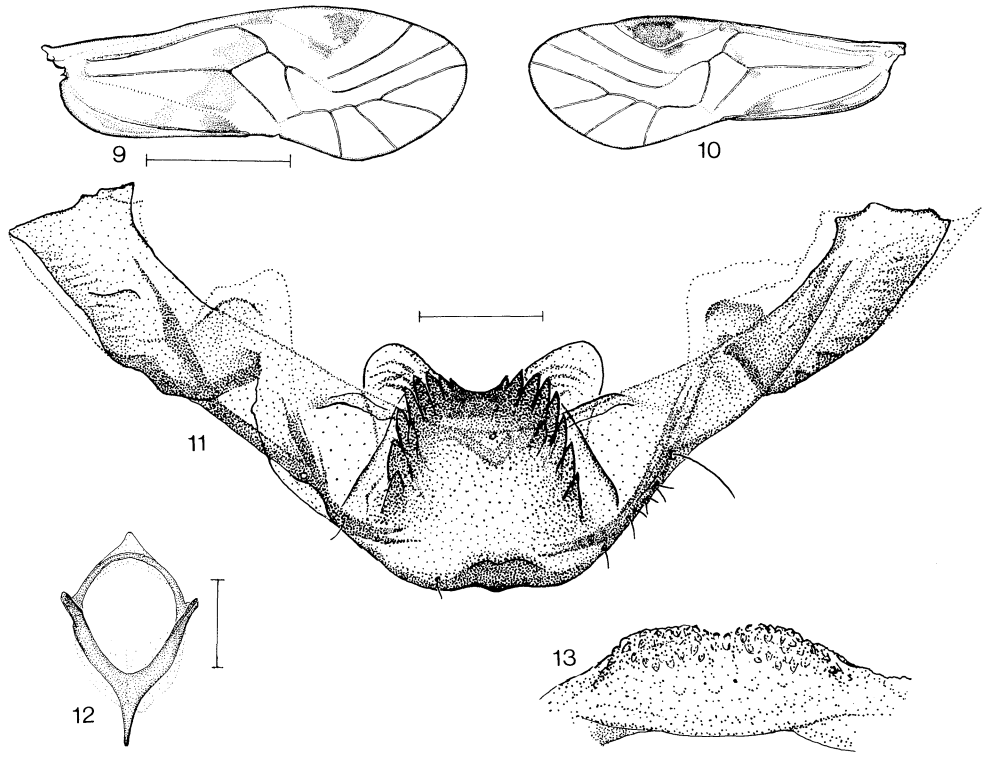

FIG. 9–13. *Ptycta apicanthoides apicanthoides:* **9,** ♀ fore wing; **10,** ♂ fore wing; **11,** hypandrium; **12,** phallosome; **13,** ♂ epiproct lobe. Fig. 9, 10 and Fig. 11, 13 to common scales.

In only 1 of the 3 males collected by Bryan is the head intact, and in this specimen the eyes are somewhat larger (I.O.:D = 1.5) than the Kamiloloa males.

This species is very closely similar to *P. peleae,* n. sp., but differs from specimens of that species, which were found within 4–15 km distance, in head pigmentation and (except the Kainalu specimen) in male eye size. It differs from *P. apicantha* in pattern of frons and gena and in male eye size.

Ptycta apicanthoides palligena Thornton, **new subspecies** Fig. 14–15

♀. Unknown.

♂. *Coloration* (freshly killed, in alcohol). As nominate subspecies except no vestiges of transverse fascia in fore wing (Fig. 14). *Morphology.* As nominate subspecies except 13 hypandrial teeth; anterior lobe of epiproct high, unlobed (Fig. 15).

Distribution. MAUI, rare.

Holotype ♂, MAUI: Olinda, 1200 m, dead branches of *Pinus,* 31.I.1963 (I.W.B. Thornton) (BPBM 12,967).

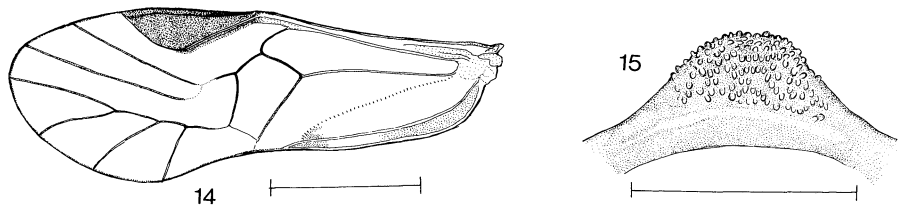

FIG. 14–15. *Ptycta apicanthoides palligena* ♂: **14,** fore wing; **15,** epiproct lobe.

Although represented by but a singleton, the differences from the nominate form are deemed sufficient to warrant subspecific distinction.

Ptycta maculifrons Thornton, **new species** Fig. 16–22

♂. *Coloration* (freshly killed, in alcohol). Vertex cream, usual markings brown. Brown mark each side of ocellar protuberance, continued as line along frons-vertex suture. Frons cream, a median brown spot vaguely defined at edges in place of usual stirrup mark. Clypeus brown, striae barely distinguishable as darker bands. Genae with broad brown band orbit to antennal socket, 2 broad brown bands below this, fusing posteriorly with each other and with antenna-orbit mark so that gena is predominantly brown. Eyes black. Maxillary palpi and antennae wholly brown. Thoracic terga brown, dorsal lobes whitish cream at lateral corners, cream band between dorsal lobes but no arrowhead mark on mesothoracic antedorsum, scutella brown. Pleura brown. Legs: coxa brown, trochanter, and tibia pale brown, tibia darker apically, tarsus dark brown. Fore wing (Fig. 16) with small vague vestige of transverse fascia, pterostigma filled with brown pigment, veins bordering basal ½ of areola postica pigmented. Hind wing hyaline, faint brown line along anterodistal margin. Abdomen brown dorsally, ventrally grayish brown. *Morphology.* Eyes relatively small, I.O.:D. = 2.4. Hind wing with 7 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 22–23; 2+1. Hypandrium symmetrical, 6 pointed teeth along apical margins of apical tongue, progressively longer apically (Fig. 17), V-shaped hyaline area formed by triangular areas of sclerotization at base of tooth-rows each side, a small smooth median prong at base of tongue. Phallosome tine (Fig. 18) simple, pointed (tip broken in type). Epiproct anterior lobe bilobed, tuberculate (Fig. 19). Paraproct with basal boss sclerotized, fairly prominent, smoothly rounded, a field of 25–27 trichobothria.

♀. *Coloration* (freshly killed, in alcohol). Head generally cream, vertex markings brown. Brown mark each side of ocellar protuberance, continued as line along frons-vertex suture. Frons cream, usual brown median stirrup mark. Clypeus with brown striae not forming a darker line medially. Genae with brown band from orbit to antennal socket, otherwise cream. Eyes black. Maxillary palpi pale brown, apical segment brown. Scape, pedicel, and most of basal flagellar segment brown, otherwise antenna light brown. Thorax color as ♂. Legs as ♂, but trochanters, femora, and tibiae cream, not pale brown. Fore wing (Fig. 20) with transverse fascia represented by a few small brown patches, only 1 patch at apex of anal cell. Hind wing as ♂. Abdomen cream, brown transverse bands dorsally and ventrally. *Morphology.* I.O.:D. = 3.3. Hind wing with 9 marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 20; 2+1. Gonapophyses and subgenital plate as Fig. 21, 22.

Distribution. HAWAII, rare.

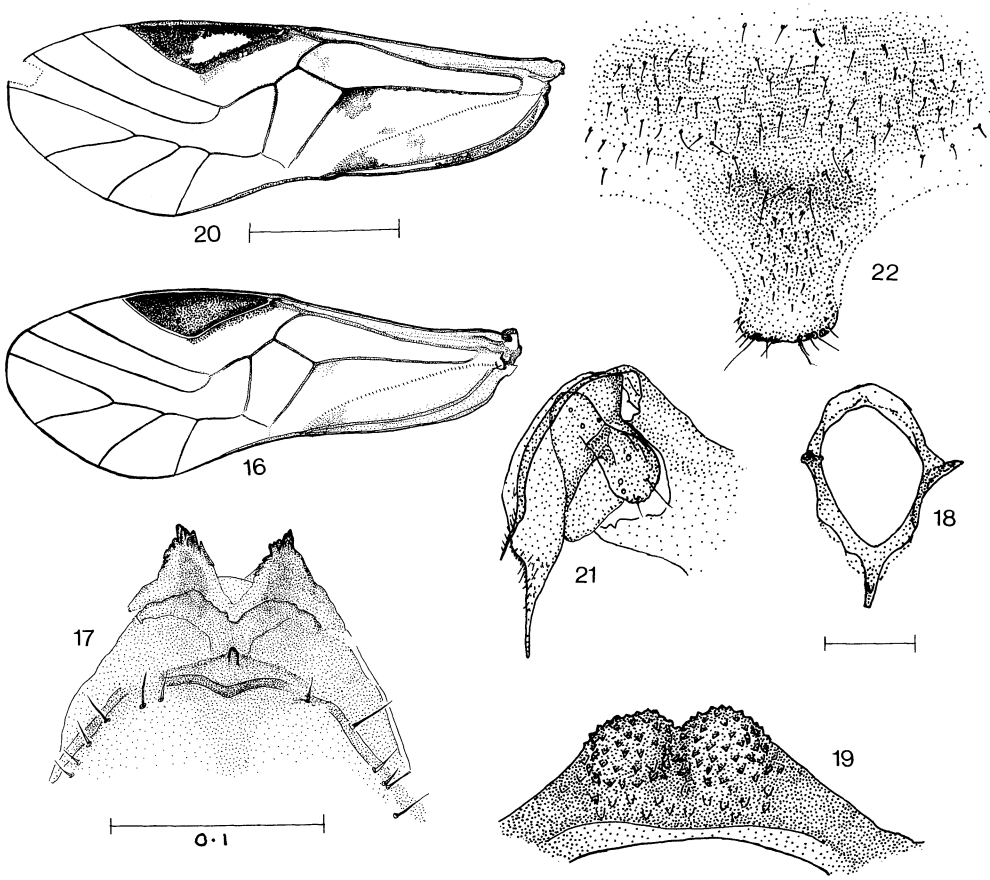

FIG. 16–22. *Ptycta maculifrons:* **16,** ♂ fore wing; **17,** hypandrium (from below); **18,** phallosome; **19,** ♂ epiproct lobe; **20,** ♀ fore wing; **21,** gonapophyses; **22,** subgenital plate. Fig. 18, 21, 22 and Fig. 17, 19 to common scales.

Holotype ♂, HAWAII: Kipuka Ki, Kilauea, 1200 m, 30.I.1963, *Acacia koa* (I.W.B. Thornton) (BPBM 12,968). Allotype ♀, data as holotype. 2♂,1♀ paratypes as holotype.

Taken on the slopes of Mauna Loa at Kipuka Ki (1200 m) and at 2000 m at the head of Mauna Loa truck trail on *Acacia koa* in January 1963. It has been taken together with *P. apicantha* from *Acacia koa* at both localities, although the latter is better represented on other trees.

This species is closely similar in genitalic features to *P. apicantha,* although it differs quite distinctly in head markings and female wing pattern.

Ptycta aaroni aaroni Thornton, **new species** Fig. 23

♀. *Coloration* (freshly killed, in alcohol). As *P. apicantha,* with following exceptions: genal markings always include 2 distinct parallel gray-brown bands on lower ½ of gena; lateral frons

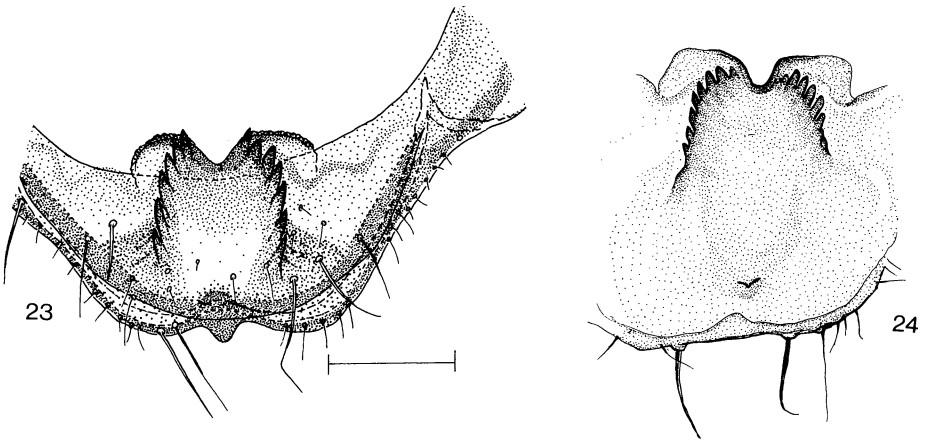

FIG. 23–24. Hypandrium of (**23**) *Ptycta aaroni aaroni* and (**24**) *Ptycta aaroni mauiensis*. Common scale.

marks rounded patches; pigmentation of veins bordering basal part of areola postica variable in extent, *rs* and *m* not infuscate distal to their bifurcation. *Morphology.* As *P. apicantha.*

♂. *Coloration* (freshly killed, in alcohol). As ♀, but fore wing with only remnants of transverse fascia. *Morphology.* As *P. apicantha* with following exceptions: I.O.:D. = 1.0–1.2, eyes fairly large; 6–7 marginal teeth each side hypandrial tongue (Fig. 23); anterior lobe of epiproct not bilobed.

Distribution. OAHU, LANAI, occasional.

Holotype ♂, OAHU: Waialae Iki, 20.I.1924 (E.H. Bryan, Jr) (BPBM 12,969). Allotype ♀, OAHU: Moanalua Golf Course, 15.IX.1957 (A.M. Nadler).

W.M. Giffard collected 2♀ on Lanai on 14.XII.1916.

P. aaroni is closely similar to *P. apicantha* but differs in genal markings and male epiproct lobe, as well as in details of the fore wing.

Ptycta aaroni mauiensis Thornton, **new subspecies** Fig. 24

♀. *Coloration* (freshly killed, in alcohol). As nominate subspecies but 2 parallel genal bands, joined anteriorly and posteriorly by gray-brown marks; lateral frons marks transversely elongate. *Morphology.* As nominate subspecies.

♂. *Coloration* (freshly killed, in alcohol). As ♀. *Morphology.* As nominate subspecies except eyes large (I.O.:D. = 0.9–1.0) and 8 marginal hypandrial teeth, teeth more bluntly pointed (Fig. 24).

Distribution. MAUI, occasional.

Holotype ♂, MAUI: Haiku, *Araucaria* in mango orchard, 12.V.1963 (I.W.B. Thornton) (BPBM 12,970). Allotype ♀, 5♂,5♀ paratypes, data as holotype.

Specimens were also found deep in the Iao Valley, W Maui, on *Cheirodendron*, in September 1963. Both localities are relatively low.

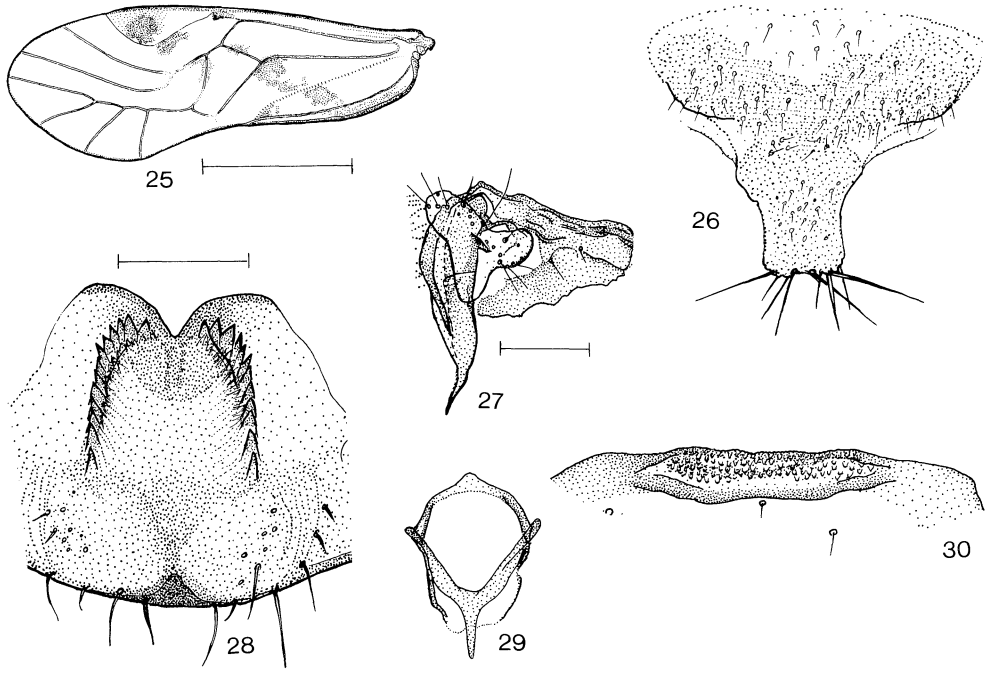

FIG. 25–30. *Ptycta pedina:* **25,** ♀ fore wing; **26,** subgenital plate; **27,** gonapophyses; **28,** hypandrium; **29,** phallosome; **30,** ♂ epiproct lobe. Fig. 26, 27, 29 and Fig. 28, 30 to common scales.

This subspecies is distinguishable from subspecies *aaroni* on head pattern.

Ptycta pedina Thornton, **new species** Fig. 25–30

♀. *Coloration* (freshly killed, in alcohol). Head generally cream, usual vertex markings dark brown. Faint buff spot in each lateral cream area on vertex. Ocelli pale, centripetal margins black. Lateral to ocellar protuberance a buff patch about size of protuberance, continuing as buff line on posterolateral margin of frons. Each side of frons stirrup-shaped mark a short buff line parallel to anterior margin of frons. Clypeus parallel striae dark brown, somewhat closer medially; labrum dark brown. Genae with brown band from orbit to antennal socket, fainter band below this, 3rd parallel faint band near distal margin. Eyes black. Maxillary palpi pale buff, distal segment dark brown. Scape and pedicel brown, basal flagellar segment brown, darkening distally, rest of flagellum dark brown. Thoracic terga brown, median pale buff arrowhead marks on meso- and metathorax, pleura brown. Legs: coxa brown, fading distally; trochanter pale; femur pale, brown distally; tibia pale, faint brown distally, setae dark; tarsus brown. Wings: fore wing (Fig. 25) with sparse dark brown markings forming an interrupted transverse fascia but giving a longitudinal effect; hind wing hyaline, anterodistal margin brown. Abdomen cream with narrow median brown line, laterodorsal and lateral longitudinal brown bands; 9th tergite dark brown. *Morphology.* I.O.:D = 3.5. Fore wing with areola postica almost completely bounded by dark veins, no crossvein stump at apex of pterostigma. Hind wing with 5 fine setae on margin between ends of *rs.* Number of ctenidia on hind tarsal segments: 19;

2+1. Subgenital plate (Fig. 26) with apical process bearing 5 long and 4 shorter setae anteriorly, body of plate broadly U-shaped. Gonapophyses (Fig. 27): outer valve with fairly long, apically rounded lobe. Gonopore plate not well sclerotized. A field of 17–19 trichobothria on each paraproct.

♂. *Coloration* (freshly killed, in alcohol). As ♀. *Morphology.* Eyes prominent, I.O.:D. = 1.0. Antennal flagellum thicker than that of ♀. Hind wing with 6 fine setae on margin between ends of *rs.* Number of ctenidia on hind tarsal segments: 24, 3+1; 23, 2+1. Hypandrium (Fig. 28) symmetrical, with a row of 12–13 squat pointed teeth on each edge of median lobe, 1 or 2 rows of ill-defined teeth within this, median prong at base of lobe, no lateral carinae. Phallosome (Fig. 29) with smooth apical tine. Epiproct with wide low anterior lobe covered with small tubercles (Fig. 30); paraproct with short sharp apical spine, large pointed hook bearing a long seta, short squat basolateral boss, field of 24 trichobothria.

Distribution. KAUAI, frequent.

Holotype ♂, KAUAI: Waimea Canyon Lookout, 1035 m, *Acacia koa,* 27.VII.1963 (I.W.B. Thornton) (BPBM 12,971). Allotype ♀, KAUAI: Kokee telephone track, 800 m, *A. koa,* 27.VII.1963 (I.W.B. Thornton). 9♀,4♂ paratypes, same data as allotype.

Like *P. placophora,* n. sp., this species occurs on Kauai throughout the *Acacia koa* forest W of Waimea Canyon, from 600 m to the Kokee plateau. Also like *P. placophora,* n. sp., it has been taken in the lowlands, at 150 m on the Na Pali Coast (*Metrosideros*), and below 150 m near Makaweli by N.L.H. Krauss. Material examined also includes specimens of both sexes from the Na Pali Kona Forest Reserve and Kalalau Lookout collected by E.L. Mockford. It has been taken in January, April, July, August, and November.

The vertex marks lateral to the ocellar protuberance, small wings, female fore wing pattern, and very low male epiproct lobe serve to distinguish this species, without dissection, from others of the species-group. *P. pedina* is easily distinguished from members of the *kauaiensis* group on genitalic characters. There is some variation among the specimens examined in the short buff frons marks, which may or may not touch the median stirrup mark, and in the hind wing pattern, which sometimes includes a faint cloud in the posterior angle of the anal cell.

Ptycta peleae Thornton, **new species** Fig. 31–33

♀. *Coloration* (freshly killed, in alcohol). As *P. aaroni* except transverse fascia of fore wing (Fig. 31) rather more extensive. *Morphology.* As *P. aaroni.*

♂. *Coloration* (freshly killed, in alcohol). As *P. aaroni. Morphology.* As *P. aaroni* (Fig. 32) except eyes relatively small (I.O.:D. = 1.5–2.0), and epiproct lobe not incipiently divided (Fig. 33).

Distribution. MOLOKAI, rare.

Holotype ♂, MOLOKAI: Halawa Val, N ridge, nr Kepookoholaa, *Pelea,* VII.1963 (I.W.B. Thornton) (BPBM 12,972). Allotype ♀, and 2♂,2♀ paratypes, same data as holotype.

This species, very similar to *P. aaroni,* may be confined to the area of Halawa Valley of E Molokai. In 1 female the area between the 2 lower genal bands is filled with gray-brown pigment.

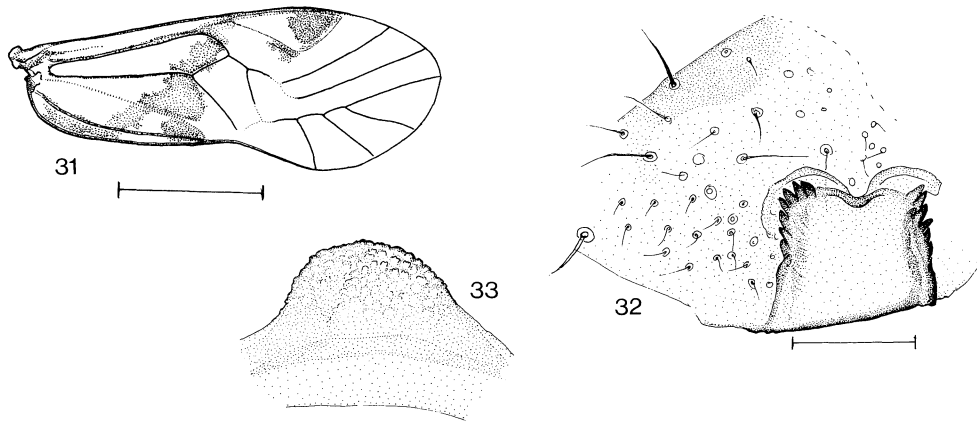

FIG. 31–33. *Ptycta peleae:* **31,** ♀ fore wing; **32,** hypandrium; **33,** ♂ epiproct lobe. Fig. 32, 33 to common scale.

diacantha group

This group consists of 1 species from Oahu. It is closely related to the *apicantha* group, but *diacantha* has distinctive hypandrial ornamentation.

Ptycta diacantha Thornton, **new species** Fig. 34–39

♀. *Coloration* (freshly killed, in alcohol). Vertex cream, usual markings brown, a large brown mark each side of ocellar protuberance, a fine brown line along vertex-frons suture. Frons cream, median stirrup mark brown, a small discrete brown mark each side. Clypeus cream, brown parallel striae merging medially into a broad median band except posteriorly. Genae cream, brown mark from orbit to antennal socket, 2 further brown bands below this. Eyes black. Maxillary palpi pale brown, apical segment brown. Scape, pedicel, and most of basal flagellar segment light brown, distal end of basal flagellar segment and rest of flagellum dark brown. Thoracic terga brown, dorsa bounded medially and laterally with fairly wide cream band, scutella brown. Thoracic pleura brown. Legs: coxa brown, cream distally; trochanter, femur and tibia pale cream, apex of femur and tibia brown; tarsus brown. Wings: fore wing (Fig. 34) with brown transverse fascia slightly angled, and with paler "windows," usually more than 1 brown patch in anal cell, no spot on *m+cu*; hind wing fairly fuscous along anterodistal margin and distal angle of anal cell. Abdomen yellowish cream, with obvious brown transverse bands except ventrally. Apical sclerites brown. *Morphology.* I.O.:D = 3.2. Hind wing with 6 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 22–23; 2+1. Subgenital plate (Fig. 36) T-shaped, angular, with broad apical process narrowing considerably posteriorly, bearing 2 longer setae at its base. Gonapophyses (Fig. 35): outer valve with fairly long lobe. A field of 17–23 trichobothria on each paraproct. Gonopore plate well sclerotized anteriorly.

♂. *Coloration* (freshly killed, in alcohol). As ♀, but much darker: transverse fascia in fore wing almost entirely absent, pterostigma pigmentation more extensive. *Morphology.* I.O.:D. = 2.0, eyes relatively small. Hind wing with 5–6 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 21–23; 2+1. Hypandrium (Fig. 38) symmetrical, bearing

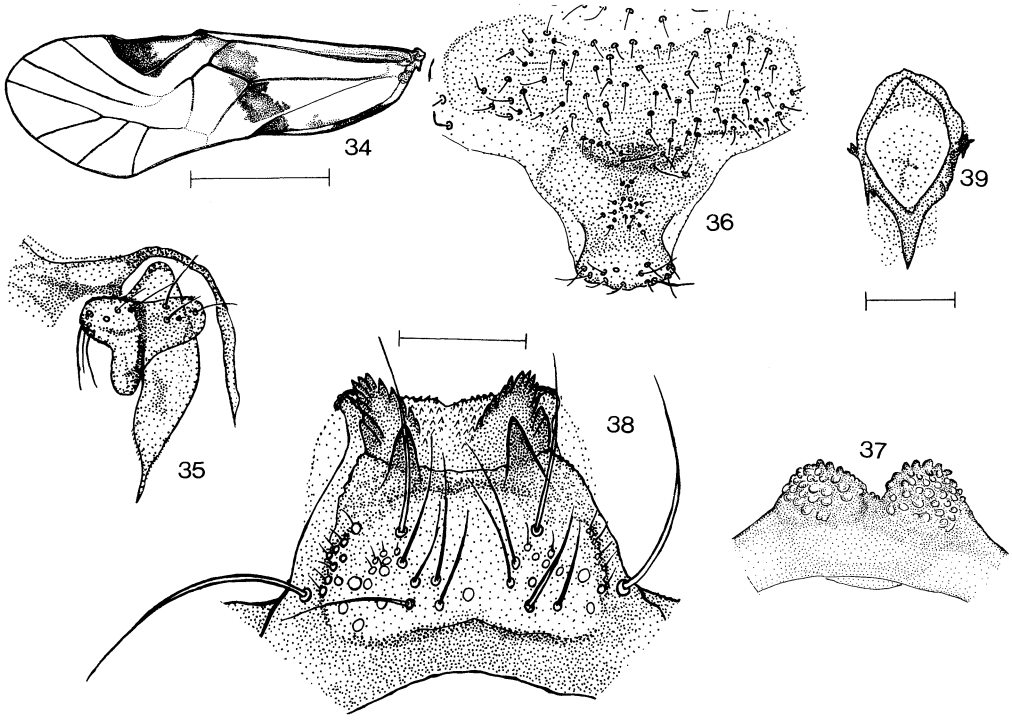

FIG. 34–39. *Ptycta diacantha:* **34,** ♀ fore wing; **35,** gonapophyses; **36,** subgenital plate; **37,** ♂ epiproct lobe; **38,** hypandrium; **39,** phallosome. Fig. 35, 36, 39 and Fig. 37, 38 to common scales.

a large stout spine each side at base of tongue, marginal teeth of tongue basally stout, blunt, progressively smaller, sharper, with finer teeth on surface near margins, no carinae. Phallosome (Fig. 39) with sharp apical tine. Epiproct anterior lobe (Fig. 37) fairly high, distinctly bilobed and tuberculate. A field of 20–23 trichobothria on each paraproct.

Distribution. OAHU, frequent.

Holotype ♂, OAHU: Waianae Distr, 30 m, in water tank, I.1963 (I.W.B. Thornton) (BPBM 12,973). Allotype ♀, same data.

This species occurs on Oahu along the length of the Koolau Range, from Pupukea in the west to Palikea in the east, on *Metrosideros* and *Acacia koa.* In January 1963, 6 specimens were found in a water tank at Waianae, and the species was collected from *Acacia koa* on Mt Tantalus (550 m) in February, from Manoa Valley in May, and from *Metrosideros* on Palikea (580 m) (W Koolau Range) in October of the same year. Giffard collected 1♂ at 400 m on Mt Tantalus in August 1905; Bryan captured 1♂ at Waulaui, on *Acacia koa,* in July 1920; Swezey collected 1♂ at Pupukea, on *A. koa,* in March 1931, and Mockford collected 5♂ in 1957 on the Nuuanu Pali. In 1963, it occurred along with *P. diadela* on *Macadamia* at the Agricultural Experimental Station, Waimanalo.

This species is easily distinguished by the unique hypandrium in the male and the large wide subgenital plate of the female.

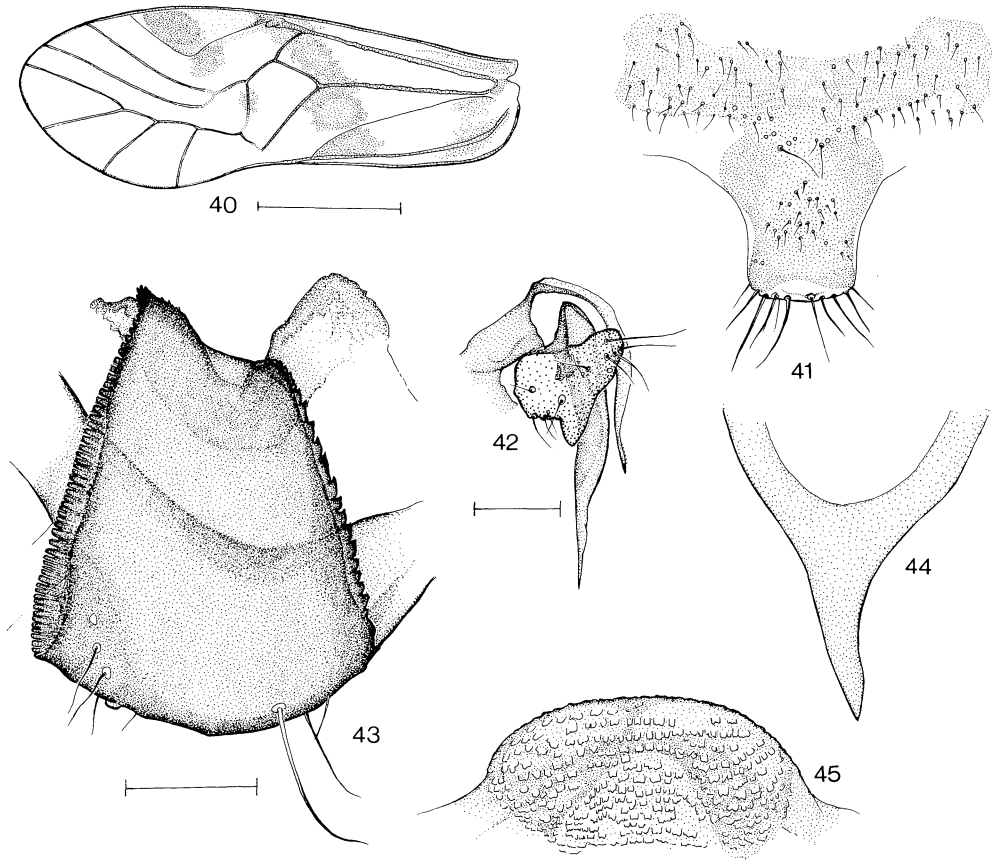

FIG. 40–45. *Ptycta haleakalae haleakalae:* **40,** ♀ fore wing; **41,** subgenital plate; **42,** gonapophyses; **43,** hypandrium; **44,** phallosome tine; **45,** ♂ epiproct lobe. Fig. 41, 42 and Fig. 43–45 to common scales.

haleakalae group

This distinctive group of 9 species has representatives on all the main islands except Kauai (Fig. 2). Four of the species occur on more than 1 island, and in 2 of these, distinct allopatric taxa are recognizable. All species appear to be strictly confined to the highlands. In female wing pattern, the group resembles the *oahuensis* group.

Ptycta haleakalae haleakalae (Perkins) Fig. 40–45

Psocus haleakalae Perkins, 1899: 77.—Enderlein, 1920: 449 (partim).—Zimmerman, 1948b: 245–246.
Clematostigma haleakalae: Enderlein, 1913: 355.
Ptycta haleakalae (Perkins): Enderlein, 1925: 102 (partim).
not *Psocus unicus* Perkins: Enderlein, 1920: 449.

The following redescription is based on an examination of the holotype and allotype of *P. haleakalae* and of other material collected more recently.

♀. *Coloration* (freshly killed, in alcohol). Head with vertex cream, usual markings brown, vague brown mark each side ocellar protuberance, brown line along frons-vertex suture. Median brown stirrup mark on frons, short transverse lines either side discrete. Clypeus with distinct parallel striae. Genae cream, brown mark from orbit to antennal socket. Eyes black. Maxillary palpi pale cream, preapical segment pale brown, apical segment brown. Antenna brown, basal flagellar segment paler basally. Thoracic terga brown, median cream band between dorsal lobes and in mesothorax along sutures of antedorsum, scutella cream. Thoracic pleura brown. Legs: coxa brown; trochanter pale cream; femur pale brown, brown mark subapically and along upper surface; tibia pale brown, dark brown apically; tarsus dark brown. Fore wing (Fig. 40). Abdomen whitish cream, granulated gray-brown markings dorsally. *Morphology.* I.O.:D. = 2.2. Thoracic sclerites dull. Hind wing with 10–15 stout marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 22; 2–4+1. Subgenital plate (Fig. 41) with fairly long apical process. Gonapophyses (Fig. 42): dorsal valve smoothly pointed; outer valve with fairly small posterior lobe. A field of 26–32 trichobothria (type 26) on each paraproct.

♂. *Coloration* (freshly killed, in alcohol). As ♀, pterostigma pigment more extensive. *Morphology.* Eyes small, I.O.:D. = 2.2–3.0. Antennae with setae on basal flagellar segment porrect. Thoracic sclerites as ♀. Hind wing with 7–8 stout marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 22–25; 3+1. Hypandrium (Fig. 43) asymmetrical, right marginal teeth large, pointed, left marginal teeth close-set, with flat tips; no median basal tooth. Phallosome with single apical tine (Fig. 44). Epiproct with anterior lobe not perceptibly bilobed (Fig. 45), beset with complex tubercles; a field of 20–30 trichobothria on each paraproct.

Distribution. OAHU, MOLOKAI, MAUI, occasional.

Specimens, other than types, on which further description based. 1♂,1♀, MOLOKAI: lee side summit Puu Kole Kole, 1200 m, *Juniperus,* 18.VII.1963.

On Oahu this subspecies was collected at Pupukea on *Metrosideros* in February 1963, and at Haleauau (300 m, S Waianae Range) on *Metrosideros* in December 1928 by Swezey. On Molokai it was collected in 1963 at Puu Kole Kole (1200 m) on *Metrosideros* and *Juniperus* in July; at 600 m in Kainalu Gulch in April; and at Puu Ha Ha (600–900 m), Kamoku Gulch (900 m), the hills near Hanalilolilo (1200 m) and in the hills (450–600 m) above Halawa Valley in July on *Metrosideros.* On Maui *P. haleakalae* was taken at Ukulele in July 1919, as well as at 1500 m on Haleakala by R.C.L. Perkins.

As pointed out by Perkins, this species differs from *P. simulator* only in male eye size and in the lack of a spot ½ way along *m+cu* in the fore wing. The 2 species are closely similar in genitalic characters. Specimens from Oahu occasionally show a second genal band, and have a suggestion of fusion of clypeal striae medially. Also, the Oahu specimens have a rather longer lateral transverse line on the frons.

I support Zimmerman's rejection of Enderlein's (1920) synonymy of *unicus* with *haleakalae*; the fore wings differ markedly in pattern and shape.

Ptycta haleakalae hualalai (Perkins), **revised combination** Fig. 46

Psocus hualalai Perkins, 1899: 79.—Zimmerman, 1948b: 247.
Clematostigma hualalai (Perkins): Enderlein, 1913: 355.
Psocus haleakalae var. *hualalai* Perkins: Enderlein, 1920: 451 (partim).
Pycta haleakalae (Perkins): Enderlein, 1925: 102 (partim).
not *Psocus simulator* Perkins: Enderlein, 1920: 451.

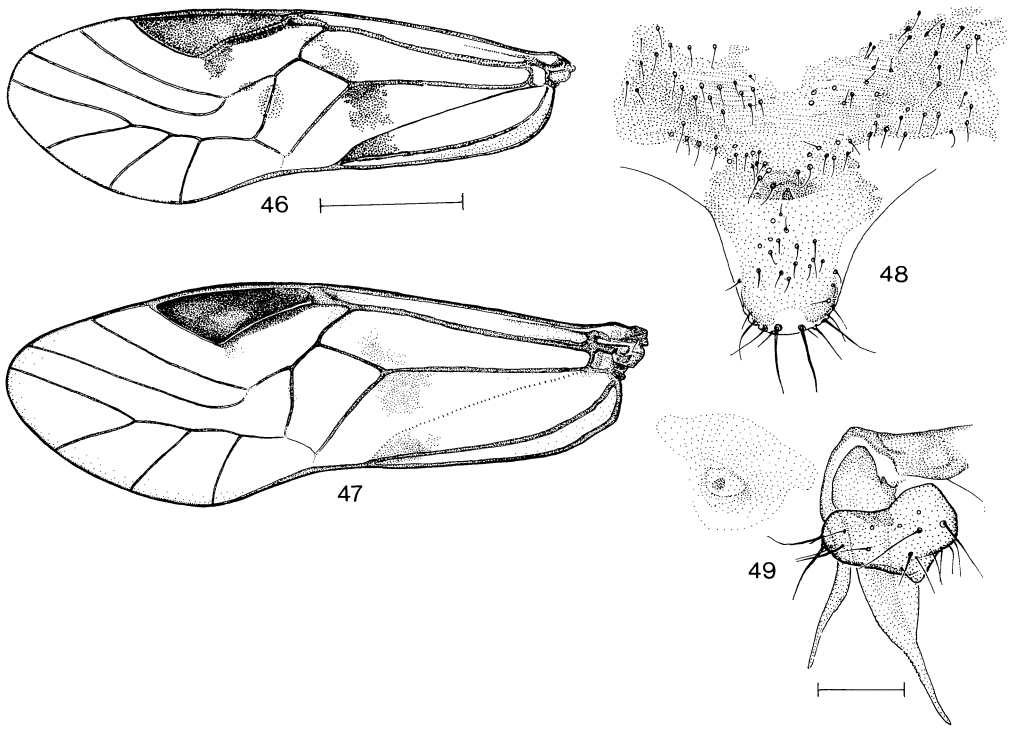

FIG. 46–49. **46,** *Ptycta haleakalae hualalai,* ♀ fore wing. **47–49,** *Ptycta hawaiiensis:* **47,** ♀ fore wing; **48,** subgenital plate; **49,** gonapophyses. Fig. 46, 47 and Fig. 48, 49 to common scales.

This subspecies differs from the nominate form in the less conspicuous wing markings (Fig. 46), as described by Perkins and figured by Zimmerman, and in having 2× as broad, more closely set teeth on the left margin of the hypandrial tongue. The number of ctenidia on the hind tarsal segments (19–20; 3+1) is less than in subspecies *haleakalae,* but the number of hind wing setae and trichobothria fall within the range exhibited by that subspecies. The male eyes (I.O.:D. = 2.0–3.6) are usually smaller.

Distribution. HAWAII, frequent.

Perkins' records are from 2440 m on Mt Hualalai, Hawaii, but the form has also been taken on *Myoporum* and *Pittosporum* in the saddle between Mauna Loa and Mauna Kea, 1800–2000 m, November 1961 and June 1963. A single ♂ collected at Nauhi Gulch (1500–1800 m), Mauna Kea, by Swezey and F.X. Williams, and labelled *sylvestris,* has rather large eyes (I.O.:D. = 2.0). Apart from this record, *P. haleakalae hualalai* seems to be confined to the west-central part of Hawaii I between Mauna Loa and Mauna Kea.

Ptycta haleakalae konae (Perkins), **revised status**

Psocus konae Perkins, 1899: 79.—Zimmerman, 1948b: 247.—Davis, 1953: 85.
Clematostigma konae (Perkins): Enderlein, 1913: 355.

Pycta haleakalae (Perkins): Enderlein, 1925: 102 (partim).
not *Psocus haleakalae* var. *molokaiensis* Perkins: Enderlein, 1920: 451.

♀. Unknown.

♂. Differs from the nominate form in the following respects: transverse fascia in fore wing much interrupted, no *m+cu* mark; hypandrial tongue rather narrow; I.O.:D. = 1.5; head pattern more distinct.

Distribution. HAWAII, rare.

Ptycta hawaiiensis Thornton, **new species** Fig. 47–49

Differs from *P. unica* in the following.

♀. *Coloration* (freshly killed, in alcohol). Vertex brown posteriorly, markings dark brown. Frons with a diffuse gray mark each side of and contiguous with median stirrup mark. Fore wing (Fig. 47) transverse fascia incomplete, often with faint infuscation around margin. Thoracic scutella brown. Abdomen with uniform gray-brown pigmentation. *Morphology.* I.O.:D. = 3.2. Number of ctenidia on hind tarsal segments: 27; 3+1. Fore wing shorter and broader than that of *P. unica.* Subgenital plate (Fig. 48). 3rd valvula of gonapophyses (Fig. 49) with small ill-defined lobe.

♂. *Coloration* (freshly killed, in alcohol). As ♀, but frons almost wholly dark brown, a small paler area each side anterolaterally, stirrup mark entirely obliterated; fore wing with transverse fascia entirely lacking, pterostigma almost entirely filled with pigment. *Morphology.* I.O.:D. = 2.2. Hind wing with 8 stout marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 21; 3+1. Hypandrial marginal teeth similar to those of *P. unica,* but slightly wider on both sides. A field of 29 trichobothria on each paraproct.

Distribution. HAWAII, occasional.

Holotype ♂, HAWAII: Kilauea area, Kipuka Ki, *Metrosideros* and *Acacia koa* collection, 1200 m, I.1963 (I.W.B. Thornton) (BPBM 12,974). Allotype ♀, HAWAII: Kilauea, Kipuka Puaulu, *Acacia koa,* VI.1963. 1♀ paratype, data as holotype.

I have identified a fore wing in the gizzard of an endemic drepanidid (*Himatione sanguinea,* the Apapane) from Volcano National Park, Hawaii I, as being of this species. Like *unica,* it is unusual in this group in lacking a pigment spot on vein *m* of the fore wing distal to its bifurcation from *rs.*

Ptycta microctena Thornton, **new species** Fig. 50–59

♀. *Coloration* (after ca. 40 years storage). Head generally cream, vertex markings brown. Brown median stirrup-mark on frons. Genae cream, brown band from orbit to antennal socket. Clypeus with distinct brown parallel striae, not merging medially. Maxillary palpi pale brown, apical segment brown. Antennae brown. Thoracic terga brown, dorsal lobes with cream borders, these wider posteriorly, cream median line between lobes, mesothoracic antedorsum with cream arrowhead mark, scutella brown. Pleura brown. Legs: coxa brown; trochanter pale brown, brown on outer surface; tibia pale brown, brown apically; tarsus brown. Fore wing (Fig. 50) with brown transverse fascia, a large spot ½ way along *m+cu* fused with fascia, single brown patch in cell *An* apically; a large spot on *m* shortly beyond its departure from *rs*; areola postica veins not largely hyaline basally; brown patch in pterostigma large, extending beyond vertex. Hind wing with brown smokiness in costal cell, along anterodistal margin, and in cell *An* apically. Abdominal color not discernible. *Morphology.* I.O.:D. = 3.5–4.0. Hind wing with

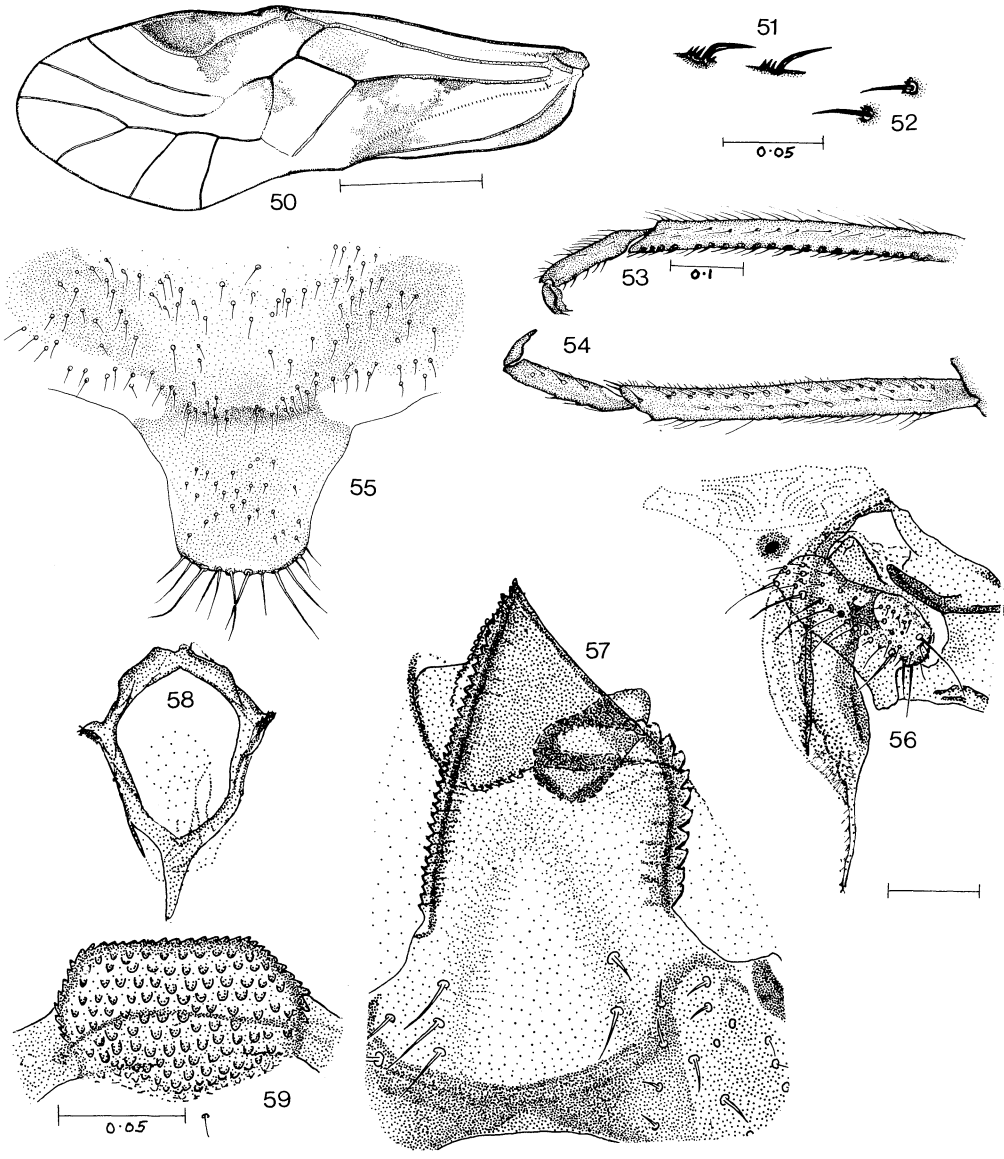

FIG. 50–59. *Ptycta microctena:* **50,** ♀ fore wing; **52,** ctenidia of basal hind tarsal segment; **54,** hind tarsus; **55,** subgenital plate; **56,** gonapophyses; **57,** hypandrium; **58,** phallosome; **59,** ♂ epiproct lobe. *Ptycta haleakalae haleakalae:* **51,** ctenidia of basal hind tarsal segment; **53,** hind tarsus. Fig. 51, 52, Fig. 53, 54, Fig. 55, 56, 58 and Fig. 57, 59 to common scales.

8 fairly stout marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segment: 12–15; 0+1, and those on basal segment much reduced in size and complexity compared, for example, to those of *P. haleakalae* (Fig. 51–54). Subgenital plate (Fig. 55) with broad apical process joined to rest of plate by wide neck, 4 slightly longer setae at base of process. Gonapophyses (Fig. 56): dorsal valve narrowing smoothly to apical spine, which is not sharply pointed but

"frayed" apically; outer valve with short posterior lobe. A field of 25 trichobothria on each paraproct. Gonopore plate not well sclerotized.

♂. *Coloration* (freshly killed, in alcohol). As ♀ except a vague brown mark each side ocellar protuberance, vertex-frons suture edged brown, gray-brown patch each side frontal stirrup mark, thoracic terga without obvious cream arrowhead mark, margins of dorsal lobes narrow, brownish cream except posteriorly cream, fore wing fascia less extensive, spot on *m+cu* sometimes separated from fascia. *Morphology.* Eyes rather small, I.O.:D. = 2.8–3.0. Basal flagellar segment with porrect setae at least 3× as long as greatest width of segment. Hind wing with 6–7 fairly stout marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 15–19; 0+1, those on basal segment small, as in ♀. Hypandrium (Fig. 57) with marginal teeth of apical lobe asymmetrical, those on right pointed, those on left close-set, narrower, median basal prong lacking. Phallosome with single pointed tine (Fig. 58). Anterior epiproct lobe high, tuberculate, slightly bilobed (Fig. 59); paraproct basal boss low, stout, sclerotized, a field of 22–23 trichobothria.

Distribution. MAUI, rare.

Holotype ♂, MAUI: Haleakala, 2500 m, beginning of Halemauu Trail, *Sophora,* 15.V.1963 (I.W.B. Thornton) (BPBM 12,975). Allotype ♀, data as holotype. Paratypes: 1♀, summit Haleakala (ca. 3050 m), V.1925 (Muir); 1♂, Haleakala, 2300 m, *Sophora,* VIII.1929 (Swezey).

This species, which seems to be restricted to the heights of Haleakala, is similar in male genitalia to other members of the *haleakalae* group. However, it differs in the structure of the apical spine of the dorsal valve of the female gonapophyses, and, most notably, in the reduction in size, complexity, and number, of the ctenidia on the tarsal segments (except the extreme apical one on the distal segment). Lack of or reduction of ctenidia is usually associated with reduction of wings and ocelli, both of which are fully developed in this species.

Ptycta microglena Thornton, **new species** Fig. 60–63

♀. Unknown.

♂. *Coloration* (freshly killed, in alcohol). Vertex buff, usual markings brown. Faint brown mark each side ocellar protuberance, continued as brown line along frons-vertex suture. Frons buff, dark brown median stirrup mark, very faint linear lateral marks. Clypeus buff, brown parallel striae merging medially. Genae buff, brown line from orbit to antennal socket. Maxillary palpi faint brown, subapical segment brown, apical segment dark brown. Antennae missing. Mesothoracic terga: antedorsum dark brown, cream median mark posteriorly and along posterior sutures: dorsal lobes dark brown, posterior margins cream; scutellum brown. Metathoracic terga dark brown, scutellum brown. Pleura dark brown. Legs: coxa dark brown; trochanter pale buff; femur pale buff, brown distally; tibia pale buff, brown distally; tarsus brown. Fore wing (Fig. 60) with well-defined narrow continuous transverse band, only a single brown patch in anal cell apically, large brown mark ½ way along *m+cu,* dark brown patch in apical ½ pterostigma, extending some distance basad from vertex, veins bordering basal ½ areola postica unpigmented, a discrete brown spot on *m* a short distance from its point of departure from *rs.* Hind wing hyaline, faint infuscation along anterodistal margin. Abdomen buff, a gray-brown granulated pigment diffused over dorsal surface. *Morphology.* I.O.:D. = 3.0–3.2, eyes very small. Hind wing with 6–7 marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 19–21; 3+1. Hypandrium (Fig. 61) with long, very narrow tongue, teeth

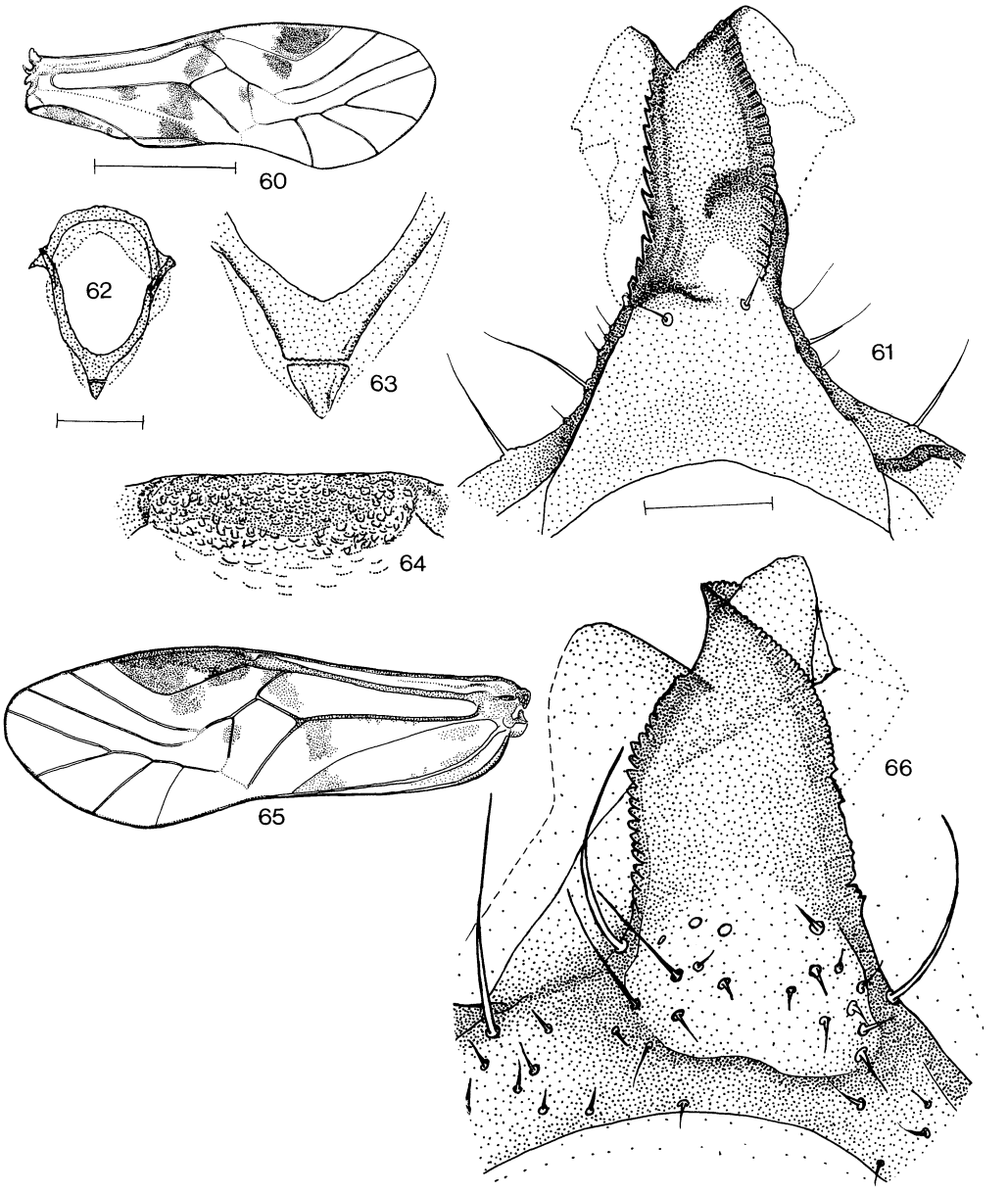

FIG. 60–66. **60–64,** *Ptycta microglena:* **60,** ♂ fore wing; **61,** hypandrium; **62,** phallosome; **63,** phallosome tine; **64,** ♂ epiproct lobe. **65–66,** *Ptycta palikea:* **65,** ♂ fore wing; **66,** hypandrium. Fig. 60, 65 and Fig. 61, 63, 64, 66 to common scales.

on left margin pointed, those on right margin close-packed, blunt; no basal median spine. Phallosome tine simple, broad, sharply pointed (Fig. 62, 63). Anterior epiproct lobe vaguely bilobed, beset with complex scalelike tubercles (Fig. 64). A field of 26–27 trichobothria on each paraproct.

Distribution. OAHU, LANAI, rare.

Holotype ♂, OAHU: Waianae Range, Mt Kaala, 550–750 m, *Metrosideros,* 14.III.1963 (I.W.B. Thornton) (BPBM 12,976).

This species is described from a ♂ taken on *Metrosideros* at over 600 m on Mt Kaala, Waianae Range, Oahu, in March 1963. Another was taken on Lanai by W.M. Giffard (no date). A 3rd ♂ was collected by Bryan on the S Waianae Mts, Oahu, on 9.XI.1919; the specimen lacks wings, hind legs, and antennae.

In size and general wing pattern the 1963 Oahu specimen is remarkably similar to *P. lanaiensis* but differs in eye size (I.O.:D. ratio) and in male genitalia. The eyes of male *lanaiensis* are outstandingly large, and the hypandrium has a broad apical tongue. The Lanai specimen is faded, but the transverse fascia of the fore wing appears to be reduced to a few disconnected spots. The male genitalia conform to those of other species of the *haleakalae* group.

Ptycta palikea Thornton, **new species** Fig. 65–66

♀. Unknown.

♂. *Coloration* (freshly killed, in alcohol). Vertex cream, brown markings, brown mark each side ocellar protuberance, brown pigment along frons-vertex suture. Frons with median brown stirrup mark only. Clypeal striae form vague T-shaped mark anteriorly. Genae cream, brown mark from orbit to antennal socket and additional vertical pigmented line from orbit. Eyes black. Maxillary palpi cream, preapical segment light brown, apical segment brown. Antenna brown, basal flagellar segment paling distally. Thoracic terga brown, sutures cream, scutella cream, pleura brown. Coxa brown; trochanter pale buff, femur light brown with subdistal patch; tibia light brown, darkening apically; tarsus dark brown. Fore wing (Fig. 65) transverse fascia slightly interrupted. Abdomen cream, gray-brown markings dorsally. *Morphology.* Eyes large, I.O.:D. = 1.0. Thoracic terga dull. Hind wing with 9 stout marginal setae between ends of *rs.* Ctenidia on hind tarsal segments: 25; 3+1. Hypandrium (Fig. 66) tongue very long, narrow, asymmetrical, teeth on right margin narrow, fused, flat, on left separate, larger, bluntly pointed, no median basal boss. Phallosome and epiproct anterior lobe as *haleakalae*; a field of 28 trichobothria on paraproct.

Distribution. OAHU, rare.

Holotype ♂, OAHU: eastern Koolau Range, Palikea, 600 m, *Metrosideros,* 31.X.1963 (I.W.B. Thornton) (BPBM 12,977). 1♂ paratype, same data as holotype.

This species is only known from the Palikea region of the eastern Koolau Range of Oahu I.

Ptycta simulator simulator (Perkins), **revised combination** Fig. 67–72

Psocus simulator Perkins, 1899: 78.—Zimmerman, 1948b: 249.

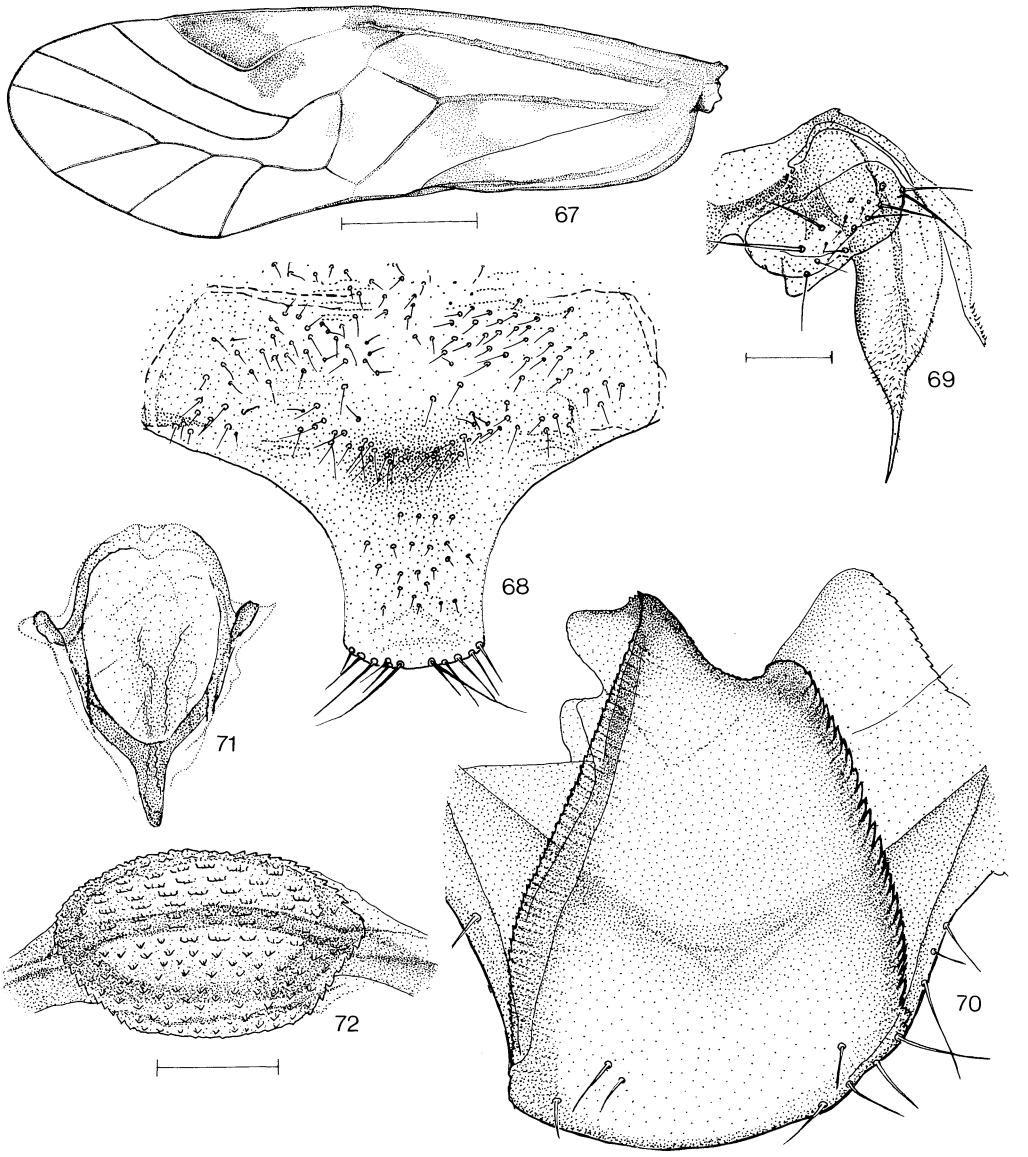

FIG. 67–72. *Ptycta simulator simulator:* **67,** ♀ fore wing; **68,** subgenital plate; **69,** gonapophyses; **70,** hypandrium; **71,** phallosome; **72,** ♂ epiproct lobe. Fig. 68, 69, 71 and Fig. 70, 72 to common scales.

Clematostigma simulator (Perkins): Enderlein, 1913: 355.
Psocus haleakalae var. *hualalai* Perkins: Enderlein, 1920: 451 (partim).
Psocus haleakalae var. *molokaiensis* Perkins: Enderlein, 1920: 451 (partim).
Ptycta haleakalae (Perkins): Enderlein, 1925: 102 (partim).

The following redescription is based on an examination of type material, and of other specimens collected more recently.

♀. *Coloration* (after ca. 15 years dry storage, then softening). Indistinguishable from *P. haleakalae haleakalae* except no lateral marks on frons, fore wing (Fig. 67) as figured by Zimmerman (1948b). *Morphology.* I.O.:D. = 3.8. Thoracic sclerites dull. Hind wing with 6 stout marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 25; 4+1. Subgenital plate (Fig. 68) very similar to that of *P. haleakalae.* Gonapophyses (Fig. 69): outer valve with short rounded posterior lobe. A field of 25–30 trichobothria (25 in type) on each paraproct.

♂. *Coloration* (after ca. 15 years dry storage, then softening). Fore wing as ♀, pterostigma pigment only slightly more extensive. *Morphology.* Eyes large, I.O.:D. = 1.4–1.6. Antennae with setae on basal flagellar segment porrect. Thoracic sclerites as ♀. Hind wing with 6–7 stout marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 28–30; 3+1. Hypandrium (Fig. 70) and phallosome (Fig. 71) as those of *P. haleakalae.* Epiproct lobe (Fig. 72) as *P. haleakalae*; a field of 30–33 trichobothria on each paraproct.

Distribution. MAUI, rare.

This is the form described by Perkins under *P. simulator.* Apart from his record of 1500 m (5000 ft) on Haleakala, October 1896, it has been taken at Puu Luau, 27.IV.1945, on *Coprosma* and *Myrsine.*

Closely similar to *P. haleakalae haleakalae, P. simulator simulator* is distinguishable by its larger size, wing shape, larger eyes of the male, and presence of a pigment mark about ½ way along vein *m+cu* in the fore wing. The 2 species are closely similar in genitalic characters.

Ptycta simulator kilauea Thornton, **new subspecies**

Differs from the nominate form in the following respects: transverse fascia in fore wing interrupted in ♂, not in ♀; *m+cu* mark only a vestige; in ♂ median stirrup mark on frons obliterated by a dark patch; smaller size; ♂ I.O.:D. = 1.0–1.1, ♀ 3.2; number of stout marginal setae on hind wing between ends of *rs*: ♂ 6–8, ♀ 7–11; number of ctenidia on hind tarsal segments: ♂ 22–24, 3+1, ♀ 21–24, 2–3+1; paraproct trichobothria: ♂ 29–37, ♀ 30; ♀ subgenital plate with small sclerotized flap in middle of apical process basally.

Distribution. HAWAII, rare.

Holotype ♂, HAWAII: Kilauea, "20 miles," 16.X.1916 (W.M. Giffard) (BPBM 12,978). Allotype ♀, HAWAII, Kilauea, "29 miles," 18.X.1916 (Giffard). Paratypes (all HAWAII): ♂, Kilauea, ohia, 28.VIII.1935 (R.L. Usinger); ♂, Glenwood, 2800 ft (850 m) (Giffard); ♀, Kohala Mts, Upper Hamakua Ditch trail, 4.X.1929 (R.R. Witten).

The flap on the female subgenital plate apical process is a feature of the *lanaiensis* group (below).

Ptycta stena Thornton, **new species** Fig. 73

♀. Unknown.

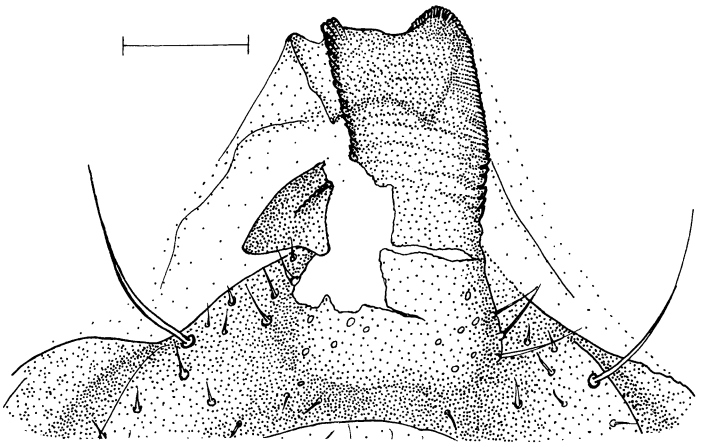

FIG. 73. *Ptycta stena*, hypandrium.

♂. *Coloration* (freshly killed, in alcohol). Vertex cream, markings brown, brown mark each side ocellar protuberance, brown line along frons-vertex suture. Frons with median brown stirrup mark only. Clypeus with distinct striae. Genae cream, brown mark from orbit to antennal socket. Eyes black. Maxillary palpi pale cream, subapical segment pale brown, apical segment darker. Antennae brown, basal flagellar segment much paler than rest. Thoracic terga brown, median cream band on mesothorax and on antedorsal sutures, scutella cream, pleura brown. Coxa brown; trochanter pale buff; femur pale brown, darker mark subapically; tibia buff, dark brown apically; tarsus dark brown. Fore wing pterostigma pigment extensive, pigment mark on *m+cu*, transverse fascia represented by only a few discrete spots. Abdomen cream, gray-brown dorsal markings. *Morphology.* I.O.:D. = 1.2. Setae of basal flagellar segment porrect. Thoracic terga dull. Hind wing with 6 stout marginal setae between ends of *rs*. Ctenidia on hind tarsal segments: 23; 3+1. Hypandrium (Fig. 73) with very narrow tongue, only slightly asymmetrical, marginal teeth differ only slightly on left and right, no basal median boss.

Distribution. MOLOKAI, OAHU, rare.

Holotype ♂, MOLOKAI: 600 m above Kamiloloa, *Acacia koa*, 19.VII.1963 (I.W.B. Thornton) (BPBM 12,979).

A male collected by Bryan on the Ewa coral plain, Oahu, from *Euphorbia*, in January 1922 differs slightly in that the teeth on the right margin of the hypandrial tongue are slightly less smooth.

The species is distinguishable from *simulator* by its small size, and from *haleakalae* by the pigment mark on *m+cu* in the fore wing.

Ptycta stenomedia Thornton, **new species** Fig. 74–80

♀. *Coloration* (freshly killed, in alcohol). Head generally cream, vertex markings brown. Brown median stirrup mark on frons. Genae whitish cream, brown mark from orbit to antennal socket, faint gray-brown line parallel to and below this, clypeus with distinct brown parallel

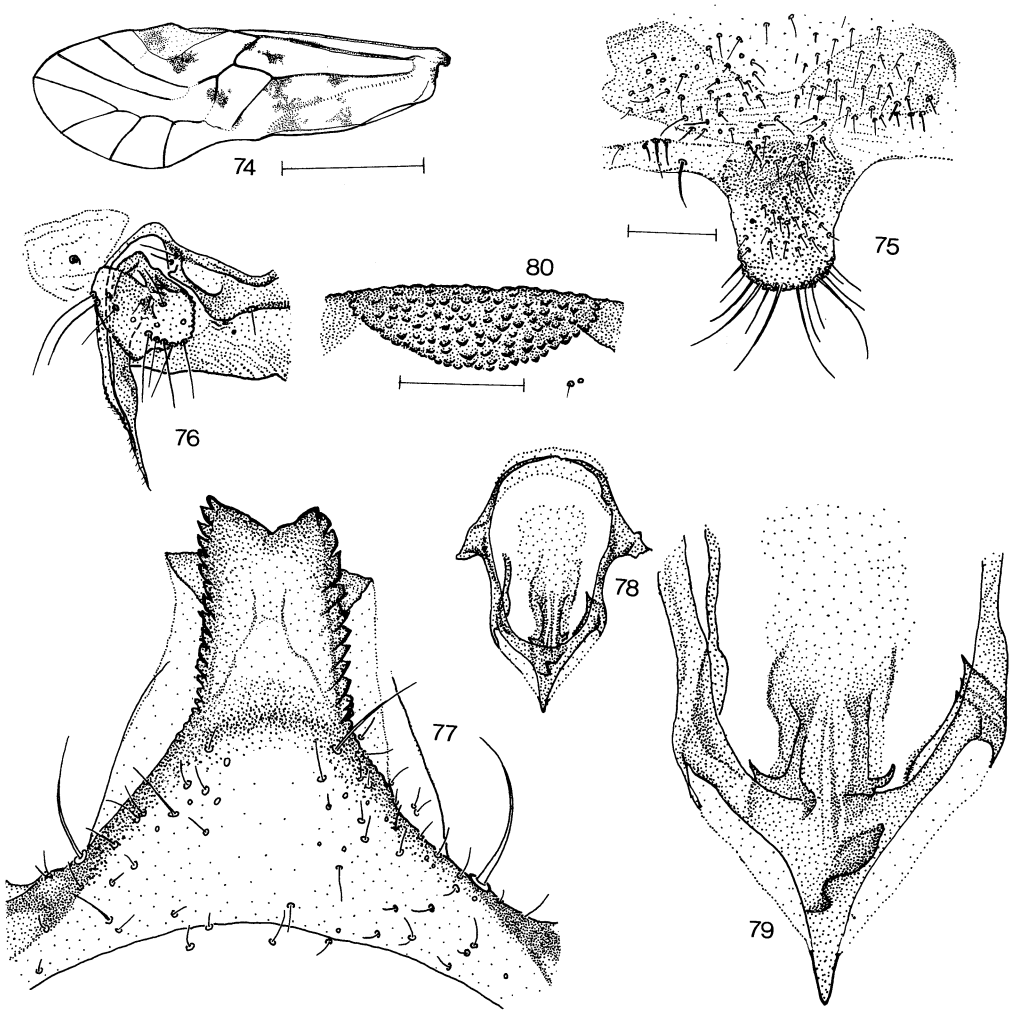

FIG. 74–80. *Ptycta stenomedia:* **74,** ♀ fore wing; **75,** subgenital plate; **76,** gonapophyses; **77,** hypandrium; **78,** phallosome; **79,** apex of phallosome; **80,** ♂ epiproct lobe. Fig. 75, 76, 78 and Fig. 77, 79, 80 to common scales.

striae, not merging medially. Maxillary palpi pale cream, apical segment brown. Antennae brown except basal flagellar segment pale brown, darkening apically. Thoracic terga brown, dorsal lobes with cream outer margins, median cream mark, arrowhead mark on antedorsum of mesothorax, scutella brown. Pleura brown. Legs: coxa brown; trochanter pale brown, brown mark on mesial surface; femur pale brown, brown on outer surface subapically; tibia pale brown, darker apically; tarsus brown. Fore wing (Fig. 74) with small distinct brown patches; transverse fascia interrupted, 2 distinct patches in apical ½ *An*; brown patch ½ way along *m+cu,* on *m* short distance beyond its departure from *rs*; brown mark in pterostigma apically

not reaching vertex; areola postica veins not wholly hyaline basally. Hind wing with very faint brown streak on anterodistal margin, brown patch in *An* apically, not contiguous with posterior wing margin. Abdomen cream, vague brown transverse bands over terga. *Morphology.* I.O.: D. = 3.2. Hind wing with 6 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 24; 2+1. Subgenital plate (Fig. 75) with 2 longer setae at base of apical process, arms of disc angular. Gonapophyses (Fig. 76): dorsal valve narrow, tapering smoothly to apical spine; outer valve with smooth low posterior lobe. A field of 21–33 trichobothria on each paraproct.

♂. *Coloration* (freshly killed, in alcohol). As ♀, except legs rather darker, mesothorax without distinct arrowhead mark on antedorsum, short median brownish-cream mark between dorsal lobes. *Morphology.* Eyes small, I.O.:D. = 3.1. Pubescence on basal flagellar segment no longer than 2× greatest width of segment, porrect, particularly on under surface. Hind wing with 7 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 20; 3+1. Hypandrium (Fig. 77) with narrow almost symmetrical apical tongue, teeth on both sides distinct, sharply pointed; no basal median prong. Phallosome (Fig. 78, 79) apical tine simple, pointed, some evident penial bulb sclerotizations. Anterior epiproct lobe low, tuberculate, not bilobed (Fig. 80); paraproct with short fairly stout sclerotized basal boss, a field of 20 trichobothria.

Distribution. HAWAII, rare.

Holotype ♂, HAWAII: Kawaihae Uka, 1050 m, live branches of *Acacia koaea,* 29.I.1963 (I.W.B. Thornton) (BPBM 12,980). Allotype ♀, data as holotype.

The species has only been found on the Kohala massif of Hawaii I.

In wing markings it somewhat resembles *P. molokaiensis,* and the male genitalia are remarkably similar. It differs, however, in the smaller eyes of the male and in the female genitalia, which show no resemblance to those of the *oahuensis* group. Its relationship to *molokaiensis* is thus remote.

Ptycta unica (Perkins), **revised combination** Fig. 81–86

Psocus unicus Perkins, 1899, 78.—Zimmerman, 1948b: 249.
Clematostigma unicus (Perkins): Enderlein, 1913: 355.
not *Psocus haleakalae* Perkins: Enderlein, 1920: 449.
not *Ptycta haleakalae* (Perkins): Enderlein, 1925: 102.

The following description supplements that of Perkins. It is based on an examination of the unique type specimen and of material collected more recently.

♀. *Coloration* (after ca. 35 years dry storage). Head cream, vertex markings brown. Brown patch each side ocellar protuberance, narrow brown line along frons-vertex suture. Frons with median brown stirrup mark. Clypeus with parallel brown striae not merging medially. Genae whitish cream, brown band from orbit to antennal socket. Eyes black. Maxillary palpi buff, preapical segment brown, apical segment dark brown. Scape and pedicel brown, flagellum dark brown. Thoracic terga dark brown, mesothoracic dorsal lobes with cream border posterolaterally, a median cream band between dorsal lobes of meso- and metathorax, scutella cream. Pleura dark brown. Legs: coxa dark brown; trochanter pale cream; femur pale buff, light brown on outer surface and towards apex; tibia buff, dark brown apically; tarsus dark brown. Fore wing (Fig. 81) and hind wing as Perkins' description and Zimmerman's figures,

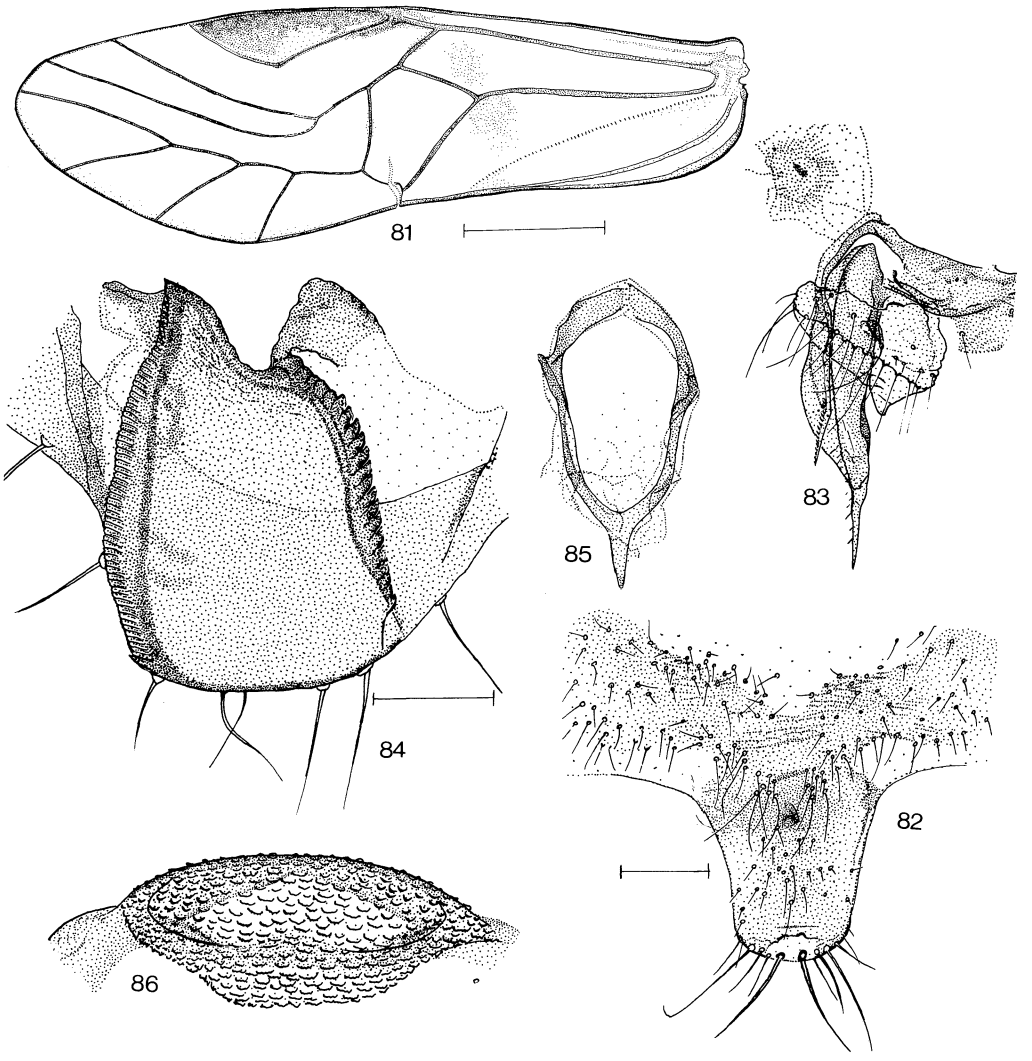

FIG. 81–86. *Ptycta unica:* **81,** ♀ fore wing; **82,** subgenital plate; **83,** gonapophyses; **84,** hypandrium; **85,** phallosome; **86,** ♂ epiproct lobe. Fig. 82, 83, 85 and Fig. 84, 86 to common scales.

pterostigma with white border by reflected light. Abdominal color not discernible. *Morphology.* I.O.:D. = 3.0, but eyes unusually prominent, offset. Flagellar pubescence very short. Hind wing with 8 stout marginal setae between ends of *rs.* Fore wing very long, narrow. Number of ctenidia on hind tarsal segments: 25; 3+1. Mesothoracic antedorsum somewhat shining anteriorly. Subgenital plate (Fig. 82) apical process with 4 longer setae at its base and a median sclerotization, main body of plate incised anteriorly in midline. Gonapophyses (Fig. 83): dorsal valve very gradually narrowing to apical spine; outer valve with small pointed lobe; articulation of dorsal and outer valves well sclerotized, prominent. A field of 24–32 trichobothria (23 in type) on each paraproct.

♂. *Coloration* (after ca. 35 years dry storage). As ♀, except frons having gray-brown lateral marks touching stirrup mark, fore wing with no pigment on membrane except within pterostigma. *Morphology.* I.O.:D. = 1.5, eyes prominent. Flagellar pubescence long, offstanding. Hind wing with 6 stout marginal setae between ends of *rs.* Fore wing narrow. Anterior of mesothoracic antedorsum somewhat shining. Hypandrium (Fig. 84) asymmetrical; with long tongue, teeth on right margin stout, pointed, those on left margin ½ width of those on right, blunt, very close-set; no basal median boss. Phallosome tine (Fig. 85) simple, stout, sharply pointed. Epiproct anterior lobe low, tuberculate, simple (Fig. 86). Paraproct with square, sclerotized basal boss, a field of 31 trichobothria.

Distribution. MAUI, rare.

Specimens, other than type, on which further description based. 1♂, E MAUI, Olinda, 27.II.1926 (Swezey); 1♀, same data, on *Metrosideros.*

P. unica was described from a single female from Haleakala on Maui at 1500 m (5000 ft). Both sexes were collected from *Metrosideros* at Olinda on the NW slopes of Haleakala, at about 1400 m, in February and May 1926, by Swezey. In March 1932, Bryan collected a single ♂ on Haleakala at 1400 m and another at 2900 m from *Styphelia.* The species is apparently confined to the E Maui mountain.

This species is easily distinguished from others of large size by the simplicity of the fore wing pattern (the male has no markings except within the pterostigma), the "neat" pterostigma (with no mark outside it next to the vertex), the narrow wings, and the faintly shining mesothoracic antedorsum.

kauaiensis group

This is a distinctive group of 8 species, all confined to Kauai, and is characterized by lateral carinae of fused teeth on the hypandrium.

All species occur in the highlands of the Waimea Plateau, although *kauaiensis* and *placophora,* n. sp., also occur in the lowlands, the latter extensively so. Both these species have a wide range of host trees, as does *telma,* n. sp., which is the only species to be found in numbers deep in the Alakai Swamp. *P. zimmermani,* n. sp., was collected some distance into the swamp, but, like *persimilis,* n. sp., was only found on *Acacia koa* and *Metrosideros* in the highlands. *P. diastema,* n. sp., is only known from *Acacia koa* in the Kokee area, and *monticola,* which also seems to be confined to the Kokee area, was collected on *Acacia koa* as well as *Metrosideros* and introduced conifers. *P. monticola* is unusual in frequenting the trunks of trees, rather than the branches.

Ptycta kauaiensis (Perkins), **revised combination** Fig. 87–92

Psocus kauaiensis Perkins, 1899: 179.—Zimmerman, 1948b: 247.
Clematostigma kauaiensis: Enderlein, 1913: 355.
not *Psocus haleakalae* var. *molokaiensis* Perkins: Enderlein, 1920: 451.
not *Ptycta haleakalae* var. *molokaiensis* (Perkins): Enderlein, 1925: 102.

The following description is based on an examination of type material and of material subsequently collected.

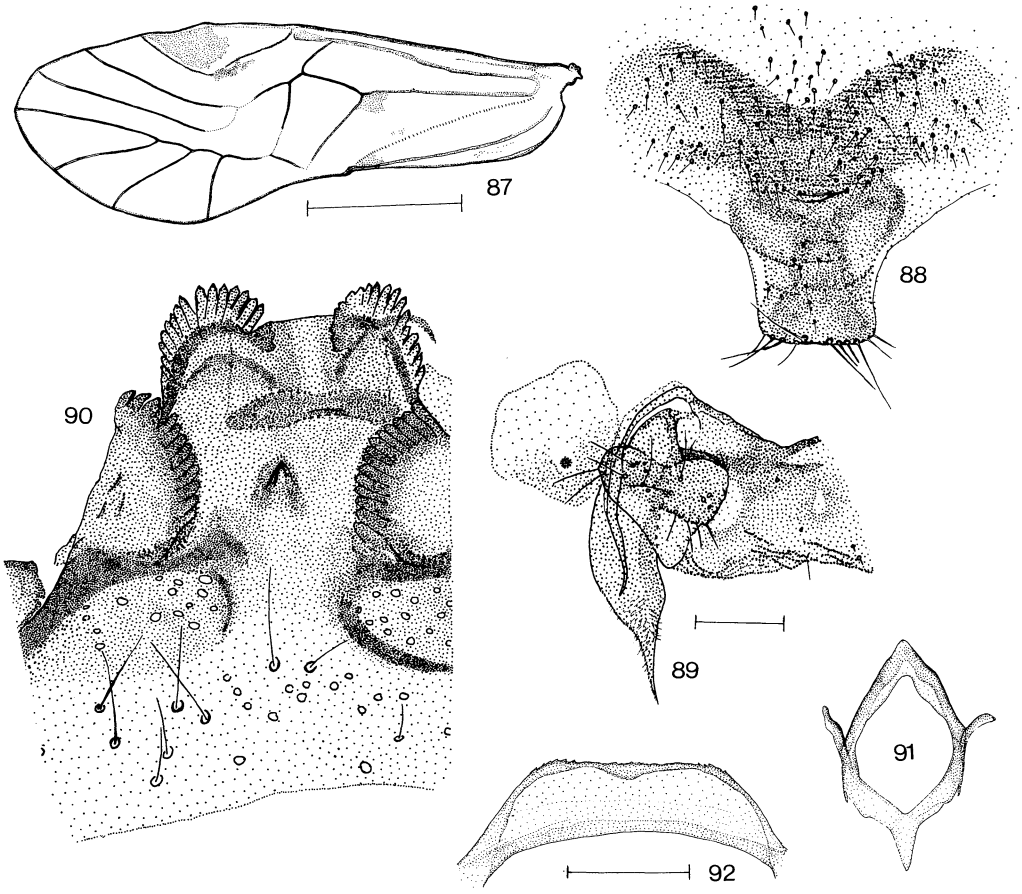

FIG. 87–92. *Ptycta kauaiensis:* **87,** ♀ fore wing; **88,** subgenital plate; **89,** gonapophyses; **90,** hypandrium; **91,** phallosome; **92,** ♂ epiproct lobe. Fig. 88, 89, 91 and Fig. 90, 92 to common scales.

♀. *Coloration* (freshly killed, in alcohol). Head generally pale cream, usual vertex markings buff. Ocelli pale, centripetal margins black. Small brown patch each side of ocellar protuberance continuing as brown line along vertex-frons suture. Median brown stirrup mark on frons with brown patch each side touching anterior suture of frons, another dark brown mark mesial to antennal socket. Clypeus pale cream, parallel striae faint brown except brown in transverse line across clypeus ½ way along its length and in median line in anterior ½, resulting in T-shaped brown mark; labrum dark brown. Genae pale cream, brown band from orbit to antennal socket, 2nd parallel band below this, sometimes interrupted. Eyes black. Maxillary palpi pale, preapical segment brown, apical segment dark brown. Antennae dark brown. Thoracic terga brown, antedorsum and anterior of dorsal lobes of mesothorax usually paler above than other terga. Dorsal lobes separated in meso- and metathorax by median cream line. Scutella pale buff. Thoracic pleura brown. Legs: coxa brown; trochanter and femur pale cream; tibia pale brown, not darkening apically; tarsus brown. Wings: fore wing (Fig. 87) with very sparse brown

markings. Hind wing hyaline, faint brown along anterodistal margin and in anal cell. Abdomen dorsally yellowish cream, usually 5 longitudinal brown bands discernible, a narrow median and 2 broader laterals; ventrally yellowish cream; 9th tergite patterned brown and pale brown. Epiproct pale buff. *Morphology.* I.O.:D. = 3.7. Hind wing with 8 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 23; 2+1. Subgenital plate (Fig. 88) with short broad apical process, 2 long setae at base. Gonapophyses (Fig. 89): outer valve with short lobe. A field of 20–23 trichobothria on each paraproct (23 in type).

♂. *Coloration* (freshly killed, in alcohol). As ♀, but abdominal bands sometimes discernible, fascia on fore wing entirely lacking. *Morphology.* Eyes prominent, I.O.:D. = 1.3. Hind wing with 4–5 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 22–26; 2+1. Hypandrium (Fig. 90) apical tongue symmetrical, stout median prong at base, margin each side basally with a carina of 10–12 fused long flat blunt teeth, apically with 14–17 shorter pointed teeth. Phallosome (Fig. 91) with smooth pointed apical tine. Epiproct lobe as Fig. 92.

Distribution. KAUAI, common above 900 m.

Specimens on which further description based, in addition to type material. 5♂,4♀, KAUAI: nr Kokee cabin, *Acacia koa,* sweeping trunks with net, 29.VII.1963.

This is the commonest species of *Ptycta* on Kauai I. It is chiefly confined to the highlands, where it has been taken on introduced conifers, *Acacia koa, Metrosideros,* and other shrubs, but it does occur in the lowlands, having been taken on *Psidium guajava* near the Sleeping Giant. In the highlands it occurs at Kokee, near Kawaikoi Stream, at Mohihi, and near Camp Slogget. Material examined also includes specimens from the fringes of the Alakai Swamp and the Na Pali Kona Forest Reserve as well as from Kokee, all collected by Mockford, and from the Kokee area collected by Nadler. A specimen from Summit Camp, at 550 m, on the eastern part of the island was collected by Swezey. The species has been taken in April, July, August, September and November.

The relative paleness of the mesothoracic antedorsum varies somewhat but is always present, and the distinctive clypeal markings are constant. The extent of pigmentation and thus completeness of the transverse fascia in the fore wing of the female varies, but the fascia is always considerably interrupted. In the male the fascia as such is lacking.

Enderlein reduced *lanaiensis* to a variety of *haleakalae* and synonymized this variety with *kauaiensis.* I can find no grounds for maintaining this synonymy, the 2 forms being quite distinct.

Ptycta diastema Thornton, **new species** Fig. 93–98

♀. *Coloration* (freshly killed, in alcohol). Head generally whitish cream, usual vertex markings dark brown. Ocelli pale, centripetal margins black. Narrow faint brown stripe from sides of ocellar protuberance along vertex-frons suture. Frons with dark brown median stirrup mark, lateral marks very faint or absent. Clypeus with brown parallel striae darker medially, and ending laterally some distance short of anterior margin. Genae whitish cream, dark brown band from orbit to antennal socket. Eyes black. Maxillary palpi whitish cream, apical segment dark brown. Scape and pedicel brown, 1st flagellar segment brown, darker distally, rest of flagellum dark brown. Thoracic terga brown, whitish cream arrowhead mark medially on mesothorax, scutella brown. Thoracic pleura brown. Legs: coxa dark brown; trochanter and femur whitish cream; tibia pale cream, dark brown distally; tarsus dark brown. Fore wing (Fig.

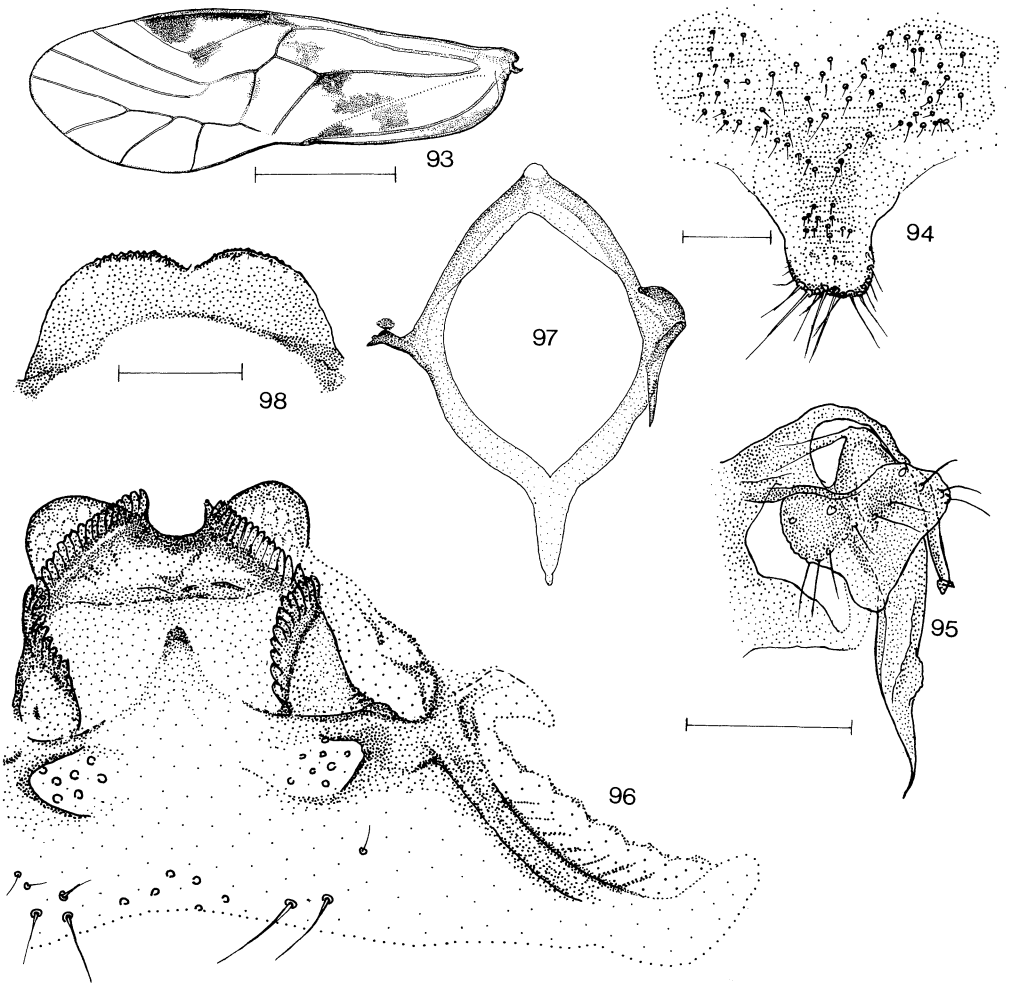

FIG. 93–98. *Ptycta diastema:* **93,** ♀ fore wing; **94,** subgenital plate; **95,** gonapophyses; **96,** hypandrium; **97,** phallosome; **98,** ♂ epiproct lobe. Fig. 95, 97 and Fig. 96, 98 to common scales.

93) with narrow interrupted transverse fascia at acute angle to wing margin, pigment within pterostigma not reaching vertex. Hind wing with brown streak on anterodistal margin, apex of anal cell faintly brown. Abdomen distinctively marked; basal 4 tergites dark gray-brown dorsally, rest cream, all tergites marked with gray-brown extremely laterally forming longitudinal band each side of abdomen; ventrally cream. *Morphology.* I.O.:D. = 2.5. Hind wing with 5 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 25; 2+1. Subgenital plate (Fig. 94) and gonapophyses (Fig. 95) closely similar to those of *P. kauaiensis.* A field of 21 trichobothria on paraproct.

♂. *Coloration* (freshly killed, in alcohol). As ♀, except angled fascia in fore wing reduced to few dark marks, pigment within pterostigma more extensive, reaching vertex. *Morphology.* Eyes fairly prominent, I.O.:D. = 1.7. Hind wing with 6 fine marginal setae between ends of *rs.*

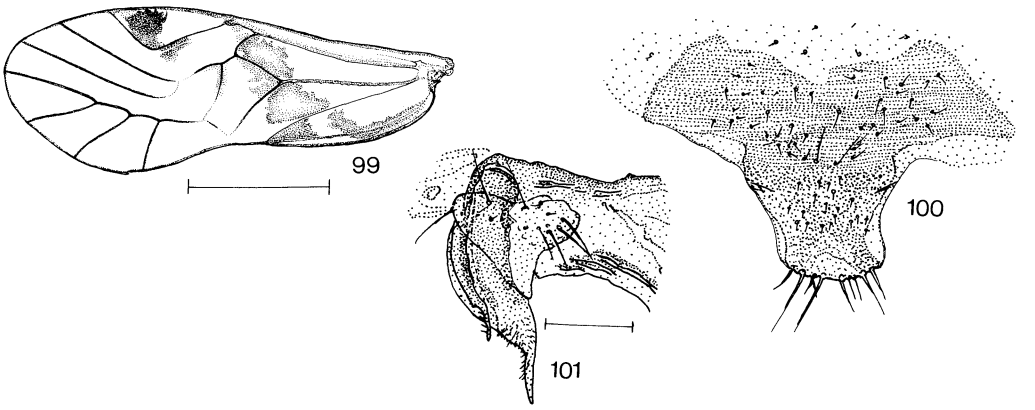

FIG. 99–101. *Ptycta gynegonia:* **99,** ♀ fore wing; **100,** subgenital plate; **101,** gonapophyses. Fig. 100, 101 to common scale.

Number of ctenidia on hind tarsal segments: 26; 2+1. Hypandrium (Fig. 96) as that of *P. kauaiensis* but apical teeth blunt; phallosome (Fig. 97) with broad smooth apical tine. Anterior epiproct lobe (Fig. 98) tuberculate, bilobed; paraproct with large apical spine only slightly curved, field of 21 trichobothria.

Distribution. KAUAI, rare.

Holotype ♂, KAUAI: Kokee cabin, searching dead and live branches and some trunks of *Acacia koa,* 1.VIII.1963 (I.W.B. Thornton) (BPBM 12,981). Allotype ♀, same data as holotype.

Occurring above 1000 m, this species was collected in 1963 on *Acacia koa* only, from near the Kawaikoi Stream, Camp Sloggett, and the Kokee area. Material examined also includes 1♂ and 1♀ from Kokee collected by Mockford, and 1♂ from the Kaunuohoa Ridge collected by Zimmerman. Specimens have been collected in July, August, and September.

It is distinguishable from other closely similar species with overlapping ranges by the distinctive abdominal color pattern.

Ptycta gynegonia Thornton, **new species** Fig. 99–101

♀. *Coloration* (freshly killed, in alcohol). Head generally yellowish cream, vertex markings brown. Brown mark lateral to ocellar protuberance continued as brown line along vertex-frons suture. Frons with median brown stirrup mark, lateral brown marks touching anterior suture. Clypeus dark, parallel striae not relatively darker medially. Genae with dark mark from orbit to antennal socket, a vague wide brown band below this. Maxillary palps dark brown. Antennae dark brown. Thoracic terga dark brown, dorsal lobes divided by cream lines, scutella dark brown. Pleura dark brown. Legs: coxa dark brown; trochanter pale buff; femur pale buff, brown apically; tibia brown, darker apically; tarsus dark brown. Fore wing (Fig. 99) with brown transverse fascia with paler "windows," 2 distinct brown patches in apical ½ of anal cell; dark brown spot in pterostigma; basal section of areola postica white by reflected light. Hind wings with brown streak on anterodistal margin, pale infuscation in anal cell apically. Abdomen yellowish cream, apical sclerites dark brown. *Morphology.* I.O.:D. = 2.6. Hind wing with 5 fine

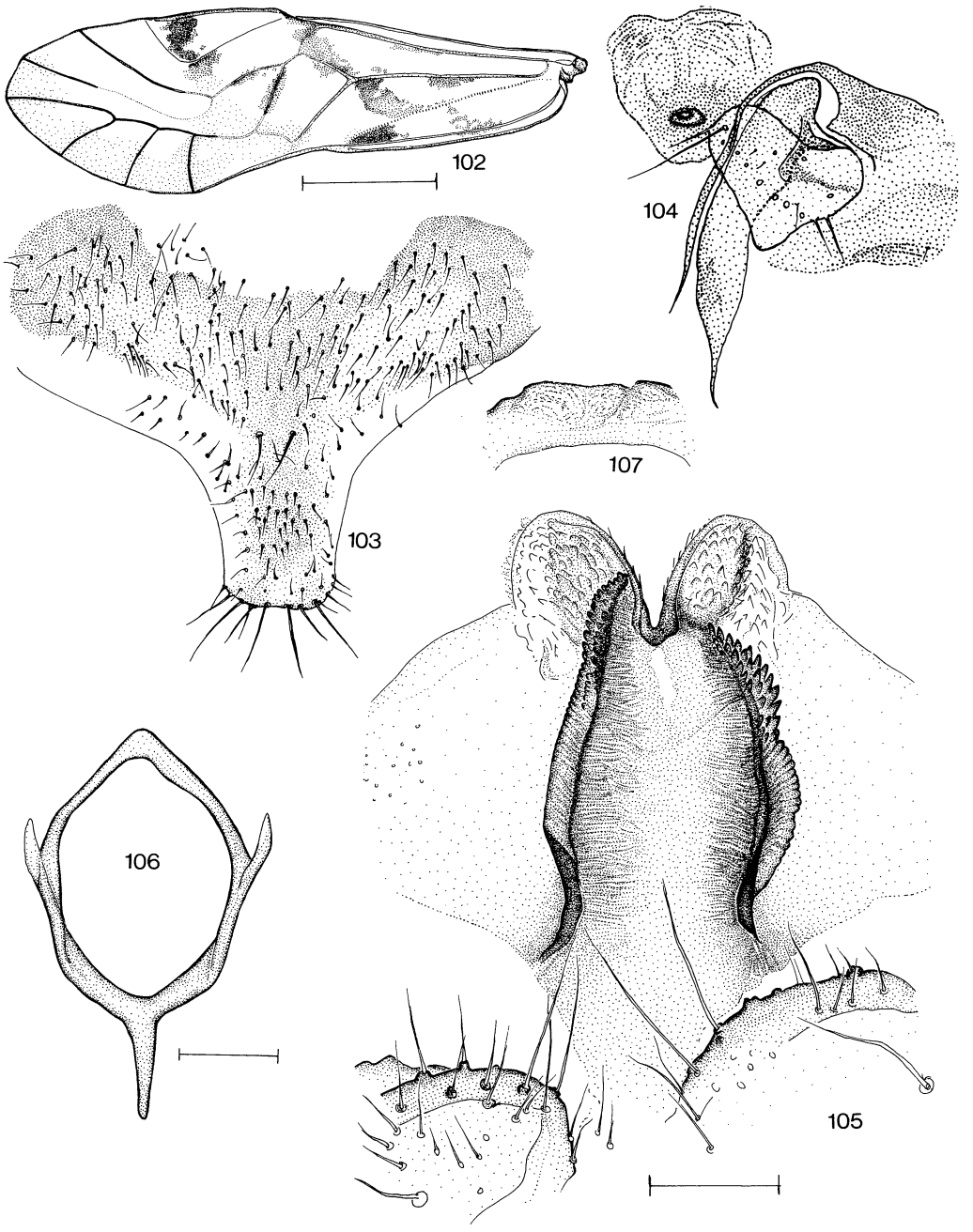

FIG. 102–107. *Ptycta monticola:* **102,** ♀ fore wing; **103,** subgenital plate; **104,** gonapophyses; **105,** hypandrium; **106,** phallosome; **107,** ♂ epiproct lobe. Fig. 103, 104, 106, 107 to common scale.

marginal setae between ends of *rs*. Number of ctenidia on hind tarsal segments: 23; 2+1. Subgenital plate (Fig. 100) squat apical process bearing 2 long setae basally, main plate with angular arms. Gonapophyses (Fig. 101): outer valve with long pointed lobe. A field of 20–26 trichobothria on each paraproct. Gonopore plate unsclerotized.

♂. Unknown.

Distribution. KAUAI.

Holotype ♀, KAUAI: Kokee, *Acacia koa* forest undergrowth, 30.VII.1963 (I.W.B. Thornton) (BPBM 12,982).

Females were collected by Nadler at Kokee in September 1957 and by Mockford near Kalalau Lookout in August 1957. Other specimens, all ♀, were taken from *Metrosideros* near the Kawaikoi Stream and from *Acacia koa* at Kokee in July 1963, and from *Metrosideros* at about 1200 m along the Kalalau-Waimea divide in November 1963. Evidently the species is restricted to the Kokee highlands.

Males are not available; the placement of the species in this group is thus doubtful and awaits confirmation of the discovery of ♂s. The general fore wing pattern is similar to several species of this group, particularly *placophora*, n. sp., and *telma*, n. sp., but differs in detail, particularly the paler areas in the transverse fascia.

Ptycta monticola (Perkins), **revised combination** Fig. 102–107

Psocus monticola Perkins, 1899: 82.—Zimmerman, 1948b: 248.
Psocus haleakalae var. *monticola* Perkins: Enderlein, 1920: 450.
Ptycta haleakalae var. *monticola* (Perkins): Enderlein, 1925: 102.

The following redescription is based on an examination of type material and material collected by the author.

♀. *Coloration* (freshly killed, in alcohol). Vertex pale cream, circular brown patch on either side of epicranial suture, usual vertex markings very pale or lacking. Ocelli pale, centripetal margins black. Brown line along and just posterior to frontal suture. Frons brown; clypeus brown, with darker parallel striae; labrum dark brown. Genae cream, broad brown vertical mark from orbit down length of gena, narrow horizontal brown line joining middle of this to antennal socket. Eyes black. Maxillary palpi light brown, apical segment slightly darker at apex. Scape and pedicel pale brown, basal flagellar segment light brown, darkening apically to very dark brown, rest of flagellum very dark brown. Antedorsum of mesothorax dark brown, rest of thoracic terga pale brown, dorsal lobes separated by median cream lines, scutella cream. Legs: coxa pale cream, a brown mark at base of pro- and mesocoxa in well-pigmented specimens; trochanter and femur pale cream; tibia pale brown, not darkening distally, tarsus brown. Fore wing patterned in various shades of brown (Fig. 102). Abdomen pale cream, basal 4 segments ringed with gray-brown even ventrally, rest of abdomen with a dorsolateral brown longitudinal stripe each side, ventrally gray-brown. 9th tergite sclerotized, patterned brown and pale brown. Epiproct pale cream. *Morphology.* I.O.:D. = 3.5. Surface of head waxy. Hind wing with 4 fine marginal setae between ends of *rs*. Number of ctenidia on hind tarsal segments: 39; 2+1. Thoracic terga waxy. Subgenital plate (Fig. 103) T-shaped, ends of crossbar widening sharply, 2 long setae at base of apical process. Gonapophyses (Fig. 104): outer valve with short lobe. A field of 26 trichobothria on each paraproct. Gonopore plate weakly sclerotized around gonopore.

♂. *Coloration* (freshly killed, in alcohol). As ♀, but fore wing fascia narrower. *Morphology.* Eyes fairly prominent, I.O.:D. = 1.9. Surface of head waxy, as ♀. Hind wing with 5 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 40; 2+1. Thoracic terga waxy. Hypandrium (Fig. 105) asymmetrical, margins of apical process with basal carinae of close-set flat blunt teeth, more apically on right side row of fine sharp teeth, on left close-set group of blunter teeth. Phallosome (Fig. 106) with smooth blunt apical tine. Anterior lobe of epiproct (Fig. 107) very flat, just perceptibly bilobed, tuberculate; large apical spine of paraproct slightly curved, basal boss squat, low, a field of 26 trichobothria.

Nymph. Color pattern as adult, except femur brown.

Distribution. KAUAI, frequent.

Specimens on which redescription based, in addition to type material. KAUAI: 1♀, Camp Sloggett, *Acacia koa,* dead branches with lichen, 1.VII.1963; 1♂, Kokee, sweeping *Acacia koa* trunks, 30.VII.1963.

The species was described from 1♂ and 1♀ from the mountains of Kauai. I have dissected these type specimens and have examined other material of both sexes taken by Perkins in May and June 1894, as well as specimens collected by Zimmerman in July 1937 (1♀), Mockford in August 1957 (both sexes), and Nadler in July and August 1963 (both sexes), all from the Kokee area of Kauai. *P. monticola* has been collected only from the Kokee plateau (above 1000 m), Kauai, in the summer months, and has not been found in the adjacent Alakai Swamp. It is found on introduced conifers and occasionally on *Metrosideros,* but its usual habitat seems to be trunks (rather than branches) of *Acacia koa,* of which there is an extensive native forest. *P. kauaiensis* has also been collected by sweeping trunks, but usually occurs on twigs and branches; the reverse is true of *monticola.*

There is some variation in the coloration of the thoracic terga, some specimens having the metathorax and the posterior part of the mesothorax quite pale dorsally. In others the usual brown markings are apparent, but in these cases the anterior of the mesothoracic terga is always very much darker. In wing pattern this species is markedly different from other species of the *kauaiensis* group and generally similar to *P. vittipennis* (Perkins) and *P. heterogamias* (Perkins). It is easily distinguished from them by head pattern and by the arrangement of dark and light sections of the fore wing veins, which is constant. The male genitalia differ quite markedly.

Ptycta persimilis Thornton, **new species** Fig. 108–113

♀. *Coloration* (freshly killed, in alcohol). Head generally whitish cream, usual markings brown. Ocelli pale, centripetal margins black. Lateral to ocellar protuberance a brown patch about size of protuberance, continuing as brown line along frons-vertex suture. Each side of frons stirrup mark a small buff area of pigment, often fused to stirrup mark and touching anterior suture of frons. Clypeus with parallel striae brown, often rather closer medially; labrum dark brown. Genae with narrow brown band from orbit to antennal socket; no other bands. Eyes black. Maxillary palpi pale cream, preapical segment brown, apical segment dark brown. Scape and pedicel brown, first flagellar segment pale brown, darkening distally, rest of flagellum brown. Thoracic terga brown, median pale cream arrowhead marks on meso- and metathorax, pleura brown. Legs: coxa brown; trochanter pale; femur pale, faint brown distally; tibia faint brown, brown distally; tarsus brown. Wings: fore wing (Fig. 108) faint brown, a hyaline area in distal angle of basal radial cell, with a distinct, broad, angled transverse fascia, including 2

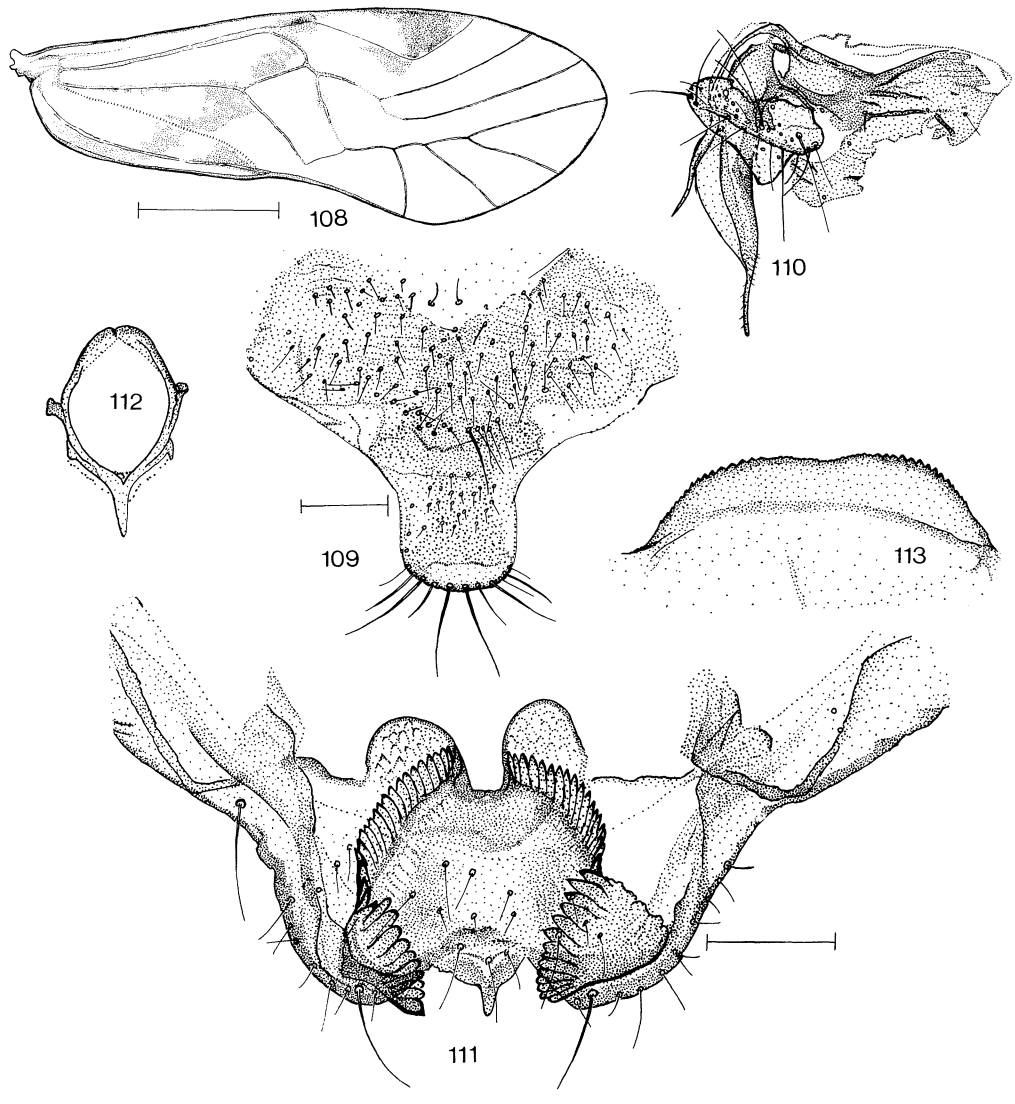

FIG. 108–113. *Ptycta persimilis:* **108,** ♀ fore wing; **109,** subgenital plate; **110,** gonapophyses; **111,** hypandrium; **112,** phallosome; **113,** ♂ epiproct lobe. Fig. 109, 110, 112 and Fig. 111, 113 to common scales.

distinct patches of pigment in anal cell, dark spot in pterostigma not usually touching vertex. Hind wing hyaline, anterodistal margin brown. Abdomen whitish cream with basal 2 or 3 terga uniformly gray-brown granulose, a fine median gray-brown line, laterodorsal and lateral longitudinal gray-brown bands; 9th tergite dark brown. *Morphology.* I.O.:D. = 3.0. Fore wing with areola postica almost completely bounded by dark veins. Hind wing with 6–7 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 22; 2+1. Subgenital

plate (Fig. 109) with short broad apical process, 2 long setae at base, arms of main plate broadening distally. Gonapophyses (Fig. 110): outer valve with fairly well-developed lobe. A field of 20 trichobothria on each paraproct. Gonopore plate weakly sclerotized.

♂. *Coloration* (freshly killed, in alcohol). As ♀, but clypeal marks darker, transverse fascia in fore wing narrower and often more interrupted but always present, pterostigma spot more extensive. *Morphology.* Eyes prominent, I.O.:D. = 1.0. Hind wing with 6–7 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 29; 2+1. Hypandrium (Fig. 111) very like that of *P. kauaiensis* (Fig. 85), apical teeth long, basal median prong prominent; phallosome with smooth pointed apical tine (Fig. 112). Epiproct (Fig. 113) anterior lobe slightly bilobed, beset with minute short setae arranged in scale-like groups; paraproct apically with large sharply curved spine bearing a long seta, short sharp apical spine, a field of 22 trichobothria and a squat basal sclerotized boss.

Distribution. KAUAI, frequent, locally common.

Holotype ♂, KAUAI: nr Kawaikoi Stream, *Acacia koa*, 27.VII.1963 (I.W.B. Thornton) (BPBM 12,983). Allotype ♀, 3♂,2♀ paratypes, data as holotype.

Apparently confined to the Waimea plateau, this species has been taken on *Acacia koa* and, more often, on *Metrosideros.* It occurs at Mohihi, the Kokee edge of the Alakai Swamp, the rim of Kalalau Valley, Kawaikoi Stream, and at Kokee, and has been collected in July, August, and November. Material examined includes specimens of both sexes collected by Mockford.

The male genitalia, usually among the best of species characters, are practically identical in the 3 species *persimilis, kauaiensis,* and *diastema. P. persimilis* is somewhat larger than the others, particularly *diastema,* and may be distinguished from *kauaiensis* by clypeal and frons pattern, and from *diastema* by abdominal and frons pattern. There is some variation in fore wing pattern, particularly in the extent of the transverse fascia, but this is always much more extensive in the female of *persimilis* than it is in *kauaiensis,* and in the male some remnant of it is always discernible. No intermediaries have been found between these 3 sympatric species, individuals always being clearly assignable to one or another species, despite the unusually close similarity of genitalic characters.

Ptycta placophora Thornton, **new species** Fig. 114–120

♀. *Coloration* (freshly killed, in alcohol). Head generally cream, usual vertex markings brown. Ocelli pale, centripetal margins black. Lateral to ocellar protuberance a buff patch continued as brown line on posterolateral margin of frons. Median brown stirrup-shaped mark, with a brown spot on each side touching anterior margin of frons. Clypeus with brown parallel striae, closer together medially; labrum dark brown. Genae with brown band from orbit to antennal socket; fainter band across gena below this, 3rd parallel faint band near distal margin. Eyes black. Maxillary palpi brown, distal segment darker. Scape and pedicel brown, flagellum dark brown. Thoracic terga brown, median pale buff arrowhead marks on meso- and metathorax, pleura brown. Legs: coxa brown, colorless distally; trochanter colorless; femur pale buff, brown distally; tibia pale brown darkening distally, setae brown; tarsus dark brown. Wings: fore wing with transverse brown band (Fig. 114), pterostigma with broad hyaline area inside posterior margin; hind wing hyaline, brown streak along anterodistal margin, anal cell faint brown distally. Abdomen dorsally with brown transverse bands, faint median longitudinal line. 9th tergite patterned dark and pale brown. *Morphology.* I.O.:D. = 3.2. Veins bounding basal ½ of

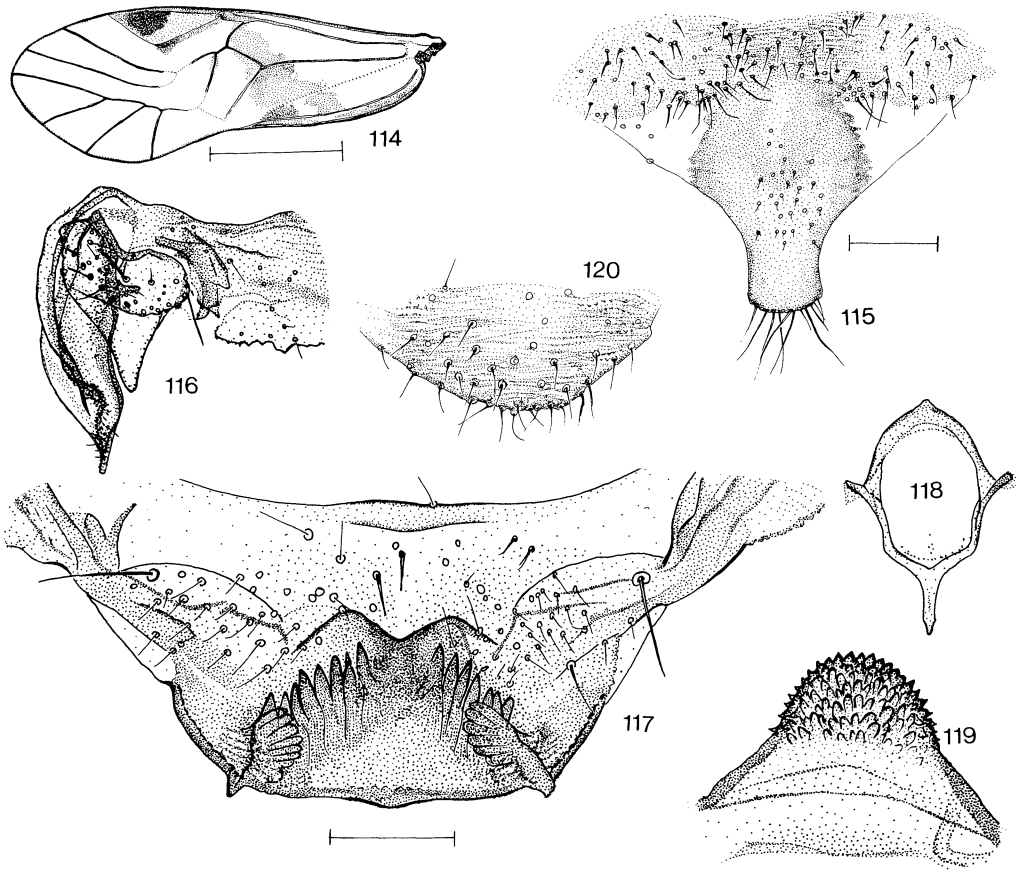

FIG. 114–120. *Ptycta placophora:* **114,** ♀ fore wing; **115,** subgenital plate; **116,** gonapophyses; **117,** hypandrium; **118,** phallosome; **119,** ♂ epiproct lobe; **120,** prehypandrial plate. Fig. 115, 116, 118 and Fig. 117, 119, 120 to common scales.

areola postica in fore wing hyaline. Hind wing with 6 fine setae on margin between ends of *rs.* Number of ctenidia on hind tarsal segments: 22; 2+1. Subgenital plate (Fig. 115) T-shaped, apical process narrowing sharply posteriorly and lacking a pair of longer setae anteriorly. Gonapophyses (Fig. 116): outer valve with long pointed lobe. A field of 24 trichobothria on each paraproct.

♂. *Coloration* (freshly killed, in alcohol). As ♀, but wing markings much reduced. *Morphology.* Eyes prominent, I.O.:D. = 1.1. Number of ctenidia on hind tarsal segments: 22; 2+1. Hind wing with 4–5 fine setae on margin between ends of *rs.* Hypandrium (Fig. 117) symmetrical, with 7 or 8 long pointed teeth each side of median lobe, sclerified ridge as basal continuation of each tooth, sharp low carina of fused flat teeth each side basally. Phallosome (Fig. 118) with finely pointed smooth posterior tine. Well-sclerotized prehypandrial plate (Fig. 120) with curved posterior border. Epiproct with high narrow posterior lobe beset with pointed tubercles (Fig. 119); paraproct with sharp spine apically, large pointed hook bearing long seta, short squat basolateral boss, field of 20–22 trichobothria.

Distribution. KAUAI, frequent to common.

Holotype ♂, KAUAI: Waimea Val, 6.I.1944 (N.L.H. Krauss) (BPBM 12,984). Allotype ♀, KAUAI: Sleeping Giant, 13.IV.1963, *Psidium guajava* (I.W.B. Thornton).

Occurring from 1200 m (W of Waimea Canyon) to the Kokee plateau (Kalalau Lookout, Mohihi, Camp Sloggett, Puu Ka Pele, Kokee), *P. placophora* is also found in the lowlands (Hanapepe, Haena, Sleeping Giant, Kalalau Valley). Other material examined includes specimens from the fringe of the Alakai Swamp, Na Pali Kona Forest, Kalalau Lookout (Mockford), Kokee (Nadler), and Lihue. The species has been taken in January, April, July, August, September, and November.

This species differs from all others of the genus treated here by the possession of a prehypandrial plate. The shape of the female subgenital plate, recognizable even without dissection, is also distinctive. Other characters that, taken together, distinguish this species are the dark maxillary palpi, partially hyaline areola postica, and 3 cheek bars. In common with other species of this group from Kauai, the hypandrium possesses basal carinae, but apart from this it seems to be fairly distantly related to the other forms.

In 4 of over 40 males examined, the dark sclerotized prehypandrial plate is lacking, and in 7 of the males and 1 of 40 females examined, the areola postica veins are pigmented normally, not hyaline basal to the apex as in the majority of specimens of this species. These 2 variations are apparently quite unrelated, nor is the venational abnormality confined to a particular region or elevation. All 4 individuals lacking the prehypandrial plate were collected in the Kokee area, together with other males possessing the structure.

Ptycta telma Thornton, **new species** Fig. 121–126

♀. *Coloration* (freshly killed, in alcohol). Head generally cream, usual vertex markings brown. Ocelli pale, centripetal margins black. Small buff-brown patch each side ocellar protuberance, continuing as buff-brown line along anterior frontal suture. Stirrup mark mid-brown, light brown transverse line each side touching stirrup mark. Clypeus with brown parallel striae closer medially, sometimes forming darker median line; labrum dark brown. Brown band across gena from orbit to antennal socket. Eyes black. Maxillary palpi pale, preapical segment brown, apical segment darker. Scape and pedicel light brown, basal flagellar segment brown, darkening distally, rest of flagellum dark brown. Thoracic terga brown, cream band between dorsal lobes of meso- and metathorax, scutella pale brown. Thoracic pleura brown. Legs: coxa dark brown; trochanter pale buff, femur pale buff, brown apically; tibia buff, brown apically; tarsus brown. Wings: fore wing (Fig. 121) with transverse brown band, usually 2 discrete brown patches in apical ½ of anal cell; vein *m* fuscous for short distance from its point of separation from *rs*; dark patch in apical ½ of pterostigma reaches vertex or nearly so. Hind wing hyaline, faint smokiness on anterodistal margin. Abdomen dorsally with gray-brown transverse marks sometimes forming discernible median line, marks often indistinct. 9th tergite patterned dark and pale brown, epiproct buff. Abdomen ventrally buff, sometimes faint broad transverse bands discernible. *Morphology.* I.O.:D. = 3.0. Hind wing with 7–13 fine setae on margin between ends of *rs*. Number of ctenidia on hind tarsal segments: 16–22; 2+1 or 3+1. Subgenital plate (Fig. 122) Y-shaped, arms of Y somewhat variable in shape, pair of very long setae at base of apical

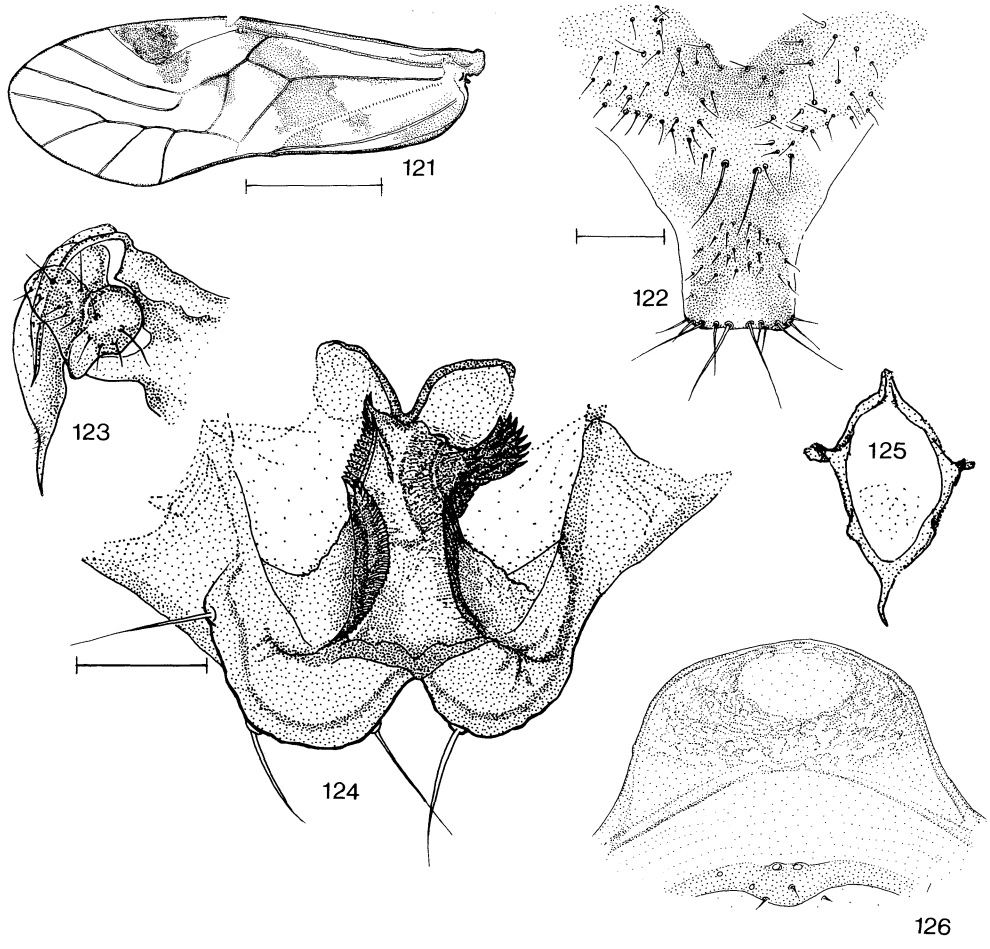

FIG. 121–126. *Ptycta telma:* **121,** ♀ fore wing; **122,** subgenital plate; **123,** gonapophyses; **124,** hypandrium; **125,** phallosome; **126,** ♂ epiproct lobe. Fig. 122, 123, 125 and Fig. 124, 126 to common scales.

process. Gonapophyses (Fig. 123): outer valve with short lobe. A pair of 20–24 trichobothria on each paraproct. Gonopore plate long, sclerotized.

♂. *Coloration* (freshly killed, in alcohol). As ♀, but transverse frontal marks often lacking; transverse fascia on fore wing less extensive though often some remnant of 2nd patch of brown in anal cell, dark mark in pterostigma more extensive. *Morphology.* Eyes prominent, I.O.:D. = 1.2. Hind wing with 9–10 fine setae on margin between ends of *rs.* Number of ctenidia on hind tarsal segments: 19–22; 3+1. Hypandrium (Fig. 124) asymmetrical, median tongue with low blunt spine basally, fairly high basal carinae formed of fused narrow flat teeth with blunt tips, on right and more apically a few broad blunt marginal teeth culminating in a group of close-set long sharp teeth forming a curved hooklike structure; on left side a row of narrow sharp teeth graded shorter apically. Phallosome (Fig. 125) with narrow smooth sharply pointed

apical tine. Epiproct anterior lobe prominent, at least as high as broad, sometimes slightly bilobed apically (Fig. 126); paraproct with fairly large boss, curved spine bearing long seta, short fine apical spine, a field of 24 trichobothria.

Distribution. KAUAI, frequent.

Holotype ♂, KAUAI: Alakai Swamp, trail to Wainiha Ridge, NW of Kawaikoi Stream, 28.VII.1963 (I.W.B. Thornton) (BPBM 12,985). Allotype ♀, 2♂,8♀ paratypes, data as holotype.

This species is apparently a true mountain form, having been collected only on the Kokee plateau above 1000 m. It occurs along the ridge bounding the south of Kalalau Valley, at Mohihi, and at various other localities in the Na Pali Kona Forest Reserve, as well as in the Kokee area. It is one of the few species of *Ptycta* to be well represented in the Alakai Swamp, occurring on both the western and eastern (Wainiha Ridge) boundaries of the swamp, as well as in the swamp proper. Material examined includes specimens of both sexes collected in the Kokee area by other workers (Nadler, Mockford, Swezey). *P. telma* is apparently quite catholic in its habitat, having been collected from *Acacia koa, Metrosideros, Styphelia, Elaeocarpus,* and introduced conifers. Collections have been made from June to September, and in November.

There is some variation in coloration, notably in the clypeus, which often has a darker transverse band forming a vaguely defined cross-shaped mark together with the darker median line. Occasionally remnants of a 2nd transverse band are visible on the gena, and in the fore wing the origin of vein *rs* is sometimes fuscous for a short distance. The extent of the transverse fascia in the fore wing varies considerably, and there is often only a single pigmented patch in the anal cell.

This species is very similar, apart from genitalic characters, to *kauaiensis, diastema* and *zimmermani,* n. sp. It may be distinguished from *kauaiensis* by clypeal pattern, from *diastema* by abdominal color pattern, and from *zimmermani* by the pattern of the transverse fascia in the female fore wing. Males are distinguishable from *zimmermani* by the greater extent of pterostigma pigmentation. The highly asymmetrical hypandrium of the male is unique in the Hawaiian complex of the genus.

Ptycta zimmermani Thornton, **new species** Fig. 127–132

♀. *Coloration* (freshly killed, in alcohol). Head generally cream, vertex markings brown. Ocelli pale, centripetal margins black. Very small buff patch each side ocellar protuberance, continuing as buff line along vertex-frons suture. Median brown stirrup mark on frons usually without lateral light brown marks. Clypeus pale cream, parallel striae not usually so much closer medially as to give effect of darker median line, never a transverse darker band; labrum dark brown. Genae pale cream, brown band from orbit to antennal socket which is ringed brown, never any other bands. Eyes black. Maxillary palpi brown, apical segment darker. Scape and pedical brown, flagellum darker. Thoracic terga brown, median cream band between dorsal lobes of meso- and metathorax; scutella brown; pleura brown. Legs: coxa brown, trochanter pale cream; femur pale cream, brown distally; tibia pale brown, dark brown distally; tarsus dark brown. Wings: fore wing (Fig. 127) with continuous brown transverse fascia, apical ½ of anal cell with single brown patch; dark patch in apical ½ of pterostigma always reaches vertex and is contiguous with *sc* for short distance basal to vertex, rest of pterostigma white by reflected light; hind wing hyaline, faintly smoky on anterodistal margin and in distal angle of anal cell. Abdomen dorsally yellowish cream, usually without discernible transverse bands,

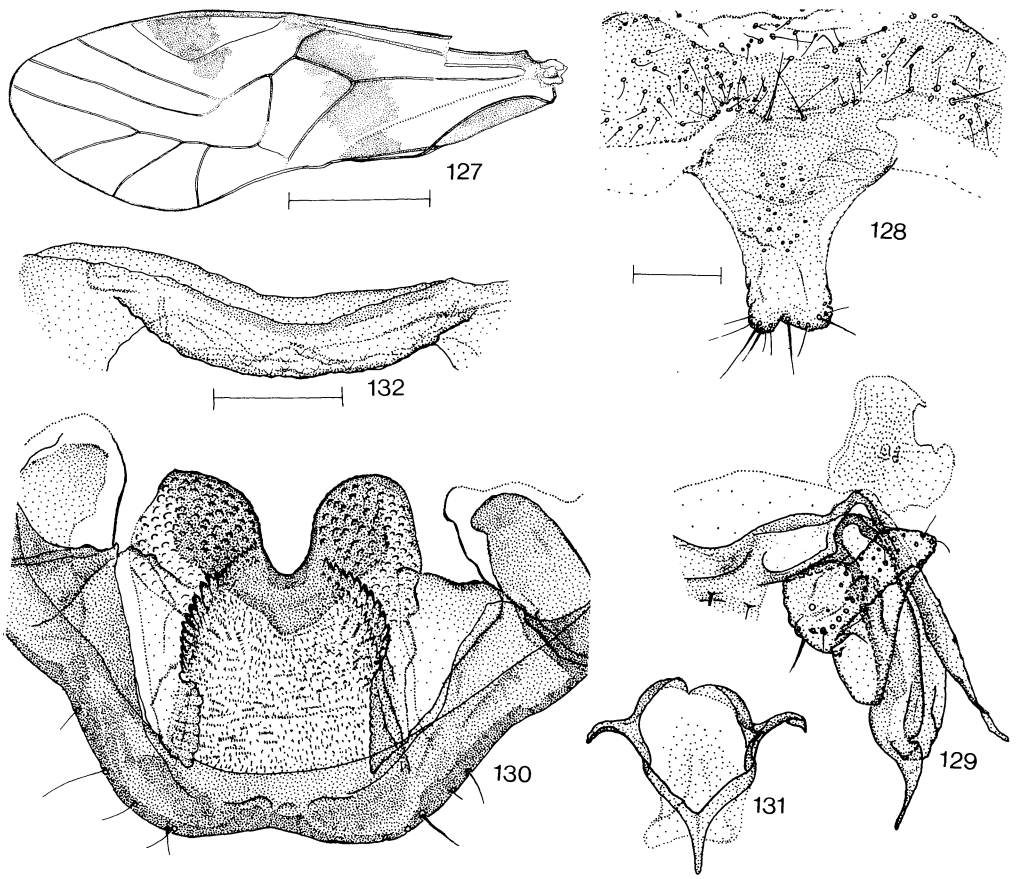

FIG. 127–132. *Ptycta zimmermani:* **127,** ♀ fore wing; **128,** subgenital plate; **129,** gonapophyses; **130,** hypandrium; **131,** phallosome; **132,** ♂ epiproct lobe. Fig. 128, 129, 131 and Fig. 130, 132 to common scales.

9th tergite patterned brown and pale brown, epiproct pale. Abdomen ventrally yellowish cream. *Morphology.* I.O.:D. = 3.6. Hind wing with 7–8 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 24; 2+1. Subgenital plate (Fig. 128) very broadly Y-shaped, apical process long, relatively narrow, a pair of long setae basally. Gonapophyses (Fig. 129): outer valve with large pointed lobe, whole valve thus as long as broad. A field of 25–28 trichobothria on each paraproct. Gonopore plate broad, unsclerotized.

♂. *Coloration* (freshly killed, in alcohol). As ♀, but clypeus darker; dark markings on vertex obliterate pale areas posteriorly; transverse fascia on fore wing almost completely absent; dark mark in pterostigma very extensive. *Morphology.* Eyes prominent, large, I.O.:D. = 1.2. Hind wing with 4–7 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 22–23; 2+1. Hypandrium (Fig. 130) symmetrical, no median boss at base of tongue, marginal carinae of fused flat teeth, margin apically with about 12 sharp teeth, often in 2 ranks towards apex. Phallosome (Fig. 131) with sharp smooth apical tine. Epiproct anterior lobe low,

vaguely bilobed, sparsely tuberculate (Fig. 132); paraproct with short sclerotized boss basally, apically with curved stout spine bearing long seta, short sharp spine, a field of 23–24 trichobothria.

Distribution. KAUAI, frequent.

Holotype ♂, KAUAI: Alakai Swamp to Wainiha Ridge, NW of Kawaikai Stream, *Metrosideros*, 28.VII.1963 (I.W.B. Thornton) (BPBM 12,986). Allotype ♀, data as holotype except *Cryptomeria*.

This species occurs from 1000 to 1200 m and the 1963 localities include the Na Pali Kona Forest Reserve at the edge of the Alakai Swamp, Mohihi, Kokee, along the upper rim of Kalalau Valley, about 2 km inside the Alakai Swamp, and at 1030 m in the Kokee *koa* forest. Other material examined includes specimens of both sexes collected by Mockford at Kokee and the fringes of Alakai Swamp, a female from the Waiaelae River in the SE Alakai Swamp, females from the Alakai Swamp and "Kalalau" collected by Swezey, and from near Kokee and the NW Alakai Swamp collected by Zimmerman. The species occurs on *Acacia koa* in the Kokee area; elsewhere it has been taken on *Metrosideros*. Collections have been made in March, April, July, August, and November.

Variation in coloration includes the clypeus, which very occasionally shows a vague median darker line, the frons, which occasionally bears lateral light brown marks, and the abdomen, which sometimes has brown transverse bands dorsally. Females are distinguishable from *kauaiensis*, *diastema*, and *telma* by the shape and orientation of the transverse fascia in the fore wing; males by the clypeal pattern, abdominal pattern, and wing pigmentation, respectively. In genitalia this species is very similar to *P. diastema*.

The species is named for Dr E.C. Zimmerman, whose works and lectures I have so much enjoyed, and who stimulated my interest in island biology in general and Hawaiian Psocoptera in particular.

oahuensis group

This close-knit and highly distinctive group of 5 fairly large species has representatives on all islands (Fig. 178), one species (*distinguenda*) occurring on the 4 eastern islands of Molokai, Lanai, Maui and Hawaii. Sympatry occurs on Molokai and Hawaii. *P. oahuensis* is unusual in the group in having the hypandrial teeth asymmetrical, recalling the condition in the *haleakalae* group, but otherwise conforms to the group characteristics. In general female wing pattern the *oahuensis* and *haleakalae* groups are similar.

Ptycta oahuensis (Perkins), **revised combination** Fig. 133–138

Psocus oahuensis Perkins, 1899: 81.—Zimmerman, 1948b: 249.
Clematostigma distinguendum var. *oahuense* (Perkins): Enderlein, 1913: 355.
Psocus distinguendus var. *oahuensis* Perkins: Enderlein, 1920: 453.
Ptycta distinguenda var. *oahuensis* (Perkins): Enderlein, 1925: 102.

The following redescription is based on an examination of type material and of other material more recently collected.

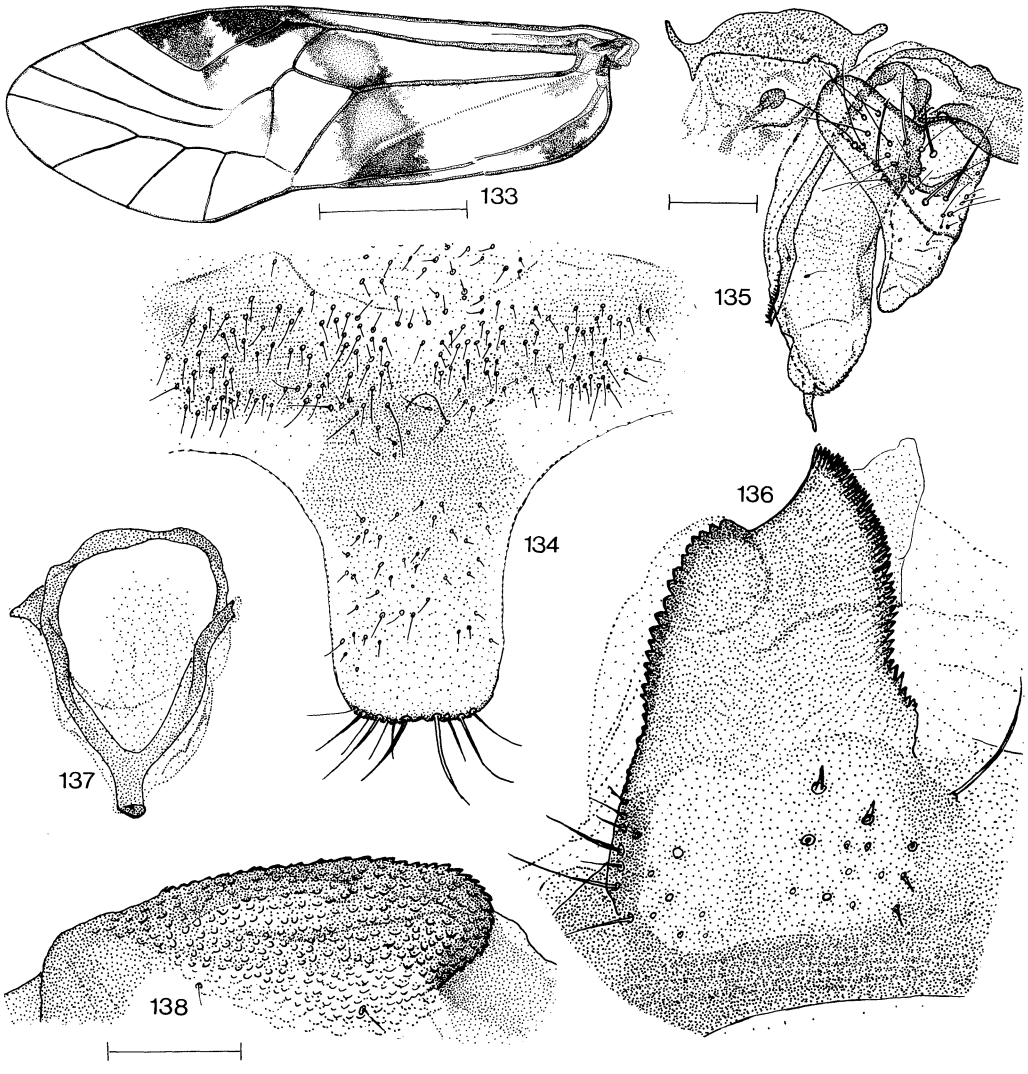

FIG. 133–138. *Ptycta oahuensis:* **133,** ♀ fore wing; **134,** subgenital plate; **135,** gonapophyses; **136,** hypandrium; **137,** phallosome; **138,** ♂ epiproct lobe. Fig. 134, 135, 137 and Fig. 136, 138 to common scales.

♀. *Coloration* (freshly killed, in alcohol). Head with vertex cream, usual markings brown, paler in middle of vertex than elsewhere; a brown line from outside ocellar protuberance along vertex-frons suture. Frons cream, median brown stirrup mark with isolated short linear brown mark each side. Clypeus cream, distinct parallel brown striae. Genae cream, narrow brown line from orbit to antennal socket. Eyes black. Maxillary palpi cream, preapical segment light brown, apical segment brown. Scape, pedicel, and most of basal flagellar segment brown, distal end of latter and rest of flagellum dark brown. Thoracic terga dark brown, median cream line

between dorsal lobes not extending into antedorsa, scutella cream. Thoracic pleura dark brown. Legs: coxa dark brown; trochanter cream; femur cream, brown spot towards apex dorsally except profemur with several brown spots dorsally; tibia cream, dark brown apically; tarsus dark brown. Wings: fore wings (Fig. 133) with discrete transverse fascia at almost right angle to long axis of wing, only ever 1 pigmented patch in cell *An*, never a pigment spot ½ way along *m+cu*, usually a discrete round patch on vein *m* shortly beyond its point of departure from *rs*, pterostigma with pigment spot reaching vertex but not filling ½ of pterostigma. Hind wings very faintly fuscous in anal cell. Abdomen pale whitish cream, transverse gray-brown bands dorsally, sometimes obliterated. Epiproct and paraprocts white except basally epiproct brown and trichobothrial fields of paraprocts brown. 9th tergite brown, darker brown patches. *Morphology.* I.O.:D. = 3.2. Mesothoracic terga, thoracic pleura, coxae, highly polished, shining; metathoracic terga less so. Hind wing with 9 stout marginal setae between ends of *rs*. Number of ctenidia on hind tarsal segments: 30; 3+1. Subgenital plate (Fig. 134) with fairly long apical process with 2 longer setae basally, relatively short and narrow anterior arms. Gonapophyses (Fig. 135): dorsal valve large, long, with short fleshy subapical lobe; outer valve with long lobe. A field of 33–38 trichobothria on each paraproct (38 in type). Gonopore plate sclerotized anteriorly.

♂. *Coloration* (freshly killed, in alcohol). As ♀ except generally darker, transverse fascia in fore wing narrower, pterostigma pigment more extensive, almost filling pterostigma. *Morphology.* Eyes not very prominent, I.O.:D. = 2.2. Thoracic terga, pleura and coxae as ♀. Hind wing with 7 stout marginal setae between ends of *rs*. Number of ctenidia on hind tarsal segments: 26; 3+1. Hypandrium (Fig. 136) slightly asymmetrical, left marginal teeth broader than those on right; no basal median tooth. Phallosome (Fig. 137) apical tine with sclerotized tip. Epiproct anterior lobe (Fig. 138) fairly flat, tuberculate; a field of 32 trichobothria on each paraproct.

Nymph. Body pattern as adult; lacks polish on thorax.

Distribution. OAHU, frequent.

Descriptions based on type material and 1♂, OAHU: Mt Tantalus, 600 m, *Acacia koa*, 22.II.1963; 1♀, OAHU: Pupukea ridge, *Metrosideros*, 19.II.1963.

This species has been taken on *Metrosideros*, *Acacia koa*, and *Dodonaeia* on both the Koolau and Waianae mountain ranges above 300 m. The adult has been collected in all months of the year. Perkins collected it at 1000 m in the Waianae Mts in April 1892; in 1963 the highest locality was at 800 m on Mt Kaala (*Metrosideros*) in March. Material examined included specimens collected by Mockford, Nadler, Swezey, Perkins, Zimmerman, Y. Kondo, Ford, Usinger, Giffard, and Moseley.

P. oahuensis may be distinguished from its close relatives by the subgenital plate, which has a distinctly smaller apical process than that of the others of this group. Moreover, it may be further distinguished from *distinguenda* by the absence of the small pigment spot ½ way along vein *m+cu* in the fore wing, and by the relative shapes and sizes of the marginal hypandrial teeth. There appears to be little variation apart from the spot on vein *m*, which may consist only of a brown pigmentation for a short distance along the vein itself. The lack of spot on *m+cu* and the shape and orientation of the transverse fascia in the fore wing are apparently constant features of the species.

Enderlein reduced this species to a variety of *P. distinguenda*. Despite the undoubted close relationships, genitalic differences are such as to warrant specific separation.

Ptycta distinguenda (Perkins) Fig. 139–149

Psocus distinguendus Perkins, 1899: 80.—Enderlein, 1920: 452 (partim).—Zimmerman, 1948b: 246.
Clematostigma distinguendum (Perkins): Enderlein, 1913: 355.
Ptycta distinguenda (Perkins): Enderlein, 1925: 102.
not *Psocus distinguendus* var. *oahuensis* (Perkins): Enderlein, 1920: 452.
not *Psocus distinguendus* var. *vittipennis* (Perkins): Enderlein, 1920: 453.

The following redescription is based on an examination of type material and of other specimens collected in the islands more recently.

♀. *Coloration* (freshly killed, in alcohol). Head generally whitish cream, vertex marks usually pale brown except extremely posteriorly. A brown line along vertex-frons suture and a second shorter line parallel to this a little more posteriorly. Frons with brown stirrup-shaped mark, a discrete spot each side. Clypeus whitish cream with distinct brown parallel striae, not merging medially. Genae cream, a brown line from orbit to antennal socket, and a second brown mark, sometimes L-shaped, below this. Eyes black. Maxillary palpi whitish cream, preapical segment light brown, apical segment brown. Scape, pedicel and most of basal flagellar segment brown, distal end of latter and rest of flagellum dark brown. Thoracic terga dark brown, whitish cream band along sutures, scutella whitish cream. Thoracic pleura dark brown. Legs: coxa dark brown; trochanter cream; femur cream, brown spot towards apex dorsally except profemur with several brown spots dorsally; tibia cream, dark brown apically, tarsus dark brown. Fore wing (Fig. 139) with fairly narrow distinct continuous transverse fascia slightly angled, only ever 1 pigmented patch in *An*, always a pigmented fleck about ½ way along *m+cu*, a discrete round brown patch on vein *m* shortly beyond its point of departure from *rs*, pterostigma pigment spot reaching vertex but not filling ½ of pterostigma. Hind wings often faintly brown in anal cell, often also a brown streak along anterodistal margin. Abdomen buff, transverse gray-brown bands dorsally, sometimes obliterated. Epiproct and paraprocts white, except basally, epiproct brown and trichobothrial fields of paraprocts brown. 9th tergite with distinct brown patterning (Fig. 140). *Morphology.* I.O.:D. = 3.2. Mesothoracic terga, pleura, coxae highly polished, shining. Metathoracic terga less so. Hind wing with 8–11 stout marginal setae between ends of *rs*. Number of ctenidia on hind tarsal segments: 25–28; 3+1. Subgenital plate (Fig. 141, 142) similar to that of *P. molokaiensis* but with longer apical lobe and more rounded arms; 2 longer setae at base of apical lobe, a field of very short fine setae centrally on apical process. Gonapophyses (Fig. 143, 144) very large, dorsal and outer valves with long lobes. A field of 33–39 trichobothria on each paraproct (39 in type). Gonopore plate with definite pattern of sclerotization anteriorly.

♂. *Coloration* (freshly killed, in alcohol). As ♀, but transverse fascia of fore wing narrower, pterostigma pigment more extensive. *Morphology.* I.O.:D. = 1.1. Thoracic terga, pleura, coxae as ♀. Hind wing with 7–11 stout marginal setae between ends of *rs*. Number of ctenidia on hind tarsal segments: 24–26; 3+1. Hypandrium (Fig. 145, 146) symmetrical, pointed teeth same on both margins of tongue, no basal median spine, no carinae. Phallosome (Fig. 147, 148) apical tine with slight subapical bulge. Apex of abdomen: epiproct anterior lobe (Fig. 149) small, tuberculate; a field of 37–38 trichobothria on each paraproct. Basal boss on paraproct very low, simply a thickening of paraproct wall.

Distribution. MOLOKAI, LANAI, MAUI, HAWAII, frequent.

Specimens, in addition to types, on which further description based. 1♂ (Fig. 146, 148), 1♀ (Fig. 140, 142, 144) HAWAII, Huehue, 27.VII.1921, Swezey; 1♀ (Fig. 139) HAWAII, Halepula, 600 m, lichen-covered *Dyospiros*, 29.I.1963.

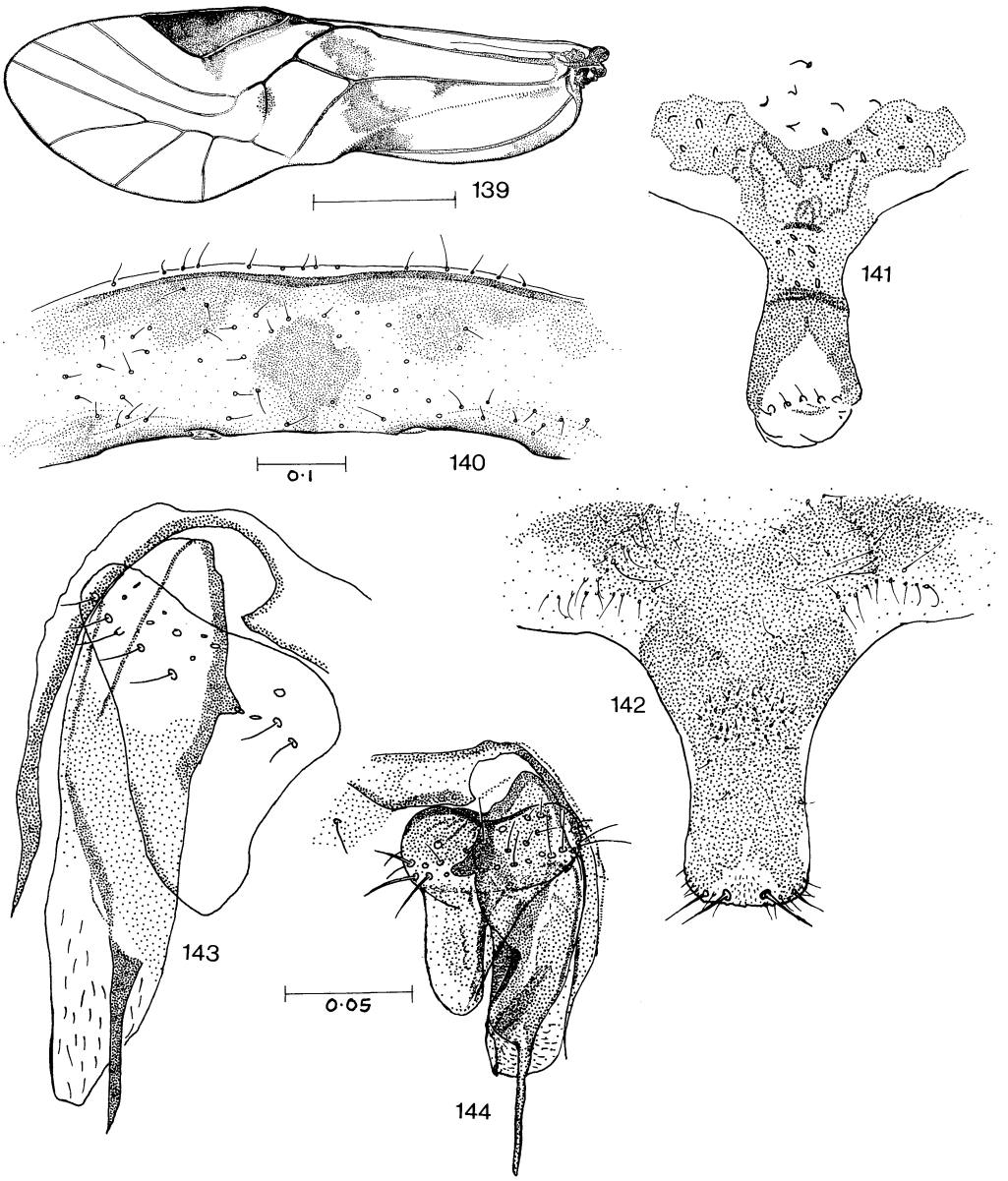

FIG. 139–144. *Ptycta distinguenda* ♀: **139,** fore wing, Halepula specimen, Hawaii; **140,** 9th tergite pattern, Huehue specimen, Hawaii; **141,** subgenital plate, sketched from type dissection; **142,** subgenital plate, Huehue specimen; **143,** gonapophyses, type, sketch; **144,** gonapophyses, Huehue specimen. Fig. 142, 144 to common scale, Fig. 141, 143 not to scale.

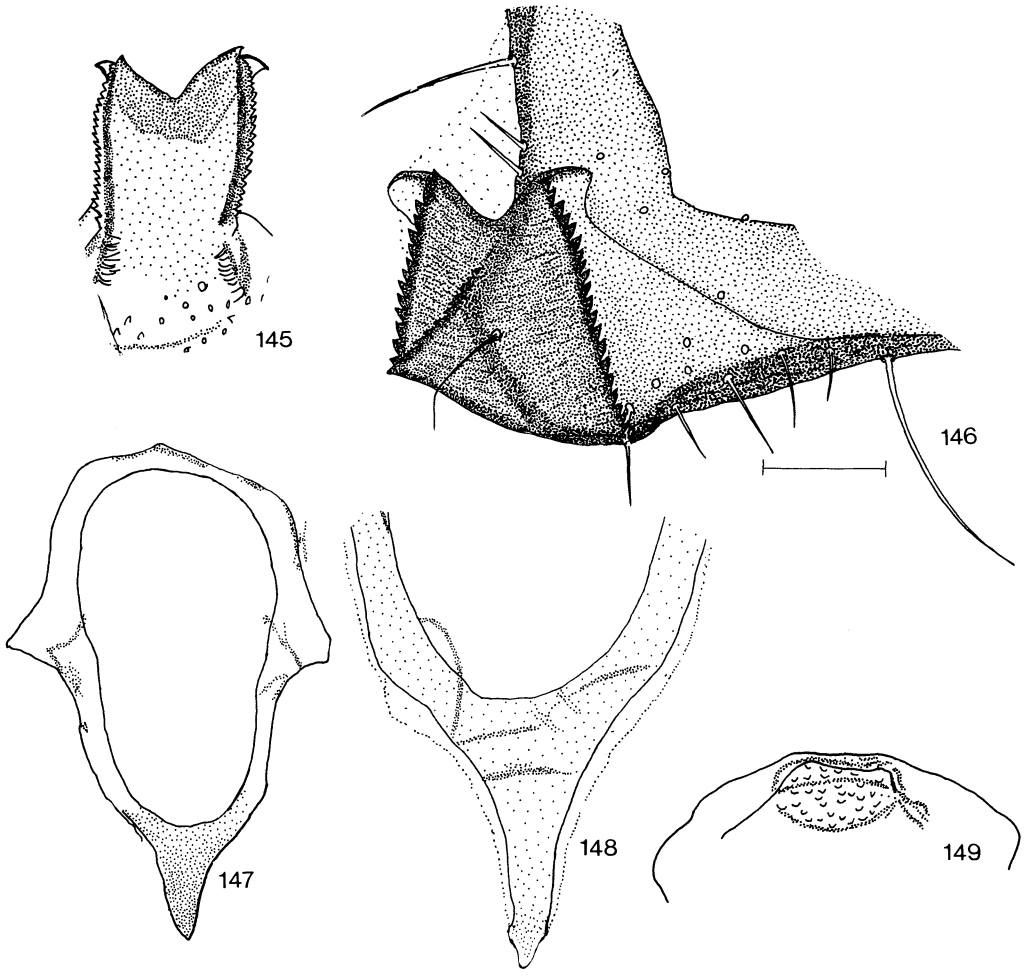

FIG. 145–149. *Ptycta distinguenda* ♂: **145,** hypandrium, type, sketch; **146,** hypandrium, Huehue specimen, Hawaii; **147,** phallosome, type, sketch; **148,** apex of phallosome, Huehue specimen; **149,** epiproct lobe, type, sketch. Fig. 146, 148 to common scale, Fig. 145, 147, 149 not to scale.

The species has been collected on all the 4 eastern islands, but not on Oahu, where the closely related *P. oahuensis* occurs, and not on Kauai. On Molokai the species has been collected in 1963 at 600 m in Dunbar's pasture, E Molokai, on *Metrosideros,* April; N ridge Hipuapua Gulch, W of Halawa Valley on *Metrosideros,* July; near Hakaaana, 490 m, July; at about 600–750 m above Kamiloloa, on *Acacia koa, Dodonaeia, Myoporum, Diospyros,* in June; and at 1000 m on the slope below Kamoku Flats, *Metrosideros,* in July. Other specimens include "Molokai Mountains," June 1896 (Perkins); Kamiloloa, 1000 m, *Coprosma,* December 1925 (Swezey); Kainalu, 460 m, *Metrosideros* and *Sadleria* (Swezey and Bryan). On Lanai, Perkins collected 2 specimens at 600 m in the Koele hills in February 1894. Other collections include Kaiholena,

and 600 m in December 1916 (Giffard); Naio, December 1935 (Usinger). In 1963 the species was collected on Maui in the Iao Valley at 460 m on *Metrosideros* and *Psidium guajava* in May; other collections include Haleakala, 1500 m, May 1896 (Perkins) and Kipahulu, *Acacia koa,* July 1920 (Bryan). On Hawaii the species was collected in February 1963 at Halepula (N Kona), 600 m, on lichen-covered *Diospyros,* and at Kawaihae Uka (Kohala), 1100 m, on dead branches of *Acacia koa.* In June it was collected at Kipuka Puaulu, 1200 m, on *Myrsine, Metrosideros,* and *Dodonaeia*; on the saddle road at the edge of the Parker Ranch, also on *Dodonaeia*; in the saddle between Mauna Kea and the Kohala massif on *Juniperus* covered with *Pleurococcus*; at Kawaihae Uka on dead and living branches of *Myoporum* and dead branches of *Acacia koaea*; at Waimea, 850 m, mango; and Halepula (N Kona), 600 m, on *Diospyros.* Other collections are from Kahuku, Kau, January 1917 (Giffard); Waimea, June 1922 (J.F.I.); Kilauea, August 1919 and June 1934, on *Suttonia, Dodonaeia,* and *Styphelia* (Swezey).

This species is superficially extremely similar to *oahuensis.* However, it may be distinguished without dissection by the invariable presence of a small brown fleck ½ way along vein *m+cu* in the fore wing, as well as by the shape and size of the subgenital plate. The transverse fascia in the fore wing is somewhat narrower than that of *oahuensis,* as was pointed out by Enderlein (1920). In the male, the eyes of *distinguenda* are relatively larger than those of *oahuensis.*

Enderlein reduced *oahuensis* to a variety of *distinguenda.* However, dissection reveals a much closer similarity in genitalic characters and in pattern of sclerotization of the 9th tergite to *P. molokaiensis* (Perkins), which is smaller and lacks the polished thorax which is a feature of this group. Clearly, *oahuensis, distinguenda,* and *molokaiensis* warrant specific status.

In some specimens the high polish on the mesothoracic terga is confined to the antedorsum and the anterior of the dorsal lobes, and sometimes the vertex marks are uniformly brown. These variations seem to be commoner on the island of Hawaii than elsewhere.

Ptycta leurothorax Thornton, **new species** Fig. 150–157

♀. *Coloration* (freshly killed, in alcohol). Head generally pale buff, usual vertex markings buff, dark brown posteriorly, a buff patch in each lateral pale area of vertex. Ocelli pale, centripetal margins black. Dark brown line along vertex-frons suture. Stirrup mark on frons brown, a brown line each side joined to stirrup mark and reaching anterior suture of frons. Clypeus whitish cream, very dark brown parallel lines; labrum dark brown. Genae with brown mark from antennal socket to orbit, antennal socket ringed brown, 2 fainter parallel bands in distal ½ of gena. Eyes black. Maxillary palpi whitish cream, preapical segment pale brown, apical segment dark brown. Scape pale cream, pedicel light brown, basal flagellar segment brown darkening distally, rest of flagellum very dark brown. Thoracic terga dark brown, antedorsum of mesothorax separated from dorsal lobes by a cream Y-shaped mark following sutures. Scutella pale. Thoracic pleura brown. Legs: coxa brown; trochanter colorless, femur pale, 1 or 2 brown spots towards apex (except fore leg—femur with 6 brown spots on upper surface); tibia pale brown, darkening distally; tarsus dark brown. Wings: fore wing with transverse brown band (Fig. 150), a brown mark ½ way along *m+cu,* a discrete brown spot on transverse section of *m*; hind wing hyaline, faint infuscation in apical part of anal cell, stalk of *rs* pale. Abdomen dorsally with very broad transverse gray-brown bands, fusing in midline.

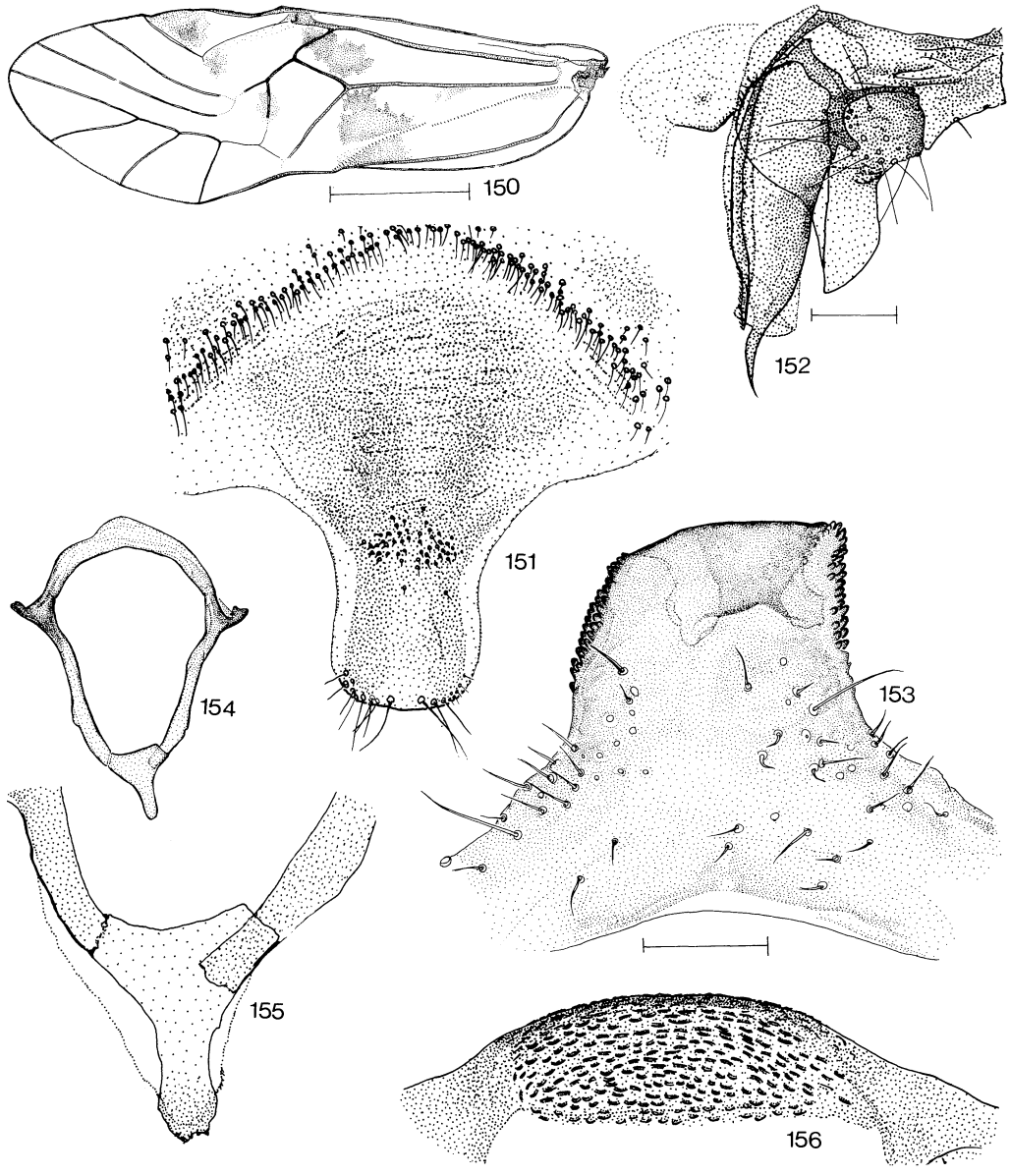

FIG. 150–156. *Ptycta leurothorax:* **150,** ♀ fore wing; **151,** subgenital plate; **152,** gonapophyses; **153,** hypandrium; **154,** phallosome; **155,** phallosome tine; **156,** ♂ epiproct lobe. Fig. 151, 152, 154 and Fig. 153, 155, 156 to common scales.

9th tergite patterned brown and buff, epiproct cream. Abdomen ventrally buff. *Morphology.* I.O.:D. = 3.0. Hind wing with 10 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 26; 3+1. Meso- and metathoracic terga, thoracic pleura and coxae highly polished, shining. Subgenital plate (Fig. 151) bordered anteriorly by a close band of several ranks of setae; anterolateral to this band, a small sclerotized patch each side. Main body of plate devoid of setae, apical process with a discrete field of very short setae. A field of 28 trichobothria on each paraproct. Gonapophyses (Fig. 152): outer valve massive, with large lobe; dorsal valve with fleshy subapical lobe.

♂. *Coloration* (freshly killed, in alcohol). As ♀, except legs generally darker; in fore wing pterostigma completely filled with pigment, transverse fascia narrower and somewhat interrupted; abdomen ventrally gray-brown. *Morphology.* Eyes large, I.O.:D. = 1.4. Flagellum thicker than that of ♀, setae more off-standing and conspicuous. Hind wing with 10 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 30; 3+1. Meso- and metathoracic terga, thoracic pleura and coxae highly polished, shining. Hypandrium (Fig. 153) almost symmetrical, simple; tongue with (basally) 2 ranks of shorter blunt teeth, slightly sharper and smaller on one side of tongue; phallosome (Fig. 154, 155) with blunt apical tine, widening subapically, having apical surface rough. Epiproct anterior lobe tuberculate, not bilobed (Fig. 156); paraprocts with apical large spine bearing long seta, sharp short seta, low basal boss, and a field of 35–36 trichobothria.

Distribution. KAUAI, rare.

Holotype ♂, KAUAI: Kokee, 1000 m, koa forest, dead branches ? apple, 26.XI.1963 (I.W.B. Thornton) (BPBM 12,987). Allotype ♀, KAUAI: Waimea Canyon Lookout, 1070 m, *Acacia koa,* 27.VII.1963.

This species has been collected only from *Acacia koa* at elevations above 850 m in the Kokee area in July and November 1963.

The size, polished thorax, and structure of the dorsal valve of the female gonapophyses place this species in the *oahuensis* group, of which it is the only Kauai representative. The subgenital plate, although like other members of the group in possessing a long apical process, is quite unusual in the shape of the disc and associated chaetotaxy.

Ptycta lobophora Thornton, **new species** Fig. 157–163

♀. *Coloration* (freshly killed, in alcohol). Head generally cream, vertex markings brown. Faint gray line along frons-vertex suture. Frons with dark brown median stirrup mark, each side a short gray linear mark parallel to but not contiguous with anterior suture, and not confluent with stirrup mark. Clypeus uniform with distinct brown parallel striae. Gena with a brown band from orbit to antennal socket, otherwise pale cream. Eyes black. Maxillary palpi pale cream, subapical segment faint brown, apical segment brown. Scape, pedicel, and most of basal flagellar segment pale brown; apex of basal flagellar segment and rest of flagellum brown. Thoracic terga dark brown, mesothoracic antedorsum with cream border along posterior sutures, a cream line between dorsal lobes, dorsal lobes of mesothorax with cream lateral and posterior margins; dorsal lobes of metathorax without such margins, with a vague small cream line posteromesially; scutella pale cream. Pleura brown. Legs: coxa dark brown, trochanter, femur and tibia pale cream, femur and tibia brown apically, tarsus brown. Fore wing (Fig. 157) with distinct complete transverse fascia, single brown patch in apical ½ of anal cell; a large brown patch ½ way along *m+cu*; a distinct rounded patch ½ way down vein *m* beyond

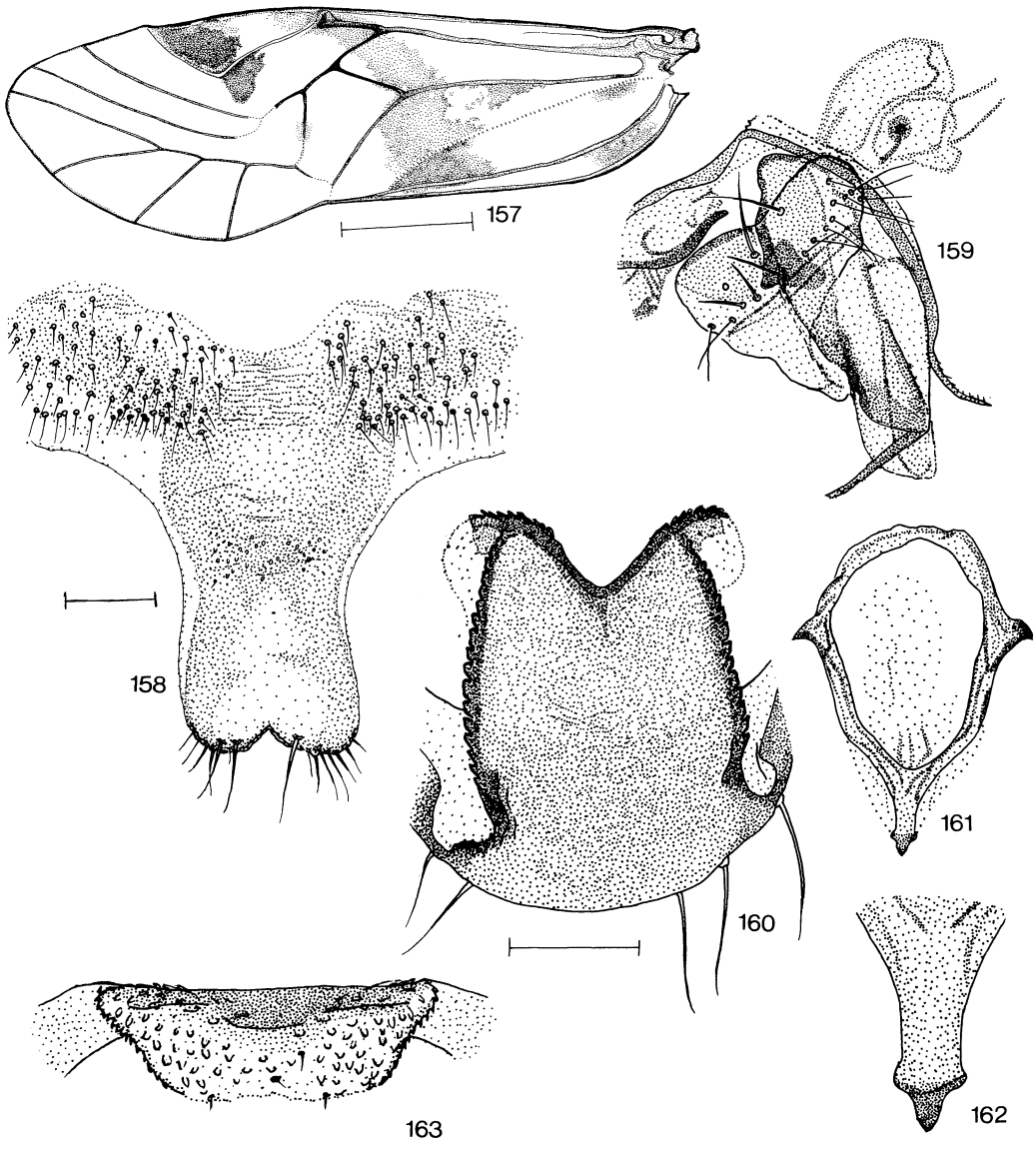

FIG. 157–163. *Ptycta lobophora:* **157,** ♀ fore wing; **158,** subgenital plate; **159,** gonapophyses; **160,** hypandrium; **161,** phallosome; **162,** phallosome tine; **163,** ♂ epiproct lobe. Fig. 158, 159, 161 and Fig. 160, 162, 163 to common scales.

its departure from *rs*; a distinct brown patch within apical ½ of pterostigma, this extending beyond vertex, a large conspicuous brown mark bordering outside of pterostigma for a short distance basad to vertex; faint infuscation along r_{2+3} and in cells M_1, M_2, and M_3. Hind wing hyaline, anal cell faint brown apically, a faint brown mark along anterodistal border. Abdomen

cream, with narrow brown transverse bands dorsally; ventrally cream, apical sclerites brown. *Morphology.* I.O.:D. = 2.3. Antennal setae short, normal. Hind wing with 8 fairly stout marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 28; 3+1. Thoracic terga waxy, but not highly polished. Subgenital plate (Fig. 158) with long apical process widening apically and incipiently bilobed, 4 long stout setae and 14 others on apical margin; lacking 2 distinctly longer setae at base of process; a field of very short sharp setae on narrow part of process; fields of long setae on disc laterally. Gonapophyses (Fig. 159): dorsal valve fleshy, with very large subapical lobe, apical spine stout, bluntly serrated at tip; ventral valve with minute sharp recurved hooks; outer valve with long lobe. A field of 34 trichobothria on each paraproct. Gonopore plate (Fig. 159) not well sclerotized.

♂. *Coloration* (freshly killed, in alcohol). As ♀. *Morphology.* I.O.:D = 0.8, eyes prominent. Setae on underside of antennae 2× as long as those of upper side, longest 2× narrowest width of basal flagellar segment, standing off at right angles; those on upper surface sloping obliquely towards apex of antenna. Hind wing with 8 fairly stout marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 30; 3+1. Thoracic terga waxy, not highly polished. Hypandrium (Fig. 160): tongue symmetrical, with marginal sharply flattened teeth, becoming pointed towards apex; no basal median spine. Phallosome (Fig. 161, 162) with stout single apical tine narrowing sharply to a point at apex. Epiproct with broad low lobe (Fig. 163), a field of approximately 40 trichobothria on paraproct.

Nymph. Head markings as adult except clypeus has a broad transverse brown band midway.

Distribution. HAWAII, rare.

Holotype ♂, HAWAII: Kilauea Crater, Devastation Trail, 1200 m, *Metrosideros,* 5.IX.1961 (I.W.B. Thornton) (BPBM 12,988). Allotype ♀, data as holotype.

Both sexes were collected at Kilauea (Devastation Trail) in November 1961 on *Metrosideros* that had been severely damaged by volcanic ash but was beginning to revive.

Another representative of the *oahuensis* group, *P. distinguenda,* is sympatric with *lobophora.*

Ptycta molokaiensis (Perkins), **revised combination** Fig. 164–171

Psocus molokaiensis Perkins, 1899: 80.—Zimmerman, 1948b: 248.
Clematostigma molokaiensis (Perkins): Enderlein, 1913: 355.
Psocus haleakalae var. *molokaiensis* Perkins: Enderlein, 1920: 451 (partim).
Ptycta haleakalae var. *molokaiensis* (Perkins): Enderlein, 1925: 102 (partim).
not *Psocus konae* Perkins, not *Psocus kauiaensis* Perkins: sensu Enderlein, 1920: 451; Banks, 1931: 437.

The following redescription is based on an examination of the type specimens, and on other material collected on Molokai. It is given as a supplement to that of Perkins.

♀. *Coloration* (freshly killed, in alcohol). Head generally cream, vertex markings brown. Light brown mark along frons-vertex suture. Frons cream, brown median stirrup mark, lateral paler marks discrete. Clypeus whitish cream, distinct parallel striae not merging medially. Genae cream, thin line from orbit to antennal socket, wider band below this. Eyes black. Maxillary palpi pale cream, apical segment brown. Antennae with scape and pedicel brown, basal flagellar segment pale brown, darker apically, rest of flagellum brown. Thoracic terga brown, wide cream border posteriorly, narrow median cream line on mesothorax, scutella pale. Pleura brown. Legs: coxa brown; trochanter pale; femur brown on upper surface, pale cream below; tibia whitish cream; tarsus dark brown. Wings: fore wing (Fig. 164) with costal

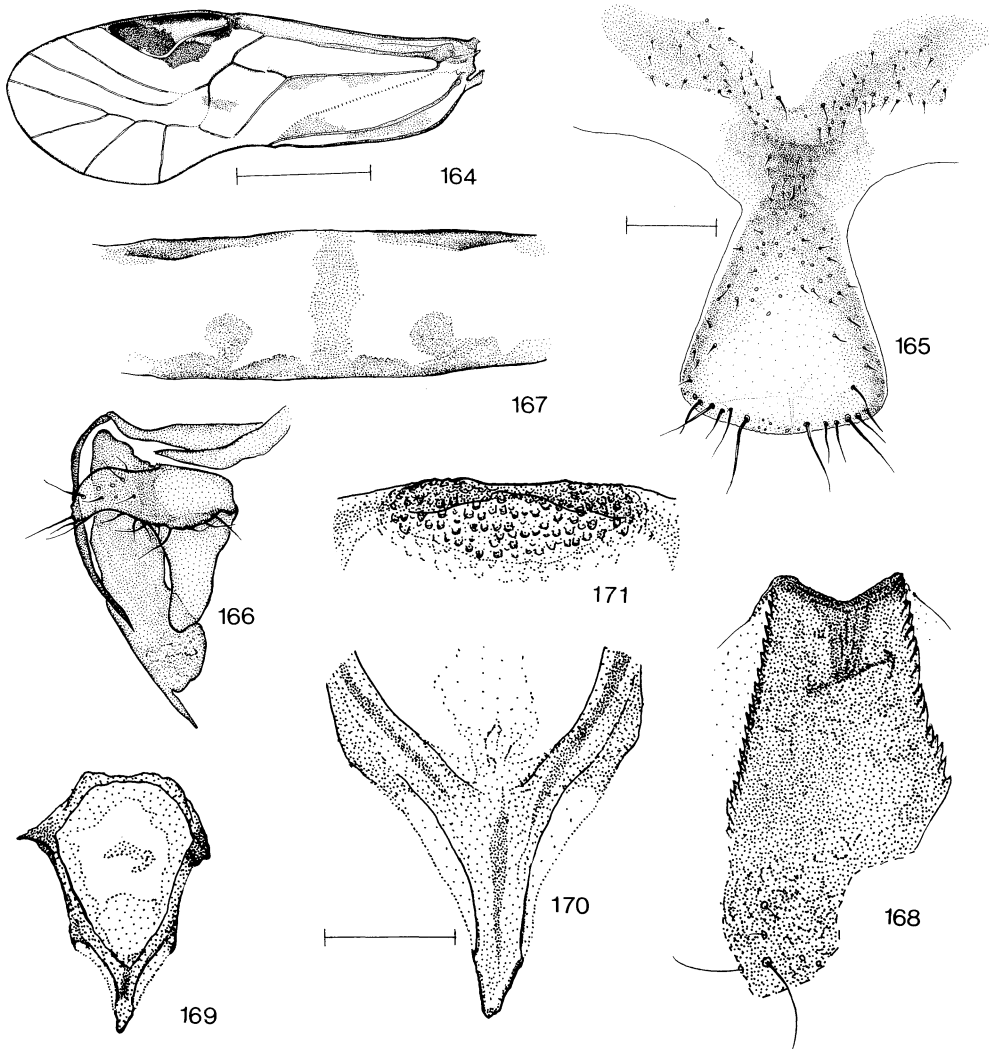

FIG. 164–171. *Ptycta molokaiensis:* **164,** ♀ fore wing; **165,** subgenital plate; **166,** gonapophyses; **167,** ♀ 9th abdominal tergite; **168,** hypandrial tongue; **169,** phallosome; **170,** phallosome tine; **171,** ♂ epiproct lobe. Fig. 165, 166, 167, 169 and Fig. 168, 170, 171 to common scales.

cell brown, distinct brown markings as described by Perkins; hind wing hyaline, slightly fuscous in apical angle of anal cell, no dark streak on anterodistal margin. Abdomen cream, gray-brown granulated markings; 9th tergite yellowish cream with brown sclerotizations, epiproct and paraprocts yellowish cream, trichobothrial fields brown. *Morphology.* I.O.:D. = 3.9. Hind wing with 5–10 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 21–23; 3+4. Thorax not shining. Subgenital plate (Fig. 165) with apical process elongate. widening apically, basal arms narrowing distally, 2 very long setae at base of apical lobe. Gonapophyses (Fig. 166): dorsal valve large, with fleshy apical lobe extending well beyond

base of apical spine; outer valve with large lobe, extending as far posteriorly as tip of ventral valve. A field of 29–34 trichobothria on each paraproct (type has 34). Epiproct long, unsclerotized at base except laterally. Gonopore plate unsclerotized. 9th abdominal tergite with very well-marked pattern of sclerotization (Fig. 167).

♂. *Coloration* (freshly killed, in alcohol). As ♀, fore wing as figured by Zimmerman (1948b). *Morphology.* I.O.:D. = 2.2. Hind wing with 7 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 23; 3. Thorax not shining. Hypandrium (Fig. 168) slightly asymmetrical, apical tongue with sharp teeth on both edges, teeth larger on one side than other, no basal spine. Phallosome with single pointed apical tine (Fig. 169, 170) with subapical bulge. Sculpturing of 9th tergite as ♀, epiproct with low tuberculate anterior lobe (Fig. 171). Basal paraproct boss low, a field of 34 trichobothria on each paraproct.

Distribution. MOLOKAI, MAUI, rare.

Further description based on types and 1♂,1♀, MOLOKAI: 600 m above Kamiloloa, on *Acacia koa,* 19.VII.1963.

This species was found on Molokai in July 1963 at 600 m above Kamiloloa on *Acacia koa,* and in June 1896 by Perkins at 900 m. A single specimen taken from W Maui near Kanaha Stream, 250 m, in December 1928 by Bryan is somewhat darker generally than the specimens from Molokai, but it is not sufficiently different to warrant subspecific distinction.

This species is clearly related to *oahuensis* and *distinguenda.* It is, however, smaller than either, and, unusually in this group, the thoracic terga are dull. The fore wing markings of this species are quite unlike any other species of the genus and are diagnostic.

vittipennis group

This group comprises the single species *vittipennis,* which possesses characters of both the *haleakalae* and *oahuensis* groups. It occurs on Kauai, on which the *haleakalae* group is unrepresented.

Ptycta vittipennis (Perkins), **revised combination** Fig. 172–177

Psocus vittipennis Perkins, 1899: 82.—Zimmerman, 1948b: 250.
Psocus distinguendus var. *vittipennis* Perkins: Enderlein, 1920: 453.
Ptycta distinguenda var. *vittipennis* (Perkins): Enderlein, 1925: 102.

The following redescription is based on an examination of type material and specimens collected more recently.

♀. *Coloration* (freshly killed, in alcohol). Head generally cream, usual vertex markings brown. Ocelli pale, centripetal margins black. A brown patch each side of ocellar protuberance, continuing as line along anterior edge of vertex. Frons pale cream, median stirrup mark dark brown, no lateral marks. Clypeus cream, parallel striae brown, darker medially; labrum dark brown. Genae pale cream, brown mark from lower edge of orbit to antennal socket, paler brown band from orbit ½ way down gena. Eyes black. Maxillary palpi brown, apical segment somewhat darker. Scape and pedicel brown, basal flagellar segment pale brown, dark brown apically, rest of flagellum dark brown. Mesothoracic terga dark brown, almost black, metathoracic terga dark brown. Dorsal lobes separated by median cream band. Scutella brown.

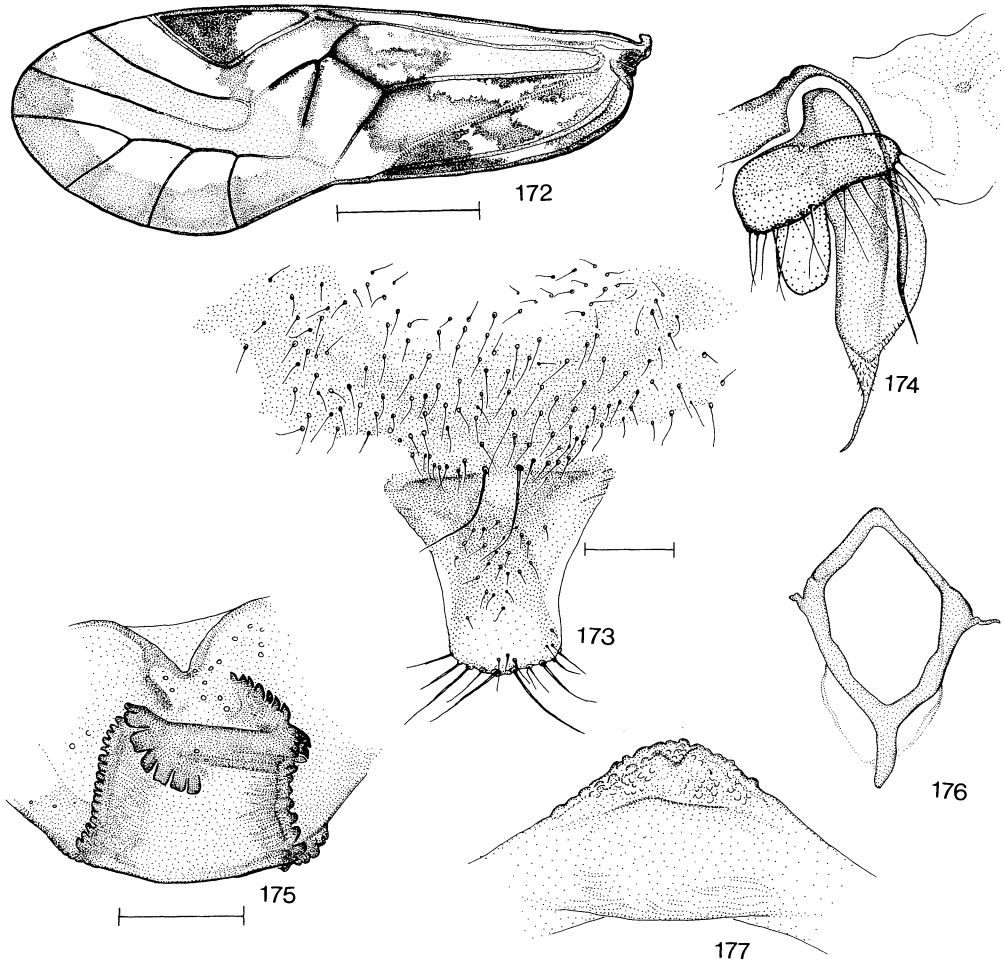

FIG. 172–177. *Ptycta vittipennis:* **172,** ♀ fore wing; **173,** subgenital plate; **174,** gonapophyses; **175,** hypandrium; **176,** phallosome; **177,** ♂ epiproct lobe. Fig. 173, 174, 176 and Fig. 175, 177 to common scales.

Thoracic pleura dark brown. Legs: coxa dark brown; trochanter pale cream, brown patch ventrally; femur pale cream, light brown dorsally; tibia pale brown, darkening preapically; tarsus dark brown. Fore wing (Fig. 172) distinctly patterned in various shades of brown; hind wing with less distinct clouds. Abdomen dorsally cream, median brown band and wider band extremely lateral each side, ventrally brown. *Morphology.* I.O.:D. = 3.0. Head shining. Hind wing with 8 fine setae on margin between ends of *rs.* Number of ctenidia on hind tarsal segments: 31; 2+1. Thoracic terga highly polished, shining. Subgenital plate (Fig. 173) with apical process narrowing markedly towards posterior, 2 long setae at base of process (these not clear in type). Gonapophyses (Fig. 174): outer valve with fairly long lobe bluntly rounded at apex. A field of 27–28 trichobothria on each paraproct. Gonopore plate large, unsclerotized.

♂. *Coloration* (freshly killed, in alcohol). As ♀, but head markings darker and more extensive. *Morphology.* Eyes fairly prominent, I.O.:D. = 2.0. Head shining. Hind wing with 7 fine setae on margin between ends of *rs.* Number of ctenidia on hind tarsal segments: 31; 2+1. Thoracic terga highly polished, shining. Hypandrium (Fig. 175) lacking median tooth at base of tongue; tongue asymmetrical; left margin with row of close-packed narrow teeth progressively wider and blunter apically, right marginal teeth large and blunt basally, progressively sharper apically; no basal carinae. Phallosome (Fig. 176) with broad apical tine beset at somewhat blunt tip with fine setae. Anterior epiproct lobe high, tuberculate, tapering to a rounded apex (Fig. 177); paraproct with large apical spine bearing long seta, fine short apical seta, basal sclerotized boss squat and low, a field of 26 trichobothria.

Distribution. KAUAI, occasional.

Based on types and 1♂,1♀, KAUI: Mohihi Stream, 2 km E of junction with Poonau Stream, 27–29.VII.1963.

The type specimens (1♂ and 1♀ from the mountains of Kauai) have been dissected, and other material examined includes 1♀ collected in the mountains, Waimea, by Perkins in 1894, 1 of each sex collected near Kokee by Zimmerman in July 1937, 6♂ from the fringe of the Alakai Swamp collected by Mockford in August 1957, and material of both sexes from Mohihi, July 1963. *P. vittipennis* is known only from the Kokee and Na Pali Kona forest plateau on Kauai. Its range evidently extends to some degree into the Alakai Swamp. It occurs on introduced conifers as well as on *Metrosideros.*

Genitalic characters are apparently constant, as are the relative lengths of dark and light sections of the veins of the fore wing. Fore wing pattern varies only slightly.

This species is distinguishable from *monticola* and *heterogamias,* which it resembles somewhat in fore wing pattern, by the arrangement of light and dark sections of the fore wing veins, the high gloss and dark color of the thoracic terga, and by genitalic characters. In the highly polished thoracic terga and the sclerotized tip of the phallosome tine, as well as hypandrial structure, *vittipennis* is similar to members of the *oahuensis* group. However, the dorsal valve is unlobed, and the subgenital plate is of a fairly normal type. It may be regarded as intermediate between the *haleakalae* and *oahuensis* groups, with fore wing characters that are unique.

disclera group

No representative of this group of 4 species has been found on Kauai, or on Lanai (Fig. 291). There is sympatry of 2 species on Hawaii, and *disclera,* which occurs on Molokai and Maui, has recognizably distinct populations on W Maui, and on Molokai and E Maui.

Ptycta disclera Thornton, **new species** Fig. 179–185

♀. *Coloration* (freshly killed, in alcohol). Head generally cream, vertex markings brown. A brown mark each side ocellar protuberance, continuing as a line along frons-vertex suture. Frons with median stirrup mark brown, lateral marks fainter brown, linear, touching anterior frontal suture. Clypeus with brown striae fusing medially anteriorly, a suggestion also of a darker transverse band across clypeus. Gena with brown band orbit to antennal socket, a 2nd L-shaped gray-brown mark below this. Eyes black. Maxillary palpi brown, apical segment

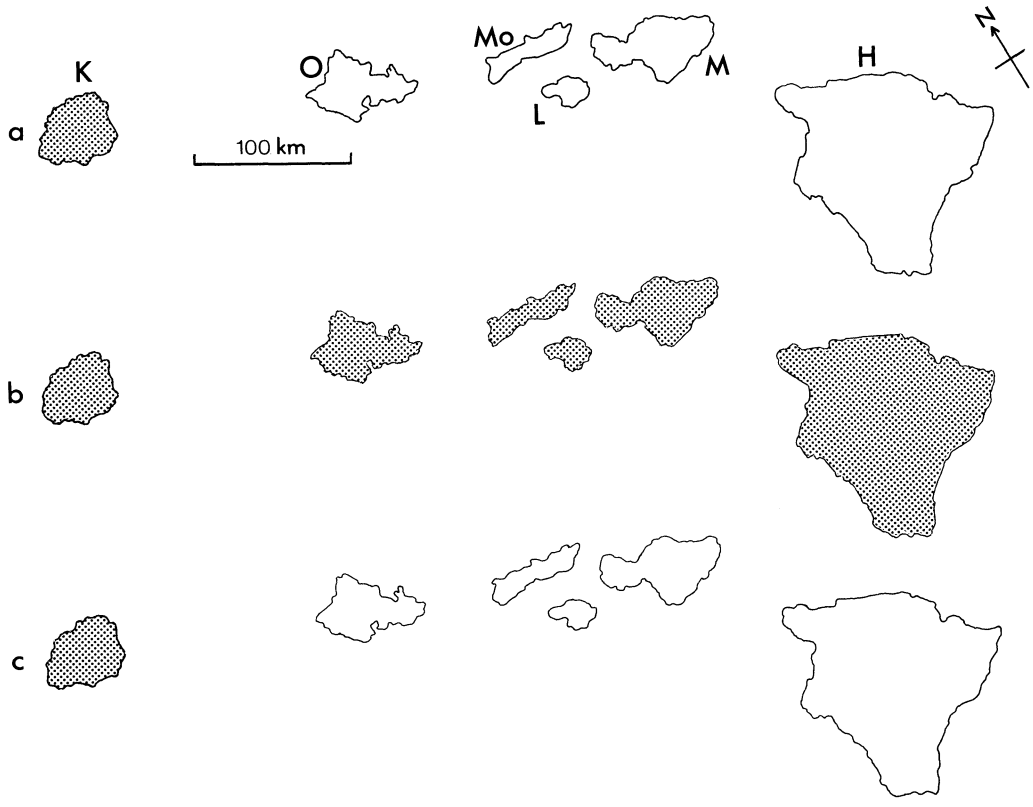

FIG. 178. Archipelago distributions of species groups of *Ptycta:* **a,** *kauaiensis* (8 species); **b,** *oahuensis* (5); **c,** *vittipennis* (1).

darker. Antenna brown, basal flagellar segment only slightly paler than rest. Thoracic terga brown, broad cream line between dorsal lobes and along their posterolateral margins. Scutella brown. Pleura brown. Legs: coxa brown; trochanter colorless; femur and tibia pale fuscous, darker at apices; tarsus brown. Fore wing (Fig. 179) with continuous brown transverse fascia, 2 brown patches in anal cell, more basal one sometimes very small, veins bounding basal ½ of areola postica pigmented, fork of *rs* and *m* with brown pigment along veins, pterostigma spot not reaching vertex. Abdomen cream, gray-brown diffuse pigment dorsally. *Morphology.* I.O.:D. = 3.0. Hind wing with 3–6 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 21–24; 2+1. Subgenital plate (Fig. 180) with broad, angular apical process, 2 longer setae at its base. Gonapophyses (Fig. 181): dorsal valve narrowing fairly gradually to apical spine; outer valve with small lobe. A field of 20–24 trichobothria on each paraproct. Gonopore plate anteriorly only slightly bilobed.

♂. *Coloration* (freshly killed, in alcohol). As ♀ but 2nd genal stripe sometimes very faint; pterostigma spot touches vertex and extends basally; transverse fascia in fore wing interrupted. *Morphology.* I.O.:D. = 1.6–1.8. Hind wing with 4 or 5 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 21–24; 2+1. Hypandrium (Fig. 182) symmetrical,

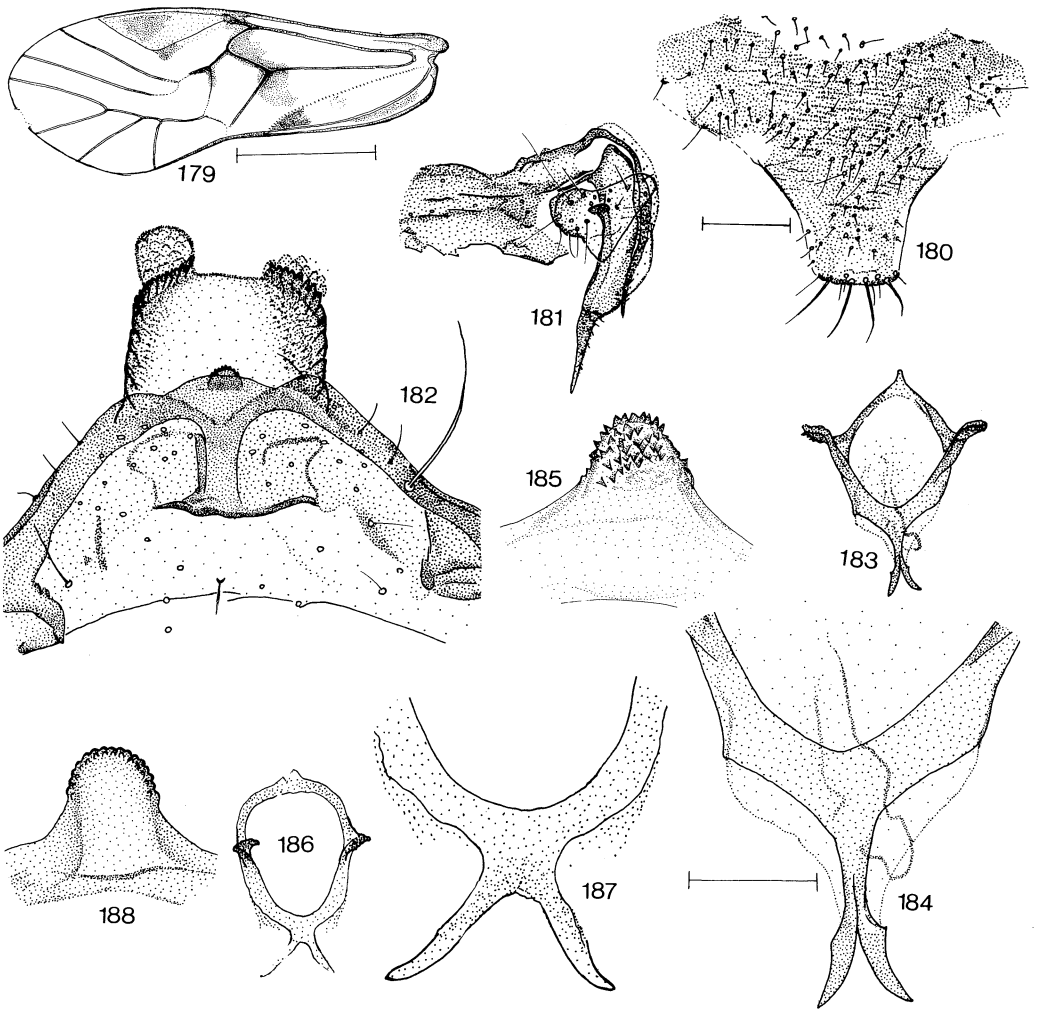

FIG. 179–188. **179–185,** *Ptycta disclera:* **179,** ♀ fore wing; **180,** subgenital plate; **181,** gonapophyses; **182,** hypandrium; **183,** phallosome; **184,** phallosome tine; **185,** ♂ epiproct lobe. **186–188,** *Ptycta iaoensis* ♂: **186,** phallosome; **187,** phallosome tine; **188,** epiproct lobe. Fig. 180, 181, 183, 186 and Fig. 182, 184, 185, 187, 188 to common scales.

teeth on margin of tongue pointed, becoming progressively smaller and narrower apically; median basal boss rugose. Phallosome tine Y-shaped, apical arms pointed, curved (Fig. 183, 184). Epiproct (Fig. 185) with fairly high, rugose anterior lobe, paraprocts each with a field of 24–25 trichobothria, basal boss sclerotized, prominent. A discrete ventral sclerotized patch each side anterior to hypandrium.

Distribution. MOLOKAI, MAUI, occasional.

Holotype ♂, MOLOKAI: valley N of Kamoku Stream, S of Hanalilolilo, 1200 m, beating

Metrosideros and other trees, 19.VII.1963 (I.W.B. Thornton) (BPBM 12,989). Allotype ♀, MOLOKAI: hills behind Halawa Val, S of Pohakuloa, on *Cibotium*, 16.II.1963 (I.W.B. Thornton). 1♂ paratype, data as allotype.

On Molokai *disclera* has been taken on *Metrosideros*, *Cibotium* and *Acacia koa*, and occurs at elevations above 600 m. Collections have been made at Kainalu Gulch (ca. 600 m) in April 1963 and June 1927 (Bryan), S of Pohakuloa in the highlands at the head of Halawa Valley (ca. 600 m) in July 1963, at about 600 m above Kamiloloa and at about 1200 m in the area S of Hanalilolilo, also in July 1963. Both sexes were collected from Olinda, E Maui (1200 m) on *Sequoia sempervirens*, in January 1963.

The hypandrium of this species is closely similar to that of *P. drepana*. *P. disclera* differs in the pigmentation of the veins bounding the areola postica in the fore wing, as well as in the shape of the epiproct lobe, structure of the phallosome tine, subgenital plate, female wing markings, and the structure of the outer valve of the female gonapophyses.

Ptycta iaoensis Thornton, **new species** Fig. 186–188

♀. Unknown.

♂. *Coloration* (freshly killed, in alcohol). Head generally cream, vertex markings brown, very dark brown mark each side ocellar protuberance continuing as line along frons-vertex suture. Frons cream, median stirrup mark brown, lateral marks darker brown, linear, forming angle with anterior frontal suture, not running along it. Clypeal striae fuse medially anteriorly, faint transverse band. Gena with brown band from orbit to antennal socket, an L-shaped brown mark below this. Eyes black. Maxillary palpi brown, apical segment darker. Antenna brown, basal flagellar segment slightly paler. Antedorsum and anterior portion of dorsal lobes of mesothorax paler brown than other principal thoracic tergites. Legs and fore wing as *P. disclera*. Abdomen cream, gray-brown diffuse dorsal markings. *Morphology*. I.O.:D. = 1.7. Hind wing with 4 or 5 fine marginal setae between ends *rs*. Ctenidia on hind tarsal segments: 21–24; 2+1. Hypandrium as *P. disclera*. Phallosome (Fig. 186, 187) tine widely bifid with short, fairly broad neck, 2 arms of tine slightly scimitar-shaped. Epiproct with crenulate anterior lobe (Fig. 188). Paraproct with field of 25 trichobothria, basal boss sclerotized. Discrete ventral sclerotized patch anterior to hypandrium each side.

Distribution. MAUI, rare.

Holotype ♂, MAUI: upper Iao Val, 500 m, *Metrosideros*, 17.IX.1963 (I.W.B. Thornton) (BPBM 12,990).

Known only from W Maui, this species is sympatric with *P. swezeyi* and *P. rhina symmetrica*, which are also known only from the male.

P. iaoensis differs from *P. rhina symmetrica* in lacking teeth on the hypandrial tongue surface, and from *P. swezeyi* in the structure of the phallosome tine and number of marginal hypandrial teeth.

Ptycta pardena Thornton, **new species** Fig. 189–193

♀. Unknown.

♂. *Coloration* (freshly killed, in alcohol). Head generally cream, vertex markings brown. Dark gray-brown mark each side ocellar protuberance continued as line along frons-vertex

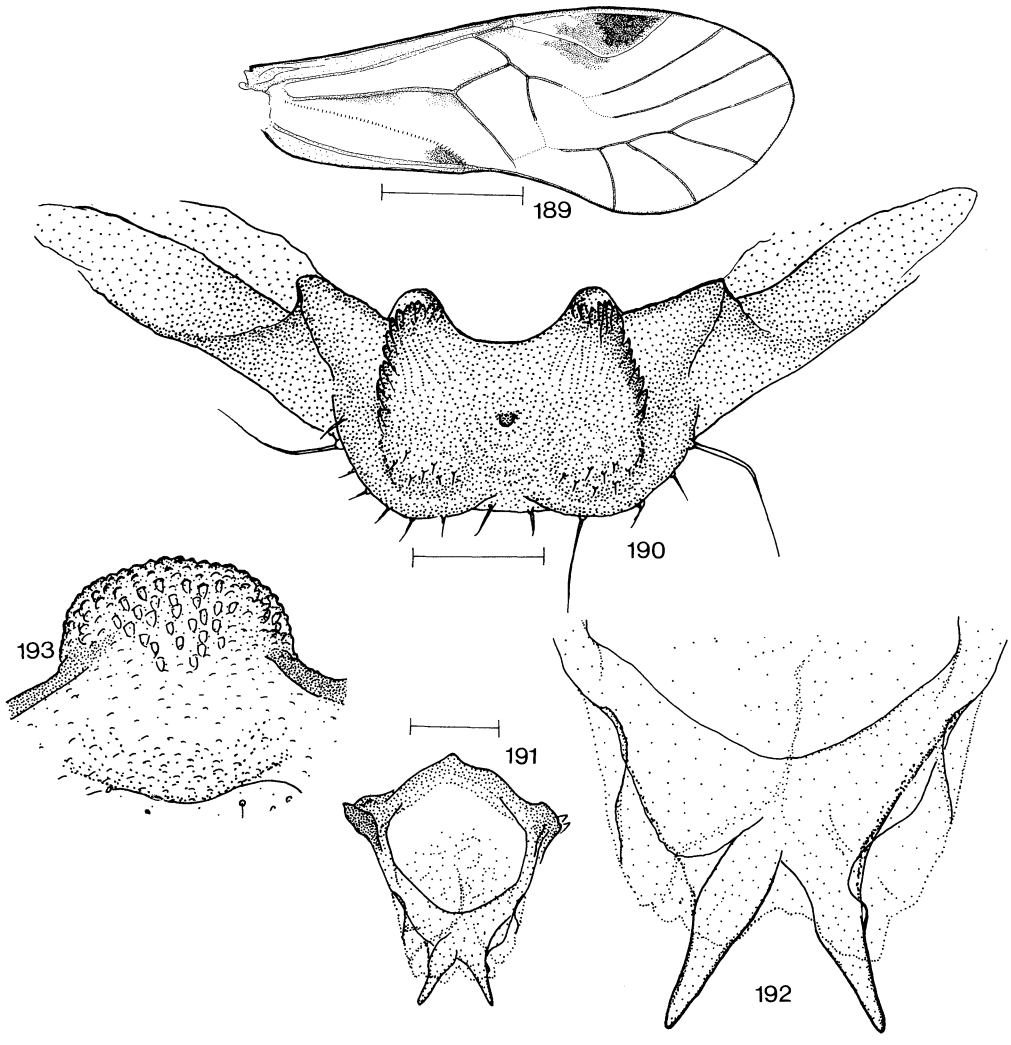

FIG. 189–193. *Ptycta pardena* ♂: **189,** fore wing; **190,** hypandrium; **191,** phallosome; **192,** phallosome tine; **193,** epiproct lobe. Fig. 190, 192, 193 to common scale.

suture. Frons with brown median stirrup mark, a dark gray-brown mark each side of this, contiguous with it at its lateral junctions with anterior frontal suture, frons otherwise whitish-cream. Clypeus cream, brown parallel striae dark gray-brown anteriorly and medially forming a wide median gray-brown mark on anterior ½ of clypeus. Genae cream, single brown band from orbit to antennal socket. Eyes black. Maxillary palpi brown except antepenultimate segment pale cream, apical segment dark brown. Antennae brown. Thoracic terga dark brown, cream arrowhead mark on mesothoracic antedorsum posteriorly, mesothoracic dorsal lobes with whitish-cream margins; metathoracic dorsal lobes with an ill-defined cream area laterally and another posteriorly; scutella pale brown. Pleura dark brown. Legs: coxa dark brown;

trochanter, femur and tibia pale cream, tibia faint brown apically; tarsus brown. Fore wing (Fig. 189, paratype) with vague vestiges of transverse fascia, a brown spot ½ way along *m+cu*, veins bordering basal ½ of areola postica hyaline, brown pigment within pterostigma extending more than ½ way towards its base, darker pigment superimposed in apical ⅓. Hind wing hyaline, very faint brown line along anterodistal border. Abdomen dorsally with dark gray-brown broad transverse bands of granulated pigment over basal 4 terga, these broken up on more apical terga into 3 patches, 1 median, 2 lateral. Pleura with gray-brown patch each segment. Ventrally abdomen with narrow transverse gray-brown band on each sternum. *Morphology.* I.O.:D. = 0.8. Hind wing with 5 fine apical setae between ends of *rs*. Number of ctenidia on hind tarsal segments: 26; 2+1. Hypandrium (Fig. 190) symmetrical, with very wide short tongue, bearing 13–16 small, fairly blunt teeth on each margin; basally a well-marked rounded prominence each side beset with setae; small rounded median boss at base of apical tongue. Phallosome with apical tine widely bifid, neck of tine broad (Fig. 191, 192). Epiproct anterior lobe fairly high, rounded, with low rugose patches (Fig. 193). Basal paraproct boss fairly small, sclerotized, rugose; a field of 27 trichobothria; paraproct basally covered with roughly square rugose patches.

Distribution. HAWAII, rare.

Holotype ♂, HAWAII: Kilauea, Kipuka Puaulu (Bird Park), *Osmanthus sandwicensis*, 24.VI.1963 (I.W.B. Thornton) (BPBM 12,991). 1♂ paratype, data as holotype, on *Charpentiera obovata*.

Males were captured at Kipuka Puaulu (1200 m) in June 1963, on *Osmanthus sandwicensis* and *Charpentiera obovata*, and have not been found elsewhere on Hawaii.

Very similar to *P. swezeyi*, n. sp. (W Maui), also known only from the male, *pardena* differs in details of genitalic characters, notably in possessing many more teeth on the hypandrial tongue.

Ptycta swezeyi Thornton, **new species** Fig. 194–197

♀. Unknown.

♂. *Coloration* (after ca. 35 years dry storage). Head generally cream, vertex markings brown; ocellar protuberance surrounded with brown pigment, ill defined on outer edge; brown line from this along frons-vertex suture. Frons with median brown stirrup mark, small discrete brown patches either side. Clypeus with brown parallel striae. Genae with brown mark between orbit and antennal socket, no other marks on gena. Eyes black. Maxillary palpi pale brown, subapical segment brown, apical segment dark brown. Antenna brown, basal flagellar segment paler, except distally. Thoracic terga brown, narrow cream band between dorsal lobes and along posterior sutures of mesothoracic antedorsum, scutella brown. Pleura brown. Legs: coxa brown; trochanter pale cream; femur pale cream, spotted with brown over upper surface; tibia pale buff, brown distally; tarsus brown. Fore wing (Fig. 194) with transverse fascia represented by rather disconnected areas of pigment, single patch of pigment in cell *An*, no clearly defined pigment spot on *m+cu*, veins *m* and *rs* with brown infuscation for a short distance beyond their separation, brown pigment filling more than ½ pterostigma, basal section of areola postica white by reflected light. Hind wing hyaline except for brown pigment along costa basally, a brown patch ½ way along costal cell, brown streak on anterodistal margin. Abdominal color not discernible. *Morphology.* I.O.:D. = 2.0. Setae on basal flagellar segment porrect on under side. Hind wing with 4–6 fine marginal setae between ends of *rs*. Number of ctenidia on hind tarsal segments: 20; 2+1. Hypandrium (Fig. 195) symmetrical; 8–11 sharp marginal teeth each side, decreasing in size apically; an apical sclerotized band; a median sculptured basal boss;

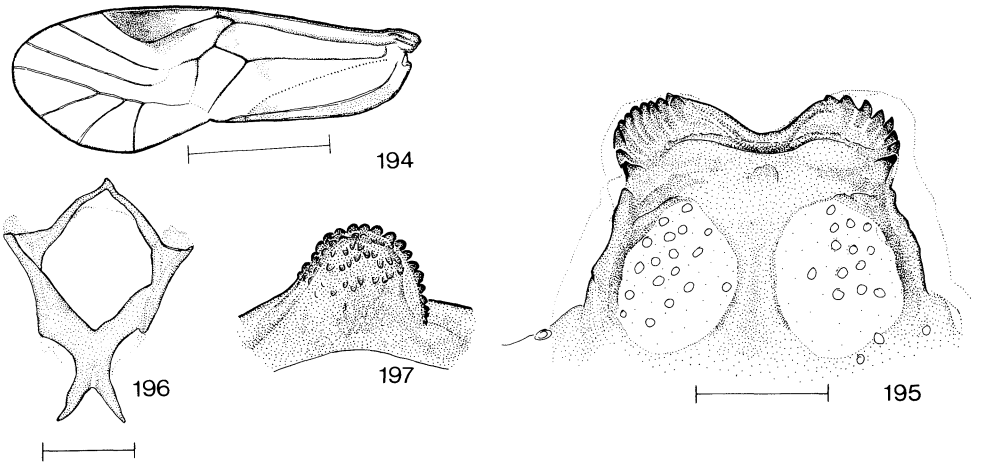

FIG. 194–197. *Ptycta swezeyi* ♂: **194,** fore wing; **195,** hypandrium; **196,** phallosome; **197,** epiproct lobe. Fig. 195, 197 to common scale.

setal fields bounded by sclerotized ridges. Phallosome (Fig. 196) with apical tine widely bifid, points sharp. Epiproct lobe high (Fig. 197), not itself bilobed, tuberculate; a field of 22–25 trichobothria on each paraproct.

Distribution. MAUI, rare.

Holotype ♂, MAUI: Halelaau (Kaulalewelewe), *Metrosideros,* 19.XII.1928 (O.H. Swezey) (BPBM 12,992). 1♂ paratype, MAUI: Iao Val, *Metrosideros,* 18.VIII.1918 (Swezey).

P. swezeyi may be distinguished from all other species of the group by fore wing pattern, and appears to be confined to Iao Valley, the eroded caldera of the W Maui volcano. It is named for the Hawaiian entomologist O.H. Swezey.

diadela group

Occurring only on the islands of Oahu and Molokai, this small distinctive group of 3 species is remarkably similar to the *oahuensis* group in female genitalic features, although the groups differ in many other characters.

Ptycta diadela Thornton, **new species** Fig. 198–204

♀. *Coloration* (freshly killed, in alcohol). Vertex pale cream, usual markings faint buff. Dark brown mark each side of ocellar protuberance continued as a conspicuous chocolate stripe along vertex-frons suture. Frons pale cream, dark brown median stirrup mark with conspicuous lateral dark brown marks along anterior border of frons. Clypeus pale cream, striae very faint buff except medially in anterior ½ and in a transverse line across clypeus, thus making up a dark T-shaped mark. Genae whitish-cream; no band from orbit to antennal socket, but an L-shaped dark brown mark in lower ½ of gena, extending to its anterior suture. Eyes black. Maxillary palpi pale buff, apical segment brown. Antennae brown. Thoracic terga brown, with

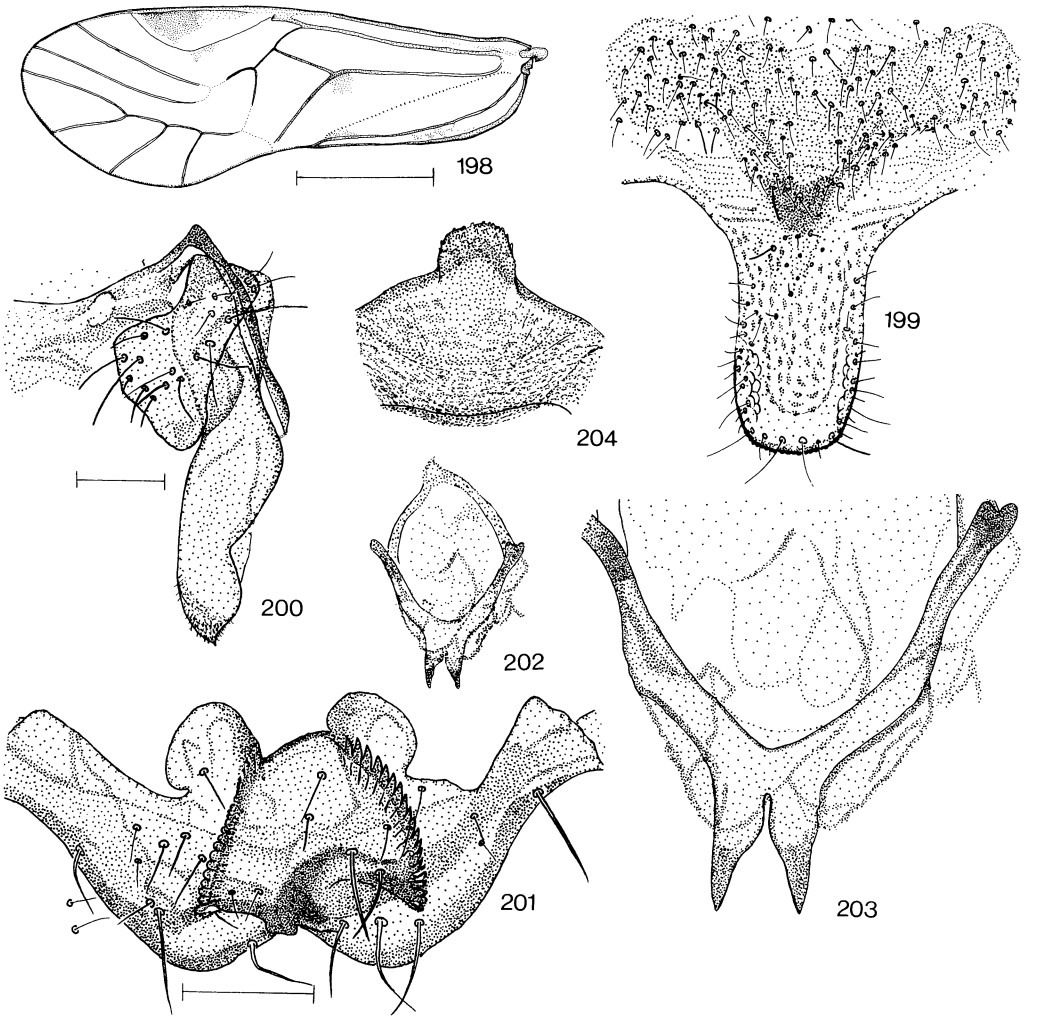

FIG. 198–204. *Ptycta diadela:* **198,** ♀ fore wing; **199,** subgenital plate; **200,** gonapophyses; **201,** hypandrium; **202,** phallosome; **203,** apex of phallosome; **204,** ♂ epiproct lobe. Fig. 199, 200, 202 and Fig. 201, 203, 204 to common scales.

broad cream borders to sclerites, scutella pale. Thoracic pleura brown, a dark brown longitudinal band just above coxae. Legs: coxa brown, trochanter, femur and tibia very pale buff, tarsus brown. Wings: fore wing (Fig. 198) without brown transverse band, brown spot in pterostigma small, not touching vertex, areola postica with basal boundary veins hyaline. Hind wing hyaline. Abdomen dorsally cream, gray-brown pigment over basal 3 terga, a narrow median gray-brown line, a rather wider line dorsolaterally and an even wider one laterally each side; ventrally cream. Apical sclerites brown, 9th tergite patterned light and dark. *Morphology.* I.O.:D. = 2.8. Hind wing with 7 fine marginal setae between ends of *rs.* Number of

ctenidia on hind tarsal segments: 22; 2+1. Subgenital plate (Fig. 199) with very long parallel-sided narrow apical process, no longer setae basally. Gonapophyses (Fig. 200): dorsal valve large, fleshy, not narrowing gradually apically; outer valve with large lobe. A field of 27–29 trichobothria on each paraproct.

♂. *Coloration* (freshly killed, in alcohol). As ♀ except vertex markings darker and pterostigma pigmentation more extensive. *Morphology.* I.O.:D. = 1.6. Hind wing with 2–4 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 22–24; 2+1. Hypandrium (Fig. 201) asymmetrical, tongue usually bulging on left side, about 24 stout sharp marginal teeth on right side, about 34 narrower close-packed blunt teeth on left, median boss at base of tongue, no carinae. Phallosome (Fig. 202, 203) with broad short double tine. Epiproct anterior lobe high, narrow, finely tuberculate (Fig. 204). Basal paraproct boss long, prominent, a field of 25–27 trichobothria.

Nymph. Head and abdominal pattern as ♀.

Distribution. OAHU, frequent.

Holotype ♂, OAHU: Waianae Range, Kole Kole Pass, 21.VII.1918 (O.H. Swezey) (BPBM 12,993). Allotype ♀, OAHU: E Koolau Range, Mt Tantalus, 550 m, *Acacia koa,* 22.II.1963 (I.W.B. Thornton).

This species occurs throughout the year on both the Koolau and Waianae mountain ranges, and is found also in the lowlands. Host plants include *Metrosideros, Acacia koa, Psidium guajava, Antidesma, Osmanthus, Suttonia, Alectryon, Eleocarpus, Newowawaiea, Acerola,* and *Macadamia.*

The dark frons and clypeal markings and the otherwise faint head marks are diagnostic.

Ptycta episcia Thornton, **new species** Fig. 205–210

♀. *Coloration* (freshly killed, in alcohol). Vertex brown, usual markings dark brown. Frons brown, darker laterally, stirrup mark very dark brown. Clypeus brown, vague darker median and transverse bands discernible. Genae dark brown. Eyes black. Maxillary palpi dark brown. Scape, pedicel and most of basal flagellar segment brown, distal end of basal segment and rest of flagellum dark brown. Thoracic terga and pleura dark brown, cream mark between mesothoracic dorsa and along their posterolateral margins. Legs: coxa dark brown; femur light brown in basal, brown in distal ½; tibia brown, darker apically; tarsus dark brown. Fore wing (Fig. 205): pterostigma with brown mark in distal angle and posteriorly along its posterior margin. A small cloud on *m+cu* distal to *rs-m* junction, transverse fascia incomplete but more extensive than *diadela,* wing membrane slightly fuscous in apical ½. Hind wing hyaline. Abdomen light brown, with brown transverse bands dorsally. *Morphology.* I.O.:D. = 3.0. Hind wing with 5 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 18; 2+1. Genitalia damaged, subgenital plate peculiar (Fig. 206), apical process narrow, with central prominence posteriorly, probably distorted. Gonapophyses, paraprocts, not available.

♂. *Coloration* (freshly killed, in alcohol). As ♀, except fore wing with distal angle of pterostigma hyaline, large dark brown spot over most of anterior ½, posterior ½ mostly brown, brown smokiness in angle of anal cell, basal ⅔ of cell *Ax* and along origins of *rs* and *m. Morphology.* I.O.:D. = 1.5. Hind wing with 4 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 17; 2+1. Hypandrium (Fig. 207) asymmetrical, one margin of tongue with 18 pointed teeth in single row, other with series of close-packed narrow blunt teeth, low median basal boss. Phallosome (Fig. 208) diamond-shaped, very long apical tine (Fig. 209) bifid for very short distance apically. Epiproct anterior lobe (Fig. 210) low, flat, just perceptibly bilobed, with few very small tubercles. Field of 28 trichobothria on paraproct.

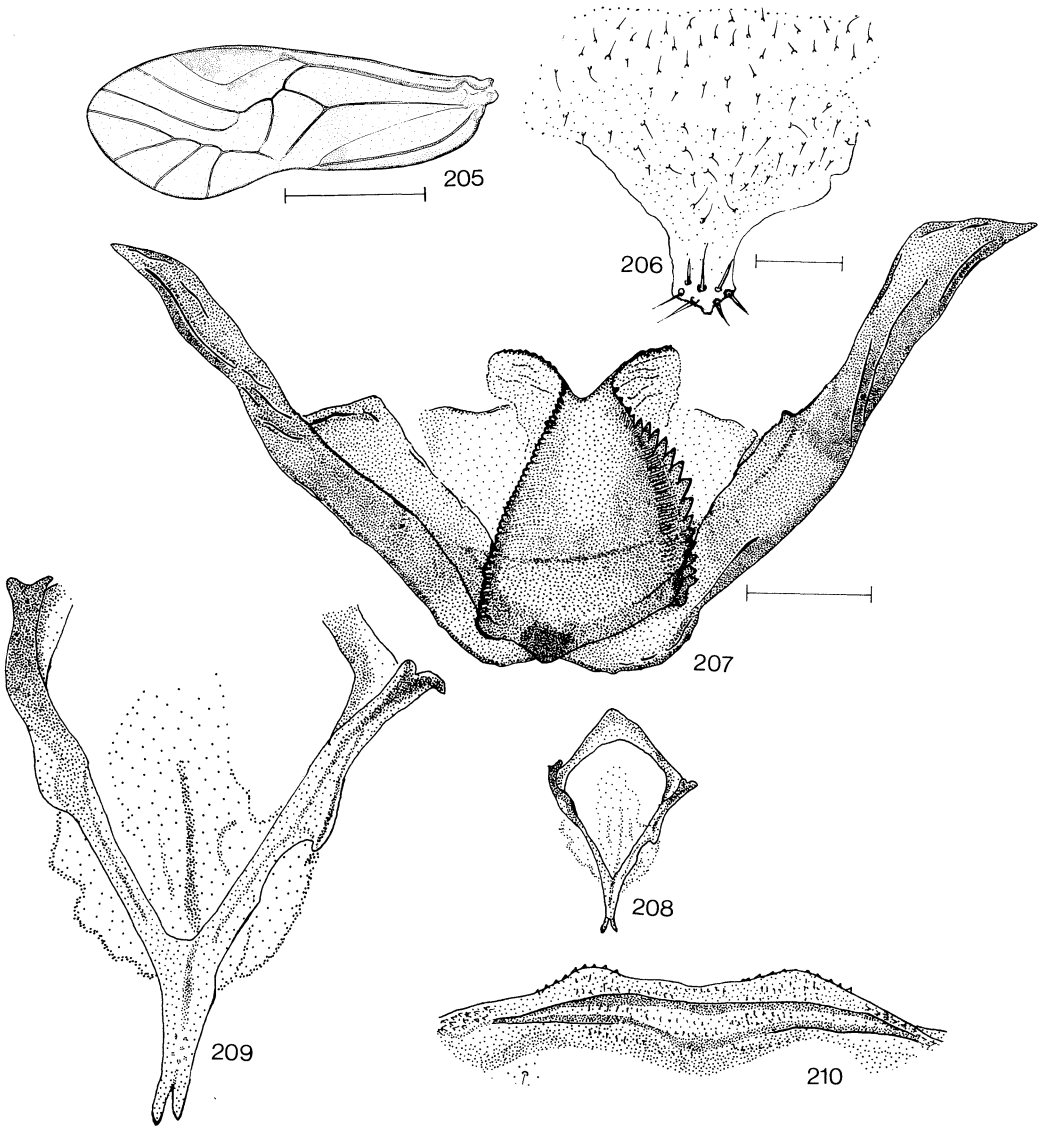

FIG. 205–210. *Ptycta episcia:* **205,** ♀ fore wing; **206,** subgenital plate (damaged); **207,** hypandrium; **208,** phallosome; **209,** phallosome apex; **210,** ♂ epiproct lobe. Fig. 206, 208 and Fig. 207, 209 to common scales.

Distribution. OAHU, rare.

Holotype ♂, OAHU: E Koolau Range, Palikea, rim of Kaau Crater, 580 m, *Metrosideros,* 31.X. 1963 (I.W.B. Thornton) (BPBM 12,994). Allotype ♀, data as holotype.

The darker head and body and structure of phallosome tine distinguish this species from *P. diadela.*

Ptycta pikeloi Thornton, **new species** Fig. 211–217

♀. *Coloration* (freshly killed, in alcohol). Head cream, usual vertex markings brown. Each side ocellar protuberance a gray-brown mark, continued as line along vertex-frons suture. Frons cream, median gray-brown stirrup mark and discrete lateral marks. Clypeus cream, brown striae merging medially. Genae cream, brown stripe from antennal socket to orbit, dark gray-brown L-shaped mark below this. Eyes black. Maxillary palpi pale buff, subapical segment brown, apical segment darker. Scape and pedicel brown, flagellum uniformly brown. Thoracic terga brown, bordered cream. Cream median band on meso- and metathorax, scutella cream. Pleura brown. Legs: coxa brown; trochanter, femur, tibia pale buff, tibia darker at apex; tarsus brown. Fore wing (Fig. 211) without transverse brown fascia, small brown patches only. Hind wing hyaline, vague brown streak along anterodistal border. Abdomen cream, gray-brown dorsally over basal 3 or 4 segments, continuing apically as 3 ill-defined lines. *Morphology.* I.O.: D. = 3.8. Hind wing with 7 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 23; 2+1. Thorax not shining. Pterostigma with smoothly rounded vertex. Subgenital plate (Fig. 212) with very long apical process, sclerotized area widening a little apically, 2 long setae at base of lobe, basal arms short, broad, rounded. Gonapophyses (Fig. 213): dorsal valve large, fleshy, not narrowing apically, apical spine short; ventral valve extending to ½ length of dorsal valve; outer valve with fairly large lobe, not extending posteriorly as far as tip of ventral valve. A field of 26 trichobothria on each paraproct. Epiproct sclerotized all along base, not unusually long. 9th abdominal tergite not so strikingly patterned as *molokaiensis.*

♂. *Coloration* (freshly killed, in alcohol). As ♀, except pterostigma pigmentation more extensive, other fore wing markings less extensive. *Morphology.* I.O.:D. = 2.8. Hind wing with 6 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 23; 2+1. Thoracic terga not shining. Pterostigma with smoothly rounded vertex. Hypandrium (Fig. 214) asymmetrical, apical tongue with short close-packed very blunt marginal teeth, wider on left side, a small prominent basal boss. Phallosome tine (Fig. 215, 216) bifid for apical ¼ of its length. Sculpturing of 9th tergite not so well marked as *P. molokaiensis,* epiproct with narrow high crenulate anterior lobe (Fig. 217). Paraproct basal boss fairly stout, a field of 25 trichobothria.

Distribution. MOLOKAI, occasional.

Holotype ♂, MOLOKAI: valley N of Kaimoku Stream, SE of Hanalilolilo, 1210 m, *Metrosideros,* 19.VII.1963 (I.W.B. Thornton) (BPBM 12,995). Allotype ♀, MOLOKAI: summit Puu Kole Kole, 1195 m, *Juniperus,* 18.VII.1963 (I.W.B. Thornton).

In hypandrium this species is similar to the *frogneri* group of species; it differs from that group in male epiproct ornamentation and in structure of female gonapophyses and subgenital plate, in which it resembles *diadela. P. diadela* and *P. pikeloi* are consistently close to one another in the phenograms based on correlation coefficients of Chui & Thornton (1972).

Named for Mr Noah Pikelo, Game Warden, Molokai, in 1963, in appreciation of his assistance in the E Molokai mountains.

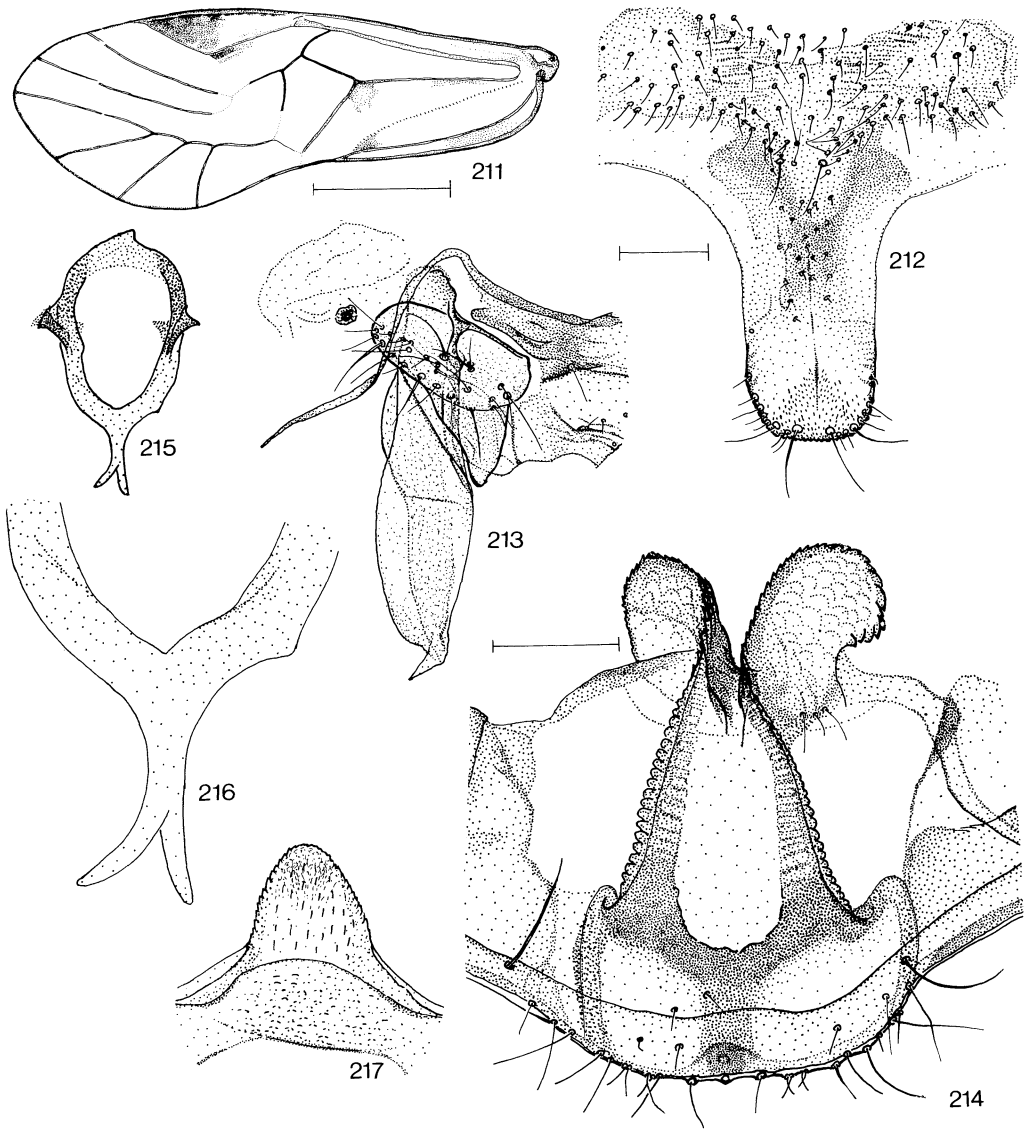

FIG. 211–217. *Ptycta pikeloi:* **211,** ♀ fore wing; **212,** subgenital plate; **213,** gonapophyses; **214,** hypandrium; **215,** phallosome; **216,** phallosome tine; **217,** ♂ epiproct lobe. Fig. 212, 213, 215 and Fig. 214, 216, 217 to common scales.

frogneri group

This well-defined group of 5 species is confined to the 4 eastern islands, Molokai, Lanai, Maui and Hawaii (Fig. 291), and resembles the *schisma* group, with whose distribution it overlaps. The shape of the dorsal valve of the female gonapophyses is distinctive.

Ptycta frogneri Thornton, **new species** Fig. 218–224

♀. *Coloration* (freshly killed, in alcohol). Head cream, usual vertex markings brown. Large gray-brown mark each side of ocellar protuberance, continued as line along vertex-frons suture. Frons cream, median brown stirrup mark, large gray-brown lateral marks, usually touching stirrup mark. Clypeus cream, brown stripe from orbit to antennal socket; gray-brown L-shaped mark below this. Eyes black. Maxillary palpi pale buff, subapical segment brown, apical segment darker. Antenna wholly brown. Thoracic terga brown, bordered, cream. Pleura brown. Legs: coxa brown; trochanter, femur and tibia very pale buff, femur faint brown apically; tarsus brown. Fore wing (Fig. 218) with somewhat interrupted angled transverse fascia, 2 distinct brown patches in anal cell, veins bordering basal ½ areola postica unpigmented, pterostigma patch barely reaching vertex, long brown mark ½ way along *m+cu*. Hind wing hyaline, brown streak on anterodistal margin. Abdomen with gray-brown granulated pigment over basal 2 or 3 tergites, narrow median and broader lateral longitudinal bands, 9th tergite patterned brown and light brown. *Morphology*. I.O.:D. = 3.2. Hind wing with 4 fine marginal setae between ends of *rs*. Number of ctenidia on hind tarsal segments: 21; 2+1. Pterostigma with smoothly rounded vertex. Subgenital plate (Fig. 219) with fairly long apical process, 2 longer setae at its base, rest of plate with characteristic pattern of sclerotization. Gonapophyses (Fig. 220): dorsal valve large, broad, not gradually narrowing apically to apical spine; ventral valve extending to over ¾ length of dorsal valve; outer valve with large lobe. A field of 25 trichobothria on each paraproct, epiproct as that of *P. pikeloi*. 9th abdominal tergite patterned, but not as strikingly as *P. molokaiensis*.

♂. *Coloration*. As ♀ except fore wing transverse fascia more interrupted, pterostigma spot more extensive, veins bounding basal ½ areola postica sometimes not completely unpigmented. *Morphology*. Eyes prominent, large. I.O.:D. = 1.1. Hind wing with 5 fine marginal setae between ends of *rs*. Number of ctenidia on hind tarsal segments: 23; 2+1. Hypandrium (Fig. 221) symmetrical, tongue with long, narrow, fairly blunt, close-packed marginal teeth, median basal boss lacking. Phallosome tine (Fig. 222, 223) Y-shaped, the 2 arms of fork smoothly rounded apically. 9th abdominal tergite as ♀; epiproct anterior lobe fairly high, distinctly bilobed (Fig. 224). Paraproct basal boss low, stout, a field of 29–30 trichobothria.

Distribution. MAUI, occasional.

Holotype ♂, MAUI: upper Iao Val, 460–610 m, *Psidium guajava*, 17.IX.1963 (I.W.B. Thornton) (BPBM 12,996). Allotype ♀, same data as holotype. 2♂,4♀ paratypes, same data.

P. frogneri is closely similar in several respects to *giffardi* of Lanai, and to a lesser degree to *pikeloi* of Molokai. It may be distinguished from *giffardi* by the shape of the phallosome tine and relative eye size in the male, and by the extent of unpigmented veins surrounding the areola postica and the shape of the subgenital plate in the female. The distinctive female genitalia of *pikeloi* preclude any confusion with *frogneri* females, and the males of these species can be clearly distinguished on relative eye size and shape of epiproct process.

Named for Mr K. Frogner in appreciation of his trail-blazing in the Puu Kukui area of W Maui.

Ptycta drepana drepana Thornton, **new species** Fig. 225–231

♀. *Coloration* (freshly killed, in alcohol). Head generally cream, usual vertex markings brown. Gray-brown patch each side of ocellar protuberance, continued as line along frons-vertex

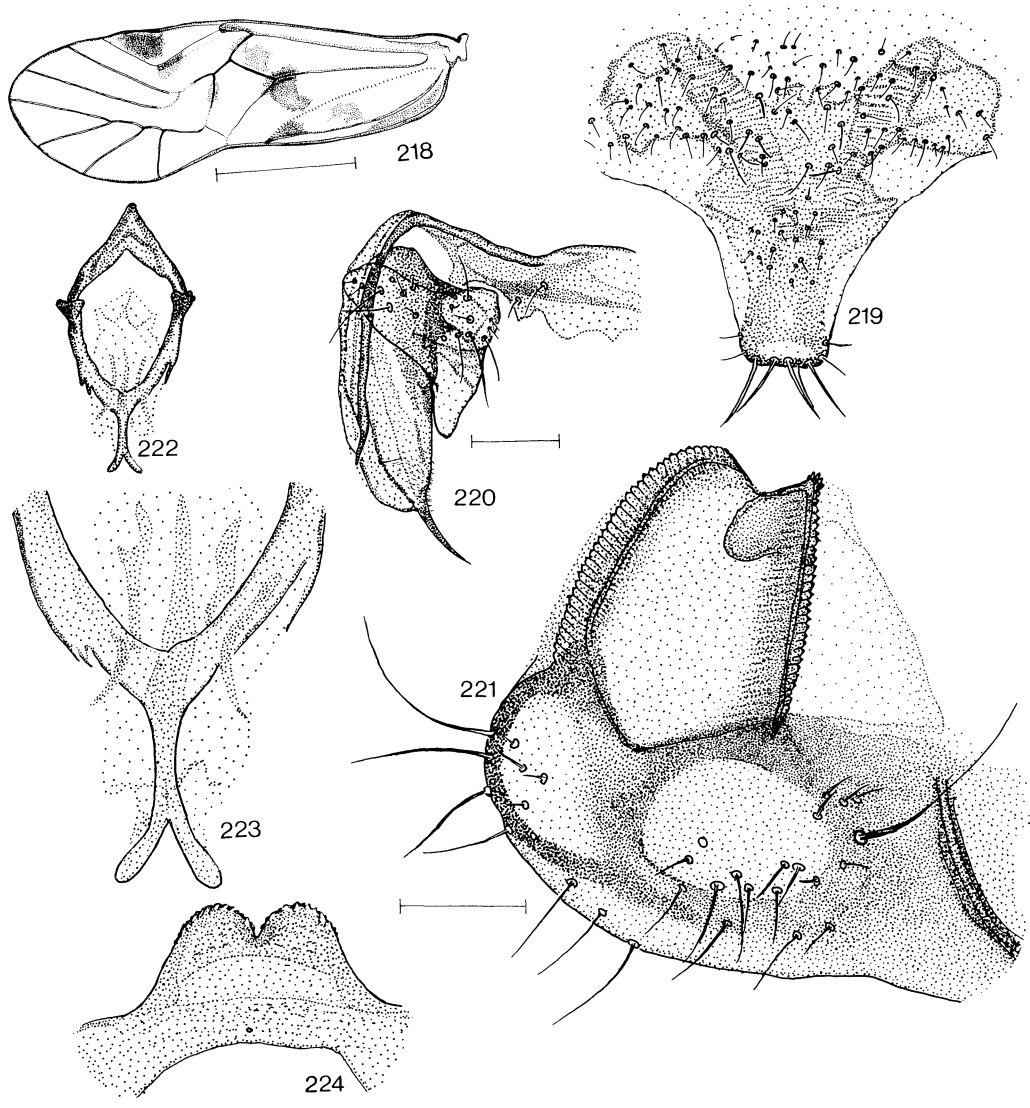

FIG. 218–224. *Ptycta frogneri:* **218,** ♀ fore wing; **219,** subgenital plate; **220,** gonapophyses; **221,** hypandrium; **222,** phallosome; **223,** phallosome tine; **224,** ♂ epiproct lobe. Fig. 219, 220, 222 and Fig. 221, 223, 224 to common scales.

suture. Frons cream, brown median stirrup-mark, darker gray-brown lateral marks sometimes contiguous. Clypeus cream, parallel striae faint brown except anterior ½ darker medially and as a transverse band across clypeus at halfway mark, producing a distinct gray-brown T-shaped mark on anterior ½ of clypeus. Genae pale buff, narrow brown band from orbit to antennal socket; a 2nd parallel gray-brown band well below this. Eyes black. Maxillary palpi buff, sub-

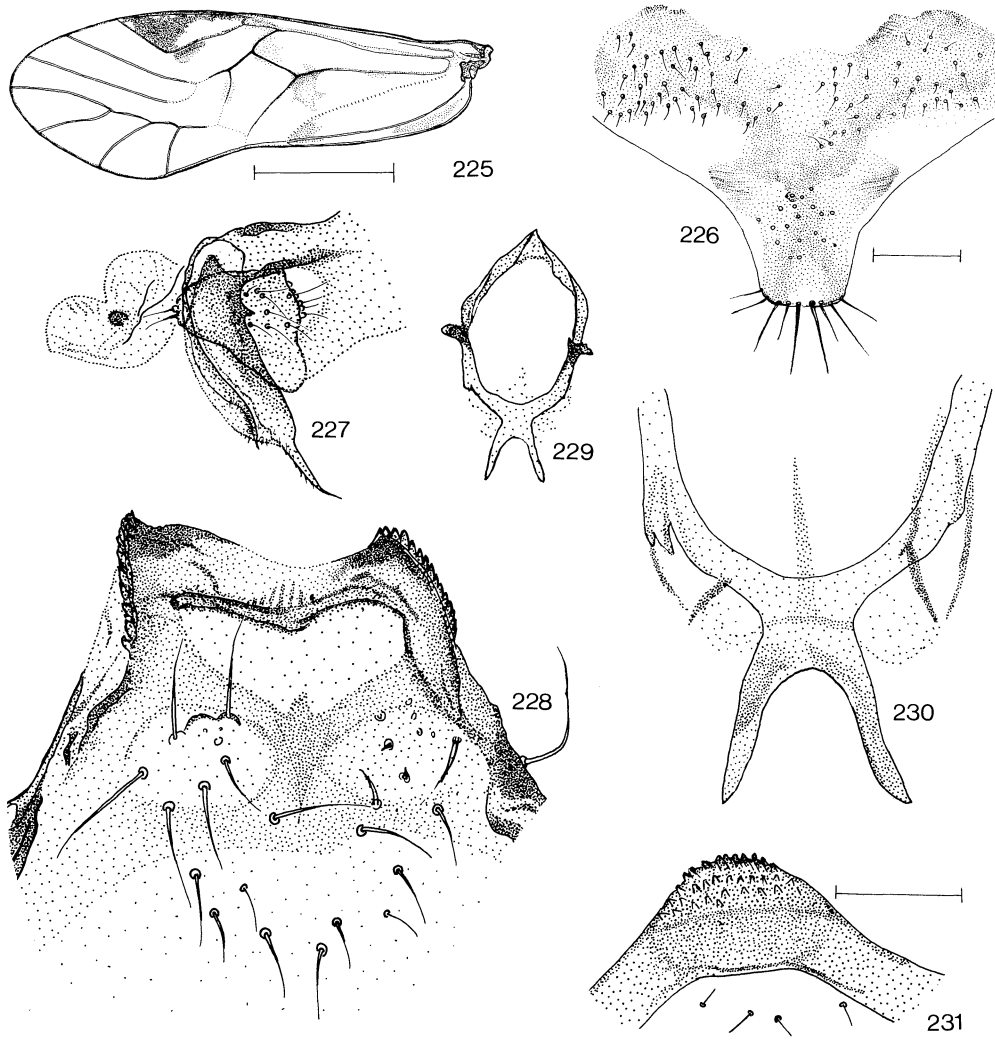

FIG. 225–231. *Ptycta drepana drepana:* **225,** ♀ fore wing; **226,** subgenital plate; **227,** gonapophyses; **228,** hypandrium; **229,** phallosome; **230,** phallosome apex; **231,** ♂ epiproct lobe. Fig. 226, 227, 229 and Fig. 228, 230, 231 to common scales.

apical segment pale brown, apical segment brown. Antennae with scape and pedicel pale brown, flagellum brown. Thoracic terga brown, margins cream, wide cream band medially on meso- and metathorax, scutella cream. Pleura brown. Legs: coxa brown, trochanter colorless, femur very pale cream, pale brown apically, tibia pale cream, tarsus brown. Fore wing (Fig. 225) with transverse fascia very interrupted, hardly recognizable as such, veins bounding basal ½ areola postica unpigmented; hind wings normal for the genus. Abdomen cream, gray-brown granu-

lated pigment dorsally, apical sclerites brown. *Morphology.* I.O.:D. = 3.0. Hind wing with 4 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 22; 2+1. Subgenital plate (Fig. 226). Gonapophyses (Fig. 227): dorsal valve wide, narrowing fairly abruptly to apical spine, outer valve with large lobe. A field of 25 trichobothria on each paraproct.

♂. *Coloration* (freshly killed, in alcohol). As ♀, but fore wing pigmentation less extensive, except within pterostigma more extensive. *Morphology.* I.O.:D. = 1.0. Eyes very large. Hind wing with 4–5 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 20–22; 2+1. Hypandrium (Fig. 228) with wide tongue apparently symmetrical at low magnifications, but marginal teeth blunt on left forming continuous smooth outer edge, sharply toothed on right; a median sclerotized bar basally and a distinct boss at base of tongue. Phallosome tine bifid almost to base, forming 2 evenly curved, pointed, subsidiary tines upon a very broad basal portion (Fig. 229, 230). Epiproct with fairly broad, just perceptibly bilobed anterior lobe (Fig. 231), basal boss of paraproct low, sclerotized, a field of 25–27 trichobothria.

Nymph. Easily recognizable by very distinct T-shaped mark on clypeus, conspicuous gray-brown frons marks, single gray-brown band along the apical edge of gena, and a gray-brown darker line along thoracic pleura.

Distribution. MAUI, MOLOKAI, occasional.

Holotype ♂, MOLOKAI: bottom of Dunbar's pasture, 600 m, *Metrosideros,* 9.IV.1963 (I.W.B. Thornton) (BPBM 12,997). Allotype ♀, same data as holotype.

This species, superficially similar to *P. lanaiensis* and undoubtedly fairly closely related to it, was also collected in 1963 on Maui at Haiku (about 600 m) on *Casuarina* and in the Iao Valley between 450 and 600 m on *Metrosideros* and *Psidium guajava.*

Ptycta drepana drepanoides Thornton, **new subspecies** Fig. 232–236

♀. Unknown.

♂. *Coloration* (after 47 years dry storage). Fore wing (Fig. 232) with transverse fascia very interrupted; pterostigma pigmentation unusually restricted for a male of this genus, not reaching vertex. Hind wing apparently without brown pigment in anal cell, but with brown anterodistal marginal streak. Otherwise color not clear. *Morphology.* I.O.:D. = 1.0–1.2, eyes large. Hind wing with 8 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 21; 2. Hypandrium (Fig. 233) with wide apical tongue symmetrical, teeth of both sides blunt, forming smooth continuous outer margin, median basal boss very small. Phallosome tine bifid almost to base (Fig. 234, 235). Epiproct with fairly high, narrow, bilobed, anterior lobe (Fig. 236), paraproct with small but distinct sclerotized boss, a field of 28–31 trichobothria.

Distribution. LANAI, rare.

Holotype ♂, LANAI: 600 m, 12.XII.1916 (W.M. Giffard) (BPBM 12,998). 6♂ paratypes, data as holotype.

This form has not been found since Giffard's collection; no females are therefore available for study. The male is very closely similar to that of the nominate subspecies, which occurs on Maui and Molokai, differing only in the symmetry of the marginal teeth of the hypandrial tongue, the small median hypandrial boss, the somewhat wider phallosome fork, and the bilobed epiproct lobe.

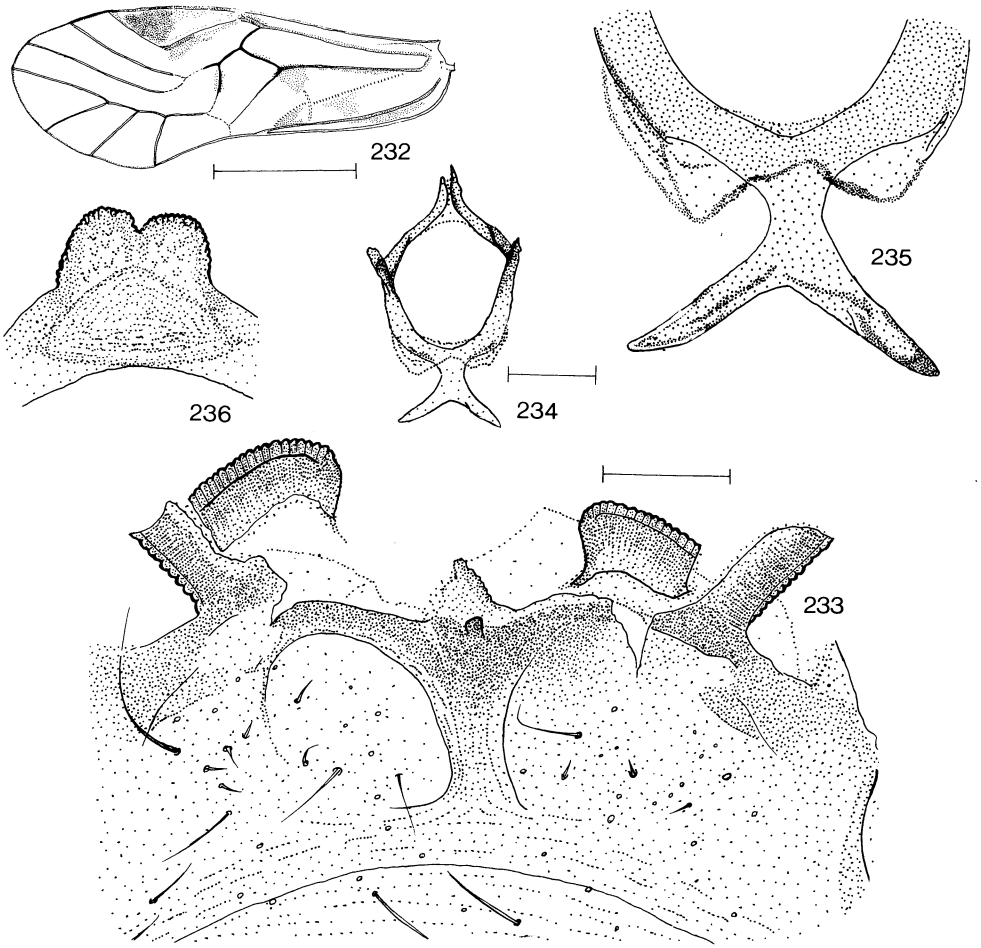

FIG. 232–236. *Ptycta drepana drepanoides* ♂: **232,** fore wing; **233,** hypandrium; **234,** phallosome; **235,** phallosome tine; **236,** epiproct lobe. Fig. 233, 235, 236 to common scale.

Ptycta giffardi Thornton, **new species** Fig. 237–243

♀. *Coloration* (after ca. 70 years dry storage). Vertex marks, clypeal striae brown, brown frontal stirrup-shaped mark with a discrete lateral brown line each side, single genal stripe from orbit to antennal socket, apical segment of maxillary palpi, tarsi, all brown. Colors of other structures indefinable. Fore wing (Fig. 237) with transverse fascia angled and very interrupted, resulting in a number of well-defined brown patches, 2 brown patches in anal cell, a long brown mark ½ way along *m*+*cu*, brown mark surrounding *m* and *rs* for a short distance beyond their bifurcation. Pterostigma pigment restricted, not reaching vertex. Veins bounding areola postica brown. Hind wing with brown streak along anterodistal margin. *Morphology.* I.O.:D. = 3.2. Hind wing with 6–10 fine marginal setae between ends of *rs*. Number of ctenidia

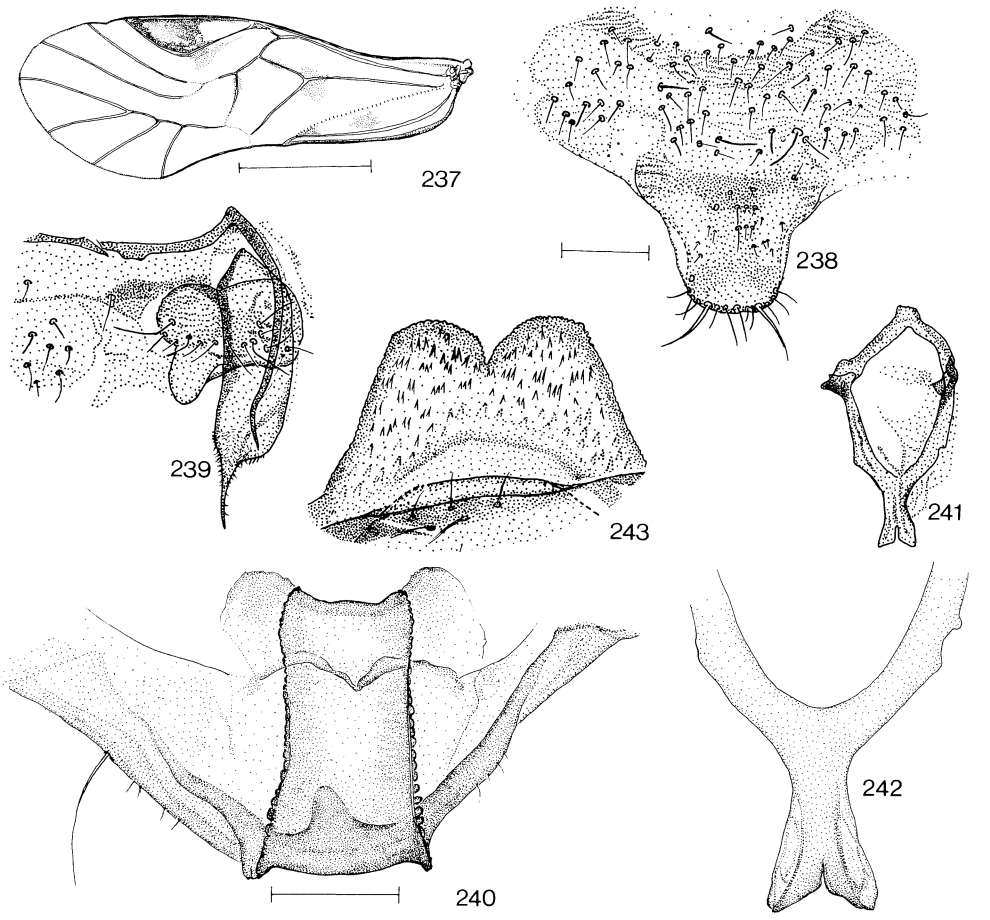

FIG. 237–243. *Ptycta giffardi:* **237,** ♀ fore wing; **238,** subgenital plate; **239,** gonapophyses; **240,** hypandrium; **241,** phallosome; **242,** phallosome tine; **243,** ♂ epiproct lobe. Fig. 238, 239, 241 and Fig. 240, 242, 243 to common scales.

on hind tarsal segments: 20; 2+1. Subgenital plate (Fig. 238) apical process narrowing abruptly subapically. Gonapophyses (Fig. 239): dorsal valve broad, narrowing abruptly to apical spine; outer valve subrectangular, with fairly large lobe. A field of 21–29 trichobothria on each paraproct. Gonopore plate sclerotized anteriorly.

♂. *Coloration* (after ca. 50 years dry storage). As ♀, except in fore wing brown pterostigma spot reaching well beyond vertex of pterostigma and brown transverse fascia rather more reduced. *Morphology.* I.O.:D. = 1.5–2.0. Hind wing with 3 fine marginal setae between ends of *rs* (broken off). Hypandrium (Fig. 240) symmetrical, teeth on both margins of tongue wide, blunt, fused; no basal boss. Phallosome (Fig. 241, 242) tine short, fairly thick, fork diverging little, arms spatulate, angular. Epiproct lobe high, clearly bilobed (Fig. 243); a field of 21–22 trichobothria on each paraproct, paraproct basal boss stout, sclerotized.

Distribution. LANAI, MOLOKAI, rare.

Holotype ♂, LANAI: 600 m, 7.XII.1916 (W.M. Giffard) (BPBM 12,999). Allotype ♀, MOLOKAI: 910 m, VI.1896 (R.C.L. Perkins). 1♀ paratype, MOLOKAI: below Kamoku Flats, 910 m, 19.VII.1963.

This species is of interest because of the similarity in male genitalia to those of *pikeloi* and *frogneri*, which occur on Molokai and Maui, respectively. *P. pikeloi*, however, has an undivided male epiproct lobe, a clearly Y-shaped phallosome tine, and the female genitalia are quite distinctive. *P. giffardi* also differs from *frogneri* quite distinctly in male and female genitalia. All 3 species, however, have a very similar hypandrium.

The species falls in the *schisma* group in the analysis of Chui & Thornton (1972); it differs in hypandrium from that group, and I suspect that the spinous male epiproct lobe was inadvertently scored as a hypandrial character state in that study.

This species is named for W.M. Giffard.

Ptycta hardyi Thornton, **new species** Fig. 244–250

♀. *Coloration* (freshly killed, in alcohol). Head generally cream, vertex markings pale brown. Large gray-brown patch (as large as ocellar protuberance) each side of ocellar protuberance, continued as line along frons-vertex suture. Frons with median gray-brown stirrup mark, an irregular gray-brown mark each side, sometimes contiguous with median mark but not touching anterior suture. Clypeus with parallel striae faint, darker in a transverse band halfway down clypeus, and merging and darkening in a median band anteriorly to produce a distinct gray-brown T-shaped mark on anterior ½. Gena with brown band from orbit to antennal socket, a gray-brown band below this widening into a square patch anteriorly. Eyes black. Maxillary palpi pale cream, subapical segment pale brown, apical segment brown. Antennae brown, basal flagellar segment paler in distal ½. Thoracic terga brown, large cream arrowhead mark posterior to mesothoracic antedorsum, mesothoracic dorsal lobes widely margined cream, metathoracic dorsal lobe with a cream patch laterally and posteriorly; scutella pale cream. Pleura brown. Legs: coxa brown; trochanter, femur and tibia pale whitish cream, femur and tibia pale brown apically, tarsus brown. Fore wing (Fig. 244) with much interrupted transverse fascia, a brown mark ½ way along *m+cu* (this sometimes lacking), pterostigma spot confined to apical ¼, not touching vertex; veins bordering basal ½ areola postica largely pigmented. Hind wing hyaline. Abdomen chalky white, gray-brown transverse bands on 2 basal terga, a median and each side a narrower lateral longitudinal gray-brown line along dorsal surface. Pleura with gray-brown markings. Abdomen ventrally with gray-brown transverse bands. *Morphology.* I.O.:D. = 3.2. Hind wing with 8 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 23; 2+1. Subgenital plate (Fig. 245) with apical process angular, very broad basally, lacking 2 setae much longer than rest at base of lobe. Gonapophyses (Fig. 246): dorsal valve with very small subapical lobe, long and distinct apical spine; outer valve with large lobe. A field of 26 trichobothria on each paraproct. Gonopore plate bilobed anteriorly.

♂. *Coloration* (freshly killed, in alcohol). As ♀, except in fore wing transverse fascia reduced to a few small patches, *m+cu* spot absent, pterostigma patch reaches vertex. *Morphology.* Eyes very large, I.O.:D. = 0.8. Hind wing with 7 fine setae on margin between ends of *rs.* Number of ctenidia on hind tarsal segments: 21; 2+1. Hypandrium (Fig. 247) with long apical tongue,

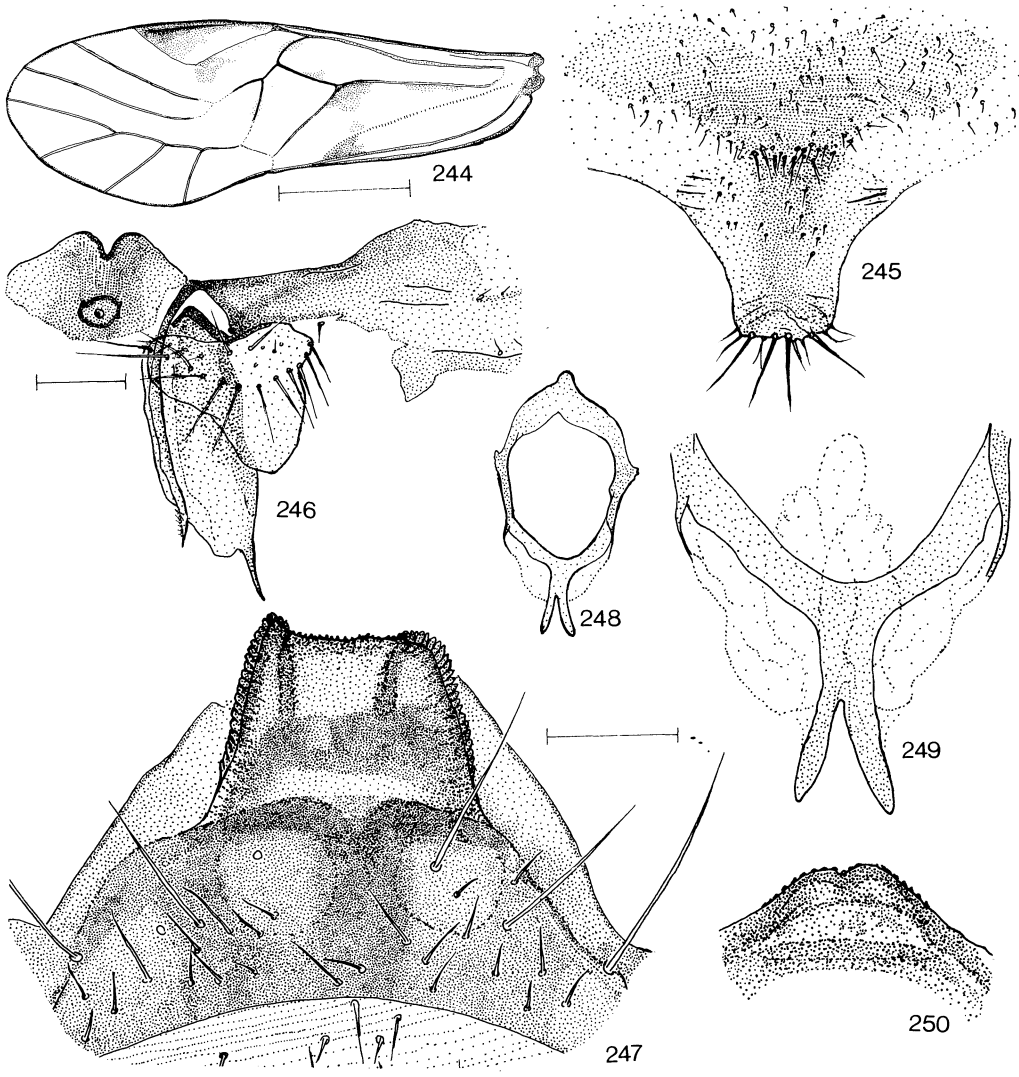

FIG. 244–250. *Ptycta hardyi:* **244,** ♀ fore wing; **245,** subgenital plate; **246,** gonapophyses; **247,** hypandrium; **248,** phallosome; **249,** phallosome apex; **250,** ♂ epiproct lobe. Fig. 245, 246, 248 and Fig. 247, 249, 250 to common scales.

symmetrical at low magnifications, but marginal teeth blunt on right forming smooth outer edge, sharply toothed and very slightly wider on left; no obvious median basal boss. Phallosome (Fig. 248) tine bifid forming 2 fairly straight subsidiary tines with smoothly rounded apices on fairly narrow basal portion (Fig. 249). Epiproct with bilobed anterior lobe, slightly tuberculate (Fig. 250); basal boss of paraproct low, smooth, sclerotized, a field of 27–39 trichobothria.

Distribution. HAWAII, occasional.

Holotype ♂, HAWAII: Kawaihaeuka, 1070 m, *Acacia koaea*, 29.I.1963 (I.W.B. Thornton) (BPBM 13,000). Allotype ♀, same data. Paratypes, HAWAII: 1♂,1♀, Waimea, *Juniperus*, VI.1963; 1♂, Pololu, VI.1922 (Swezey).

The above localities are on the edge of the Kohala volcano at the NW tip of Hawaii I. Evidently this is the most easterly representative of the *frogneri* group and is possibly confined to this old volcanic massif.

In general structure of genitalia and in color pattern, this species closely resembles *P. drepana*, which occurs on Molokai and Maui. It differs, however, in details of pigmentation of the areola postica veins, and in the structure of the dorsal valve of the female genitalia, the hypandrium, and the phallosome.

The species is named for Dr D.E. Hardy, who first suggested I study Hawaiian Psocoptera and whose assistance in many ways during this study is much appreciated.

Ptycta perkinsi Thornton, **new species** Fig. 251–257

♀. *Coloration* (after 60 years dry storage). Vertex marks brown, brown patches each side ocellar protuberance, median brown stirrup-mark on frons, clypeal striae not merging, genal mark from orbit to antennal socket. Fore wing pigmentation not discernible, veins bordering basal ½ areola postica hyaline. Other color not clear. *Morphology.* I.O.:D. = 2.5. Hind wing with 6 fine marginal setae between ends of *rs*. Number ctenidia on hind tarsal segments: 23; 2+1. Pterostigma with smoothly rounded vertex. Subgenital plate (Fig. 252) with fairly long apical process, 2 longer setae at base of lobe. Gonapophyses (Fig. 253): dorsal valve large, broad, fleshy, with short but distinct fleshy lobe; ventral valve not extending more than ⅔ way along dorsal valve; outer valve with long, fairly narrow lobe. A field of 28 trichobothria on each paraproct. Gonopore plate sclerotized anteriorly. No pattern discernible on 9th abdominal tergite.

♂. *Coloration* (after over 60 years dry storage). Not clearly discernible. Veins borderig basal ½ of areola postica hyaline (Fig. 251). *Morphology.* Eyes prominent, I.O.:D. = 1.0. Hind wing with 7 fine marginal setae between ends of *rs*. Number of ctenidia on hind tarsal segments: 25; 2+1. Hypandrium (Fig. 254) symmetrical, marginal teeth blunt, smooth, close-set, teeth also on surface of tongue laterally and apically; a small median boss at base of tongue, a median sclerotized bar basal to this. Phallosome tine (Fig. 255, 256) Y-shaped, arms of fork curved. Epiproct (Fig. 257) anterior lobe high, bilobed. Paraproct basal boss low, rounded, sclerotized, a field of 30–31 trichobothria.

Distribution. MAUI, rare.

Holotype ♂, MAUI: Haleakala, 5000 ft [1500 m], "May, 1896," labelled "Psocus kauaiensis" by R.C.L. Perkins (BPBM 13,001). Allotype ♀, data as holotype.

This species is described from *Fauna Hawaiiensis* material in the Bishop Museum, labelled "*Psocus kauaiensis*," and collected by Perkins on Haleakala at 1500 m (5000 ft) in May 1896. The species has not been collected since.

P. perkinsi is placed in this group on features of male epiproct lobe and female genitalia; the small hypandrial teeth on the surface of the tongue also suggest relationship with the *schisma* group, although in that group there is no basal median prong.

Named for R.C.L. Perkins, whose prodigious work on the Hawaiian fauna has been the basis of so many subsequent studies.

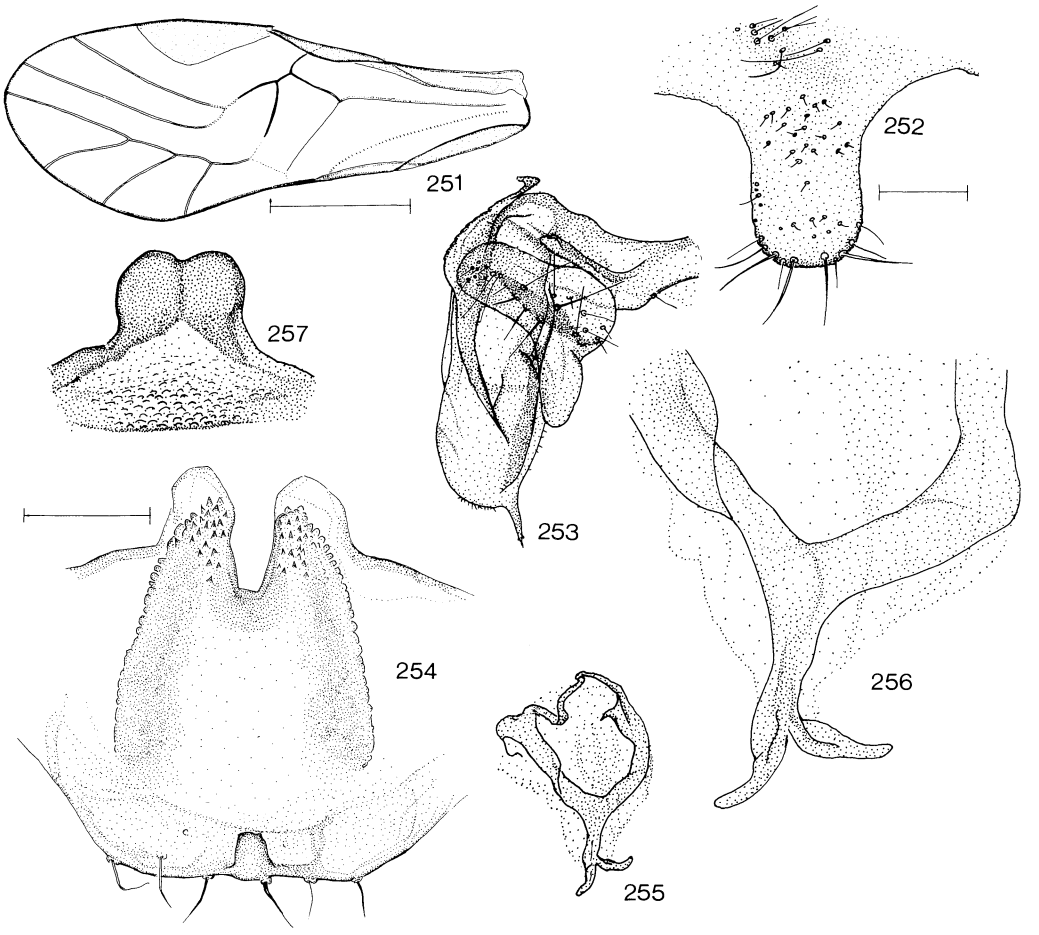

FIG. 251–257. *Ptycta perkinsi:* **251,** ♂ fore wing; **252,** subgenital plate; **253,** gonapophyses; **254,** hypandrium; **255,** phallosome; **256,** phallosome tine; **257,** ♂ epiproct lobe. Fig. 252, 253, 255 and Fig. 254, 256, 257 to common scales.

lanaiensis group

The 3 species of this group are related to the *disclera* group. Species of the *lanaiensis* group, however, have a distinctive sclerotized flap on the subgenital plate and an asymmetrical hypandrium. *P. lanaiensis* has 4 recognizable populations, 1 each on Lanai and Maui and 2 on Molokai, but these are allopatric and, in relation to the degree of difference of sympatric taxa, are not considered sufficiently distinct to be regarded as separate species (see Discussion); the Lanai population is the most distinct.

Ptycta lanaiensis lanaiensis (Perkins), **revised status** Fig. 258–260

Psocus lanaiensis Perkins, 1899: 81.—Zimmerman, 1948b: 247.

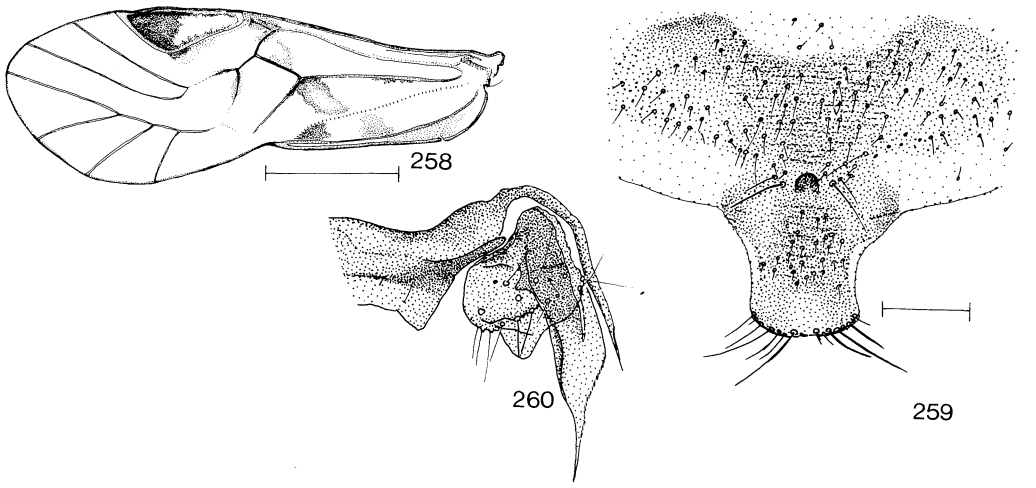

FIG. 258–260. *Ptycta lanaiensis lanaiensis* ♀: **258,** fore wing; **259,** subgenital plate; **260,** gonapophyses. Fig. 259, 260 to common scale.

Clematostigma lanaiensis (Perkins): Enderlein, 1913: 355.
Psocus haleakalae var. *lanaiensis* Perkins: Enderlein, 1920: 450 (partim).
Ptycta haleakalae var. *lanaiensis* (Perkins): Enderlein, 1925: 102 (partim).
not *Psocus sylvestris* Perkins: Enderlein, 1920: 451.
not *Psocus heterogamias* Perkins: Enderlein, 1920: 451.

The following further description, based on the type specimens, is given to supplement that of Perkins.

♀. *Coloration* (after ca. 50 years dry storage). Fore wing (Fig. 258) with transverse brown fascia, 2 distinct brown patches in anal cell, veins bordering basal ½ of areola postica unpigmented. Hind wing with brown streak on anterodistal border, anal cell very faintly fuscous. *Morphology.* I.O.:D. = 5.5. Hind wing with 5 fine marginal setae between ends of *rs.* Subgenital plate (Fig. 259) with apical process squat, bearing an internal sclerotized flap, 2 long setae at its base. Gonapophyses (Fig. 260): dorsal valve large, broad, narrowing abruptly to apical spine; outer valve with short lobe. A field of 23–24 trichobothria on each paraproct (type 24).

♂. *Coloration* (after ca. 50 years dry storage). As ♀, transverse wing fascia less extensive, single brown patch in anal cell. *Morphology.* I.O.:D. = 0.9. Eyes very large. Hypandrium of type damaged, but pointed teeth discernible at base of both margins of tongue, a median basal boss of rough, not smooth, outline. Phallosome tine and epiproct missing (?eaten).

Distribution. LANAI, rare.

This subspecies is that taxon described by Perkins as *Psocus lanaiensis.* I have dissected the types and based the further description also on a single female collected by Giffard at 1200 m on Lanai in December 1916. The state of the male genitalia in the type is bad, but sufficient remains for some comparison to be made with the

following subspecies. The type female subgenital plate shows the sclerotized flap only indistinctly. All 3 specimens agree in size and in wing venation and pattern.

Ptycta lanaiensis fusca Thornton, **new subspecies** Fig. 261–266

♀. *Coloration* (freshly killed, in alcohol). Head generally cream, usual vertex markings brown. A brown line along frons-vertex suture. Frons cream, brown median stirrup mark anteriorly with 2 almost discrete spots, a discrete gray-brown spot lateral to this each side. Clypeus cream, brown striae merging medially, particularly anteriorly, forming a vague brown wedge-shaped mark on clypeus. Genae cream, 3 or 4 brown spots merge to form a line from orbit to antennal socket. Eyes black. Scape and pedicel brown, basal flagellar segment light brown, brown apically; rest of flagellum brown. Thoracic terga brown, sometimes dark brown, bordered whitish cream, a median cream arrow-shaped mark on antedorsum of mesothorax and a median cream line between dorsal lobes of meso- and metathorax, scutella brown. Thoracic terga dark brown. Legs: coxa dark brown; trochanter and femur pale buff, femur brown subapically; tibia light brown, darker apically; tarsus brown. Fore wing (Fig. 261) with membrane faintly cloudy in apical ½, transverse fascia rather broader, otherwise pattern of pigmentation as in *P. lanaiensis lanaiensis,* veins bounding basal ½ of areola postica hyaline. Hind wing with brown streak on anterodistal margin and brown cloudiness in anal cell apically. Abdomen dorsally with granulated gray-brown pigmentation forming transverse bands along tergites, fusing laterally to give effect of 2 broad lateral bands, a narrow median gray-brown line; ventrally gray-brown pigment on sterna fusing only medially; apical sclerites brown. *Morphology.* I.O.:D. = 5.0. Hind wing with 7–8 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 22–23; 2+1. (1 specimen: 30; 3+1). Thorax alutaceous. Subgenital plate (Fig. 262) apical process with well-sclerotized internal flap, 2 long setae at base of process. Gonapophyses (Fig. 263): dorsal valve broad, narrowing rather abruptly to apical spine; outer valve with short lobe. A field of 25–30 trichobothria on each paraproct.

♂. *Coloration* (freshly killed, in alcohol). As ♀ except fore wing fascia less extensive, single brown patch in anal cell. *Morphology.* I.O.:D. = 1.5–2.0. Hind wing with 7 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 24; 2+1. Thorax alutaceous. Hypandrium (Fig. 264) slightly asymmetrical, marginal teeth of tongue large and stout on left side, particularly subapically, those on right more nearly uniform, narrower; median boss at base of tongue has a spinose outline at high magnifications. Phallosome tine long, split in apical ½ and forking in apical ¼ (Fig. 265). Epiproct anterior lobe high, fairly narrow (Fig. 266). Paraproct with stout basal boss, a field of 29–30 trichobothria.

Distribution. MOLOKAI, frequent.

Holotype ♂, MOLOKAI: nr Kole Kole cabin, *Metrosideros,* 18.VII.1963 (I.W.B. Thornton) (BPBM 13,002). Allotype ♀, data as holotype.

This subspecies differs from the nominate form in size (it is consistently larger) and in pigmentation of the female fore wing membrane. The typical form of *fusca,* as described above, was found in 1963 at about 1200 m at the western end of the main Molokai mountain mass in the forest bogs to the SE of the Waikolu Valley. Five specimens were collected by J.L. Gressitt in April and May 1955 "above Waikolu Valley" at over 1200 m on *Metrosideros,* and other specimens available are from near Puu Kole Kole and S of Hanalilolilo, collected in July 1963 on *Metrosideros* and *Juniperus.* Two specimens among the latter show a darkening of the pigmentation of

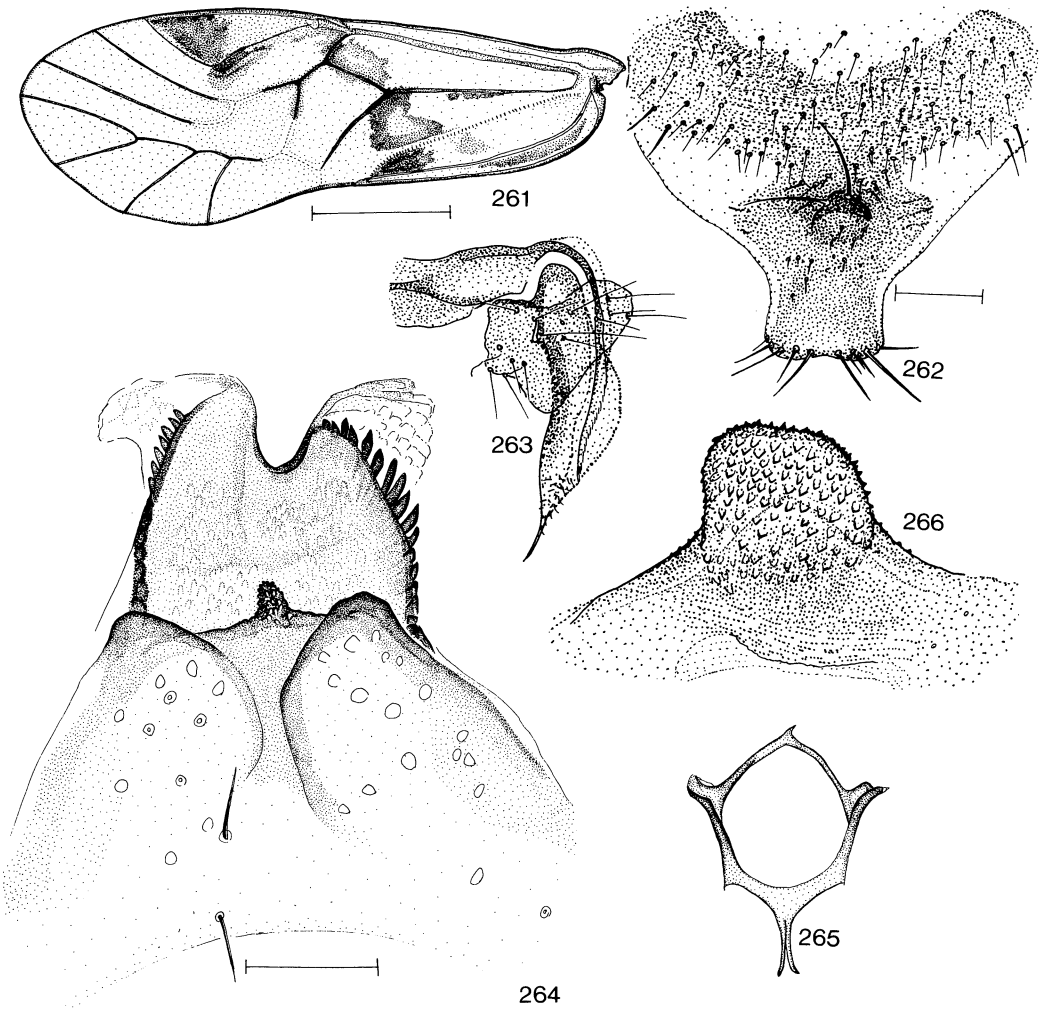

FIG. 261–266. *Ptycta lanaiensis fusca:* **261,** ♀ fore wing; **262,** subgenital plate; **263,** gonapophyses; **264,** hypandrium; **265,** phallosome; **266,** ♂ epiproct lobe. Fig. 262, 263, 265 and Fig. 264, 266 to common scales.

the wing membrane, particularly near the veins and margin. The most extreme example is unusually large, with the number of ctenidia on the hind tarsal segments as high as 30 and 3+1. Moreover, both specimens show very little merging of the clypeal striae, so that the clypeus lacks the dark wedge-shaped mark. These characters, though extreme, intergrade into those of the other specimens, with which they are sympatric.

Ptycta lanaiensis halawa Thornton, **new subspecies** Fig. 267–273

Differs from *P. lanaiensis fusca* in the following respects:

♀. *Coloration* (freshly killed, in alcohol). Clypeal striae fused medially anteriorly, forming very distinct and well-marked wedge-shaped mark on clypeus. Median stirrup mark on frons accompanied by 2 discrete spots anteriorly. Fore wing (Fig. 267) membrane hyaline in apical ½. *Morphology.* Subgenital plate (Fig. 268): pair of longer setae not discernible at base of process. Gonapophyses (Fig. 269): outer valve lobe very small.

♂. *Morphology.* I.O.:D. = 0.6–0.8. Eyes large. Hypandrial teeth (Fig. 270) rather smaller than those of *lanaiensis fusca.* Phallosome tine (Fig. 271, 272) divided only apically at low magnifications. Epiproct lobe (Fig. 273) rather lower, rounded.

Distribution. MOLOKAI, frequent.

Holotype ♂, MOLOKAI: W of Halawa Val, Hipuapua Gulch N ridge, collecting from *Metrosideros* and *Cheirodendron,* 15.VII.1963 (I.W.B. Thornton) (BPBM 13,003). Allotype ♀, data as holotype.

Specimens of this subspecies have been collected only from the forest bogs to the W of Halawa Valley, on the eastern side of the main mountain mass of Molokai, from *Metrosideros, Cheirodendron, Cibotium* and *Pelea,* in July 1963.

The differences from *fusca* in head pattern, that of subspecies *halawa* being much more distinct and well defined, are of degree only. The difference in male eye size is, however, quite striking, the I.O.:D. ratio of *fusca* being 2× that of *halawa.* These 2 subspecies are of the same size, have the same fore wing pigmentation pattern (apart from the darkening of the apical membrane), and very similar genitalic characters. They thus differ from each other less then either does from subspecies *lanaiensis.*

Ptycta lanaiensis persclera Thornton, **new subspecies** Fig. 274–276

Differs from *P. lanaiensis fusca* in the following respects:

♀. *Coloration* (freshly killed, in alcohol). Lateral frons marks lacking; costal cell of hind wing brown; pigment in cubital cell of fore wing (Fig. 274) rather more extensive. *Morphology.* Hind wing with 12 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 27; 2+1. Posterior lobe of outer valve rather narrow (Fig. 276), apical process of subgenital plate rather broad (Fig. 275).

♂. Unknown.

Distribution. MAUI, rare.

Holotype ♀, MAUI: Haleakala, 2000 m, on *Picea abies,* 20.XI.1963 (I.W.B. Thornton) (BPBM 13,004).

P. l. persclera is very close to *fusca,* on E Molokai, but *persclera* differs in head pattern.

Ptycta heterogamias (Perkins), **revised combination** Fig. 277–283

Psocus heterogamias Perkins, 1899: 82.—Zimmerman, 1948b: 247.
Clematostigma heterogamias (Perkins): Enderlein, 1913: 355.

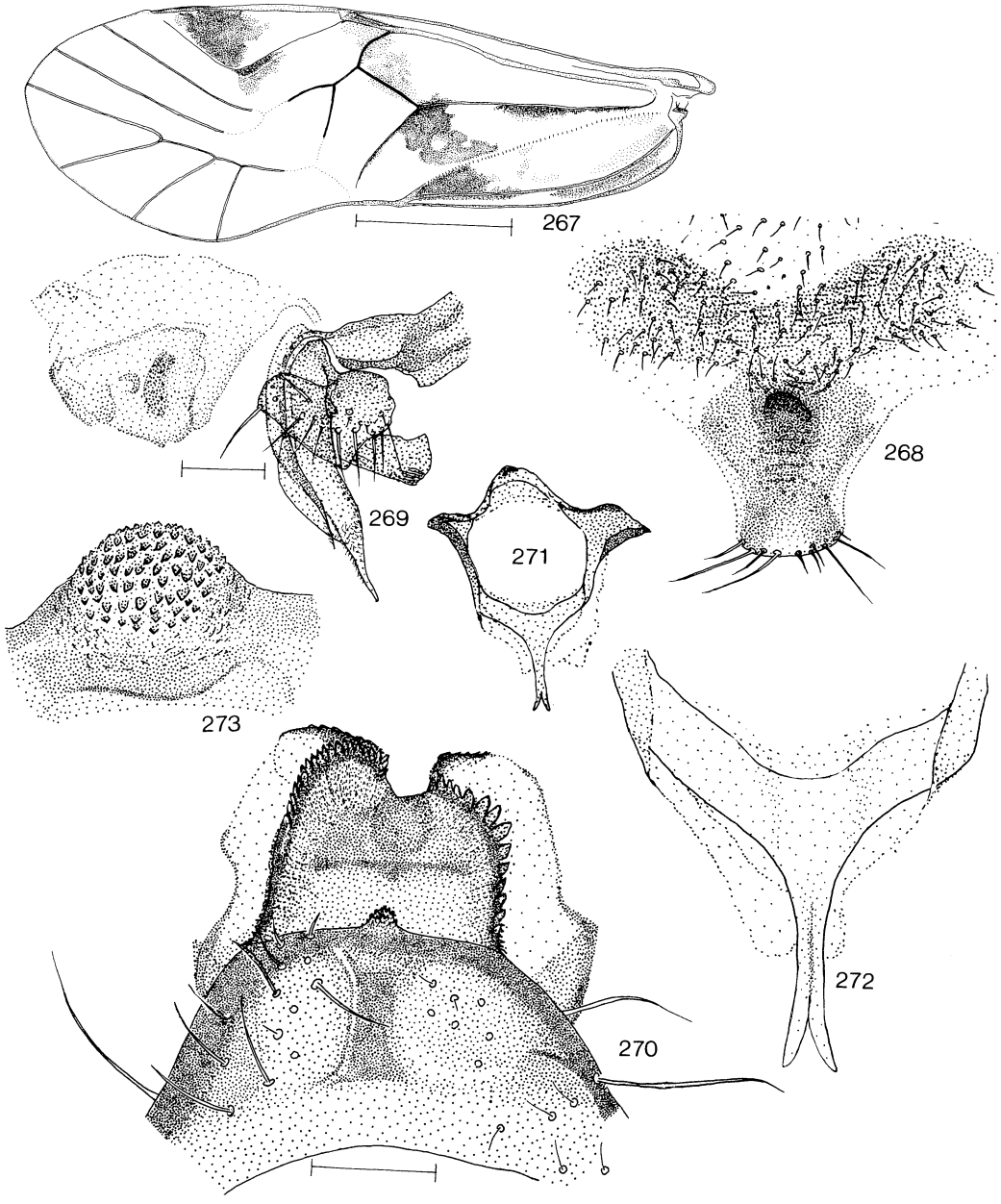

FIG. 267–273. *Ptycta lanaiensis halawa:* **267,** ♀ fore wing; **268,** subgenital plate; **269,** gonapophyses; **270,** hypandrium; **271,** phallosome; **272,** phallosome tine; **273,** ♂ epiproct lobe. Fig. 268, 269, 271 and Fig. 270, 272, 273 to common scales.

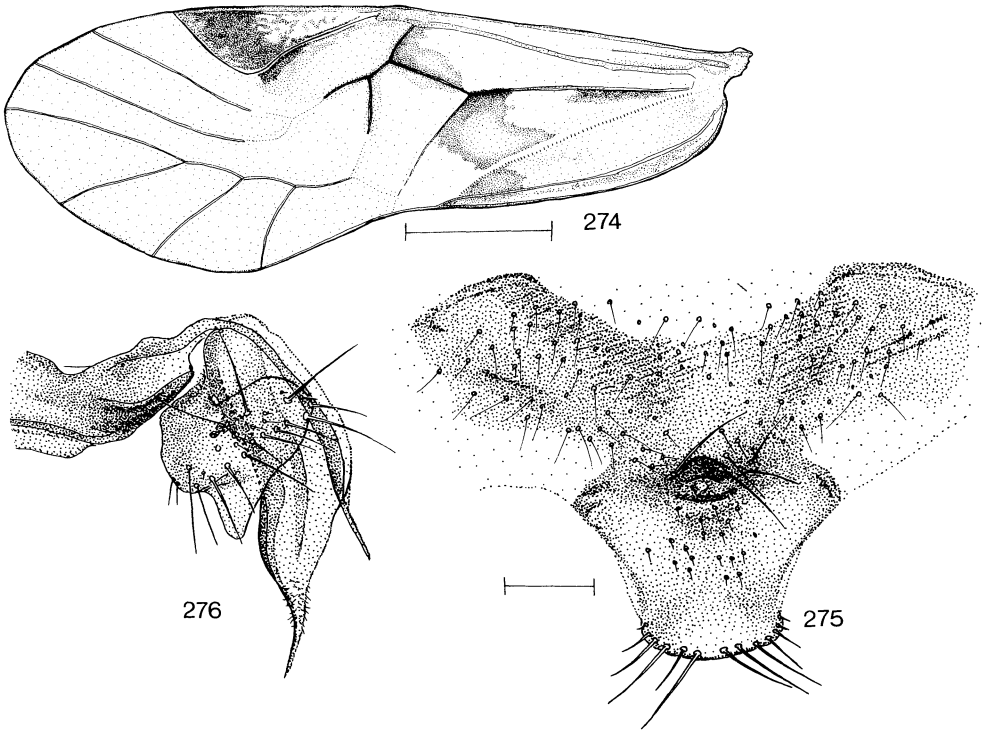

FIG. 274–276. *Ptycta lanaiensis persclera* ♀: **274,** fore wing; **275,** subgenital plate; **276,** gonapophyses. Fig. 275, 276 to common scale.

not *Psocus haleakalae* var. *lanaiensis* (Perkins): Enderlein, 1920: 450.
not *Ptycta haleakalae* var. *lanaiensis* (Perkins): Enderlein, 1925: 102.

The following further description is based on an examination of male type material, there being no female type material, and of other dry material in the collections of the Hawaiian Sugar Planters' Association and the B.P. Bishop Museum.

♀. *Coloration* (after ca. 40 years dry storage). Head with vertex uniformly buff, frons and clypeus fairly dark. Gena with brown line from antennal socket to orbit, 2 parallel lines below this. Maxillary palpi brown, apical segment darker. Antenna brown, basal flagellar segment somewhat paler, except distally. Thorax brown, dorsal lobes of mesothorax paler in some specimens. Wings: fore wing (Fig. 277) as holotype ♂ but clouds in apical cells often with more and larger hyaline areas, that part of *m* forming vertex of areola postica always dark for a very short distance. Hind wing with brown smokiness in anal cell along *an* and at distal angle. Leg and abdominal color not distinguishable. *Morphology.* I.O.:D. = 2.2. Hind wing with 5 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 32; 2+1. Subgenital plate (Fig. 278) with nonuniform sclerotization, apical process broad, squat, with 2 close-set long setae basally. Gonapophyses (Fig. 279): dorsal valve narrow, outer valve with a narrow, fairly long lobe. A field of 28 trichobothria on each paraproct.

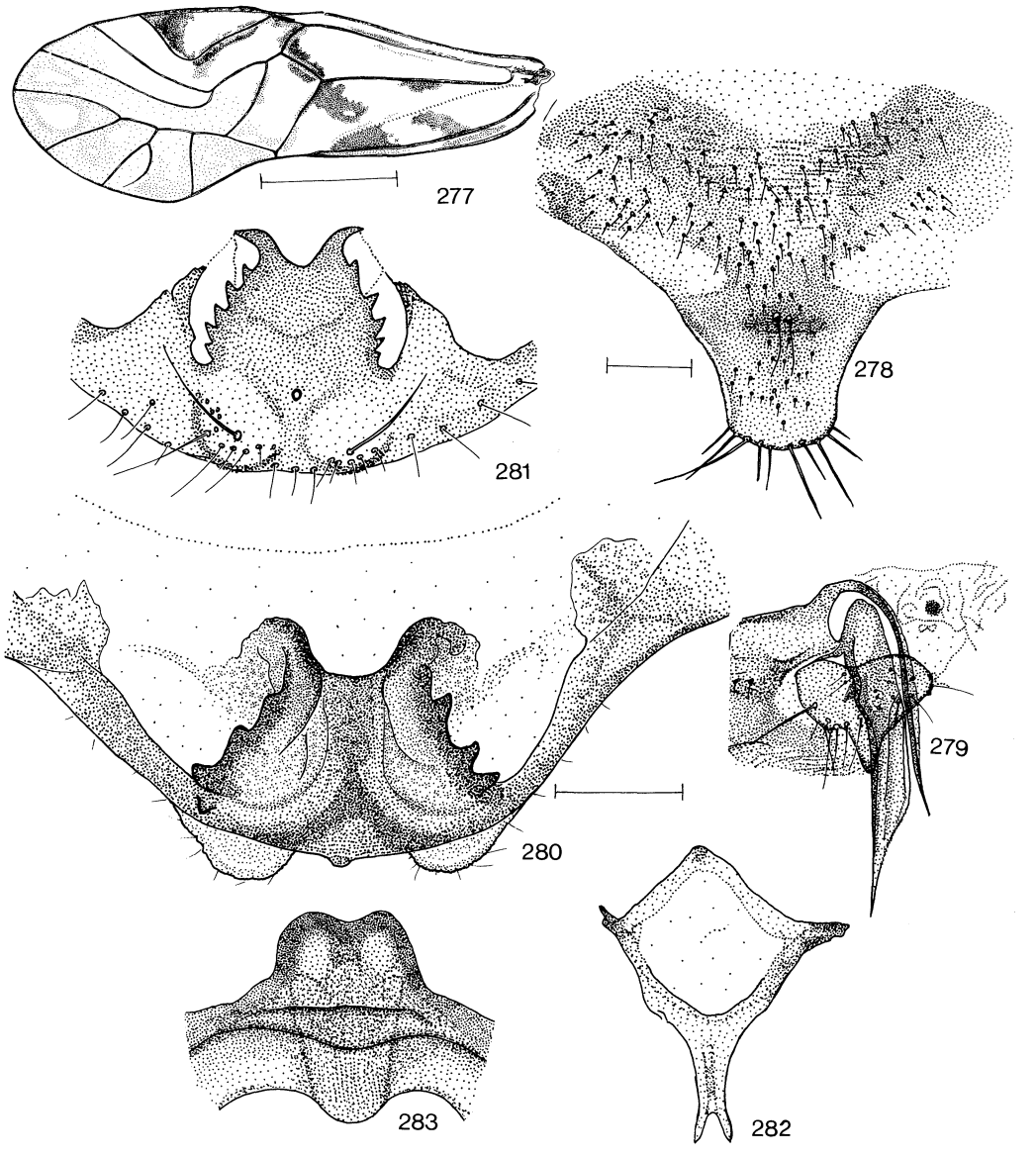

FIG. 277–283. *Ptycta heterogamias:* **277,** ♀ fore wing; **278,** subgenital plate; **279,** gonapophyses; **280,** hypandrium; **281,** type hypandrium; **282,** phallosome; **283,** ♂ epiproct lobe. Fig. 281 not to scale, sketched from type; all others from Haleauau specimens. Fig. 278, 279, 282 and Fig. 280, 283 to common scales.

♂. *Coloration* (after ca. 60 years dry storage). As ♀ except vertex not obviously buff. Wing markings as in holotype but often 2 hyaline windows in cell M_1, and veins r_{4+5} and m_1 often with a fairly short dark section subapically. *Morphology.* Eyes fairly prominent. I.O.:D. = 1.5. Hind wing with 5 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal

segments: 30; 2+1. Hypandrium (Fig. 280) symmetrical, with only 4 or 5 (5 in the holotype, Fig. 281) large well-spaced teeth each side on margin of tongue, basal one low and blunt, a median bluntly rounded boss at base of tongue, highly convex areas bearing setae basally. Phallosome (Fig. 282) with a very long tine, bifurcating in apical ⅓. Anterior lobe of epiproct high, narrow, bilobed (Fig. 283). Paraprocts each with a field of 26–28 trichobothria.

Distribution. OAHU, rare.

Specimens, other than type ♂, on which the above further description is based. 1♂,1♀, OAHU, S Waianae Range, Haleauau, 1.XII.1929 (Swezey).

This species has not been found in recent years, despite the visits of 3 specialist collectors and the fact that Oahu received more attention generally than the other islands. It is known from both the Waianae and Koolau mountain ranges, and has been collected at as low an elevation as 280 m in the Nanakuli Valley. It has been taken on *Elaeocarpus* and other trees. Perkins' collections were from the Waianae and Honolulu mountains, and the species has also been taken on Mt Kaala and at Kole Kole Pass by Swezey. The adult has been collected in February, March, April, July, and December.

The original description by Perkins was of the male, the nymphs being mistaken for females, hence the specific name. Enderlein, 1920, synonymized *heterogamias* with *lanaiensis* and pointed out that Perkins' type females were in fact nymphs. I can find no grounds for maintaining the synonymy with *lanaiensis*, the 2 species being quite distinct in several characters; most notably, the distinctive sclerotized flap of the subgenital plate of *lanaiensis* is represented in *heterogamias* by a thickening of the plate only, in the same position.

There is considerable individual variation in extent of the dark brown transverse fascia in the fore wing, and in the extent of hyaline patches in the clouds in the apical cells. Nevertheless, the fore wing pattern is quite distinctive, and the species may be recognized on this alone. The hypandrium is also quite distinctive in the shape of the tongue and number and arrangement of the teeth.

Ptycta sylvestris (Perkins), **revised combination** Fig. 284–290

Psocus sylvestris Perkins, 1899: 81.—Zimmerman, 1948b: 249.
Clematostigma sylvestris (Perkins): Enderlein, 1913: 355.
not *Psocus haleakalae* var. *lanaiensis* Perkins: Enderlein, 1920: 450.
not *Ptycta haleakalae* var. *lanaiensis* (Perkins): Enderlein, 1925: 102.

The following description is based on an examination of type material labelled *Psocus immaturus* Perkins (which, as Zimmerman implies, agrees with the description of *P. sylvestris* and which was not described under the name *immaturus*), and of material collected more recently. It supplements that of Perkins.

♀. *Coloration* (freshly killed, in alcohol). Head generally cream, vertex markings brown. Small vague brown patch each side ocellar protuberance, very narrow brown line along frons-vertex suture. Frons cream, median brown stirrup mark, no other marks. Clypeus with brown parallel striae merging medially. Gena cream, brown band from orbit to antennal socket, no other bands. Eyes black. Maxillary palpi pale buff, preapical segment brown, apical segment

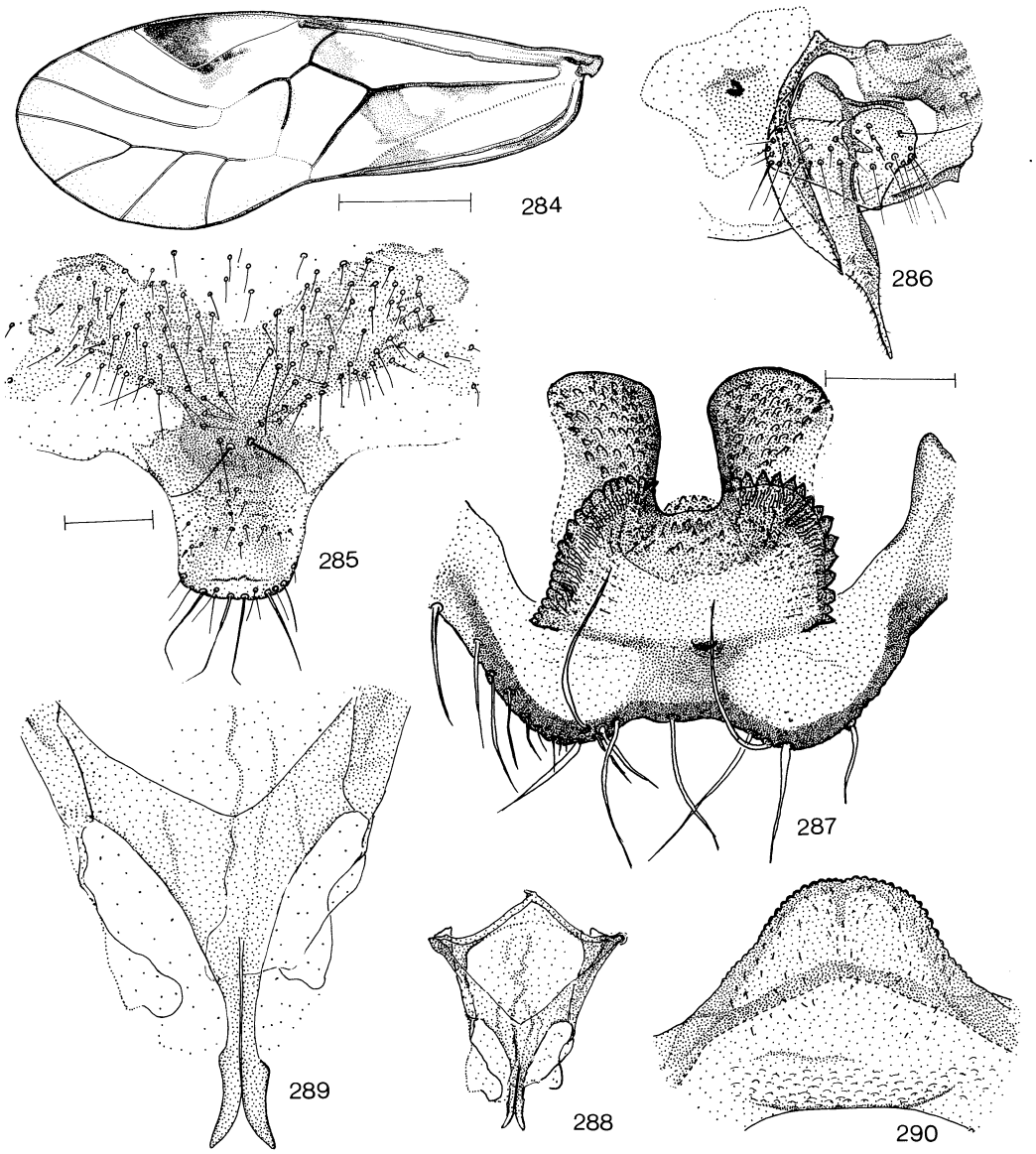

FIG. 284–290. *Ptycta sylvestris:* **284,** ♀ fore wing; **285,** subgenital plate; **286,** gonapophyses; **287,** hypandrium; **288,** phallosome; **289,** phallosome tine; **290,** ♂ epiproct lobe. Fig. 285, 286, 288 and Fig. 287, 289, 290 to common scales.

darker. Antennae brown. Thoracic terga brown, widely bordered yellowish cream, obvious large cream arrowhead mark on antedorsum of mesothorax, wide median cream band between dorsal lobes of meso- and metathorax, scutella brown. Pleura brown. Legs: coxa brown, trochanter very pale buff; femur very pale buff, pale brown apically; tibia pale brown; tarsus

brown. Fore and hind wings as drawn by Zimmerman (1948b) for ♂ type, but in fore wing fascia rather more extensive and 2 patches of pigment in anal cell (Fig. 284), veins *sc* and *m+cu* very pale; hind wing with brown streak on anterodistal margin, costal cell brown. Abdomen white, dorsally with blackish-gray pigment forming a wide longitudinal band in midline over basal 4 segments, more apically such a band each side dorsolaterally over segments 5–8; some scattered pigment extremely laterally; abdomen ventrally white, apical structures brown where sclerotized, cream where unsclerotized. *Morphology.* I.O.:D. = 2.6. Hind wing with 8 marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 26; 2+1. Subgenital plate (Fig. 285) with 2 extremely long setae on a heavily sclerotized area at base of process. Gonapophyses (Fig. 286): dorsal valve tapering gradually to apical spine; ventral valve rather short; outer valve with very small lobe. A field of 26 trichobothria and 2 setae not in rosette sockets on each paraproct. Gonopore plate (not seen in type) as in Fig. 286.

♂. *Coloration* (freshly killed, in alcohol). As ♀, wings as drawn by Zimmerman (1948b), *sc* of fore wing very pale. *Morphology.* I.O.:D. = 0.7. Hind wing with 5 marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 30; 2+1. Hypandrium (Fig. 287) with apical tongue semicircular, sharply marked off from more basal structures, teeth on left margin sharply pointed, those on right blunt, closer packed, a small median spine basally. Phallosome tine (Fig. 288, 289) deeply split, forked only apically. Epiproct (lacking in type) with fairly high bilobed anterior lobe (Fig. 290). Paraproct with fairly prominent boss, a field of 25 trichobothria.

Distribution. HAWAII, occasional.

Further description based on types, and 1♂,1♀, HAWAII: Kilauea area, Kipuka Puaulu, *Acacia koa,* 25.VI.1963.

P. sylvestris was taken on *Acacia koa* in Kipuka Puaulu (1200 m) in June 1963. A male was captured by Swezey in September 1931 at Nauhi Gulch on *Myoporum* at 1500–1800 m, and Perkins' types were collected in July 1892 at Kona (the male and female types' labels were reversed).

This species is similar in size and fore wing markings to the larger subspecies of *P. lanaiensis.* It differs, however, in genitalic characters. In *sylvestris,* the female subgenital plate lacks the sclerotized flap, the male epiproct lobe is double and the phallosome tine, although very similar to that of *P. lanaiensis,* has the arms somewhat curved, similar to those of *P. disclera.* Although lacking the distinctive sclerotized flap of the subgenital plate, it is placed in this group on the asymmetrical hypandrium.

The synonymy with *lanaiensis,* as a variety of *P. haleakalae* (Enderlein 1920), is not supported by detailed studies.

schisma group

This group of 6 species is centered on Oahu (Fig. 335), although 1 species is endemic to Molokai, and another occurs on Maui. The group is characterized by the possession of teeth on the surface of the hypandrial tongue in all but the Molokai species. Evidence of relationship with the *lanaiensis* group is seen in the female subgenital plates of *schisma* and *kaala,* which, like species of that group, have a sclerotized flap at the base of the apical process.

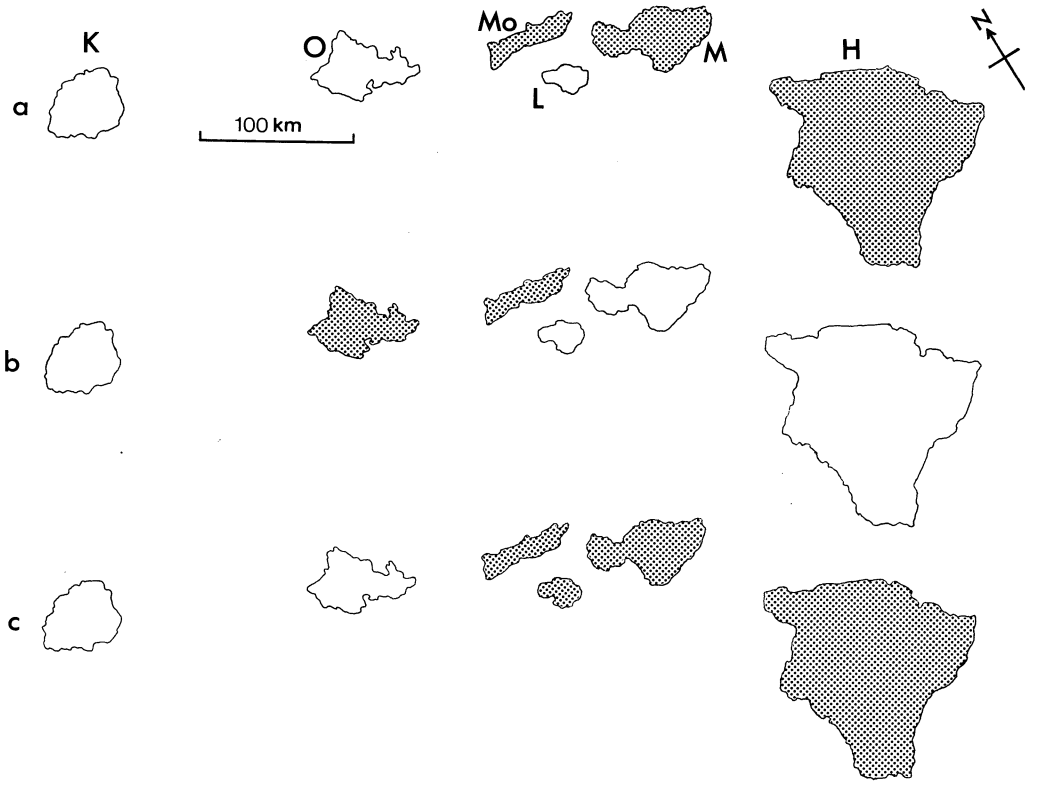

FIG. 291. Archipelago distributions of species groups of *Ptycta:* **a,** *disclera* (4 species); **b,** *diadela* (3); **c,** *frogneri* (5).

Ptycta schisma Thornton, **new species** Fig. 292–298

♀. *Coloration* (freshly killed, in alcohol). Vertex pale cream, usual markings pale brown medially and posteriorly, pale buff laterally. Light brown patch each side ocellar protuberance, dark brown line along vertex-frons suture. Frons with pale brown median stirrup mark, dark brown spot lateral to and not touching this. Clypeus pale cream, dark transverse band and anterior median band forming well-defined T-shaped brown mark. Gena pale cream, very pale light brown band from antennal socket to orbit. Maxillary palpi pale cream, apical segment brown. Scape, pedicel, basal flagellar segment pale brown, apex of basal segment and rest of flagellum brown. Mesothoracic terga: antedorsum cream, brown anteriorly; dorsal lobes largely cream, a brown spot posteromesially, scutellum brown. Metathoracic terga brown, bordered cream. Pleura brown. Legs: coxa brown, trochanter, femur, tibia pale cream, basal tarsal segment very pale brown, 2nd segment brown. Wings: brown transverse fascia in fore wing (Fig. 292) angled, interrupted, 2 distinct brown patches in anal cell, brown mark ½ way along *m+cu,* pterostigma pigment confined to distal ¼, not touching vertex, veins bounding basal ½ areola postica hyaline; hind wing hyaline, longitudinal brown mark in anterodistal border. Abdomen cream, distinctively patterned. Dark gray-brown pigmentation on basal 3 segments

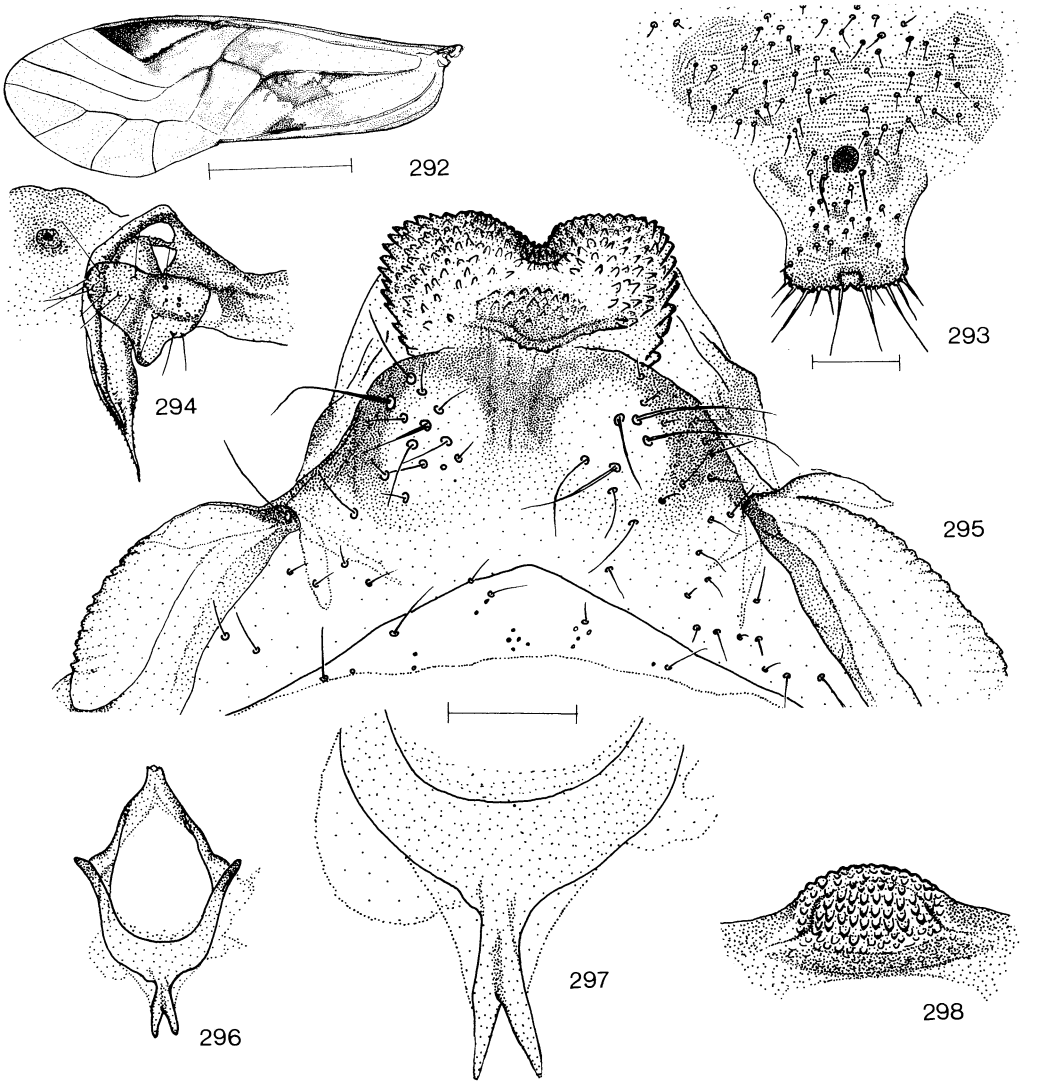

FIG. 292–298. *Ptycta schisma:* **292,** ♀ fore wing; **293,** subgenital plate; **294,** gonapophyses; **295,** hypandrium; **296,** phallosome; **297,** phallosome tine; **298,** ♂ epiproct lobe. Fig. 293, 294, 296 and Fig. 295, 297, 298 to common scales.

confined (except extremely laterally) to dorsal surface of terga, on more distal segments confined to dorsolateral position, thus producing 3 short longitudinal bands, 1 medial anteriorly, and 2 dorsolateral posteriorly. Abdomen ventrally cream, apical sclerites brown. *Morphology.* I.O.:D. = 2.2. Hind wing with 9 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 21–25; 2+1. Subgenital plate (Fig. 293) with apical process narrowing distally, very long setae at its base; heavily sclerotized small flap. Gonapophyses (Fig. 294):

dorsal valve narrowing smoothly apically, outer valve with small but well-defined lobe. A field of 21–23 trichobothria on each paraproct. Gonopore plate sclerotized anteriorly.

♂. *Coloration* (freshly killed, in alcohol). As ♀ except basal tarsal segment brown, pterostigma pigmentation reaches vertex. *Morphology.* Eyes prominent, I.O.:D. = 0.8. Hind wing with 5–6 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 29; 2+1. Hypandrium (Fig. 295) symmetrical, margin and surface of tongue toothed, no median basal boss. Phallosome apical tine bifid (Fig. 296, 297). Epiproct anterior lobe fairly high, tuberculate (Fig. 298). Basal boss of paraproct long, prominent, a field of 27 trichobothria.

Nymph. Markings on abdomen as adult, distinctive.

Distribution. OAHU, frequent.

Holotype ♂, OAHU: Palolo Val, 26.XII.1914 (O.H. Swezey) (BPBM 13,005). Allotype ♀, OAHU: Tantalus trail, 550 m, *Acacia koa,* 20.II.1963 (I.W.B. Thornton).

This species has only been taken on *Acacia koa* at the eastern end of the Koolau Range, i.e., the mountains behind Honolulu, from 400–600 m, in February, August, September, and December.

P. schisma is easily distinguished from any other species by the combination of areola postica, and face and abdominal patterns. The sclerotized flap on the female subgenital plate indicates relationship to the *lanaiensis* group.

Ptycta dicrosa Thornton, **new species** Fig. 299–305

♀. *Coloration* (freshly killed, in alcohol). Head generally pale buff, vertex markings brown. Brown line each side of ocellar protuberance continued as line along vertex-frons suture. Frons pale buff, median brown stirrup mark, lateral gray-brown marks may be contiguous. Clypeus pale buff, parallel striae faint, darker and merging medially and in a transverse band across clypeus, thus forming a cross-shaped mark on clypeus. Gena pale buff, narrow brown band from orbit to antennal socket, sometimes a gray-brown mark below this. Eyes black. Maxillary palpi pale, apical segment brown. Antennae with scape, pedicel and most of basal flagellar segment pale brown; basal segment darker apically, rest of flagellum brown. Thoracic terga brown, margined cream; cream median line on meso- and metathorax, scutella brown; pleura brown. Legs: coxa brown; trochanter, femur and tibia pale cream; femur light brown subapically; tarsus brown. Fore wing (Fig. 299) with angled, somewhat interrupted transverse fascia, 2 distinct patches in apical ½ cell *An,* pigment within pterostigma barely reaching vertex, areola postica usually bounded by pigmented veins basally. Hind wing hyaline, very faintly fuscous in apical angle of anal cell, faint brown streak on anterodistal margin. Abdomen buff, with scattered gray-brown granulated pigment. *Morphology.* I.O.:D. = 3.0. Hind wing with 10 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 22; 2+1. Subgenital plate (Fig. 300) with short apical process bearing 2 very long setae basally. Gonapophyses (Fig. 301): dorsal valve smoothly pointed; outer valve with apical lobe. A field of 29 trichobothria on each paraproct and 1 seta not in rosette socket.

♂. *Coloration* (freshly killed, in alcohol). As ♀ except lateral frons marks very small or absent, only 1 stripe on gena. *Morphology.* I.O.:D. = 1.2, eyes large. Hind wing with 8 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 20; 2+1 (1 specimen 20; 1+1). Hypandrium (Fig. 302) symmetrical, with about 10 pointed teeth along each margin of tongue, small and blunt apically, no basal spine. Phallosome tine (Fig. 303, 304), duplex, apices sharply pointed, angular. Epiproct with low tuberculate anterior lobe, not itself bilobed (Fig. 305); paraproct boss very low, a field of 22 trichobothria and 2 setae not in rosette sockets.

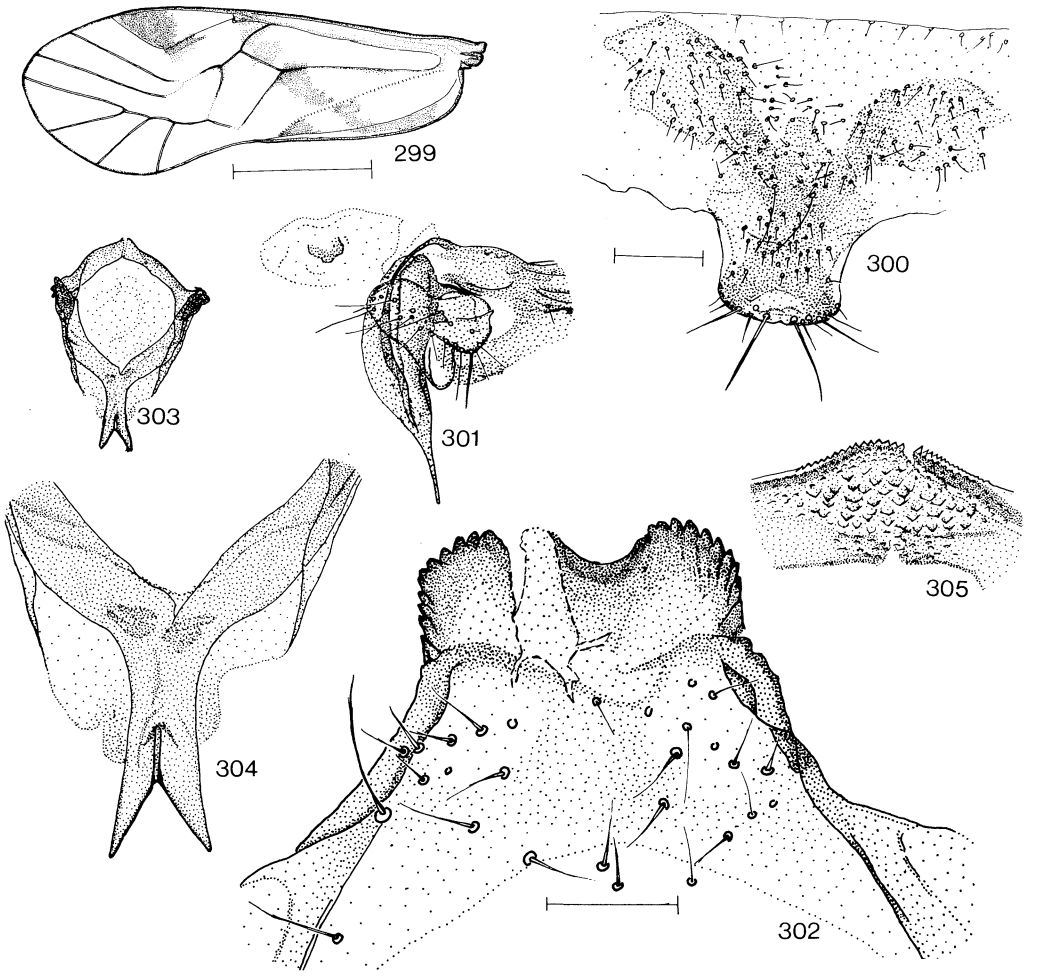

FIG. 299–305. *Ptycta dicrosa:* **299,** ♀ fore wing; **300,** subgenital plate; **301,** gonapophyses; **302,** hypandrium; **303,** phallosome; **304,** phallosome tine; **305,** ♂ epiproct lobe. Fig. 300, 301, 303 and Fig. 302, 304, 305 to common scales.

Distribution. MOLOKAI, occasional.

Holotype ♂, MOLOKAI: above Waikolu Val, 1210 m, 2.V.1955, *Metrosideros* (J.L. Gressitt) (BPBM 13,006). Allotype ♀, MOLOKAI: N ridge Halawa Val, 520 m, nr Kepookoholoaa, *Pelea,* 16.VII.1963 (I.W.B. Thornton).

Three ♂s and 2 ♀s were collected at about 520 m in the mountains W of Halawa Valley, E Molokai, in July 1963, on *Pelea,* and 1♂ was collected on *Metrosideros* by Gressitt at over 1200 m "above Waikolu Valley" in May 1955.

Superficially similar to *P. lanaiensis, dicrosa* may be distinguished by the fact that the veins bordering the basal ½ of the areola postica are, at least to some extent,

pigmented, as well as by details of the genitalia. It differs from other members of the group in the pigmentation of the areola postica veins, and in wing markings.

The Waikolu specimen has the hypandrial teeth at the apex shorter, blunter, and with a wider gap between them than those of the specimens from Halawa, and there are slight differences in the shape and proportions of the phallosome tines.

The placement of this species is difficult; in hypandrium it resembles the *disclera* group, but like members of the *schisma* group, it lacks the central basal boss at the base of the tongue. In female fore wing pattern it is more similar to species of the *schisma* group than to the *disclera* group.

Ptycta kaala Thornton, **new species** Fig. 306–311

♀. *Coloration* (after 34 years dry storage). Vertex buff, usual markings brown. Light brown patch each side ocellar protuberance, continued along vertex-frons suture as light brown line. Frons with brown median stirrup mark, no other marks discernible. Clypeus pale buff, brown parallel striae darker medially but distinct. Gena buff, brown band from orbit to antennal socket. Maxillary palpi pale, subapical segment brown, apical segment dark brown. Scape, pedicel, basal flagellar segment pale brown, apex of segment and rest of flagellum brown. Thoracic terga brown, pleura brown. Legs: coxa brown, trochanter, femur and tibia colorless, femur and tibia pale brown apically, tarsus brown. Fore wing (Fig. 306) with broad, angled, uninterrupted transverse fascia, 2 patches of pigment in anal cell fusing, small brown mark ½ way along *m+cu*, pigment within pterostigma confined to distal ½ and reaching vertex, distinct brown patch on *m* close to its point of separation from *rs*, veins bordering basal ½ areola postica hyaline. Hind wing hyaline, longitudinal brown mark on anterodistal border, anal cell clouded pale brown in apical ½. Abdomen color pattern not discernible. *Morphology.* I.O.:D. = 3.0. Hind wing with 6 fine marginal setae between ends of *rs*. Number of ctenidia on hind tarsal segments: 23; 2+1. Subgenital plate (Fig. 307) T-shaped, apical process broad, bearing 2 long setae and an inner sclerotized rounded flap near base. Gonapophyses (Fig. 308): dorsal valve narrowing smoothly apically, outer valve with small lobe. A field of 21–25 trichobothria on each paraproct. Epiproct only slightly marginate on anterior edge.

♂. *Coloration* (after 34 years dry storage). As ♀, but lateral brown marks on frons discernible; transverse fascia of fore wing narrower, single pigmented patch in anal cell. *Morphology.* I.O.:D. = 1.0. Eyes large. Hind wing with 6 fine marginal setae between ends of *rs*. Number of ctenidia on hind tarsal segments: 22; 2+1. Hypandrium (Fig. 309) with approximately 12 teeth each side of apical tongue and many sclerotized teeth on surface towards apex. Phallosome tine (Fig. 310) apparently bifid in apical ½. Epiproct anterior lobe (Fig. 311) high, rather pointed. A field of approximately 22 trichobothria on each paraproct.

Distribution. OAHU, rare.

Holotype ♂, OAHU: Mt Kaala, *Metrosideros*, 21.VII.1929 (O.H. Swezey) (BPBM 13,007). Allotype ♀, same data as holotype.

This is 1 of several examples among Hawaiian insects of a species collected by Swezey in 1 locality and not recovered since. Both sexes were collected from *Metrosideros* in July 1929 on Mt Kaala, Waianae Range.

Like *P. schisma, kaala* shares with the *lanaiensis* group the sclerotized flap on the female subgenital plate, and its placement in the *schisma* group is based on *hypandrial* characteristics.

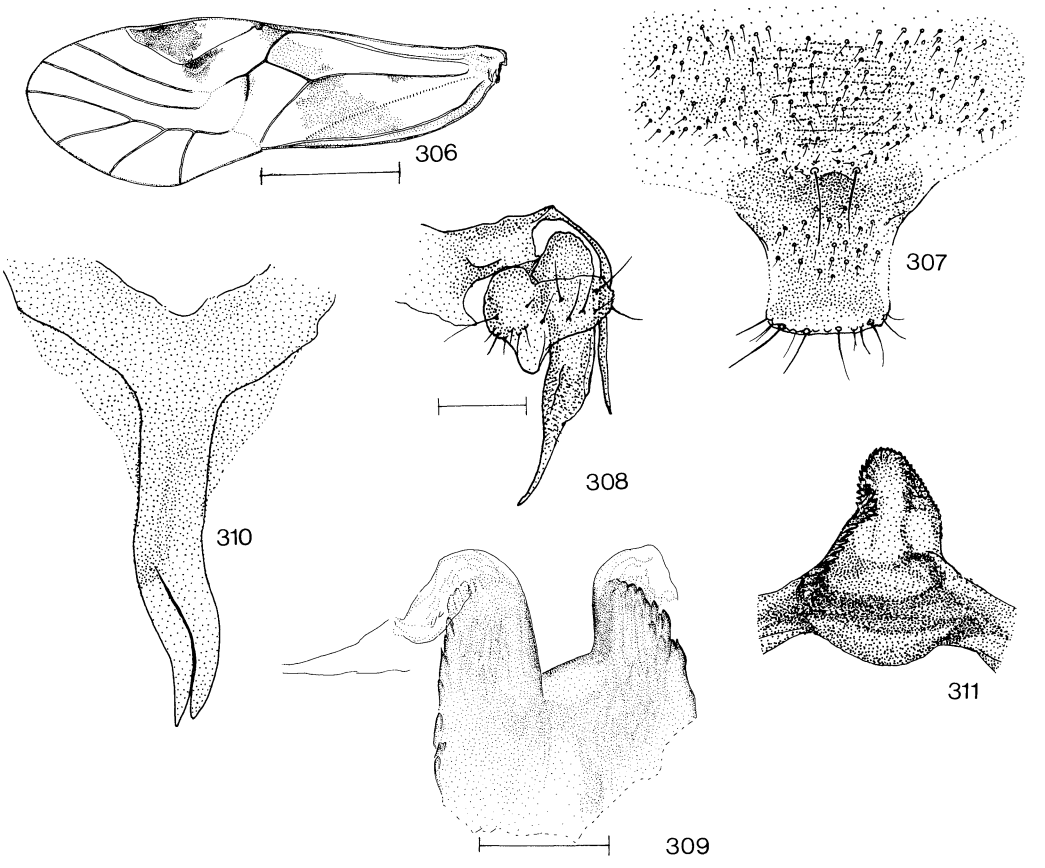

FIG. 306–311. *Ptycta kaala:* **306,** ♀ fore wing; **307,** subgenital plate; **308,** gonapophyses; **309,** hypandrium; **310,** phallosome tine; **311,** ♂ epiproct lobe. Fig. 307, 308 and Fig. 309–311 to common scales.

Ptycta oligocantha Thornton, **new species** Fig. 312–318

♀. *Coloration* (freshly killed, in alcohol). Vertex cream, usual markings brown. Light brown patch each side ocellar protuberance continued as brown line along vertex-frons suture. Frons cream, median brown stirrup mark with large brown spot contiguous laterally. Clypeus buff, parallel striae merging to form median brown band, wider anteriorly. Gena cream, brown band from antennal socket to orbit, a 2nd parallel band below this. Maxillary palpi pale, apical segment brown. Scape, pedicel and 1st flagellar segment pale brown, rest of flagellum brown. Mesothoracic terga: antedorsum brown, cream arrowhead mark posteriorly; dorsal lobes brown, cream margins; scutellum brown. Metathoracic terga brown, bordered cream. Pleura brown. Legs very pale buff, except coxa, apices of femur, tibia, and tarsus brown. Fore wing (Fig. 312) with continuous, angled transverse band, 2 brown patches in cell *An*, pterostigma patch confined to apical ⅓, not reaching vertex or apical angle, veins bordering basal ½ areola postica hyaline, veins *m* and *rs* fuscous for a short distance from their point of separation, wider along vein *m*,

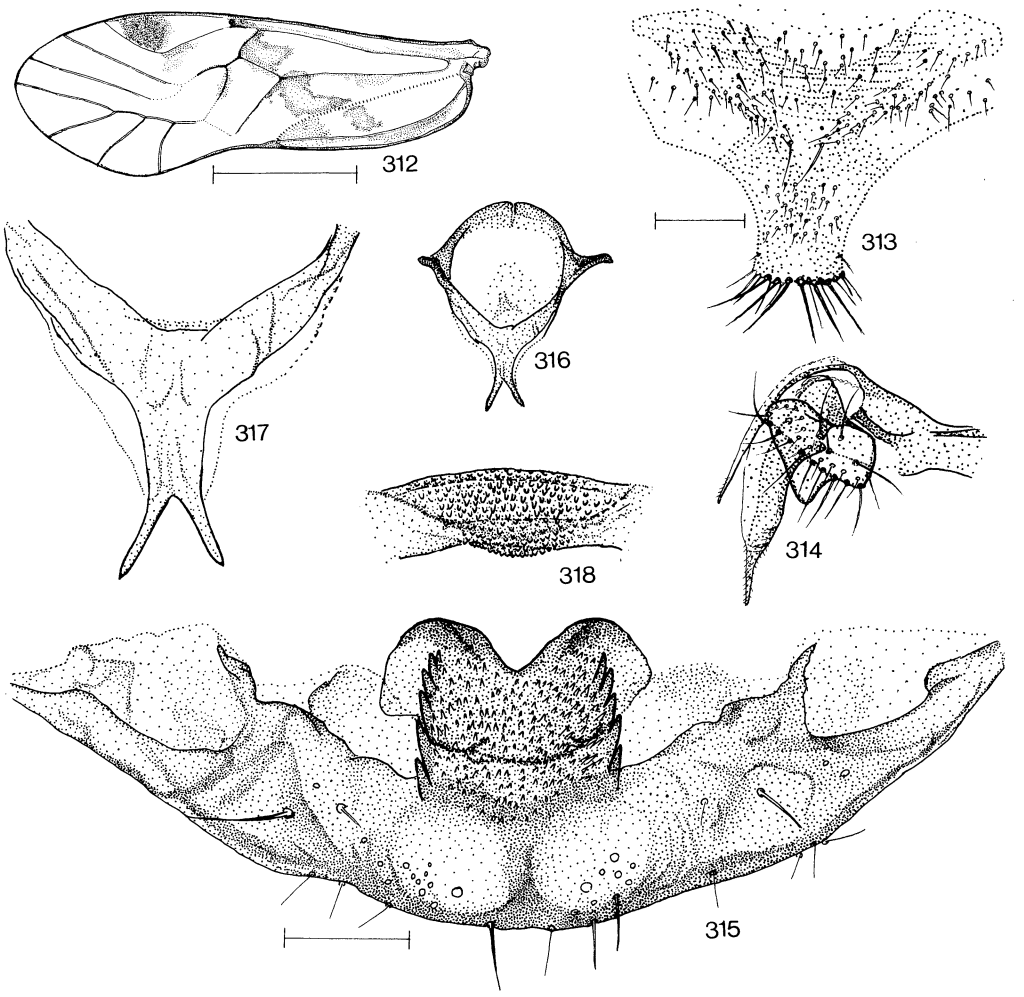

FIG. 312–318. *Ptycta oligocantha:* **312,** ♀ fore wing; **313,** subgenital plate; **314,** gonapophyses; **315,** hypandrium; **316,** phallosome; **317,** phallosome tine; **318,** ♂ epiproct lobe. Fig. 313, 314, 316 and Fig. 315, 317, 318 to common scales.

small brown mark ½ way along *m+cu.* Hind wing hyaline, longitudinal brown mark on antero-distal border, anal cell faintly cloudy apically. Abdomen cream, dark gray-brown granulation over 1st 2 tergites, 1 median and 2 dorsolateral narrow broken longitudinal bands; ventrally cream, transverse gray-brown bands; apical sclerites brown. *Morphology.* I.O.:D. = 3.0. Hind wing with 8 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 21; 2+1. Subgenital plate (Fig. 313) with 2 long setae at base of apical process. Gonapophyses (Fig. 314): very like those of *P. schisma* and *P. pupukea,* n. sp. A field of 21 trichobothria on each paraproct.

♂. *Coloration* (freshly killed, in alcohol). As ♀ but lateral frons marks not touching stirrup

mark, pterostigma spot more extensive, reaching vertex. *Morphology.* Eyes prominent, I.O.:D. = 0.8. Hind wing with 4–6 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 21–23; 2+1. Hypandrium (Fig. 315) with short parallel-sided tongue bearing 6–8 marginal teeth, a field of small sharp teeth on surface (in some specimens 12 very small teeth in addition apically); prominent median sclerotized bar basal to tongue. Phallosome apical tine widely bifid (Fig. 316, 317). Epiproct (Fig. 318) anterior lobe low, tuberculate. Basal boss of paraproct large, prominent, a field of 26 trichobothria.

Distribution. OAHU, occasional.

Holotype ♂, OAHU: E Koolau Range, Palikea Pali, 580 m, *Metrosideros,* 12.IX.1963 (I.W.B. Thornton) (BPBM 13,008). Allotype ♀, data as holotype except 31.X.1963.

Ptycta oligocantha has been collected in February, June, August, September, October, and December on the E Koolau Range, from 460–600 m, on *Metrosideros, Suttonia, Hibiscus,* and *Acacia koa.* It is thus sympatric with *schisma,* though apparently not with *pupukea,* n. sp., which it most closely resembles.

The number of teeth on the hypandrial tongue margin is variable; as many as 10 teeth have been observed, and as few as 6.

This species, like *kaala,* differs from the other species of the *schisma* group in the shape of the hypandrial tongue, but apart from this the differences are slight. The clypeal and abdominal pattern are distinct from those of *schisma,* but the females of *pupukea* and *oligocantha* are extremely similar. *P. oligocantha* has paler legs, generally a less extensive pterostigma spot, and the genal stripes differ in shape from those of *pupukea.* The median sclerotized bar on the hypandrium is also found in *kaala.*

Ptycta pupukea Thornton, **new species** Fig. 319–325

♀. *Coloration* (freshly killed, in alcohol). Vertex pale cream, usual markings brown. Light brown patch each side of ocellar protuberance continued as brown line along vertex-frons suture. Frons cream, brown median stirrup mark, a brown spot lateral to this which may be contiguous. Clypeus buff, parallel striae brown, merging medially to form an ill-defined brown median stripe. Genae cream, brown band from antennal socket to orbit, a 2nd L-shaped mark below this. Maxillary palpi very pale cream, apical segment brown. Scape brown, pedicel and basal flagellar segment buff, rest of flagellum brown. Mesothoracic terga: antedorsum brown, cream arrowhead mark posteriorly; dorsal lobes brown, with cream margins; scutellum brown. Metathoracic terga brown, bordered cream. Pleura brown. Legs: coxa brown; trochanter and femur very pale buff; tibia buff, darker apically; tarsus buff-brown. Wings: brown transverse fascia in fore wing (Fig. 319) almost continuous, 2 distinct brown patches in anal cell, brown mark ½ way along *m+cu,* pterostigma pigment dark brown, confined to distal ½, not filling apical angle and only just reaching vertex, veins bordering basal ½ of areola postica hyaline, a brown spot on *m* a short distance from its point of departure from *rs*; hind wing hyaline, longitudinal brown mark on anterodistal border. Abdomen cream, dorsally dark gray-brown pigmentation pattern as that of *P. schisma* but an additional narrow median streak of gray-brown on distal segments; ventrally cream; apical sclerites brown. *Morphology.* I.O.:D. = 2.8. Hind wing with 7 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 22; 2+1. Subgenital plate (Fig. 320) Y-shaped, arms of Y at wider angle than in *P. schisma,* 2 very long setae at base of apical lobe. Gonapophyses (Fig. 321): dorsal valve tapering

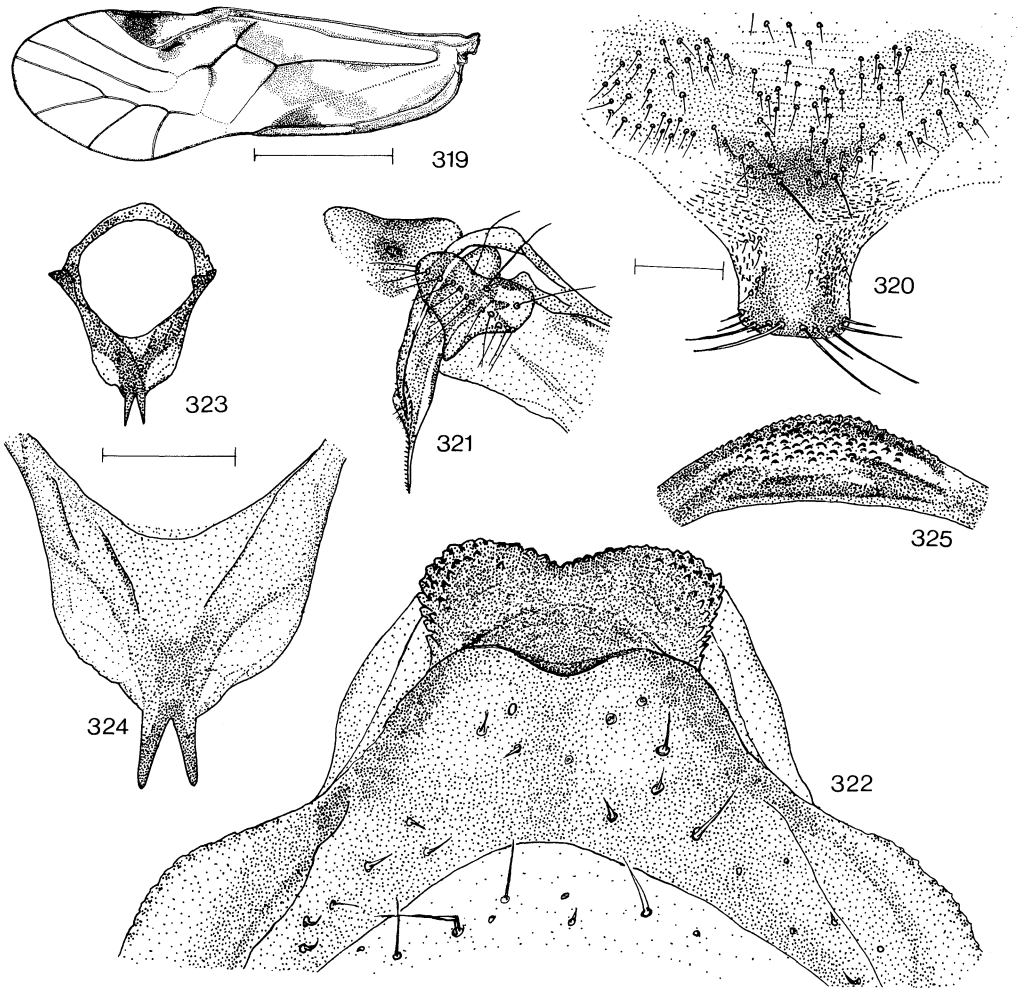

FIG. 319–325. *Ptycta pupukea:* **319,** ♀ fore wing; **320,** subgenital plate; **321,** gonapophyses; **322,** hypandrium (slightly from below); **323,** phallosome; **324,** phallosome apex; **325,** ♂ epiproct lobe. Fig. 320, 321, 323 and Fig. 322, 324, 325 to common scales.

gradually apically; outer valve with small but well-defined lobe. A field of 19 trichobothria on each paraproct. Gonopore plate sclerotized anteriorly.

♂. *Coloration* (freshly killed, in alcohol). As ♀, but pterostigma pigmentation extends some distance basad of vertex. *Morphology.* Eyes prominent, I.O.:D. = 0.8. Hind wing with 6 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 22; 2+1. Hypandrium (Fig. 322) very like that of *P. schisma,* but marginal teeth of tongue in more than 1 main rank basally, surface of tongue untoothed basally. Phallosome tine divided (Fig. 333, 334). Epiproct anterior lobe wider and somewhat lower than that of *P. schisma* (Fig. 335). Basal boss of paraproct long, prominent, a field of 21 trichobothria.

Distribution. OAHU, occasional.

Holotype ♂, OAHU: Pupukea Ridge Trail, *Metrosideros,* 19.II.1963 (I.W.B. Thornton) (BPBM 13,009). Allotype ♀, data as holotype.
P. pupukea has been taken on *Eugenia sandwicensis* and *Metrosideros,* in February, at 600 m.

Closely related to *P. schisma,* which also occurs only on the Koolau range, *pupukea* is nevertheless allopatric with it, being confined to the Pupukea region at the western end of the Koolaus. The 2 species are very similar in genitalic features, but differ consistently, without intermediaries, in color pattern of clypeus, gena, mesothorax, abdomen and fore wing. Moreover, *pupukea* is generally darker and slightly larger. *P. schisma* has only been collected at the eastern end of the Koolau Range, and neither species has been found in intervening areas, thus there is no information on intergradation. Despite this lack, and the close similarities in genitalia, the 2 forms are considered specifically distinct in view of the number and constancy of the differences between them.

Ptycta rhina rhina Thornton, **new species** Fig. 326–330

♀. Unknown.

♂. *Coloration* (after 30 years dry storage). Vertex buff, usual markings brown. Frons markings not clearly discernible. Clypeus buff, distinct brown parallel striae not merging medially. Gena buff, a single brown stripe from orbit to antennal socket. Maxillary palpi pale, subapical segment brown, apical segment dark brown. Scape and pedicel brown, flagellum brown, basal segment paler. Thoracic terga brown, including antedorsum of mesothorax, cream borders. Pleura brown. Legs: coxa brown; trochanter and femur pale buff; tibia buff, brown apically; tarsus brown. Wings: transverse fascia of fore wing (Fig. 326) angled, continuous, large brown patch in apical angle of anal cell, much smaller brown mark more basally, pterostigma with brown patch in apical ½, brown mark at point of separation of *m* and *rs,* no brown spot on *m+cu,* veins bordering basal ½ areola postica hyaline; hind wing hyaline, longitudinal brown mark on anterodistal border, faint fuscous cloud in apical ½ anal cell. Abdominal pigmentation not discernible. *Morphology.* Eyes prominent, I.O.:D. = 1.0. Hind wing with 5 fine marginal setae between ends of *rs.* Number of ctenidia on hind tarsal segments: 23; 2+1. Genitalia: hypandrium (Fig. 327) with teeth of tongue not confined to margins, covering surface. Phallosome tine (Fig. 328, 329) widely bifid. Epiproct anterior lobe narrow, high, rounded, tuberculate (Fig. 330). Basal boss of paraproct large, prominent, a field of 25 trichobothria.

Distribution. OAHU, rare.

Holotype ♂, OAHU, Koolau Range, Kahauiki, "ohia ha," 29.I.1933 (O.H. Swezey) (BPBM 13,010).
This description is based on a single specimen collected on *Metrosideros* in the eastern Koolau Range.

Although there is only a single pigmented patch in the anal cell of the fore wing, the acutely angled transverse fascia agrees with other members of this group, and the heavily toothed surface of the hypandrial tongue is typical of it.

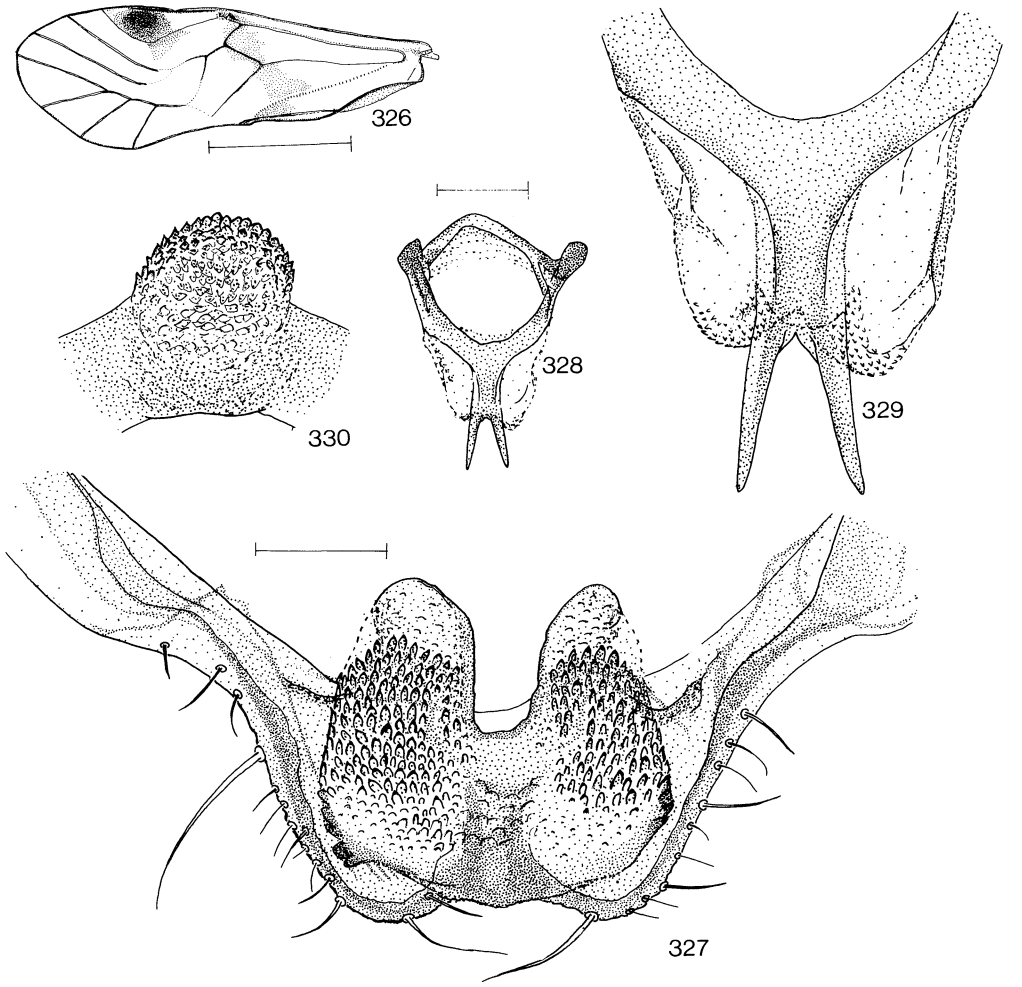

FIG. 326–330. *Ptycta rhina rhina* ♂: **326,** fore wing; **327,** hypandrium; **328,** phallosome; **329,** phallosome tine; **330,** epiproct lobe. Fig. 327, 329, 330 to common scale.

Ptycta rhina symmetrica Thornton, **new subspecies** Fig. 331–334

♀. Unknown.

♂. *Coloration* (freshly killed, in alcohol). As nominate subspecies, with following differences: angled transverse fascia of fore wing (Fig. 331) less extensive, and a faint, interrupted gray-brown stripe below antennal socket to orbit mark on gena. *Morphology.* I.O.:D. = 2.8, eyes small. Neck of phallosome tine (Fig. 333) broad. Hypandrium (Fig. 332) with 11 marginal teeth on tongue, weakly sclerotized teeth over surface. Epiproct lobe (Fig. 334) smaller, rather more pointed, less rugose. Field of 22 trichobothria on paraproct.

Distribution. MAUI, rare.

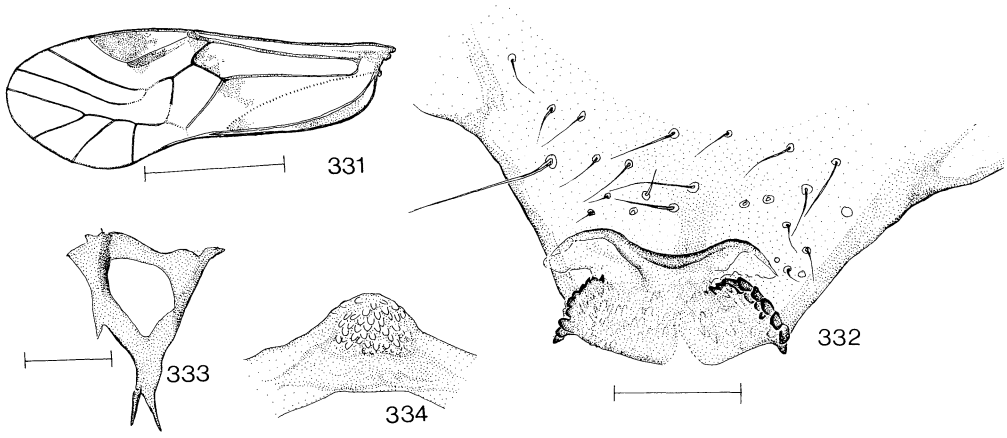

FIG. 331–334. *Ptycta rhina symmetrica* ♂: **331,** fore wing; **332,** hypandrium, from above; **333,** phallosome; **334,** epiproct lobe. Fig. 332, 334 to common scale.

Holotype ♂, MAUI: middle ridge at head of Iao Val, 760 m, *Metrosideros*, 19.IX.1963 (I.W.B. Thornton) (BPBM 13,011).

This singleton is sympatric with *P. swezeyi*; the hypandrial tongue is of the same form as that species, but the presence of surface teeth distinguishes it, as does the more extensive transverse fascia.

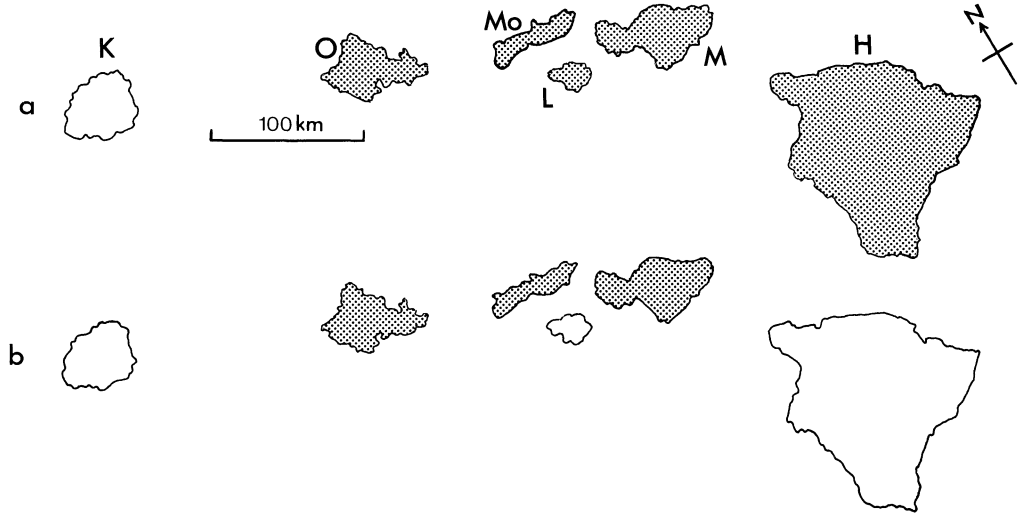

FIG. 335. Archipelago distributions of species groups of *Ptycta:* **a,** *lanaiensis* (3 species); **b,** *schisma* (6).

DISCUSSION

The genus Ptycta

There are good reasons for believing that the *Ptycta* species of Hawaii have a common origin. The overlapping mosaic of character distributions makes it impossible to devise a cladogram without repetition of character states in different lineages. Parallelisms are rather frequent. Examples are the long outer valve lobe of the female gonapophyses and long distal process of the subgenital plate (egg guide) in both the *oahuensis* and *diadela* groups, which on phallosome structure fall into different sections of the complex (see below); the asymmetrical dentition of the hypandrial tongue in the *haleakalae* and *vittipennis* groups of Section A (a section of the genus comprising species groups having a single phallosome tine, see Table 1, Fig. 336, and the section titled Evolution of *Ptycta* in Hawaii, below) which is repeated in the *lanaiensis* and *diadela* groups of Section B (groups having a bifid tine); the small sclerotized flap at the base of the apical process of the female subgenital plate, which occurs in the *haleakalae* group (*simulator kilauea*) of Section A, and in the *lanaiensis* (*lanaiensis*) and *schisma* (*schisma, kaala*) groups of Section B. These parallelisms suggest that the 2 lineages have a common origin in an ancestral population in which these characters were heterozygous, not fixed (Throckmorton 1967).

The endemic Hawaiian species of Psocidae must, thus, all be placed in the single genus *Ptycta,* of which *Ptycta haleakalae* is the type-species. In order to include the diversity of the Hawaiian species, *Ptycta* must have wider parameters than is usual in genera of the family (see Introduction for a revised diagnosis). Extra-Hawaiian species that have been placed in *Ptycta* are from Africa (Badonnel 1969, 1979; New 1975; Broadhead & Richards 1980), Madagascar (Smithers 1964; Badonnel 1967, 1976), the Mascarene Islands (Turner 1976), Aldabra (New 1977), the Oriental Region (Enderlein 1925, Thornton 1960, New 1975, New & Thornton 1976), Australia (New 1974, Smithers 1977), the Ryukyu Islands (Tsutsumi 1964), Micronesia (Thornton et al. 1972), Fiji (Thornton 1981a), Tonga (Thornton 1981b), Galapagos (Thornton & Woo 1972); South America (New 1972; New & Thornton 1975, 1981), the Antilles (Mockford 1974, Turner 1975), Cape Verde Islands (Meinander 1966), Israel (Galil 1981), and Spain (Meinander 1981). The species are thus mainly, but not exclusively, tropical.

It is likely that 2 of the Galapagos species and some South American species should now be placed in *Indiopsocus* Mockford, 1974 (Turner 1976, Meinander 1981). Eight of the 9 Fiji species and 1 Tongan species previously placed in *Ptycta* are now to be assigned (Smithers 1984) to *Copostigma* Enderlein following a redefinition of that genus. Although some extra-Hawaiian species, for example *Ptycta parvidentata* Tsutsumi from the Ryukyus and those from the Mascarene Islands, appear to fall into *Ptycta* as understood from a consideration of Hawaiian species, the position of others, such as *Ptycta hispanica* Meinander from Spain, requires reconsideration. One species, *Ptycta lineata* Mockford from Cuba, possesses a bifid phallosome tine and is the only extra-Hawaiian species to exhibit this character state.

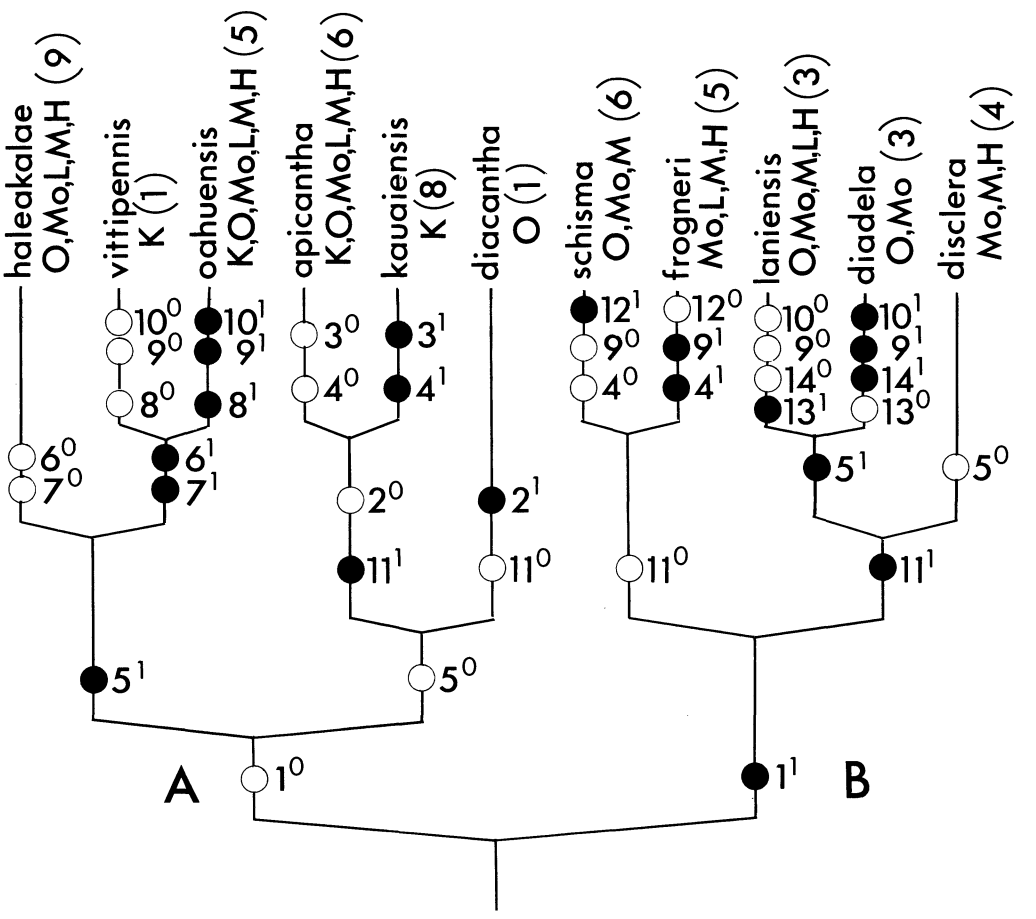

FIG. 336. Archipelago distribution and cladistic analysis of species groups of Hawaiian *Ptycta* based on 14 characters. Character states, apomorphic first (solid circles), plesiomorphic in parentheses (open circles): **1,** phallosome tine bifid or forked (single); **2,** pair of stout spines at base of hypandrial tongue (absent); **3,** hypandrial tongue marginal teeth fused basally into carinae (not so fused nor so distinct from apical teeth); **4,** ♂ epiproct anterior process bilobed (single); **5,** hypandrial tongue asymmetrical, teeth on 2 lateral margins differ (symmetrical, teeth same on each side); **6,** phallosome tine swollen subapically (smoothly pointed); **7,** thoracic terga glossy (dull); **8,** dorsal valve with large subapical lobe (lobe barely perceptible or valve smoothly tapering to apex); **9,** outer valve lobe long (short); **10,** apical process of subgenital plate long, parallel-sided (trapezoid, no more than 2× as long as broad); **11,** basal stem of vein *cu* in areola postica of fore wing unpigmented (pigmented); **12,** hypandrial tongue with teeth on surface (teeth confined to margins); **13,** apical process subgenital plate with central sclerotized flap basally (flap absent); **14,** dorsal valve massive, fleshy (normal size and shape). When a character is not shown in a lineage, it may be taken to be plesiomorphous. **K** = Kauai, **O** = Oahu, **Mo** = Molokai, **L** = Lanai, **M** = Maui, **H** = Hawaii; number of species in brackets.

Ptycta is clearly related to *Maheella* Enderlein, 1931, species of which are known from Madagascar and the Seychelles. It has long been acknowledged that the *Copostigma-Clematostigma-Ptycta-Maheella* complex is in need of revision (Thornton 1960, Badonnel 1967, Smithers 1972, Broadhead & Richards 1980, Meinander 1981), but a thorough knowledge of *Ptycta* species from the Hawaiian Islands, the locality of the type-species, is a necessary prerequisite. It now would be appropriate to reconsider extra-Hawaiian *Ptycta* species, as well as species assigned to *Maheella, Copostigma* and *Clematostigma,* in the context of our knowledge of *Ptycta* in Hawaii.

Species and subspecies

It is clear from the preceding section that within this endemic complex there is a wide range of taxonomic divergence; however, because of the geographical discontinuities of the area, information on zones of overlap is often absent. Within the well-studied Hawaiian Drosophilidae all populations apparently in a "speciating" state have been clearly assigned to species rather than subspecies (Carson & Kaneshiro 1976). In the present study, which lacks the advantages of chromosomal, hybridization, and behavioral data, such decisions were not always so clearly justified. Thus, decisions as to specific status of allopatric populations were made by comparing degrees of taxonomic divergence with those of sympatric species, and by analysis of a numerical taxonomic study (Chui & Thornton 1972).

Forty-four species are regarded as monotypic; all but 5 of these are confined to single islands. *P. disclera* and *P. molokaiensis* (on Molokai and Maui), *P. microglena* (on Oahu and Lanai), and *P. stena* (on Oahu and Molokai), each show some degree of divergence in each of their 2 populations; *P. distinguenda* (found on Hawaii, Molokai, Lanai and Maui) is separable into 2 populations, 1 on Hawaii and 1 on the other 3 islands. These differences are sometimes based on few specimens, are small, involve only 1 or 2 characters, and are not absolute. In none of these species are subspecific names given to the island subpopulations.

On examining the correlation coefficient phenogram (Chui & Thornton 1972, Fig. 1) for the *Ptycta* taxa, it can be seen that taxa 14 (*distinguenda*) and 36 (*molokaiensis*), towards the top of the phenogram, join at a phenon level of about 0.55. These 2 distinguishable taxa both occur on Molokai and Maui and can be regarded as good species. They join at the highest phenon level of any pair of sympatric taxa. Thus, taxa that join at this or lower phenon levels are regarded as being of specific status. Taxa joining at higher levels than this (3,5; 6,7; 15,16; 47,57; 27,28,29,30; 21,22,50; 49,52; and 31,38), all of which are allopatric with their sibling taxa, were referred to on the distance phenogram (Fig. 2 of Chui & Thornton 1972) to see if the situation was confirmed. It is repeated almost exactly above the phenon level at which taxon 4 joins 3 and 5 (about phenon 9.15). The only difference is that on the distance phenogram, taxa 31 (*leurothorax*) and 38 (*oahuensis*) join at a much lower level (about phenon 8.94). Accordingly, all the taxa considered above except *leurothorax* and *oahuensis* are regarded as being of subspecific status.

This criterion is a conservative one. Other taxa join at a higher phenon level than 14 and 36 (i.e., are more closely related) and are sympatric in the sense that they occur on the same island: 28 and 29 (*lanaiensis fusca* and *lanaiensis halawa*) on Molokai, and 22 and 50 (*haleakalae hualalai* and *haleakalae konae*) on Hawaii. However, the first 2 occur on different parts of the E Molokai range and have not been found together, and the 2 latter are allopatric on Hawaii. Thus, there is no sympatry at the local level, as there is in the case of 14 (*distinguenda*) and 36 (*molokaiensis*), which were collected together at 600 m above Kamiloloa, Molokai in June 1963. These 2 taxa, as the most closely similar strictly sympatric taxa under study, provide a conservative base-line criterion of specific status. Taxa which just make specific status on this basis are 4 (*peleae*), 39 (*oligocantha*), and 46 (*pupukea*).

Isolation in Hawaii

The various factors conducive to isolation of populations and diversification in the windward, or main, group of Hawaiian islands were first described and emphasized by Zimmerman (1948a) and have since been repeated and stressed by other workers (e.g., Carlquist 1970, Carson & Kaneshiro 1976, and Carson 1981). Isolating factors exist at several levels.

The Hawaiian archipelago itself is one of the most isolated island groups in the world; it lies over 3500 km from the nearest continent (North America) and over 3000 km from the nearest high islands (the Marquesas). The main group is 1000 km from the nearest atoll (Johnston Island). The fauna of Hawaii has been shown to be taxonomically disharmonic (Zimmerman 1948a, Carlquist 1970), the result of waif dispersal with the success of colonists determined to a great extent by chance. Among the Psocoptera, such families as Archipsocidae, Calopsocidae, Myopsocidae, Philotarsidae, and Stenopsocidae are absent, although the Archipsocidae, Myopsocidae, and Philotarsidae are well represented in Micronesia (Thornton et al. 1972). The Pseudocaeciliidae, with 18 species in Micronesia, and one of the best represented families in Fiji, where considerable speciation has taken place (Thornton 1981a), has but 2 species in Hawaii. In contrast, the Elipsocidae, with over 100 endemic taxa in Hawaii, is absent from Micronesia and from Fiji.

Natural selection in novel ecosystems, together with a genetic revolution occasioned by the success of a small number of founders (Mayr 1942, 1954; Carson 1971, 1975, 1976, 1981), has resulted in major evolutionary departures from parent stock in some Hawaiian insect groups, e.g., Drosophilidae (Carson et al. 1970, Carson & Kaneshiro 1976), Neuroptera (Zimmerman 1948a, 1957), Tipulidae, Delphacidae, Odonata (Zimmerman 1970), and Lepidoptera (Montgomery 1982). In the Psocoptera no such bizarre adaptations have been detected, although the large genus *Kilauella* is found only in the Hawaiian Islands, and Section B of the Hawaiian *Ptycta* (see below) differs from all but 1 of the many extra-Hawaiian species in a distinctive apomorphic character.

The configuration of islands within the archipelago provides the second level of

isolation, and this has changed considerably several times in the last few million years (see below). Not only has the number of islands changed, and the distances between them, but they are of different ages (Table 2), from Kauai, 5.14 m.y., to Hawaii, 0.4 m.y. and still growing, thus providing striking habitat differences between islands. The succession of island transfers and founding events which were envisaged by Zimmerman (1948a) have been largely documented for the Drosophilidae by Carson et al. (1970) and Carson & Kaneshiro (1976).

The majority of *Ptycta* species (38 of 51 species, Table 1) and of all recognizable taxa (52 of 61 taxa) are confined to a single island. Seven species occur on 2 islands, in all cases involving islands of the Maui complex (Molokai, Lanai, Maui and Kahoolawe), and in 4 cases being confined to 2 of these; 2 occur on Molokai, Lanai and Maui; and 2 species occur on 4 islands, one on Oahu, Molokai, Maui and Hawaii, and the other on Molokai, Lanai, Maui and Hawaii.

Seven species are polytypic (number of subspecies in parentheses): *aaroni*—Oahu and Lanai (1), Maui (1); *apicanthoides*—Molokai (1), Maui (1); *haleakalae*—Oahu, Molokai and Maui (1), Hawaii (2); *simulator*—Maui (1), Hawaii (1); *drepana*—Lanai (1), Molokai and Maui (1); *lanaiensis*—Lanai (1), Molokai (2), Maui (1); *rhina*—Oahu (1), Maui (1).

Although 2 subspecies of *lanaiensis* and *haleakalae* occur on the same island, the populations concerned are in fact allopatric. *P. lanaiensis fusca* occurs at 1200 m at the western end of the main Molokai range, and *P. lanaiensis halawa* has only been found in the forest bogs W of Halawa Valley at the extreme eastern end of the island. Similarly, *P. haleakalae hualalai* seems to be confined to the west-central part of the island of Hawaii between Mauna Kea and Mauna Loa, and *P. haleakalae konae* has only been taken in the Kona area of Hawaii I.

No polytypic species inhabits Kauai, the oldest and most isolated island at the western end of the group. Two inhabit Hawaii, the easternmost island, 3 are on Oahu, 3 on Lanai, 4 on Molokai, and all 7 of the polytypic species occur on Maui. Of the 6 cases of monotypic species occurring on more than a single island, Maui is included in the range of 3, Molokai in 5, Lanai in 3, Oahu in 2, and Hawaii in 1. Again, no multi-island monotypic species occurs on Kauai. Thus, Maui and Molokai are most frequently included in the distribution of the 13 multi-island species (Maui 10, Molokai 9, Lanai 6, Oahu 5, Hawaii 3, Kauai 0). These 2 islands, both of which have 2 distinct volcanic domes, lie in the middle of the eastern group of islands, close to the islands of Lanai and Kahoolawe.

The Maui complex (E and W Molokai, Lanai, E and W Maui, Kahoolawe) in the recent past has been a dynamic area of separating and anastomosing islands, probably highly conducive to speciation. Pleistocene changes in sea level of the island group, documented in Macdonald & Abbott (1970), include a change from −400 m 1.5 m.y. ago to +366 m 350,000 years ago, followed by a drop to −107 m 17,000 years ago and a subsequent rise to the present level (see also Chappel 1974).

The Maui complex is separated from Oahu by a depth of 700 m and from Hawaii

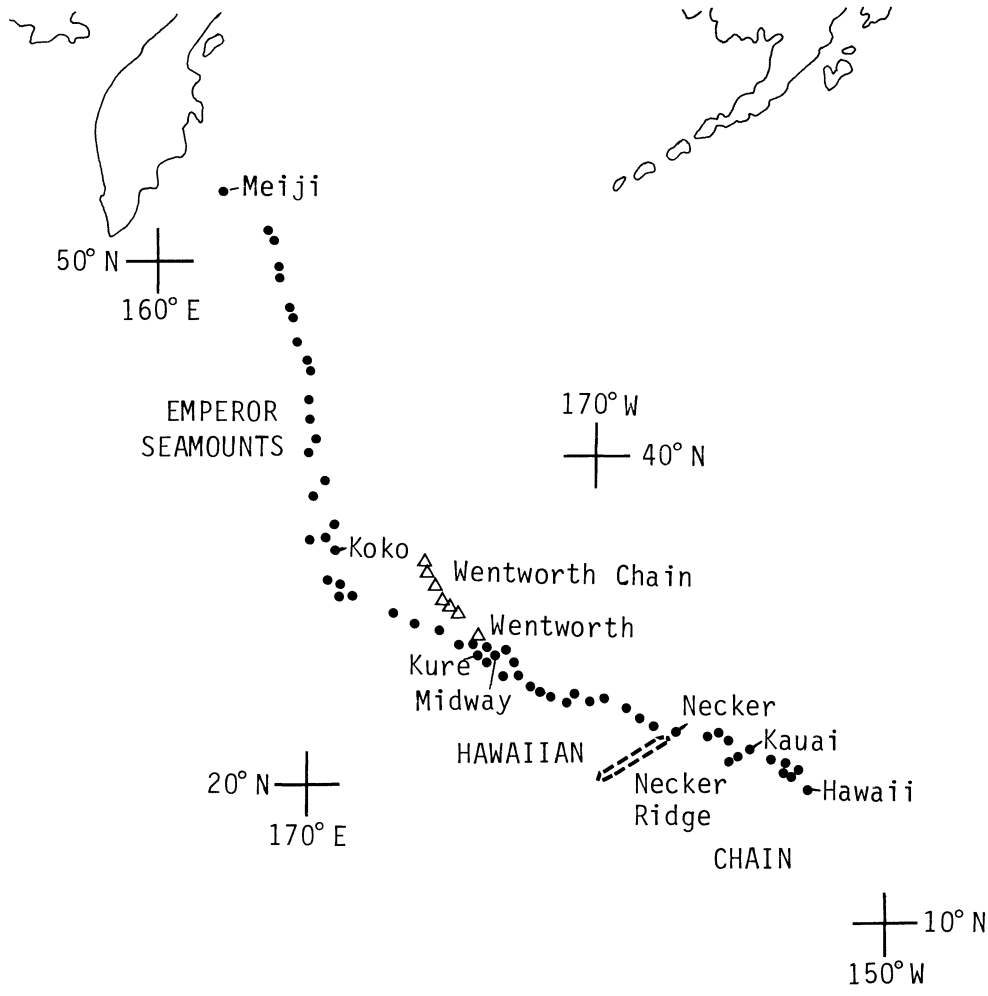

FIG. 337. Hawaiian-Emperor chain of islands, reefs and seamounts (after Rotondo et al. 1981). Open triangles represent seamounts of the Wentworth Chain, dashed line the Necker Ridge.

by a strait 1890 m deep, so that the above changes would not have affected its isolation as a whole during or since its formation (from 1.89 to 0.84 m.y.). Within the complex, however, the interisland straits are shallow enough (Fig. 1) to have been exposed (Molokai-Maui 244 m, Molokai-Lanai 80 m, Lanai-Maui 33 m, Kahoolawe-Maui 143 m) and the saddles between the Molokai and Maui volcanoes are low enough (at 130 m and 38 m elevation, respectively) to have isolated the component volcanoes as separate islands on several occasions (the Oahu ranges are separated by a plain 290 m at its highest and would also have been separate islands 1½ m.y. ago). Thus, in

the geologically recent past, the present 4 islands of the Maui complex were most probably at times a single large island (Maui Nui) and at other times up to 6 separate islands.

Table 2 shows the number of single island endemic taxa (species and subspecies) on each island, the total number of taxa on each island, and the islands' percentage endemicities. The endemicity of Hawaii, the youngest, largest, and highest island is greater than that of all but Kauai, the oldest, which is also smaller, lower, and more isolated than Maui and Hawaii. Endemicity is unrelated to the age, size, climate, or altitude of the islands, but rather is associated with isolation, whether measured as distance from the nearest island or average (or sum) of distances from all other islands (see Thornton 1967). Emdemicity is lowest on Molokai, Lanai and Maui, which nevertheless harbor the majority of subspecies and endemic subspecies. This suggests that speciation in the closely grouped central islands is at an earlier stage than it is in the other islands, in spite of the fact that they were connected, separated, and reconnected in part during pleistocene glaciations, events conducive to speciation by vicariance or fragmentation of populations, which, other things being equal, might be expected to produce more, rather than less, diversification.

Subpopulations established within the central group may be subject to immigration from closely neighboring islands, which may impede the speciation process. However, should one of the several incipient species of the Maui complex colonize a more isolated island, speciation would proceed more rapidly. The Maui complex (before the destruction of most of Lanai's native vegetation for agriculture, and before Kahoolawe was denuded) can thus be regarded as an area where initial segregation of demes may have occurred relatively quickly, providing a number of quasi-separate populations for the colonization of and speciation on more distant islands, but which proceeded more slowly to full speciation within the complex.

Hawaii, Maui, Molokai, and Oahu each consist of more than 1 volcano (Fig. 1). Hawaii comprises 5, the Kohala, Mauna Kea, Hualalai, Mauna Loa, and Kilauea volcanic domes, while the other 3 islands are each the result of 2 volcanoes (Haleakala and W Maui; E and W Molokai; and the Koolau and Waianae volcanoes of Oahu). There are differences between the ages of these volcanoes, even on the same island (Table 2), which provide an additional ecological component of isolation. Thus, *Ptycta kaala* is confined to the Waianae Range of Oahu, while *pupukea, schisma, oligocantha, r. rhina,* and *palikea* are confined to the Koolau Range. On Maui, *swezeyi* and *r. symmetrica* occur only on the W Maui volcano, *microctena* and *perkinsi* only on Haleakala. On the island of Hawaii, *hardyi* and *stenomedia* have only been found on the Kohala massif, *maculifrons* only on the Mauna Loa dome.

There is unpublished evidence that the several volcanoes of the island of Albermarle (Isabella) in the Galapagos Is carry isolates of *Indiopsocus,* a genus close to *Ptycta,* that are as distinct from each other as are those from separate islands, and this phenomenon is well documented for other parts of the Galapagos fauna, for example the giant tortoises (*Geochelone* species) (see Thornton 1971 for a general account).

TABLE 2. Indices of habitat heterogeneity, isolation, and endemicity of *Ptycta* taxa on the Hawaiian Islands.

			Rainfall (mm/yr)*			Distance (km)		Taxa			Species (subsp.)		
	Area (km^2)	Max. alt. (m)	Max. $\bar{X}$	Min. $\bar{X}$	Max. age (m.y.)†	To nearest island	$\bar{X}$ to all other islands‡	Total no.	No. endemic	% endemicity	Total no.	No. endemic	% endemicity
Kauai	1437	1576	11,455	460	5.14	118	163	11	11	100	11 (0)	11	100
Oahu	1564	1227	7690	315	3.70 2.60	40	69	15	11	73	15 (3)	10 (1)	66
Molokai	673	1515	3910	235	1.89 1.52	15	53	13	6	46	12 (5)	3 (3)	25
Lanai	365	1027	1060	292	1.28	15	60	6	2	33	6 (3)	0 (2)	0
Maui	1886	3056	9690	282	1.32 0.86	15	60	16	11	69	16 (7)	6 (5)	38
Hawaii	10,483	4201	7645	190	0.40 0.00	47	99	12	11	92	11 (3)	8 (3)	73

* Figures from Dep. of Land and Natural Resources, Hawaii, for the station with the maximum or minimum median rainfall on each island, over periods of from 11–46 years.

† From Dalrymple et al. (1981): includes component volcanoes on Oahu, Molokai and Maui, and Kohala and Kilauea on Hawaii.

‡ In arbitrary units. See Thornton (1967).

Volcanic activity can itself result in 2 other levels of isolation. First, lava flows frequently bifurcate and rejoin, leaving areas untouched while the surrounding vegetation is incinerated and covered by the flow. In this way, islands of vegetation are left which are at a different, older successional stage from the regenerating plant associations surrounding them, and a flow may not be reclothed in vegetation for years. Such enclaves (called *kipukas* in Hawaii) may be from a few hectares to many square kilometres in area, and separated from others by considerable stretches of subclimax vegetation or barren lava. Some kipukas are lower than the surrounding flow; others, like those on Bindloe (Marchena) in the Galapagos, are higher than their surroundings. An area which has been spared by one flow may also escape obliteration by a subsequent one, for the same reason, so that some kipukas may be quite long-lasting. On the island of Hawaii, *Ptycta pardena* has been found only in Kipuka Puaulu, a large kipuka in the Kilauea area, and not in the surrounding area or in another nearby kipuka, Kipuka Ki.

A second level of isolation resulting directly from volcanic activity is due to the fact that lava from the Hawaiian volcanoes varies in its chemical composition, substrate texture, and drainage qualities, as well as in age. Ash and cinder falls can form rich deep soils in places. Edaphically based patchworks of plant associations may thus result from a sequence of eruptions, providing a mosaic of different habitats for terrestrial animals, although no clear example of this effect is identifiable in the *Ptycta* fauna.

The high topography of the islands (see Table 2, Fig. 1), which lie in the path of the NE trade winds, also results in additional types of isolation. Altitudinal zonation, extreme patchiness of habitat due to local rainfall patterns, and the topographical effects of erosion can all favor the isolation of populations.

Few *Ptycta* species can now be regarded as lowland forms. *P. diacantha* and *P. diadela* both occur at low elevations on Oahu, particularly on introduced *Macadamia* trees, although the former is also found high on the Koolau Range and the latter on both the Koolau and Waianae ranges. *P. aaroni* has been collected only at low elevations on Oahu and Maui, and is the only species not to have been found in upland habitats. On Kauai, *pedina, kauaiensis,* and *placophora* are found in the lowlands as well as at high altitudes. All the other species are strictly upland forest insects. Evidently the introduction of *Macadamia* has provided a favorable lowland habitat for 2 species of *Ptycta,* and this suggests that others may also have been distributed in the lowlands before the lowland native forests were destroyed by man. Moreover, it is probable that, like the endemic birds (Olsen & James 1982), many strictly lowland species have been lost, along with their habitats.

Gagné (1979, 1981) and Gagné & Howarth (1981) have studied the altitudinal zonation of canopy arthropods of 2 dominant trees (*Metrosideros collina* subspecies *polymorpha* and *Acacia koa*) on the island of Hawaii in transects from the *Metrosideros* tree line of Mauna Loa at about 2440 m, SE through the area of the Kilauea Volcano, to sea level. The high frequency of psocopterans and their very high numbers com-

pared to other arthropods, particularly at mid and high elevations (1200–2440 m), has been pointed out above, in the Introduction.

In the Blue Mountains of Jamaica, Turner & Broadhead (1974) were able to relate psocid diversity at 8 altitudes to indices of microepiphyte diversity. Broadhead & Richards (1980) examined the gut contents of 4 East African highland species of *Ptycta* and found the main components to be fungal spores and protococcal algae, along with pollen grains and, infrequently, bryophyte rhizomes and a multicellular alga. In the Hawaiian transect, although Doty & Watson (1981) found no marked altitudinal zonation of terrestrial algae, algae on leaf and bark surfaces were not sampled. Stoner & Baker (1981) did examine samples of leaf fungi, but found no clear evidence of zonation; lichens, on which some psocopterans are known to feed almost exclusively (Broadhead 1958, Broadhead & Richards 1980), were not studied.

In the *Acacia koa* forest at Kokee, Kauai, 8 species of *Ptycta* were found on *A. koa* in 1963 from 600 m to 1200 m. *P. pedina* was collected from 600–1000 m, but not on the Kokee plateau itself (1000–1200 m); *placophora* occurred at all stations sampled above 600 m; *telma* and *anacantha* were taken only above 900 m; and *diastema* and *monticola* were only found on the plateau at heights above 1000 m. *P. kauaiensis*, which was common on the plateau, also occurred lower, to 900 m. There is some suggestion here of altitudinal zonation; *kauaiensis, diastema,* and *monticola* are apparently true highland species, *pedina* being restricted to the midlevel forest. When the Hawaii I transect collection is analyzed, altitudinal zonation of *Ptycta* species on Mauna Loa may be revealed. If the indication from Kauai is confirmed by the collection from Hawaii, sampling of surface microepiphytes (including lichens) from these areas, as well as gut-content analyses, should be undertaken.

In Hawaii, rainfall distribution is largely influenced by the trade winds, which predominate during most of the year, and the terrain; extremes of high and low rainfall are found in close proximity on each island. Maximum rain falls on the windward side of the mountain ranges from 600–1200 m and on or near the summits of mountains less than 1800 m high, with the leeward or kona side of islands lying in rain shadows and mountain peaks above 2500 m being relatively dry (Mueller-Dombois 1981). Thus, the summit of Mt Waialaeale on Kauai (about 1500 m) is said to be the "wettest spot on earth," with a median annual rainfall of 11,455 mm reaching over 15,200 mm, while the area 24 km to the SW is arid with an annual rainfall of only some 350 to 500 mm. The lush vegetation of the windward coast of Oahu contrasts markedly with the xeric cover of the leeward coast; rainfall gradients are sometimes very steep, reaching 1800 mm per km on Kauai. Such rainfall patterns contribute to the patchiness of the habitat for psocopterans, and thus the isolation of their populations. Moreover, Paik & Sung (1981) found a correlation between saturation deficit and the frequencies of chromosomal gene arrangements in *Drosophila immigrans* on Mauna Loa, Hawaii I, and the fact that environmental dryness can affect the gene pools of insects in various ways is well established.

Erosion has also contributed indirectly to the isolation of Hawaiian populations.

The peculiar combination of forces operating in Hawaii, graphically described by Zimmerman (1948a), have resulted, particularly on the older volcanoes, in knife-edged ridges separating steep-sided amphitheater-headed valleys. The valley bottoms have often been covered by lava flows, and no doubt much extinction of valley populations has occurred in the past. After such an event, populations on the ridges would be separated from one another by barren lava sometimes 500 m or so below them and often a kilometre or more in width. In time, depending on the particular climatic regime and the nature of the substrate, the valley floors would become reforested, but even then populations adapted to either the ridges or valley floors would still be effectively ecologically separated from other such populations. This topographical-ecological isolation appears to have been an important factor in the speciation of several Hawaiian animal groups, most notably the land snails. Although its effects are not as striking in Psocoptera as in some other groups, there are indications that the Psocoptera may have been affected. For example, 2 taxa of *Ptycta, peleae* and *lanaiensis halawa,* have only been collected in the Halawa Valley area of E Molokai, not on other Molokai ridges or in other valleys, and on Oahu the species *pupukea* and *palikea* were found only on the Koolau Range ridges for which the species were named.

All the above factors are conducive to the isolation of terrestrial populations in Hawaii. Their effectiveness in preventing gene flow will depend upon intrinsic characteristics of the organisms concerned, such as normal range of movement and breadth of ecological tolerance.

The normal cruising range of winged psocopterans is probably small (Broadhead & Thornton 1954), and psocopterans do not readily take to flight. Moreover, considering that they do not feed directly upon their host plants but rather feed on microepiphytes harbored by them, some endemic psocopteran species are remarkably host-specific. In the lowlands of Oahu and Hawaii the introduced *Acerola glabra* and *Macadamia ternifolia* were growing in close proximity in 1963. Many nonendemic psocopteran species occurred on both these plants in about equal numbers. In contrast, 3 species of *Kilauella* (a large endemic Hawaiian genus to be treated in a later work) occurred in much greater numbers on *Acerola* than on *Macadamia* (238 individuals to 21, 82 to 5, 6 to 0), but in 3 species of *Ptycta, diadela* and *diacantha* (on Oahu) and *apicantha* (on Hawaii), the reverse was the case, the 2 latter not being found on *Acerola* at all (2 to 16, 0 to 30, 0 to 18, respectively). Evidently these endemic species of *Kilauella* and *Ptycta* were differentially preadapted to the microenvironment provided by the 2 introduced plants, resulting in their distributions, even at this very local level, being different.

Evolution of Ptycta *in Hawaii*

The 51 species have been placed in 11 fairly well-knit species groups (above) and a cladistic analysis of the groups is shown in Fig. 336, the synapomorphic characters used being listed in the legend, the plesiomorphic states in parentheses. It will be seen

that the complex may be divided into 2 large sections on the state of the phallosome tine, which is highly apomorphic (bifid) in several groups (Section B, Fig. 336). Both this character and the presence of a median basal prong on the hypandrium provide equally parsimonious cladograms as first dividers. The former was preferred because it is so unusual, being found in only 1 of many extra-Hawaiian species of the genus (a Cuban species).

Of Section A, all groups have representatives on Kauai except the *haleakalae* and *diacantha* groups, the *kauaiensis* and *vittipennis* groups being confined to that island. The more apomorphic Section B is not represented on Kauai (Fig. 336). One explanation of this contrasting pattern is that the *Ptycta* complex originated on Kauai, the bifid tine having arisen in an extra-Kauaian population which speciated on the eastern islands but was unable to reinvade Kauai. A similar scenario would explain the distribution of the *haleakalae* and *diacantha* groups of Section A. The *kauaiensis* and *vittipennis* groups appear to be autochthonous Kauai groups.

The *apicantha* group, a fairly homogeneous group of 6 species without a synapomorphy, is represented on all islands and subspeciation is evident in 2 species on the Maui complex. In contrast, the *kauaiensis* group of 8 species, with 2 synapomorphies, is confined to Kauai. The species *diacantha,* which is related to these 2 groups, is found only on Oahu. In the large close-knit *haleakalae* group of 9 species, subspeciation is evident in 2 species, and Kauai lacks a representative. The *oahuensis* group of 5 species, which has representatives on all 6 islands, is particularly well-defined, having 3 synapomorphies, and includes the largest Hawaiian psocids; the Kauai species is the most aberrant. The species *vittipennis* constitutes its sister-group and is confined to Kauai.

The highly apomorphic characters exhibited by the *kauaiensis* group are quite unrelated to those of any of the other groups, and it probably evolved on Kauai. This would not necessarily involve sympatric speciation, despite the fact that speciation on a single island is postulated. The normal cruising range of psocids is small, and topographical effects associated with volcanism (kipuka formation, amphitheater-headed valleys) mentioned above, together with submergence (isolation of ridges) could have provided barriers in the 5.1 m.y. of the island's existence, resulting in the effective spatial isolation of populations. Reduction of native forest largely to the eroded summit of a single volcanic dome (and Kauai is unique among the large islands in consisting of a single large shield volcano) may have resulted in a considerable overlap in ranges of the surviving species. The fauna of the adjacent island of Niihau, which is about 5.5 m.y. old and now only some 390 m high, is almost unknown; it could have played an important role in the evolution of the Kauaian fauna. As might be expected of an old line that has evolved in isolation, the *kauaiensis* group has a combination of primitive and specialized traits.

The remaining 5 groups (Section B, Fig. 336) all share a highly specialized character, suggesting their common origin; the groups are less well-defined than those of Section A, and none of them is represented on Kauai. It has been suggested above

that this line evolved later, on the younger eastern islands, and has been unable to successfully reestablish populations on isolated Kauai. That the line had a common origin with Section A is suggested particularly by characters of the *diadela* and *lanaiensis* groups (see above) and to a lesser extent by the female genitalic characteristics of the *frogneri* group.

The *disclera* group, with representatives on Molokai, Maui, and Hawaii, has no obvious synapomorphies, but is evidently the sister-group of the *lanaiensis* and *diadela* groups. The *lanaiensis* group, with representatives on all islands but Kauai, exhibits considerable subspeciation on the Maui complex and appears to be the sister-group of the *diadela* group, which occurs only on Oahu and Molokai. The *frogneri* group is absent from both Kauai and Oahu and appears to have arisen on the Maui complex, to which 4 of its 5 species are confined, and where subspeciation is evident. The *schisma* group is something of a problem. The species are closely similar, and in the case of 2 of the Oahu forms the decision as to specific status was difficult. It seems possible that the group evolved on Oahu, to which 4 of its 6 species are confined, from a population retaining many of the characteristics of the *disclera* group and has not yet colonized the 2 extreme islands, Hawaii and Kauai.

The hypothesis is advanced that the Hawaiian *Ptycta* complex derives from a single ancestral population, probably on Kauai, which speciated on all the high islands, including Kauai itself (to which 2 species groups were confined). Later evolution on the eastern islands resulted in a line (Section B) which speciated considerably, probably largely on the isolation-producing Maui complex called Maui Nui (Big Maui) by Macdonald & Abbott (1970), the geography of which has been much affected by sea level changes; this line was not able to recolonize Kauai.

So far as this genus is concerned, Kauai, the oldest and most isolated of the islands, shows the most faunal peculiarities: it is the home of the most divergent species group; it is the only island with 2 island-endemic species groups; it is the only island to lack a representative of the double-tined section of the genus (Section B); it is the only island to lack any representative of a polytypic species; and it is the only island with 100% endemicity. Of all the interisland barriers, the strait between Kauai and Oahu, which is the widest and deepest, appears to be the most effective. It forms the boundary to distribution of 7 of the 11 species groups, as compared to the Oahu-Molokai disjunction which forms a boundary for 3, Molokai-Maui 1, and Maui-Hawaii 1. Clearly, the Kauai-Oahu channel has played an important role in the evolution of Hawaiian *Ptycta*.

The Oahu-Kauai strait is 118 km wide and reaches a depth of over 2935 m and, like the Maui-Hawaii (47 km) and Oahu-Molokai (40 km) channels, would have been little affected by sea level changes. The Kauai-Niihau channel is 27 km wide and reaches some 780 m in depth, and also probably was never fully exposed, although from 5.14 to 5.5 m.y. ago, when Kauai and Niihau, respectively, originated, the channel may have been shallower, and a more complete Niihau (the eastern part of the volcano extending some 8–13 km E of the present island has been removed)

would have been much closer to Kauai, particularly during low stands of the sea. On the other hand, a sea level of +366 m would have reduced Niihau and Kahoolawe to small islets.

The Maui complex, also, was probably always isolated from the rest of the group, but, in contrast to Kauai, Maui Nui underwent considerable geographic changes within itself (see above). Such a set of circumstances would be conducive to both the isolation and the diversification of the 21 species of the apomorphic lineage of the genus (Section B), which very probably was centered in the Maui complex and evolved largely within the last 2 m.y.

Possible "pre-Kauaian" evolution

In considering the evolution of the biota of the present main Hawaiian islands, the geological history of the whole Hawaiian-Emperor chain must be borne in mind (Fig. 337). Stretching roughly WNW for some 2000 km from the island of Kauai are the Northwestern Hawaiian Islands which are now eroded rocks, coral atolls, or flat-topped submarine seamounts (guyots) and are progressively older as one proceeds WNW to Midway and Kure atolls. From here an entirely submarine chain continues for about another 1000 km, then, as the Emperor Seamounts, extends for 2300 km almost due N, the furthest seamount, Meiji, being close to the Kurile and Aleutian trenches. Wilson (1963a, 1963b) proposed that the configuration of the Hawaiian chain is due to the movement of the Pacific plate over an intermittently active hot spot. Sporadic surges or thermal plumes from the mantle resulted in a succession of islands which were carried away from their point of origin by plate movement, subsiding and becoming worn down by erosion as they aged. Morgan (1972) extended Wilson's idea to include the Emperor Seamounts chain, and suggested that the directional change at the junction of the Northwestern Hawaiian and Emperor chains, which are geologically uniform, represents a change in direction of movement of the plate about 42 or 43 m.y. ago (Jackson et al. 1972, Clague & Jarrard 1973) possibly associated with large-scale tectonic phenomena elsewhere, although such an association has yet to be definitely established (Jackson et al. 1980). Thus, at one extreme the Meiji Seamount, with sediments bearing fossils 70 m.y. old (Dalrymple et al. 1973), is poised for subduction into the Kurile-Aleutian trench, and at the other an active submarine volcano (Loihi) off the E coast of Hawaii has been recognized as the probable site of an emerging island (Malahoff et al. 1982).

On this extended model, ages of the volcanoes making up the combined chain should increase with distance from the hot spot, the lava of the volcanoes should be chemically similar, and the nature of the eruptions should follow a similar pattern. There is now evidence from some 33 volcanoes of the Hawaiian-Emperor chain (Rotondo et al. 1981, Dalrymple et al. 1981) that these predictions are substantially correct. The Emperor Seamounts were once islands and have subsided 2000 m or more since their formation (Jackson et al. 1980); they are "Hawaiian" islands long dead. Koko Seamount, for example, has a layer of coral limestone on its submerged

summit; it evidently sank to a depth too great for coral growth or moved into waters too cold, about 9 m.y. ago (Schlanger & Gillet 1976). The basement volcano of Midway has a 385 m thick cap of coral limestone; it has not yet subsided below reef-building depth. The age of the bend or "elbow" at the junction of the Hawaiian and Emperor chains is believed to be 42–43 m.y. (Jarrard & Clague 1977).

If the Hawaiian hot spot is stationary with respect to the plate (one theory), then all components of the chain originated at the site of the present hot spot. There is palaeomagnetic evidence (Grommé & Vine 1972) that the Midway volcano was formed at a site close to the existing Kilauea Volcano of the island of Hawaii.

The implication of this scenario for the Hawaiian biota is of great importance. It has been suggested above that the present species swarm of *Ptycta* on the main islands originated from a Kauai ancestor, with the Maui complex playing an important role in diversification. Carson et al. (1970) and Carson & Kaneshiro (1976) came to a similar general conclusion as a result of the long-term intensive interdisciplinary study of the evolution and distribution of Hawaiian Drosophilidae, a conclusion which, of course, is much more soundly based than the suggestion resulting from the present, admittedly limited, analysis. But whence came the Kauai source faunas?

The possibility must be seriously entertained that Kauai in its turn received a remnant of the fauna of older islands now eroded and stretching to its WNW (see also Hardy & Kaneshiro 1981) in the same way that the present fauna of the young late-Pleistocene island of Hawaii may be regarded as being the result of a handing-on process or processes from the Kauai source. Isolation, speciation, colonization of younger emergent islands, and subsequent bursts of speciation (see Carson 1976, 1981), no doubt with some reinvasions and some extinctions, might have been going on for as long as the existing hot spot was island producing [over 70 m.y. and, possibly (Rotondo 1980) 100 m.y.], providing that new islands arose in time to receive the faunas of ageing ones, thus compounding these processes and resulting in the quite extraordinary diversity now evident in so many components of the Hawaiian biota.

Charlesworth & Smith (1982) constructed a computer model of speciation by the founder effect and concluded that reproductive isolation was unlikely to result in a single step (e.g., Kaneshiro 1976) by this process, one which they do not regard as a major cause of speciation. However, the chance of speciation is evidently highest when the population bottleneck is preceded by many generations of relaxed selection, when the bottleneck is not prolonged, and when it does not have a very small population size. The chances of all these criteria being met are considerably increased when the geological history of the whole Hawaiian-Emperor chain, as outlined above, is taken into account. The process of change from high volcanic island to atoll evidently takes about 15 m.y. (Schlanger & Gillett 1976) and gaps in island production, as shown by the dates for successive components of the chain, are generally very much less than this. The largest time gap between components of the chain dated by "best K-Ar age" (Dalrymple et al. 1981) is 15 m.y., and this is between 2 unnamed volcanoes, numbers 63 and 67 under their system. Thus, during this time 3 other

volcanoes arose. The maximum gap between successive components is 6.7 m.y., between Laysan and Northampton Bank, but a period of less than 1 m.y. would appear to be the average gap between successive volcanoes (unnamed volcano 91 is dated at 64.7 m.y.). Nor is there reason to believe that the age-spacing of the present main Hawaiian volcanoes (maximum 1.44 m.y.) is generally closer than that of the older parts of the chain. Thus, the islands of the chain have probably all succeeded one another quickly enough for transfer of components of their faunas to be possible.

The Galapagos Islands are of about the same age as the main (high islands) Hawaiian group, yet the Galapagos finches have not achieved the diversification of the Hawaiian drepanidids, nor have their *Indiopsocus* species yet achieved the degree of speciation found in Hawaiian *Ptycta*, to which they are related. To be sure, nemataths (submarine volcanic traces) on the Cocos and Nazca plates testify to geological processes operating over the Galapagos hot spot similar to those outlined above for the Hawaiian hot spot, but in the Galapagos case there is no evidence that the submarine traces represent previous islands that were ever above water. Thus the Galapagos biota is probably, unlike that of Hawaii, a "first-generation" biota. Hey (1977) suggested that biological evolution on the Galapagos Islands has all occurred in the past 3–5 m.y. in the essentially closed system of the existing islands, and that the long evolution on a "succession of Galapagos islands," as suggested by Holden & Dietz (1972), is unlikely.

Rotondo et al. (1981) have recently put forward an intriguing possibility of "biotic fusion" in the case of the Hawaiian chain. The morphology and geology of the submarine Necker Ridge and Wentworth Chain (Fig. 337) led Clague & Dalrymple (1975) to advance the theory that Necker I and Wentworth Seamount originated to the SE of the Hawaiian hot spot, near the Mid-Pacific Rise, and moved NW with the Pacific plate to become incorporated into the Hawaiian chain. The Necker basement is very much older, at some 77 m.y., than the above-water portion (10 m.y.), which is in accord with its position in the chain. Wentworth is similarly much older at a depth of over 1500 m (71 m.y.) than its position would warrant. Rotondo et al. (1981) have provided some evidence for the suggestion that Necker could have remained subaerial during at least part of its journey to the chain. The evidence is less supportive in the case of Wentworth. Thus Necker, and possibly Wentworth, may be intruders into the chain, and may have kept their heads above water sufficiently during their journey to the hot spot to have passed on their biota to react with the presumably already existing proto-Hawaiian biota. The mixing of 2 biotas would have resulted in drastic changes in selection pressures over a short period of time, with important consequences for the genetic balances of the populations concerned. The existing Hawaiian biota may thus be the resultant of 2 unrelated ancestral components: a strictly Hawaiian one of unknown but probably considerable age, and an immigrant one carried from the SE. If this latter component indeed exists, it also, like the former, must have arisen by transoceanic dispersal: there is no evidence or suggestion of a vicariant or fragmentation origin for Necker. Moreover, any "handing over" of biota, if it occurred at all, would have involved dispersal; the suggestion of Rotondo

et al. (1981) that such biotic integration would in some way be an alternative to the founder principle as a mechanism in the formation of Hawaiian island endemism appears to be unwarranted.

Whether or not island integration, as proposed by Rotondo et al. (1981), is accepted, there is little doubt that, as suggested by Zimmerman (1948a), long before the theory of plate tectonics was fashionable, the existing biota of the main Hawaiian group has origins much older than the present islands. Its long history probably has been frequently and fairly regularly punctuated by population and genetic bottlenecks followed by flushes, thus providing just the conditions conducive to successive bouts of speciation. The evolutionary processes that we can now recognize on the present high island group, including those discussed above, may have occurred many times over on proto-Hawaiian groups of islands long before Kauai broke the surface of the ocean some 5 m.y. ago.

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LITERATURE CITED

Badonnel, A. 1967. Insectes psocoptères. *Faune Madagascar* **23:** 1–235.

1969. Psocoptères de l'Angola et de pays voisins avec révision de types Africain d'Enderlein (1902) et de Ribaga (1911). *Publ. Cult. Cia. Diamant. Angola* **79:** 137–40.

1976. Compléments a l'étude des Psocoptères de Madagascar. *Bull. Mus. Natl. Hist. Nat. Zool.* Ser. 3 (410), **287:** 1143–97.

1979. Psocoptères de la Cote d'Ivoire. *Rev. Suisse Zool.* **86**(1): 11–22.

Baldwin, P.H. 1953. Annual cycle, environment, and evolution in the Hawaiian honeycreepers (Aves: Drepaniidae). *Univ. Calif. Publ. Zool.* **52**(4): 285–398.

Ball, A. 1943. Contributions à l'étude des Psocoptères. III. *Ectopsocus* du Congo Belge. *Bull. Mus. R. Hist. Nat. Belg.* **19**(38): 1–28.

Broadhead, E. 1958. The psocid fauna of larch trees in northern England—an ecological study of mixed species populations exploiting a common resource. *J. Anim. Ecol.* **27:** 217–63.

Broadhead, E. & A.M. Richards. 1980. The Peripsocidae and Psocidae (Psocoptera) of East Africa. *Syst. Entomol.* **5:** 357–97.

Broadhead, E. & I.W.B. Thornton. 1954. An ecological study of three closely related psocid species. *Oikos* **6**(1): 1–50.

Broadhead, E. & A.P. Wapshere. 1966. *Mesopsocus* populations on larch in England—the distribution and dynamics of two closely related coexisting species of Psocoptera sharing the same food resource. *Ecol. Monogr.* **36:** 327–88.

Carlquist, S. 1970. *Hawaii: A natural history.* Natural History Press, New York. 463 p.

Carson, H.L. 1971. Speciation and the founder principle. *Univ. Mo. Stadler Symp.* **3:** 51–70.

1975. The genetics of speciation at the diploid level. *Am. Nat.* **109:** 83–92.

1976. The unit of genetic change in adaptation and speciation. *Ann. Mo. Bot. Gard.* **63:** 210–23.

1981. Microevolution in insular systems, p. 471–82. *In:* Mueller-Dombois, D., K.W. Bridges & H.L. Carson, eds., *Island ecosystems.* Hutchinson Ross.

Carson, H.L., D.E. Hardy, H.T. Spieth & W.S. Stone. 1970. The evolutionary biology of the Hawaiian Drosophilidae, p. 437–543. *In:* Hecht, M.K. & W.C. Steere, eds., *Essays in evolution and genetics in honor of Theodosius Dobzhansky.* Appleton-Century-Crofts, New York.

Carson, H.L. & K.Y. Kaneshiro. 1976. *Drosophila* of Hawaii: Systematics and ecological genetics. *Ann. Rev. Ecol. Syst.* **1976**(7): 311–45.

Chappel, J. 1974. Relationships between sea levels, variations and orbital pertubations, during the past 250,000 years. *Nature (Lond.)* **252:** 199–202.

Charlesworth, B. & D.B. Smith. 1982. A computer model of speciation by founder effects. *Genet. Res.* **39:** 227–36.

Chui, W.D. & I.W.B. Thornton. 1972. A numerical taxonomic study of the endemic *Ptycta* species of the Hawaiian Islands (Psocoptera: Psocidae). *Syst. Zool.* **21**(1): 7–22.

Clague, D.A. & G.B. Dalrymple. 1975. Cretaceous K-Ar ages of volcanic rocks from the Musicians Seamounts and the Hawaiian Ridge. *Geophys. Res. Lett.* **2:** 305–08.

Clague, D.A. & R.D. Jarrard. 1973. Tertiary Pacific plate motion deduced from the Hawaiian-Emperor chain. *Geol. Soc. Am. Bull.* **84**(4): 1135–54.

Dalrymple, G.B., D.A. Clague, M.O. Garcia & S.W. Bright. 1981. Petrology and K-Ar ages of dredged samples from Laysan and Northampton volcanoes, Hawaiian Ridge, and evolution of the Hawaiian-Emperor chain. *Geol. Soc. Am. Bull.* Part II. **92**(6): 884–933.

Dalrymple, G.B., E.A. Silver & E.D. Jackson. 1973. Origin of the Hawaiian Islands. *Am. Sci.* **61:** 294–308.

Davis, C.J. 1952. New host and insect records from the islands of Hawaii. *Proc. Hawaii. Entomol. Soc.* **15**(1): 85–86.

Doty, M.S. & L. Watson. 1981. Terrestrial algae, p. 165–71. *In:* Mueller-Dombois, D., K.W. Bridges & H.L. Carson, eds., *Island ecosystems.* Hutchinson Ross.

Enderlein, G. 1913. Beitrage zur Kenntnis der Copeognathen. I. Zur Kenntnis der Copeognathen Hawaii. *Zool. Anz.* **41:** 354–58.

1920. Die Copeognathen der Hawaii-Inseln. *Zool. Jahrb. Abt. Syst.* **43:** 449–60.

1925. Beitrage zur Kenntnis der Copeognathen. IX. *Konowia* **4:** 97–108.

1931. Die Copeognathenfauna der Seychellen. *Trans. Linn. Soc. Lond. (Zool.)* (2) **19:** 207–40.

Gagné, W.C. 1979. Canopy-associated arthropods in *Acacia koa* and *Metrosideros* tree communities along an altitudinal transect on Hawaii Island. *Pac. Insects* **21**(1): 56–82.

1981. Canopy-associated arthropods, p. 118–27. *In:* Mueller-Dombois, D., K.W. Bridges & H.L. Carson, eds., *Island ecosystems.* Hutchinson Ross.

Gagné, W.C. & F.G. Howarth. 1981. Arthropods associated with foliar crowns of structural dominants, p. 275–88. *In:* Mueller-Dombois, D., K.W. Bridges & H.L. Carson, eds., *Island ecosystems.* Hutchinson Ross.

Galil, B. 1981. On some Psocoptera from Israel and descripton of new species. *Isr. J. Entomol.* **15:** 53–58.

Grommé, C.S. & F.J. Vine. 1972. Palaeomagnetism of Midway Atoll lavas and northward movement of the Pacific plate. *Earth Plan. Sci. Lett.* **17:** 139–68.

Hardy, D.E. & K.Y. Kaneshiro. 1981. Drosophilidae of Pacific Oceania, p. 309–42. *In:* Ashburner, M., H.L. Carson & J.N. Thompson, Jr, eds., *The genetics and biology of Drosophila.* Vol. 3a. Academic Press, London.

Hey, R. 1977. Tectonic evolution of the Cocos-Nazca spreading centre. *Geol. Soc. Am. Bull.* **88**(10): 1404–20.

Holden, J.C. & R.S. Dietz. 1972. Galapagos Gore, NazCoPac triple junction and Carnegie and Cocos ridges. *Nature (Lond.)* **235:** 266–69.

Jackson, E.D., I. Koizumi, G.B. Dalrymple, D.A. Clague, R.J. Kirkpatrick & H.G. Green. 1980. I. Introduction and summary of results from DSDP Leg 55, the Hawaiian-Emperor hot-spot experiment, p. 5–32. *In:* Shambach, J., ed., *Initial reports of the deep sea drilling project, Vol. 55.* U.S. Govt. Printing Office.

Jackson, E.D., E.A. Silver & G.B. Dalrymple. 1972. Hawaiian-Emperor chain and its relation to Cenozoic circum-Pacific tectonics. *Geol. Soc. Am. Bull.* v, **83:** 601–18.

Jarrard, R.D. & D.A. Clague. 1977. Implications of Pacific island and seamount ages for the origin of volcanic chains. *Rev. Geophys. Space Phys.* **105:** 57–76.

Kaneshiro, K.Y. 1976. Ethological isolation and phylogeny in the *planitibia* subgroup of Hawaiian *Drosophila*. *Evolution* **30:** 740–45.

Macdonald, G.A. & A.T. Abbott. 1970. *Volcanoes in the sea: Geology of Hawaii.* University of Hawaii Press, Honolulu. 441 p.

Malahoff, A., G.M. McMurtry, J.C. Wiltshire & Hsuey-Wen Yeh. 1982. Geology and chemistry of hydrothermal deposits from active submarine volcano Loihi, Hawaii. *Nature (Lond.)* **298:** 234–39.

Mayr, E. 1942. *Systematics and the origin of species.* Columbia Univ. Press, New York. 334 p.

1954. Change of genetic environment and evolution, p. 157–80. *In:* Huxley, J.S., A.C. Hardy & E.B. Ford, eds., *Evolution as a process.* Allen & Unwin, London.

Meinander, M. 1966. Psocoptera from the mid-Atlantic islands and Morocco. *Notulae Entomol.* **46:** 107–21.

1981. Descriptions of three Mediterranean Psocidae: *Blaste hilaris* (Navas, 1907), *Neopsocopsis aegyptiacus* n. sp. and *Ptycta hispanica* n. sp. (Psocoptera). *Entomol. Scand.* **12:** 448–52.

Mockford, E.L. 1974. Records and descriptions of Cuban Psocoptera. *Entomol. Am.* **48:** 103–215.

Montgomery, S.L. 1982. Biogeography of the moth genus *Eupithecia* in Oceania and the evolution of ambush predation in Hawaiian caterpillars (Lepidoptera: Geometridae). *Entomol. Gen.* **8**(1): 27–34.

Morgan, W.J. 1972. Deep mantle convection plumes and plate motions. *Bull. Am. Assoc. Pet. Geol.* **56:** 203–13.

Mueller-Dombois, D. 1981. Some bioenvironmental conditions and the general design of IBP research in Hawai'i, p. 3–32. *In:* Mueller-Dombois, D., K.W. Bridges & H.L. Carson, eds., *Island ecosystems.* Hutchinson Ross.

New, T.R. 1972. A collection of Psocidae (Psocoptera) from Central Brazil. *Arq. Zool. Estado Sao Paulo* **22**(4): 193–237.

1974. Psocidae (Psocoptera) from southern Australia. *J. Austral. Entomol. Soc.* **13:** 285–304.

1975. New species and records of Psocidae (Psocoptera) from Kenya. *J. Nat. Hist.* **9:** 535–44.

1977. Psocoptera from Aldabra and the Chagos Archipelago. *Orient. Insects* **2**(1): 89–112.

New, T.R. & I.W.B. Thornton. 1975. Psocomorpha (Psocoptera) collected on recent expeditions to South America. *J. Entomol.* (B), **44**(1): 27–80.

1976. Psocomorpha (Psocoptera) from the Malayan Peninsula, including collections from forest canopy. *Orient. Insects* **9**(4): 375–418.

1981. Psocoptera from central and southern Chile. *Pac. Insects Monogr.* **37:** 136–78.

Olsen, S.L. & H.F. James. 1982. Fossil birds from the Hawaiian Islands: Evidence for wholesale extinction by man before western contact. *Science* **217**(4560): 633–35.

Paik, Y.K. & K.C. Sung. 1981. Genetics of island populations of exotic *Drosophila*, p. 455–64. *In:* Mueller-Dombois, D., K.W. Bridges & H.L. Carson, eds., *Island ecosystems.* Hutchinson Ross.

Perkins, R.C.L. 1899. Neuroptera, p. 31–89. *In: Fauna Hawaiiensis.* Vol. 2. Cambridge.

Rotondo, G.M. 1980. A reconstruction of linear island chain positions in the Pacific. M.A. thesis (61 p.). Sinclair Library, Univ. Hawaii.

Rotondo, G.M., V.G. Springer, G.A.J. Scott & S.O. Schlanger. 1981. Plate movement and island integration—a possible mechanism in the formation of endemic biotas, with special reference to the Hawaiian Islands. *Syst. Zool.* **30**(1): 12–21.

Schlanger, S.O. & G.W. Gillett. 1976. A geological perspective of the upland biota of Laysan atoll (Hawaiian Islands). *Biol. J. Linn. Soc.* **8**(3): 205–16.

Smithers, C.N. 1964. On the Psocoptera of Madagascar. *Rev. Zool. Bot. Afr.* **70:** 209–94.

1972. The classification and phylogeny of the Psocoptera. *Aust. Mus. Mem.* **14:** 1–349.

1977. The Psocoptera of Muogamarra Nature Reserve. *Rec. Aust. Mus.* **31**(7): 251–306.

1984. Redefinition of *Copostigma* Enderlein (Psocoptera: Psocidae). *Aust. Entomol. Mag.* (in press).

Stoner, M.F. & G.E. Baker. 1981. Soil and leaf fungi, p. 171–80. *In:* Mueller-Dombois, D., K.W. Bridges & H.L. Carson, eds., *Island ecosystems.* Hutchinson Ross.

Thornton, I.W.B. 1960. New Psocidae and an aberrant new myopsocid (Psocoptera) from Hong Kong. *Trans. R. Entomol. Soc. Lond.* **112**(10): 239–61.

1967. The measurement of isolation on archipelagos, and its relation to insular faunal size and endemism. *Evolution* **21**(4): 842–49.

1971. *Darwin's islands, a natural history of the Galapagos.* Natural History Press, New York. 322 p.

1981a. Psocoptera of the Fiji Islands. *Pac. Insects Monogr.* **37:** 1–105.

1981b. Psocoptera of the Tongan Archipelago. *Pac. Insects Monogr.* **37:** 106–35.

1981c. Psocoptera of the Hawaiian Islands. I & II. Introduction and the nonendemic fauna. *Pac. Insects* **23**(1–2): 1–49.

Thornton, I.W.B., S.S. Lee & W.D. Chui. 1972. Psocoptera. *Insects Micronesia* **8**(14): 45–144.

Thornton, I.W.B. & K.T. Woo. 1972. Psocoptera of the Galapagos Islands. *Pac. Insects* **15**(1): 1–57.

Throckmorton, L.H. 1966. The relationships of the endemic Hawaiian Drosophilidae. *Univ. Tex. Publ.* **6615:** 335–96.

Tsutsumi, C. 1964. Two new species of Psocoptera from the Ryukyu Islands, Japan. *Kontyu* **32**(2): 265–69.

Turner, B.D. 1975. The Psocoptera of Jamaica. *Trans. R. Entomol. Soc. Lond.* **126**(4): 533–609.

1976. Psocoptera of the Mascarene Islands. *Syst. Entomol.* **1:** 201–25.

Turner, B.D. & E. Broadhead. 1974. The diversity and distribution of psocid populations on *Mangifera indica* L. in Jamaica and their relationship to altitude and microepiphyte diversity. *J. Anim. Ecol.* **43:** 173–90.

Wilson, J.T. 1963a. A possible origin of the Hawaiian Islands. *Canad. J. Phys.* **41:** 863–70.

1963b. Evidence from islands on the spreading of ocean floors. *Nature (Lond.)* **197:** 536–38.

Zimmerman, E.C. 1948a. Introduction, p. 1–191. *Insects of Hawaii.* Vol. 1. Univ. Hawaii Press, Honolulu.

1948b. Corrodentia, p. 217–52. *Insects of Hawaii.* Vol. 2. Univ. Hawaii Press, Honolulu.

1957. Neuroptera, p. 19–169, 179. *Insects of Hawaii.* Vol. 6. Univ. Hawaii Press, Honolulu.

1970. Adaptive radiation in Hawaii with special reference to insects. *Biotropica* **2**(1): 32–38.