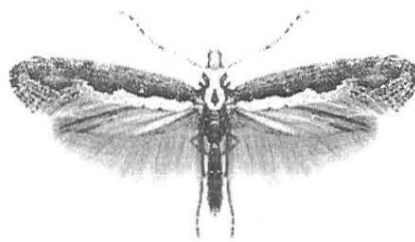

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PLUTELLA IN THE HAWAIIAN ISLANDS:
RELATIVES AND HOST-RACES OF
THE DIAMONDBACK MOTH
(LEPIDOPTERA: PLUTELLIDAE)

GADEN S. ROBINSON
AND
KLAUS SATTLER



BISHOP MUSEUM PRESS
HONOLULU

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A SPECIAL PUBLICATION OF THE
RECORDS OF THE HAWAII BIOLOGICAL SURVEY FOR 2000

Cover illustration: *Plutella xylostella* (Linnaeus) by N.L. Evenhuis

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BISHOP MUSEUM

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***Plutella* in the Hawaiian Islands: Relatives and Host-Races of the Diamondback Moth (Lepidoptera: Plutellidae)**

GADEN S. ROBINSON & KLAUS SATTLER (Department of Entomology, The Natural History Museum, London SW7 5BD, UK; email: gsr@nhm.ac.uk)

Abstract. A systematic revision of the Hawaiian representatives of *Plutella* is given with keys, descriptions and illustrations of adults and genitalia of both sexes. Four species are recognized, 3 of them endemic to the Hawaiian Islands (and 2 of these are described as new): *Plutella capparidis* Swezey (2 island races on O'ahu and Maui); *P. noholio*, **sp. n.** (Hawai'i); *P. kahakaha*, **sp. n.** (Kaua'i); *P. xylostella* (L.) (widespread). *Plutella xylostella* exhibits a rare individual aberration unique to Hawai'i (originally described and named as *Plutella albovenosa* Walsingham) and also has distinct host-races feeding on *Capparis* on Kaua'i, O'ahu, and Hawai'i. The origins and taxonomic context of the Hawaiian *Plutella* are discussed. It is suggested that in *Plutella* at least 2 prehistoric colonization events of the Hawaiian chain have occurred. The first was of a perhaps *Plutella porrectella*-like ancestor and gave rise to the present-day endemic species (the *capparidis*-subgroup), 2 of which feed on *Capparis* (the hostplant of *P. kahakaha* is unknown). The second involved a *xylostella*-like ancestor evolving into at least 2 separate *Capparis*-feeding host-races that preceded the introduction or immigration of typical Brassicaceae-feeding *Plutella xylostella* in historic times. An overview of *Plutella* worldwide is provided together with a systematic checklist of world Plutellidae. Eleven new combinations and 2 new synonyms are established; 1 species is transferred from Plutellidae to Ypsolophidae.

INTRODUCTION

***Plutella* in Hawai'i**

Plutella Schrank, 1802, is a poorly defined genus with a worldwide distribution containing 22 species. Its composition, and that of related genera, is reviewed and adjusted later in this paper. The type species, *Plutella xylostella* L., the Diamondback moth or Cabbage moth (the latter common name is ambiguous), is a notorious migratory pest of brassicaceous crops — it occurs practically everywhere on earth with the exception of extreme alpine and arctic habitats (CIE, 1953). The observation by Talekar & Shelton (1993) that the worldwide management cost of *P. xylostella* in 1992 was \$1 billion makes it the more remarkable that a satisfactory taxonomic context for this pest has never been established.

Plutella xylostella (under its earlier name *P. maculipennis* Curtis) was first recorded from Hawai'i by Walsingham (1907) from material collected as early as 1892 (Zimmerman, 1978). It is a serious pest of *Brassica* cultivars and it has been the subject of attempts at biocontrol using introduced parasitoids both in Hawai'i and elsewhere (Zimmerman, 1978). Clearly an introduced species, it is widespread in Hawai'i; Zimmerman (1978) recorded it from all islands except Lāna'i.

Walsingham (1907) described an apparently endemic Hawaiian *Plutella* species — *P. albovenosa* Walsingham — but Zimmerman (1978) was of the opinion that this was merely a color variant of *P. xylostella* and synonymized the two. We have re-examined the relevant specimens and agree with his conclusion.

Until now, only one named endemic species was known from the Hawaiian Islands

(Zimmerman, 1978): Swezey (1920) described an endemic *Plutella*: *P. capparidis* Swezey — clearly distinct from *xylostella* and reared from *Capparis sandwichiana* DC (Capparaceae) on O'ahu. It should be noted, however, that the taxonomic status of *Capparis sandwichiana* is uncertain, and it may be identical with the widespread Pacific *Capparis cordifolia* Lam. (Wagner *et al.*, 1999).

Zimmerman (1978: 758-766) noted in his introduction to *Plutella*:

“. . . after my manuscript was completed . . . the Hawaiian insect collections at the Sugar Planters' Experiment Station were given to the Hawaiian [sic] State Department of Agriculture, and . . . I have recently been able to make a brief preliminary study of several specimens of *Plutella* from series reared from *Capparis* by Dr. Swezey. One series of specimens is from the Ewa Coral Plain, Oahu, the second series is from Diamond Head, Oahu, and the third is from Kailua and Napoopoo, Hawaii. From external appearances these series appear to represent three or, possibly, four species. Surprisingly, however, their male genitalia are confusingly similar, and without further detailed study I cannot express an opinion regarding their status. . .”.

These are host-plant races of *P. xylostella* and are discussed further below.

Endemic species of the genus *Plutella* are rare and extremely local in the Hawaiian fauna. No specimens were collected by R.C.L. Perkins during his historic *Fauna Hawaiiensis* surveys (Walsingham, 1907). *Plutella capparidis* Swezey must now be considered as extinct, at least on O'ahu, its type-locality island.

However, further material, apparently comprising *Plutella* and not referable to *xylostella*, is present in collections in Hawai'i and UK (see below); most of these specimens were obtained by rearing larvae from *Capparis sandwichiana* collected in the lowlands of O'ahu and Maui. Additionally, 3 specimens of an as yet undescribed species were attracted to MV light in upland Kaua'i in 1982 (specimens in BMNH; figured by Howarth & Mull, 1992: 119, fig. 111). Further, a recent survey by S.L. Montgomery resulted in additional specimens from Maui and the island of Hawai'i (the Big Island).

Chang *et al.* (1997) examined genetic variation among 6 strains of *P. xylostella* together with 2 “undescribed Hawaiian *Plutella* species”; this work is discussed further below.

Many years ago, the US Fish & Wildlife Service (USFWS) Endangered Species Office identified native Hawaiian *Plutella* as under potential threat from continued introductions of biological control agents against *Plutella xylostella*. However, as the species characterizations were unsatisfactory, no regulatory context could be established. The purpose of this paper is to characterize the morphologically distinguishable taxa of endemic Hawaiian *Plutella* from the material available, review their significance and distribution, and provide for them a global context with a revisionary catalogue of *Plutella* and its allies.

Overview of Plutella worldwide

The family Plutellidae *sensu stricto* (Dugdale *et al.*, 1999) comprises 5 genera containing 58 species — *Eidophasia* (11 species), *Lunakia* (1 species), *Plutella* (22 species, 12 attributable to *Plutella sensu stricto*), *Leuroperna* (2 species) and *Rhigognostis* (2 species). Two further genera, the brachypterous subantarctic *Embryonopsis* (1 species) and the Australasian *Proditrix* (2 species) are only tentatively associated with the family (Dugdale *et al.*, 1999).

Species of *Plutella sensu stricto* form 2 clearly distinct species-groups. The *geniatella*-group contains 7 Holarctic species (of which 2 may prove to be synonyms), and the *xylostella*-group 5 species from the Holarctic region and Hawai'i. In the latter group, the 3 Hawaiian endemic species form the *capparidis*-subgroup; *P. porrectella* L. occurs in North America, Europe and the Neotropical region, while *P. xylostella* is, effectively, cosmopolitan and has been introduced into New Zealand and Australia where it is an established pest. In Japan it is the only *Plutella* recorded.

The remaining species associated with *Plutella* are of uncertain affinity and are listed in the Appendix below as *Plutella sensu lato*. They comprise 5 species from the Neotropical region and 2 from New Zealand; 3 species have not been examined by us (it is unlikely that syntypic material of *P. canaella* even exists) and we list these as "*incertae sedis*". Seven Afrotropical "*Plutella*" species are transferred below to *Rhigognostis*. The taxonomy of *Plutella* is unsatisfactory and the genus needs revision.

The classification used here follows Kyrki (1990), except that the Acrolepiinae are not included within Plutellidae following Dugdale *et al.* (1999). *Distagmos* was included in Plutellinae by Vives Moreno (1994) but placed in Praydinae by Kyrki (1990) followed by Karsholt & Razowski (1996). The synonymy of *Plutella hyperboreella* with *Plutella geniatella* was suggested but not established by Karsholt & Razowski (1996); the valva of *geniatella* from the European Alps and Pyrenees is sharply rhomboidal but that of the Arctic *hyperboreella* is a rounded rhomboid, identical to that of *P. polaris* with which we synonymize it below. Both *P. haasi* Staudinger and *P. mariae* Rebel may prove to be additional synonyms of *P. polaris*.

The checklist (see Appendix) includes all names of Plutellidae known to us, together with author, date of original description, genus of original combination and type locality.

MATERIAL AND METHODS

Relevant material was located in 3 depositories and examined: The Natural History Museum, London (BMNH) — material from the *Fauna Hawaiiensis* survey [only *xylostella* (including types of *albovenosa* Walsingham)], K. & E. Sattler survey [only *kahakaha* from upland Kaua'i and *xylostella*]; Bernice P. Bishop Museum, Honolulu, Hawai'i (BPBM) — material reared on Maui and Hawai'i by Montgomery and on O'ahu by Bridwell, also *xylostella* from the Leeward Islands (Kure, Midway, Pearl & Hermes Reef, Laysan) and O'ahu; Hawai'i Department of Agriculture, Honolulu (HDOA) — material reared on O'ahu and Maui by Swezey and Bridwell and on Hawai'i by Matayoshi.

An exhaustive search for Hawaiian *Plutella* material in the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM) failed to unearth further specimens. The constraints placed upon this study by the quality and quantity of specimens were considerable. Regrettably, some genitalia slide preparations from past studies by Busck and Zimmerman (including some made by KS for Zimmerman's study) could no longer be traced at BPBM and/or HDOA.

Protocols followed for dissection and preparation of genitalia and slides of wing venation have been described by Robinson (1976) and Robinson & Nielsen (1993) respectively. In the male genitalia of *Plutella* the saccus is three-dimensional to the point that it is invariably distorted in a standard preparation. In contrast to standard practice we did not remove the female genitalia from the abdomen in order to preserve the position of the antrum relative to the posterior margin of abdominal segment VIII.

Color photographs of forewings were made using the *Synoptics* (Cambridge) composite image analysis system and images processed using *Montage* for Windows; Corel's *Photo-Paint* was employed for post-processing, etching and background coloring.

Future studies should ensure the recording of precise biological and locality data on labels; voucher material from DNA studies should be clearly marked as such (see also Discussion). The voucher specimens re-examined here of UPA (Nāpō'opo'o) and UPB (Kaloko) from the study of Chang *et al.* (1997) are identically labelled "Kona, HAWAII" but come from different localities in the Kailua-Kona District on Hawai'i (Kumashiro, pers. comm.) and may represent different populations. The identity of UPB (Kaloko) is uncertain. It was part of a sample designated 96/085 (see Material Examined), but according to Kumashiro (pers. comm.) that sample may have been mixed and the specimen used for DNA analysis may have been unique.

SYSTEMATICS

Plutella Schrank

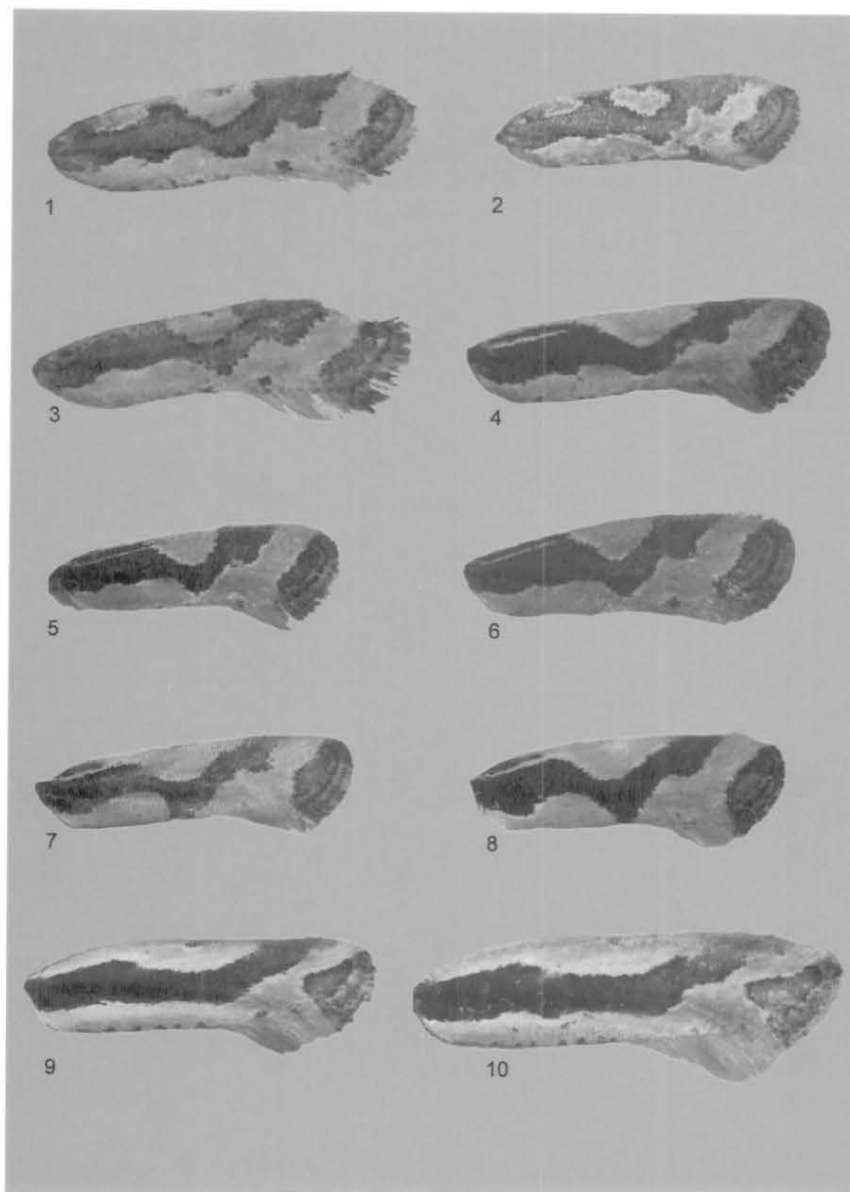
Plutella Schrank, 1802: 169. Type species: *Cerostoma maculipennis* Curtis, 1832 [= *Phalaena* (*Tinea*) *xylostella* Linnaeus, 1758].

♂, ♀ Ocellus present. Antenna about 3/4 length of forewing, scape with dense pecten, flagellum in distal 1/2 with series of black rings. Proboscis present, naked. Labial palpus recurved, segment 2 with forward-directed triangular tuft. Forewing with 12 veins, R1 to CuA2 arising free from cell; hind wing with 9 veins, M1+M2 stalked (Figs. 20, 21). Female frenulum with 2 acanthae. Tibial spurs 0-2-4, epiphysis present. Forewing more or less dark with light contrasting dorsum ('diamond back').

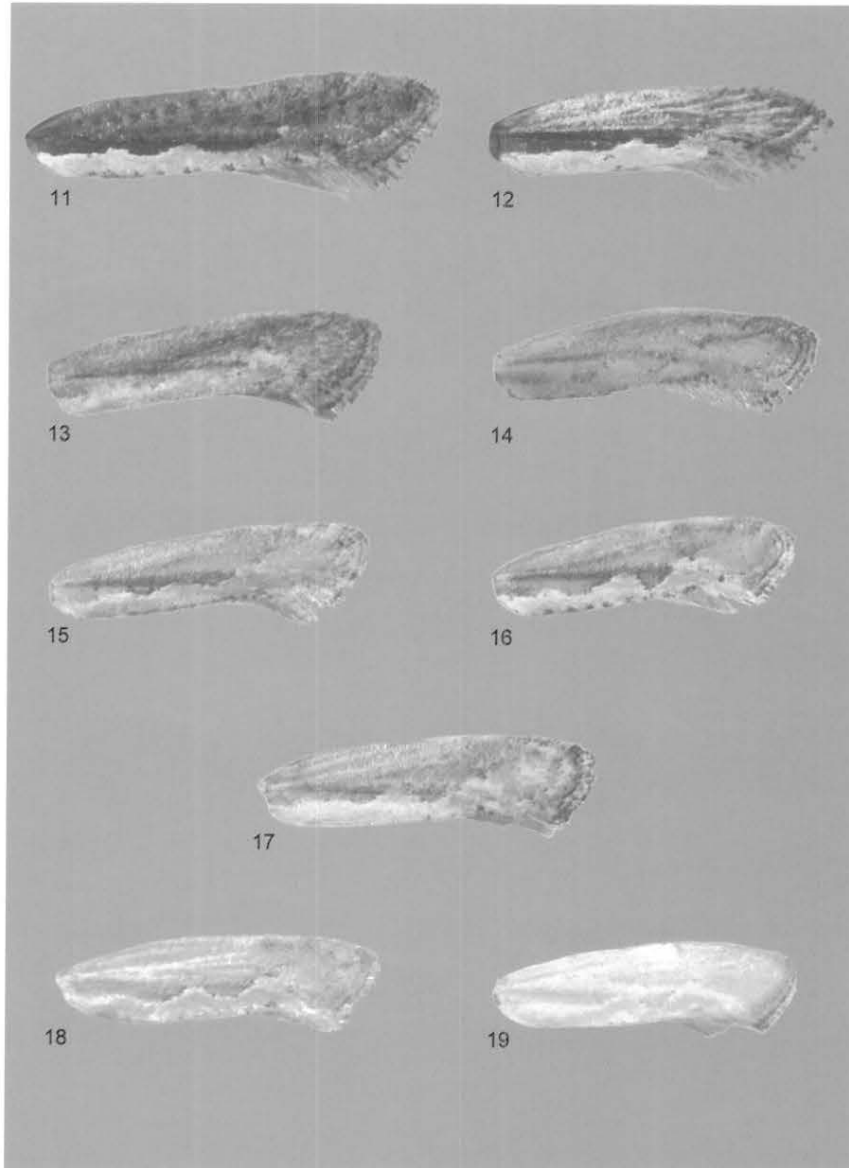
GENITALIA ♂ (Figs. 27-38). Uncus absent, socii reduced, gnathos absent, tegumen unremarkable, saccus large. No sclerotized anellus structures. Valva simple, broad, usually without clearly defined sacculus, base with valval apodeme. Aedeagus straight (*P. xylostella*) or variously curved, without cornuti. Pregenital abdomen (Fig. 39), segment VIII with pair of rounded lateral flaps characteristic of Yponomeutoidea, abdominal tergites without spines. Pair of long coremata brushes present in VIII/IX intersegmental membrane, rarely absent (*P. noholio*).

GENITALIA ♀ (Figs. 40-49). Ovipositor short, papillae anales unremarkable, apophyses posteriores short. Apophyses anteriores short, rod-like, divided; dorsal branch terminating in tergal sclerotization; posterior margin of tergite VIII set with a small number of long sensilla trichodea. Ventral branch directed mesad, terminating in paired, minutely spinose sternal pad bearing a small number of sensilla trichodea. Antrum a short sclerotized ring or funnel; ductus bursae short, straight, thin; corpus bursae membranous, without signa. Pregenital abdomen unremarkable in endemic Hawaiian species, segment VII specialized in *P. xylostella*.

BIOLOGY. Host-plants: Predominantly Brassicaceae (Cruciferae) including many cultivated varieties of *Brassica*; 2 Hawaiian *P. xylostella* host-races and endemic species of *capparidis*-subgroup only known from *Capparis sandwichiana* DC (Capparaceae), an endemic plant found on all islands at low altitudes, from 0-100 (-575) m (but see *P. kahakaha* sp. n., below). Ovum usually laid singly on underside of leaf, not observed in *capparidis*-subgroup. Larva usually solitary, feeding on lower surface of leaf, sometimes covered by flimsy web. Pupa on host-plant, in cocoon of delicate network. Larvae and/or adults of *P. xylostella* observed practically all year round, those of *capparidis*-subgroup observed in x, xii-iii, vi, but possibly also present throughout entire year.



Figures 1–10. Hawaiian *Plutella* spp., right forewing (or reversed image – 1, 3, 4, 6, 8–10): 1, *capparidis*, ♂, O'ahu; 2, *capparidis*, ♂, O'ahu; 3, *capparidis*, ♀, O'ahu; 4, *capparidis*, ♀, Maui; 5, *capparidis*, ♀, Maui; 6, *capparidis*, ♂, Maui; 7, *noholio*, sp.n., holotype ♂, Hawai'i; 8, *noholio*, paratype ♀, Hawai'i; 9, *kahakaha*, sp.n., paratype ♂, Kaua'i; 10, *kahakaha*, holotype ♂, Kaua'i. Specimens not to scale.



Figures 11–19. Hawaiian *Plutella xylostella*, right forewings (or reversed image: 11, 13, 14). 11–12, *Brassica* host-races; 13–19, *Capparis* host-races (13–17: race 1; 18, 19: race 2). 11, ♂, Hawai‘i, typical form; 12, ♂, O‘ahu, Waianae, “*albovenosa*” form; 13, ♂, O‘ahu, Mokapu, ex *Capparis*; 14, ♀, O‘ahu, Diamond Head, ex *Capparis*; 15, ♀, O‘ahu, Diamond Head, ex *Capparis*; 16, ♂, O‘ahu, Diamond Head, ex *Capparis*; 17, ♂, O‘ahu, Ewa, ex *Capparis*; 18, ♂, Hawai‘i, Kailua-Kona, ex *Capparis*; 19, ♂, Hawai‘i, Kailua-Kona, ex *Capparis*. Specimens not to scale.

Key to the Hawaiian species of *Plutella* (forewings)

1. Contrasting pattern, always with large dark patch on termen (Figs. 1–10, 22–26).. 2
- . Uniform or with yellowish white dorsum, never with dark terminal patch (Figs. 11–19) *xylostella*
2. Large species (12.0–16.0 mm). Light costal band broad, uninterrupted to base (Figs. 9, 10, 26)..... *kahakaha*, **sp. n.**
- . Small species (6.0–9.5 mm). Never with broad, uninterrupted costal band (Figs. 1–8, 22–25)..... 3
3. Light dorsum broken at 1/2 by dark mark (Figs. 7, 8, 25) *noholio*, **sp. n.**
- . Dorsum entirely light (Figs. 1–6, 22–24) 4
4. Base with narrow white subcostal streak (Figs. 4–6, 24)..... *capparidis* (Maui)
- . Base with large oval subcostal mark (Figs. 1–3, 22, 23).. *capparidis*, s. str. (O'ahu)

Key to the Hawaiian species of *Plutella* (♂ genitalia)

1. Aedeagus straight, bulbous base bearing pair of lateral hooks (Figs. 37, 38) *xylostella*
- . Aedeagus curved or sinuous, not straight, base simple, without hooks (Figs. 29, 30, 33, 34) 2
2. Ventral margin of valva sharply angled; aedeagus evenly curved (Figs. 32, 34) *kahakaha*, **sp. n.**
- . Valva with even margins; aedeagus more or less sinuous (Figs. 27–31, 33) 3
3. Valva distally broader than at base; aedeagus distinctly sinuous (Figs. 27–30) *capparidis*
- . Valva basally broader than distally; aedeagus weakly sinuous (Figs. 31, 33) *noholio*, **sp. n.**

Key to the Hawaiian species of *Plutella* (♀ genitalia)
(♀ of *P. kahakaha* unknown)

1. Abdominal segment VII specialized beneath ostium bursae (Figs. 40, 41) *xylostella*
- . Abdominal segment VII unremarkable (Figs. 42–49) 2
2. Antrum large, at least 1/3 width of segment VII (Figs. 44, 47–47) ... *noholio*, **sp. n.**
- . Antrum small, at most 1/5 width of segment VII (Figs. 42, 43, 45, 46) 3
3. Substernal plate large (Figs. 42, 45)..... *capparidis*, s. str. (O'ahu)
- . Substernal plate rudimentary (Figs. 43, 46) *capparidis* (Maui)

Plutella capparidis Swezey s. str. (O'ahu)

Figs. 1–3, 22, 23, 27, 29, 42, 45

Plutella capparidis Swezey, 1920, *Proc. Hawaii. Entomol. Soc.* 4: 383. Lectotype ♂, Hawaiian Islands, O'ahu, Ewa Coral Plain, 8.vi.1919 (*Bridwell*) (BPBM) [examined]. Designated (as 'holotype') by Zimmerman, 1978: 760, fig. 505, top figure.

♂, ♀ (Figs. 1–3, 22, 23). 8.0–8.5 mm wingspan. Head off-white, vertex with pair of indistinct pale brown longitudinal lines, area behind compound eye and beneath ocellus dark brown. Labial palpus drooping, segment 2 with forward-directed, triangular, brown tuft; segment 3 slightly upturned, about as long as 2, outer surface brown. Antenna about 2/3 length of forewing, scape with dense pecten, flagellum dorsally off-white, with several dark rings in distal half. Thorax as head, with thin, indistinct,

pale brown median line; tegula dark brown. Forewing dark grey-brown with off-white to yellowish dorsum, demarcation line between both areas irregularly sinuous; dark area with light elongate costal mark occupying basal fourth and larger, usually sub-triangular costal mark at about one-half. Light dorsal band obliquely extended to reach costa subapically; termen between apex and tornus with broad, proximally concave, greyish brown mark. Costa often with small black dot in light sub-triangular mark; dorsum with half a dozen similar dots.

GENITALIA ♂ (Figs. 27, 29). Valva simple, broadly ovoid, narrowest at base, broadest at about distal 2/3, cucullus evenly rounded. Saccus broad, evenly tapered from base to 2/3, distal 1/3 with parallel margins, apex rounded. Aedeagus thin, tubular, characteristically sinuous.

GENITALIA ♀ (Figs. 42, 45). Apophyses posteriores distinctly less than 2 × length of apophyses anteriores. Rod-like part of ventral branch of apophyses anteriores relatively long, merging mesad with round to oval, minutely spinose, pad that bears about 6 sensilla trichodea on caudal margin. Antrum small, cup-like, on broad substernal plate.

REMARKS. *Plutella capparidis* was described from 20 specimens of both sexes reared from *Capparis sandwichiana*. A series of original specimens seen by us bears small yellow printed labels "Paratype", except 1 male which bears a white, black-edged label reading "*Plutella capparidis* Swezey" (in an unidentified handwriting) to which a small red printed label "Holotype" has been pasted. This last specimen was illustrated by Zimmerman (1978: 760, fig. 505, top figure) as the "holotype" and this is accepted as constituting a valid lectotype designation.

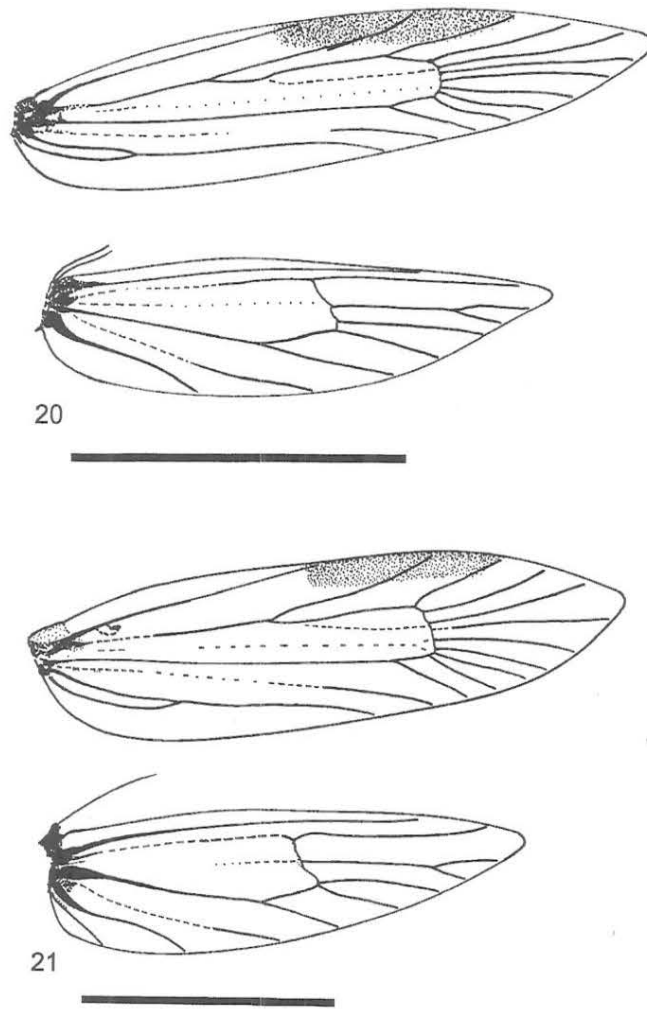
The type-material is not in the best condition; the specimens are faded, many abdomens have been destroyed by psocids and several specimens lack the head and parts of the antennae. The dark antennal rings are probably much as in the Maui form (described below) but are now faded and indistinct.

Some variation can be observed in the extent of the dark forewing markings and the size of the light basicostal mark; however, both marks never merge. A small dark spot is often present in the large costal mark; it is absent in the Maui form. With regard to the color description it should be borne in mind that the available specimens are now about 80 years old and somewhat faded; reference should therefore also be made to Swezey's original description.

Plutella capparidis was apparently last observed in 1926 and is now believed to be extinct on O'ahu.

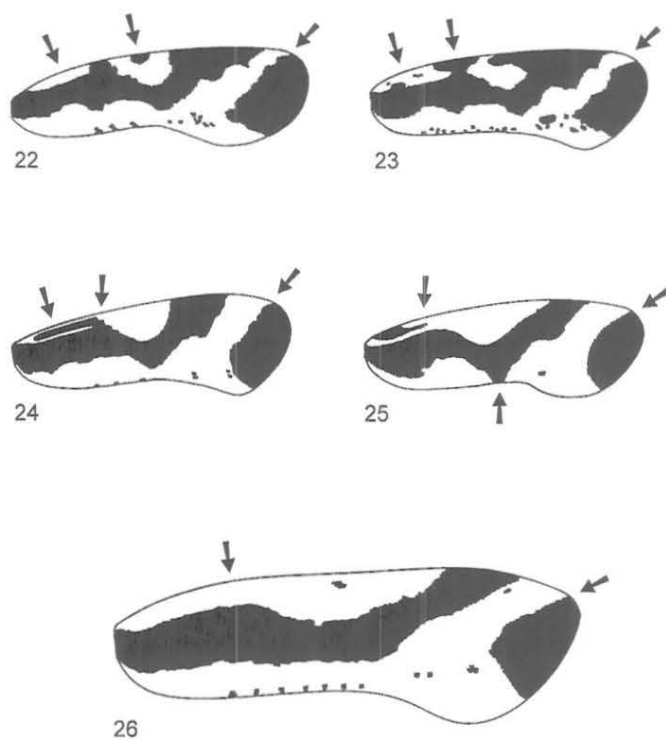
BIOLOGY. Host-plant: *Capparis sandwichiana*. The type-series was reared from green larvae feeding in June on the leaves by shaving one surface and leaving the epidermis of the other intact thus causing dead spots in the leaf. The larvae are usually exposed but sometimes are covered by a slight web; they occasionally mine the leaf. Pupation takes place *in situ* in a cocoon that is denser than in *P. xylostella* but thin enough for the pupa to be visible within. Parasitism by *Chelonus blackburni* Cameron (Hymenoptera: Braconidae) was upwards of 60% (Swezey, 1920: 383-384). According to label data also reared subsequently in December-February.

It is noteworthy that a form of *P. xylostella* was reared from larvae in *Capparis* fruits in some of the localities of *P. capparidis* (see below).



Figures 20–21. Wing venation. 20, *Plutella xylostella*, ♀, Jordan (scale line = 5 mm); 21, *Plutella capparidis*, ♂, Maui (scale line = 1 mm).

MATERIAL EXAMINED (including 2♂, 2♀ genitalia preparations). Lectotype as above; 6♂, 3♀, O‘AHU: Ewa Coral Plain, 8.vi.1919, ex leaves of *Capparis* (Bridwell, HDOA) [1♂ without abdomen] paralectotypes [associated label stating ‘18 specimens ex leaves of *Capparis*’; 1♂, 1♀, with individual label ‘*Capparis* leaves’]; 1♂ with same data but without “paralectotype” label; 1 unsexed, unsexed specimen with label ‘paratype ♂ entire/♀ abdomen to/ ECZ 7-18-61’ [ECZ slide



Figures 22-26. Forewing pattern of endemic Hawaiian *Plutella* (schematic) with key features arrowed: 22, *capparis* (O'ahu); 23, *capparis* (O'ahu — variant); 24, *capparis* (Maui); 25, *noholio* (Hawai'i); 26, *kahakaha* (Kaua'i).

information.]; 1 ♂, O'ahu, Ewa Coral Plain, 8.vi.1919, ex leaves of *Capparis* (Bridwell, BPBM), paralectotype [genitalia slide 138, Busck, not traced]; 1 ♀, O'ahu, Ewa Coral Plain, 8.vi.1919, ex leaves of *Capparis* (Bridwell, BPBM), paralectotype [genitalia slide 139, Busck, not traced]; 1 ♂, 1 ♀, O'ahu, Ewa Coral Plain, 8.vi.1919, ex leaves of *Capparis* (Bridwell, BPBM), paralectotypes [♂ head and abdomen missing]. 2 ♂, O'ahu, Ewa Coral Plain, 19.xii.1926, ex *Capparis* leaves, (Swezey, HDOA) [1 ♂ without abdomen]. 5 unsexed, O'ahu, Ewa Coral Plain, 29.i.1922, emerged 11/12.ii.1922 (Swezey, BPBM) [damaged, without abdomens].

Plutella capparidis Swezey (Maui)

Figs. 4–6, 21, 24, 28, 30, 43, 46

♂, ♀ (Figs. 4–6, 21). 6.0–8.5 mm. Head off-white, vertex with pair of indistinct light to greyish brown longitudinal lines. Area behind compound eye and beneath ocellus black. Labial palpus drooping, segment 2 with forward-directed triangular, dark greyish brown tuft; segment 3 about length of 2, slightly upturned, outer surface grey. Antenna about 2/3 length of forewing; scape with dense pecten, flagellum dorsally off-white, with several dark rings in distal half. Thorax as head; tegula black. Forewing black with off-white to fawn dorsum; demarcation line between both areas irregularly sinuous; dark area with narrow white subcostal streak in basal quarter and large sub-triangular mark at about one-half. Light dorsal band obliquely extended to reach costa subapically; termen between apex and tornus with broad, proximally concave, black mark. Costa never with small black dot in light sub-triangular mark; dorsum with half a dozen similar dots.

GENITALIA ♂ (Figs. 28, 30). As in *capparidis* s. str. (O'ahu).

GENITALIA ♀ (Figs. 43, 46). As in *capparidis* s. str. (O'ahu) but antrum a short sclerotized ring on vestigial substial plate.

REMARKS. *Plutella capparidis* (Maui) closely resembles *P. capparidis* (O'ahu) but differs in the presence of a narrow subcostal streak rather than a large oval patch in the basal quarter of the forewing. The light sub-triangular costal mark always lacks the small black dot that is often present in the O'ahu form. A difference between the 2 forms in the forewing color — the dark pattern of the Maui form is black rather than brown as in the O'ahu form — may be age-related rather than real, as black tends to turn dark brown with time. The male genitalia are indistinguishable from those of the O'ahu form while in the female the antrum is shorter, ring- rather than cup-like, and the substial plate is much reduced.

It might be argued that, in view of constant differences in the forewing pattern and because the 2 occur on different islands, the Maui population should be treated as a separate species. As, however, the male genitalia, which so clearly separate *noholio* and *kahakaha* from *capparidis*, are identical in the O'ahu and Maui populations, we hesitate to accord full species status to the latter without further corroborating evidence such as DNA studies or cross-breeding experiments.

BIOLOGY. Host-plant: *Capparis sandwichiana*. Reared in December 1928 and March 1999. Larva green, feeding on the leaves (Montgomery, pers. comm.).

In 1980 all stages of a *capparidis*-like *Plutella* were observed on a single large *Capparis* plant on NE Kaho'olawe, Hakiowawa, 400 ft, but no voucher specimens were collected. No evidence of *Plutella* was seen on Lāna'i, NE coastal Lae HI, where eight plants were examined (Montgomery, pers. comm.).

MATERIAL EXAMINED (including 4♂, 2♀ genitalia preparations). MAUI: 1♂, West Maui, Lahaina, 23.xii.1928, ex *Capparis* (Swezey, BPBM) [*capparidis*, det. Swezey]; 35♂, 33♀, East Maui, Kanaio to Kinau coast, 10 ft, *Capparis*, 27.iii.1999 (Montgomery, BPBM; 3♂, 3♀, BMNH); 2 unsexed and unsuitable for analysis, East Maui, La Perouse, ex *Capparis*, i.1997 (Starr & Martz, BPBM) [possibly also *capparidis* (Maui) but specimens damaged, forewings rubbed, 1 without abdomen].

Plutella noholio Robinson & Sattler, sp. n. (Hawai'i) Figs. 5, 6, 25, 31, 33, 44, 47–49

♂, ♀ (Figs. 5, 6, 25). 8.5–9.5 mm wingspan. Head off-white, vertex pale greyish brown, area behind compound eye and beneath ocellus black. Labial palpus drooping, segment 2 with forward-directed triangular, dark grey tuft, leading edge white; segment 3 upturned, as long as 2, greyish white. Antenna about two-thirds length of forewing; scape with dense pecten, flagellum dorsally off-white to grey, with several black rings in distal half. Thorax greyish brown, sometimes with thin, indistinct, darker longitudinal line; tegula black. Forewing off-white with light ochreous brown suffusion and contrasting black, sinuous longitudinal band. Latter extended at about 2/3 across plical fold to dorsum. Light subcostal streak open to broadly based costal triangle. Costa and dorsum without small black dots; termen with broad, black-edged, proximally convex brown mark.

GENITALIA ♂ (Figs. 31, 33). Valva long, narrow, broadest in basal third, gently tapered in middle third, distal third with margins sub-parallel, cucullus evenly rounded. Saccus with broad base, abruptly tapered at about 1/3, distal 2/3 narrow, apically rounded. Aedeagus long, thin, medial three-fifths moderately curved. Coremata absent.

GENITALIA ♀ (Figs. 44, 47–49). Apophyses posteriores about twice length of apophyses anteriores. Rod-like part of ventral branch of apophyses anteriores short, imperceptibly changing to narrow, minutely spinose sclerotized band terminating in short transverse arc bearing 4–5 sensilla trichodea. Antrum broad, simple, funnel-shaped, more or less trapezoid in outline.

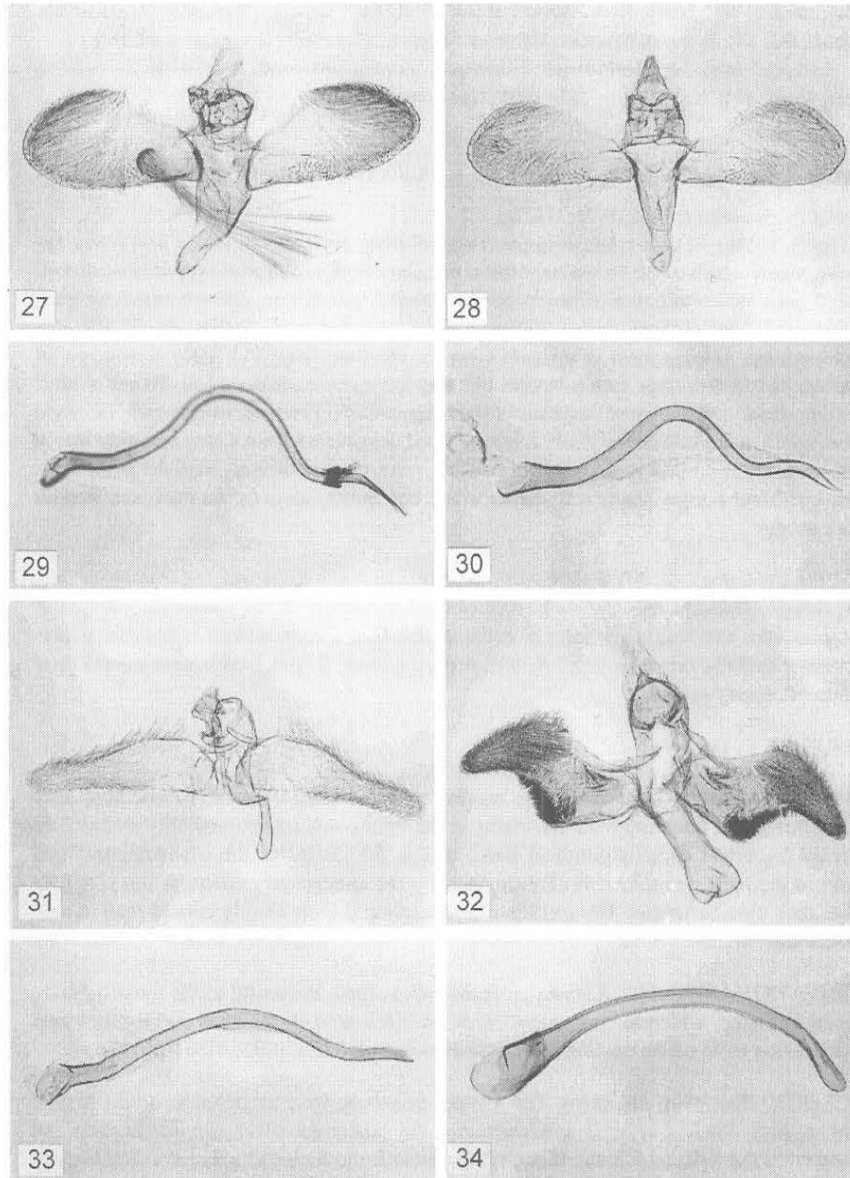
REMARKS. *Plutella noholio* superficially resembles *P. capparidis* but is distinguished in the forewing pattern. The black longitudinal marking usually touches the dorsum at about two-thirds, whereas in *capparidis* it never reaches that far. The subcostal streak at the forewing base, which it shares with *capparidis* from Maui, is always open, whereas in the Maui form it is always isolated from the large sub-triangular costal mark. In the male genitalia *noholio* is easily distinguished from other Hawaiian *Plutella* in the narrow valva, abruptly constricted saccus, weakly sinuous aedeagus and the absence of coremata. Coremata hairs are deciduous and are easily cleared away during dissection; however, the patches of scale sockets are usually preserved and cannot be missed by an observant preparator; none were seen in this instance. The presence or absence of the coremata in closely related and otherwise extremely similar species is not unusual. Examples are found in other Yponomeutoidea, for instance, in some European species of the genus *Kessleria* Nowicki (Yponomeutidae) (Huemer & Tarmann, 1991).

Among the specimens from North Kona Airport Road there is an identically labelled female of an unidentified *Tamsica* Zimmerman, 1958, species (Crambidae: Crambinae). Although the host-plants of *Tamsica* are poorly known, all evidence points to them being grass or grass roots feeders as other Crambinae (Zimmerman, 1958: 346–52); the record of *Capparis* for this specimen is almost certainly an error.

DERIVATION OF NAME. *Noho lio*, Hawaiian, saddle. Referring to the dark forewing marking that touches the dorsum and forms a saddle on the moth in resting posture.

BIOLOGY. Host-plant: *Capparis sandwichiana*. Reared in March 1999. Larva green, feeding on the leaves (Montgomery, pers. comm.).

MATERIAL EXAMINED (including 2♂, 2♀ genitalia preparations). Holotype ♂, HAWAII: North Kona, Keauhou, 300 ft, ex *Capparis*, 25.x.2000 (Montgomery) (genitalia slide no. H.021; BPBM).



Figures 27–34. Male genitalia of endemic Hawaiian *Plutella*: 27, 29, *capparidis*, paralectotype, O‘ahu (slide no. H.014; HDOA); 28, 30, *capparidis*, Maui (slide no. H.015; BPBM); 31, 33, *noholio*, paratype, Hawai‘i (slide no. H.009; BPBM); 32, 34, *kahakaha*, paratype, Kaua‘i (slide no. 29521; BMNH).

Paratypes: 1 ♂, 5 ♀, North Kona, Airport Road, 10 ft, ex *Capparis*, 13.iii.1999 (Montgomery, BPBM); 9 ♂, 8 ♀, N. Kona, Keauhou, 300 ft, ex *Capparis*, 25.x.2000 (Montgomery, BPBM).

Excluded from the type-material: 2 damaged, unsexed specimens, HAWAII: North Kona Airport Road, 10 ft, ex *Capparis*, 13.iii.1999 (Montgomery, BPBM).

Plutella kahakaha Robinson & Sattler, sp. n. (Kaua'i) Figs. 9, 10, 26, 32, 34

Plutella sp.: Howarth & Mull, 1992: 119, fig. 111.

♂ (Figs. 9, 10, 26). 12.0–16.0 mm wingspan. Head off-white, frons slightly darker than vertex, latter with pair of indistinct pale brown longitudinal lines, area behind compound eye and beneath ocellus dark blackish brown. Labial palpus drooping, segment 2 with forward-directed, triangular, greyish brown tuft with light leading edge; segment 3 slightly upturned, greyish white, about length of 2. Ocellus present. Antenna about 2/3 length of forewing, off-white; scape with dense pecten; apex of flagellum dark, 3 dark rings, each composed of 2 flagellar segments, in distal half. Thorax as head, with thin, indistinct pale brown longitudinal line. Tegula black. Forewing whitish grey with light brown suffusion and contrasting blackish brown, broad, longitudinal band. Latter obliquely bent at about 2/3, reaching costa at about 4/5 where distinctly paler. Costa with small black dot at about 3/5; dorsum with half a dozen similar dots; termen with orange brown sub-triangular mark with blackish brown margin.

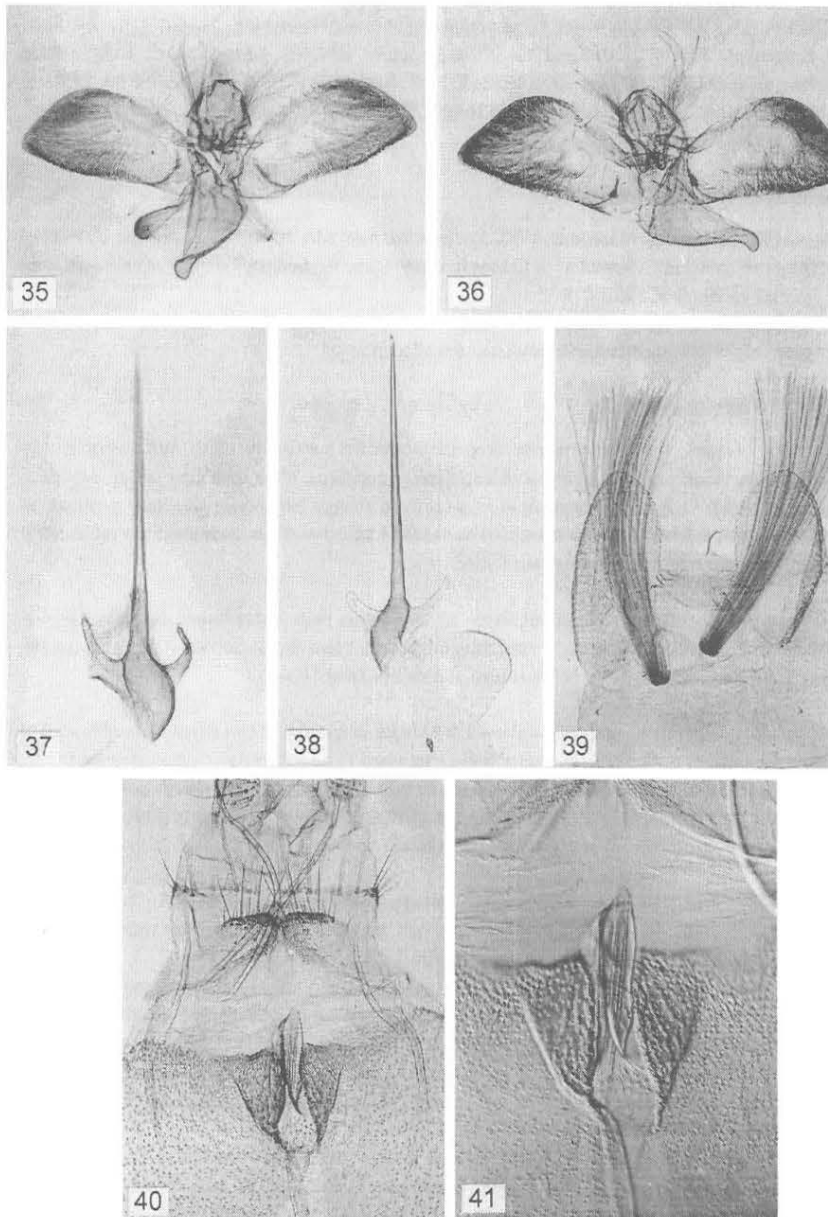
GENITALIA ♂ (Figs. 32, 34). Socii narrow, strongly sclerotized. Valva with angular sacculus and large, broadly beak-like cucullus; distal edge of sacculus densely set with moderately long stiff spines, cucullus with long, dense hair-like scales. Saccus long, almost as broad as tegumen, weakly constricted medially, broadly rounded distally. Aedeagus evenly curved, base slightly inflated apex rounded. Coremata present.

GENITALIA ♀. Unknown.

REMARKS. *Plutella kahakaha* is the biggest of the endemic Hawaiian *Plutella* species and differs in the forewing from the others in the light costa, interrupted only at the distal fifth by the broad dark longitudinal band, and in the distinctly sub-triangular terminal mark. In the male genitalia it is characterized by the angular valva and the sub-scapulate rather than tapered saccus. The aedeagus is stronger and more evenly curved than in *capparis* and *noholio*.

DERIVATION OF NAME. *Kahakaha*, Hawaiian, striped. Referring to the longitudinally striped forewing, which in conjunction with the black area on the head and tegula forms a continuous band on the resting moth (see Howarth & Mull, 1992: 119, fig. 111).

BIOLOGY. Host-plant unknown. The 3 type-specimens were attracted as adults to MV light in June 1982. *Capparis sandwichiana*, the host-plant of *P. capparis*, was not observed in the field by KS and is probably absent from the localities of *P. kahakaha*, all of which are at 1000 m or above. As there is no other endemic species of Capparaceae known from Kaua'i, the potential host-plant should be looked for amongst endemic species of Brassicaceae. We considered as a potential candidate *Lepidium serra* H. Mann which is recorded on Kaua'i as rare in widely scattered localities, where it is found "on rocky ledges and cliffs in mesic forest, (450–) 610–1160 m" (Wagner *et al.*, 1999: 409). However, we have been informed that, according to botanist Ken Wood, that plant may be absent from all 3 collecting sites (Montgomery, pers. comm.).



Figures 35–41. Male and female genitalia of Hawaiian *Plutella xylostella*: 35, 37, race 1, ♂, O'ahu (slide no. H.003; HDOA); 36, 38, race 2, ♂, Hawai'i (slide no. H.018; HDOA); 39, abdominal segment VIII of race 2, ♂, Hawai'i (slide no. H.018; HDOA); 40, 41, race 2, ♀, Hawai'i (slide no. H.020; HDOA).

MATERIAL EXAMINED (including 1 ♂ genitalia preparation). Holotype ♂, KAUA'I: Koke'e State Park, Kahuama'a Flat, 4000 ft, 7.vi.1982 (K. & E. Sattler, BMNH); paratypes, 1 ♂, Koke'e State Park, Awa'awapuhi Trail, 4000 ft, 17.vi.1982 (K. & E. Sattler, BMNH) (genitalia slide no. 29 521), 1 ♂, Na Pali – Kona Forest Reserve, Miloli'i Ridge, 3000 ft, 26.vi.1982 (K. & E. Sattler, BPBM).

Plutella xylostella (Linnaeus)

Phalaena (Tinea) xylostella Linnaeus, 1758, *Systema Naturae*, edn. 10, 1: 538. Lectotype ♂, lacking abdomen, labelled "Xylostella" in Linnaeus's hand (Linnean Society, London) [examined], designated by Bradley, 1966: 219.

Plutella xylostella L.: Zimmerman, 1978: 762–66.

[For synonymy of this species, see checklist (Appendix) below.]

1. Typical *Plutella xylostella*

Figs. 11, 20

♂ ♀. 11.0–17.0 mm. Forewing typically deep purple-brown varying to sandy-buff (especially in examples from desert regions), often speckled in paler specimens, often with grey costal and apical suffusion; dorsum with conspicuous field of whitish to orange-buff scales that may continue as speckles into apical fascia, sinuous margin of dorsal field with 3 scallops such that a dorsal line of 3 pale diamonds is evident when wings are folded.

GENITALIA ♂. Socii terminating in relatively large, elongate pads. Valva broad, simple, ventrodorsally more or less distinctly angled; ventral margin straight, costa evenly curved. Aedeagus straight, sharply pointed, needle-like with bulbous base and pair of lateral hooks.

GENITALIA ♀. Apophyses posteriores about 1.5 × length of apophyses anteriores. Ventral branch of apophyses anteriores weak, lamella postvaginalis composed of paired oval pads, posterior margin set with small number of long sensilla trichodea. Ostium bursae on apex of conspicuous protuberance of posterior margin of abdominal sternite VII, at end of sunken channel between pair of sternal folds. Ductus bursae thin, straight, corpus bursae membranous, without signa.

REMARKS. Chang *et al.* (1997) slightly misquoted Zimmerman (1978), who did not claim that *xylostella* was introduced into Hawai'i about 100 years ago but merely recorded the first specimens to have been observed in 1892.

The origin of the cosmopolitan *P. xylostella* is still unclear. Having examined most of the described *Plutella* s. str. species and a variety of other genera of Plutellidae we are still unable to identify the sister species or any really close relatives because, with specializations in the aedeagus (pair of basal hooks) and the abdominal segment VII of the female (pair of sternal folds), *P. xylostella* stands morphologically quite isolated within its genus as currently defined.

Although a European or Mediterranean origin has been repeatedly suggested for *xylostella* (e.g., Talekar & Shelton, 1993), no reasons for such an assumption have ever been given. It may well have been based on the idea that the present cosmopolitan distribution of *xylostella* is the result of accidental transport with cultivated brassicas as European agriculture spread around the world. More recently, Kfir (1998) has advanced an "out of Africa" hypothesis for *P. xylostella*, suggesting a southern African origin for the species. Evidence adduced for this is, broadly, the diversity of Brassicaceae in southern Africa, the diversity of parasitoids of *P. xylostella* there, coupled with the endemism and

specificity of several of them, and the observation that one apparently host-specific parasitoid, *Diadromus collaris*, reproduces sexually in southern Africa but is thelytokous elsewhere. There are, however, numerous weaknesses in this hypothesis. Host specificity is rarely provable and the 'host-specific' parasitoids of *xylostella* could easily have other hosts among the poorly known Microlepidoptera fauna of southern Africa. The parasitoid loading of *xylostella* in southern Africa is actually less than in Moldavia (compare data in Talekar & Shelton, 1993). Thus, on the subject of the geographical origin of *P. xylostella*, the case is still open. The geographical distribution of *Plutella* is most suggestive of a Holarctic origin for both species-groups of *Plutella* *sensu stricto*.

Studies of the genitalia of *Plutella xylostella* from all parts of the world (including the superficially distinct host-plant races from Hawai'i) have not yet shown evidence that *xylostella* comprises more than one morphologically distinct species.

BIOLOGY. Notorious as a pest of *Brassica* cultivars, *xylostella* has also been recorded from a wide range of other host-plants across the world (Talekar & Shelton, 1993; HOSTS database, BMNH — see Robinson, 1999 and Robinson *et al.*, 2000). Amongst Brassicaceae it is recorded from *Alyssum*, *Arabis*, *Armoracia*, *Barbarea*, *Brassica*, *Bunias*, *Capsella*, *Cardamine*, *Conringia*, *Descurainia*, *Erysimum*, *Hesperis*, *Iberis*, *Isatis*, *Lepidium*, *Lobularia*, *Matthiola*, *Pringlea*, *Raphanus*, *Rorippa*, *Sinapis*, *Sisymbrium* and *Thlaspi*. Host-plant records from other families are practically all uncorroborated by similar observations or by voucher material and most are downright implausible. They are Basellaceae (*Basella*), Caprifoliaceae (*Lonicera*), Chenopodiaceae (*Beta*, *Spinacia*), Compositae (*Galinsoga*), Dipterocarpaceae (*Shorea*), Gramineae (*Saccharum*, *Zea*), Leguminosae (*Arachis*, *Vicia*), Rubiaceae (*Guettarda*), Solanaceae (*Solanum*) and Umbelliferae (*Apium*, *Daucus*). In Hawai'i, however, there is ample evidence that *xylostella* feeds also on *Capparis* (Capparaceae) but the individuals involved differ consistently in external adult features from typical *xylostella* — see below. We can find no records of *xylostella* feeding on *Capparis* elsewhere in the world.

MATERIAL EXAMINED. O*AHU: 10♂, Honolulu, Kaimuki, 50 m, 18, 25.iii., 19.iv.1978, ex *Alyssum* sp. (Uchida, BPBM). HAWAI'I: 1♀, Puna District, Volcano, 3800 ft, 11.vi.1973 (K. & E. Sattler, BMNH); 1♂, 1♀, larvae 31.v. on Chinese cabbage [*Brassica chinensis* L.], pupated 4.vi., em. 11, 12.vi.1976 (K. & E. Sattler, BMNH); 2♂, Volcanoes National Park, Mauna Loa Strip Road, 6600 ft, 8, 10.v.1973 (K. & E. Sattler, BMNH); further specimens from various Hawaiian localities.

OTHER MATERIAL EXAMINED. Approx. 500 exx. from all continents.

DISTRIBUTION. Worldwide in practically all habitats except for extreme arctic and alpine zones and equatorial lowland rainforest.

2. *Plutella xylostella* "ab. *albovenosa* Walsingham"

Fig. 12

Plutella albovenosa Walsingham, 1907: 653, pl. 25, fig. 11. Lectotype ♂, **HAWAI'I**: Kona District, 4000 ft, vii.1892 (*Perkins*) (genitalia slide no. 2150, BMNH) [designated as 'holotype' by Zimmerman, 1978: 763, fig. 508 (top)].

P. albovenosa was described from 4 field-collected adults. When proposing the taxon, Walsingham wondered about its validity as a good species but stated that amongst a long series of extra-Hawaiian *xylostella* he had not noticed any other specimens with similar white veins in the costal area of the forewing. Having ourselves compared numerous *xylostella* from many parts of the world we confirm that the *albovenosa* form appears to be restricted to Hawai'i. Taking into account that the type-specimens come from 2 different islands and that 3 of them were collected at altitudes above the range of *Capparis*, *albovenosa* is almost certainly a rare individual aberration of *xylostella* rather than one of its host-plant races. The type-specimens of *albovenosa*, including the only lowland specimen, the male from Waialua beach, differ superficially from *Capparis*-bred O'ahu specimens including those identified by Bridwell (1920: 316) as *albovenosa*.

MATERIAL EXAMINED (including 1 ♂ genitalia preparation). **HAWAI'I**: lectotype ♂, Kona District, 4000 ft, vii.1892 (*Perkins*) (genitalia slide no. 2150, BMNH) [designated as 'holotype' by Zimmerman, 1978: 763, fig. 508 (top)]. **O'AHU**: paralectotypes, 1 ♂, 1 ♀, Waialua (beach), iii.1892 (*Perkins*) (♂ BPBM; ♀ BMNH); 1 ♂, Wai'anae Mts, Mt Ka'ala, 1000–2000 ft, iii.1892 (*Perkins*, BMNH); other material: 1 ♂, 1 ♀, Honolulu, 12.iii, 21.iii.1917 (*Bridwell*, BPBM).

3. *Plutella xylostella* host-race 1 (O'ahu)

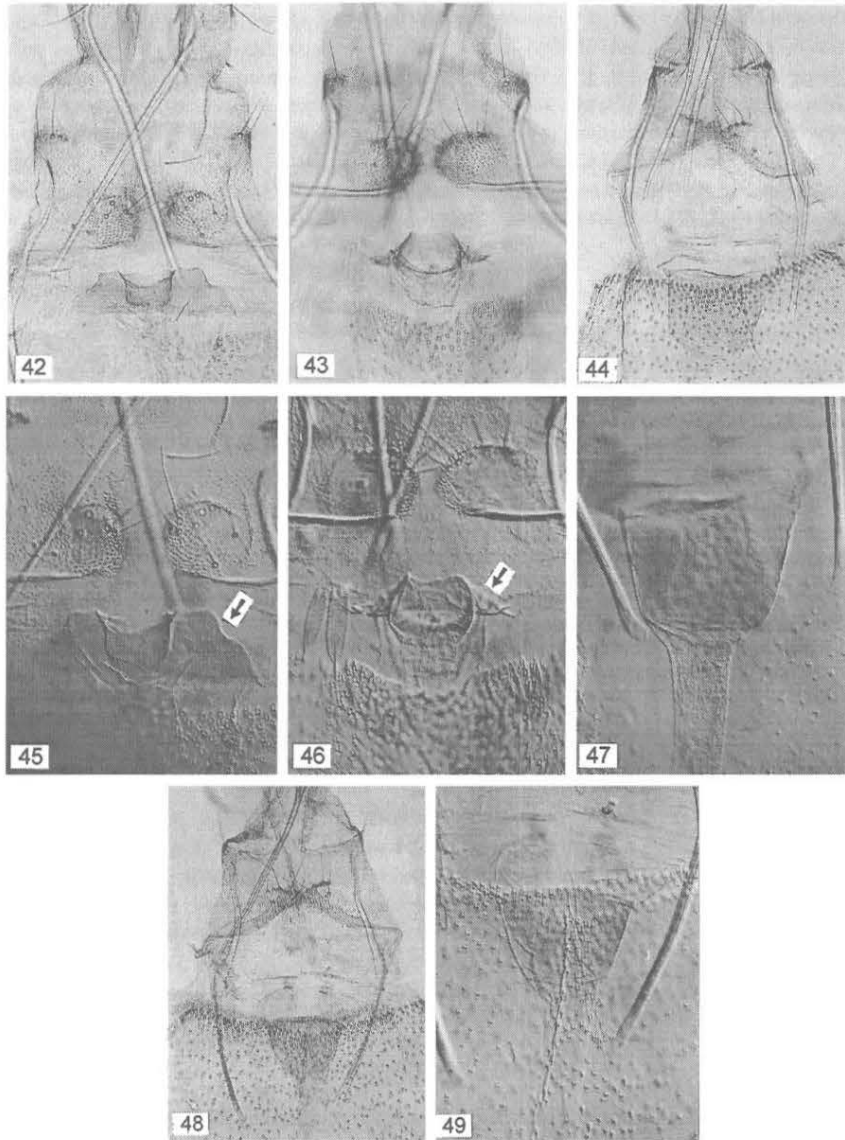
Figs. 13–17, 35, 37

[*Plutella albovenosa* Walsingham: Bridwell, 1920, *Proc. Hawaii. Entomol. Soc.* 4: 316. Misidentification.]

A fairly uniform population of small (8.5–13.0 mm wingspan) brown specimens with forewing pattern of typical *xylostella* faded or at best weakly indicated. Occasionally dorsum light but usually suffused with brown. As far as detail is recorded, the larva of this form feeds predominantly in the fruits, rarely on the leaves of *Capparis* (two specimens are labelled as having been reared from leaf-feeding larvae). It should be noted that the *Capparis* fruit is a berry, although notes (by Bridwell and/or Swezey) associated with specimens in the collection refer to 'pods' or 'seed pods' (see Material Examined). The young larva feeds under the cuticle of the green fruits with the older larva burrowing into the fleshy walls. It should also be noted that some of the specimens are from the type-locality of the leaf-feeding *capparidis*, or very close to it, and it would now be interesting to know whether both species may have co-existed on the same plants.

Montgomery had visited Bridwell's locality Ewa several times in the past without ever encountering *Plutella* adults at MV light or flying at dusk, a time when *P. noholio* and *P. xylostella* race 2 were active and obvious in Kona (Hawai'i). However, on a repeat visit in late December 2000 he found evidence of larval feeding by *Plutella* in green fruits of *Capparis*. About one-third of 24 fruits examined by him had 1–4 holes of 2 mm diameter; 2 green larvae of about 10 mm length later exited and pupated.

MATERIAL EXAMINED (including 2 ♂, 1 ♀ genitalia preparations). **O'AHU**: 15 ♂, 20 ♀, [Honolulu,] Diamond Head, 30.xii.1917 (*Swezey*, HDOA; 1 ♂, BMNH); 6 ♂, 1 ♀, [Honolulu,]



Figures 42–49. Female genitalia of endemic Hawaiian *Plutella*: 42, 45, *capparidis*, paralectotype, O‘ahu (slide no. H.016; HDOA); 43, 46, *capparidis*, Maui (slide no. H.013; BPBM); 44, 47, *noholio*, paratype, Hawai‘i (slide no. H.017; BPBM); 48, 49, *noholio*, paratype, Hawai‘i (slide no. H.012; BPBM).

Diamond Head, 16.iv.1917, ex *Capparis* (Swezey, HDOA) [♀ without abdomen]; 1♂, [Honolulu,] Mānoa, 27.vi.1920 (Swezey, HDOA) [reared]; 1♂, [?] Mokapu, 29.viii.1920, ex *Capparis* pods (Swezey, HDOA); 3♂, 1♀, Ewa Coral Plain, 5.xii.1916 ex *Capparis sandwichiana* seed pods (Bridwell, BPBM) [1♂ genitalia slide no. 109, Busck, 1♂ without abdomen] [misidentified as *Plutella albovenosa* Walsingham] [6 associated pupal cocoons, also identified as 'albovenosa']; 4♂, Ewa Coral Plain, 17.iii.1918, ex *Capparis* pods (collector not recorded, HDOA); 4♂, 1♀, Ewa Coral Plain, vii.1919 [reared but no host recorded] (Bridwell, HDOA) [2♂ without abdomen]; 1♂, Ewa Coral Plain, 29.i.1922, ex *Capparis* (Swezey, HDOA) [without abdomen].

4. *Plutella xylostella* host-race 2 (Hawai'i)

Figs. 18, 19, 36, 38–41

This unusual very pale host-plant race is known only from the island of Hawai'i, where it has been reared from several localities and on several occasions (1919, 1920, 1995, 1996 and 2000) exclusively on *Capparis*. The palest specimens are white to cream with faded yellow markings primarily along dorsum and termen; the costal 1/3–1/2 of the wing is unmarked. The hind wings are greyish brown, distinctly darker than the forewings. This is the form referred to as "undescribed *Plutella* species A" (UPA) by Chang *et al.* (1997). It was locally referred to as "Napoopoo" because it matches a series of specimens from Nāpō'opo'o, a locality in the South Kona District of Hawai'i (Kumashiro, pers. comm.). A second, slightly darker form with slightly more distinct sinuous plical markings, "undescribed *Plutella* species B" (Chang *et al.*, 1997), was referred to as "Kaloko" because it was collected at Kaloko, near Kailua-Kona (Kumashiro, pers. comm.). But the identity of this taxon is uncertain; see Material and Methods.

Typical *xylostella* is also present on Hawai'i, where it has been reared from Chinese cabbage (KS); it was also caught in the wild amongst predominantly native vegetation at an altitude of 6600 feet in Volcanoes National Park (KS) (see above).

MATERIAL EXAMINED (including 3♂, 5♀ genitalia preparations). HAWAII: 3♂, 5♀, [S. Kona District] Nāpō'opo'o, 9.viii.1919, ex *Capparis* (Swezey, HDOA) [♀ without abdomen; 1♂ slide no. Z-70-20.]; 5♂, 1♀, [North Kona District] Kailua, 4.vi.1922 (Swezey, HDOA) [reared specimens, all with associated pupal cases, but no host recorded; 1♀ without abdomen]; 3♂, Kona, 28.ix.1995, ex *Capparis sandwichiana* (Matayoshi, HDOA) [1♂ without abdomen.] (UPA); 1♂, 1♀, 1 unsexed, Kona, 20.iii.1996, ex roadside *Capparis sandwichiana* 'pilo' (Matayoshi, HDOA) (1996-085) (?UPB) [specimens mostly unspread, poorly collected; unsexed specimen comprises head, thorax and left-hand forewing only and lacks right-hand wings]; 3♂, 3♀, N. Kona, Keauhou, 300 ft, ex *Capparis*, 25.x.2000 (Montgomery) (BPBM; 1♂, BMNH).

DISCUSSION

The genus *Plutella* is represented in the Hawaiian Islands by a small complex of endemic species (*capparidis*-subgroup), the cosmopolitan *P. xylostella* and at least 2 host-plant races of the latter.

The *capparidis*-subgroup is recorded from the islands of Kaua'i (*P. kahakaha*, sp. n.), O'ahu (*P. capparidis* Swezey), Maui (*P. capparidis* Swezey form), Kaho'olawe (*P. capparidis* form?) and Hawai'i (*P. noholio*, sp. n.). No evidence of *Plutella* was found on Lanai (Montgomery, pers. comm.) whilst Moloka'i remains to be sampled. The O'ahu population of *P. capparidis* is now probably extinct and the other lowland species must be considered as vulnerable due to the paucity of host-plants, small size of populations, pre-

TABLE 1: Characters supporting tentative cladogram of relationships of *Plutella* (Fig. 50); apomorphic states precede plesiomorphic states; character 7 occurs twice as a parallelism.

1.	Hind wing M1 and M2 stalked / M1 and M2 free
2.	Wing apex with dark termen / termen no darker than remainder of wing
3.	Base of aedeagus with pair of lateral hooks / aedeagus without basal hooks
4.	Abdominal sternites melanized / sternites not melanized
5.	Bulbus ejaculatorius helical / bulbus ejaculatorius simple
6.	Forewing pattern of discrete dark blotches / forewing pattern gradational
7.	Hostplant Capparaceae / hostplant Brassicaceae
8.	Forewing dorsum fascia blurred into remainder of wing / dorsum fascia clearly demarcated
9.	Aedeagus sinuate / aedeagus evenly curved
10.	Coremata absent / coremata present
11.	Aedeagus strongly sinuate / aedeagus weakly sinuate
12.	Valva strongly elongated / valva broadly rounded
13.	Antrum with substial plate / antrum without substial plate
14.	Substial plate large / substial plate small

dation by non-native species of ants (Montgomery, pers. comm.) and non-native parasitoid wasps. The taxonomic status of *capparidis* (Maui) is uncertain; there are slight but apparently consistent differences in the forewing pattern and in the female genitalia although the male genitalia do not differ from those of typical *capparidis* from O'ahu. *Plutella kahakaha* sp. n. differs more strongly from the rest of the *capparidis*-subgroup in the larger size and the male genitalia (female as yet unknown). It is also likely to have a different host-plant because *Capparis* is absent at higher altitudes where *kahakaha* was collected. Should the as yet unknown host-plant turn out to be the endemic *Lepidium serra* H. Mann (Brassicaceae), as we consider possible, *kahakaha* might be closer to the ancestral immigrant than the rest of the subgroup which underwent a shift of host-plant from Brassicaceae to Capparaceae.

The sister-group of the *capparidis*-subgroup is uncertain. There are 3 contenders from within *Plutella* sensu stricto — the monophyletic *geniatella*-group, *Plutella porrectella* and *P. xylostella*. The *geniatella*-group (see checklist, below) is characterized by strong melanization of the abdominal sternites, the male genitalia have short sub-quadrate valvae and a short, tapered aedeagus with a strongly contorted, helical bulbous ejaculatorius. None of these apparently derived features is shared with the *capparidis*-subgroup. *Plutella porrectella* shares with the *capparidis*-subgroup the feature of a dark terminal forewing fascia; the valva tapers apically to form a defined process and as such is reminiscent of that of *P. kahakaha*. In all other *Plutella* and in *Leuoperla* and *Rhigognostis* the "diamond-back" pattern is expressed to a greater or lesser extent but there is no dark apical mark and neither is an apical process developed on the valva. We can find no derived features to link the morphologically isolated *xylostella* with any other group within *Plutella* s.s. (see checklist below).

The suggested relationships of the Hawaiian *Plutella* may be expressed in a tentative cladogram (Fig. 50) supported by the characters listed in Table 1. This hypothesis of rela-

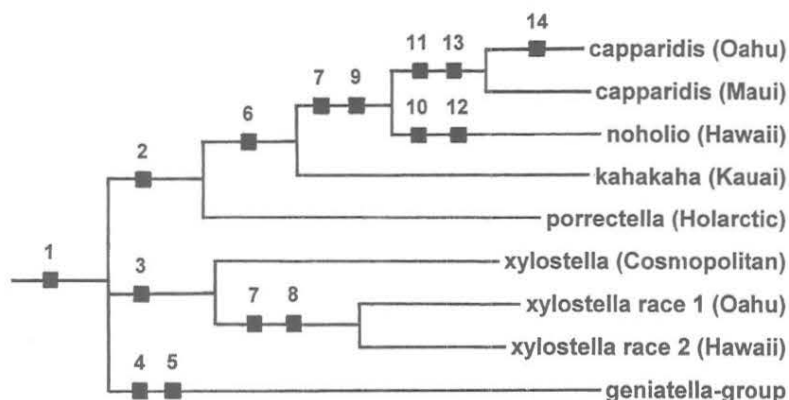


Figure 50. Tentative cladogram of relationships of Hawaiian *Plutella* and related taxa; numbers refer to apomorphic states of characters (see text and Table 1).

tionship requires much more rigorous testing using other character systems including molecular data.

Plutella xylostella (L.) was first collected in Hawai'i in 1892 (Walsingham, 1907: 652) but may have become established there earlier, soon after the arrival of European agriculture and cultivated brassicas. It is now a pest of cultivated Brassicaceae but is sometimes also found in areas with predominantly native vegetation.

On the islands of Kaua'i¹, O'ahu, and Hawai'i there exist several forms indistinguishable from *P. xylostella* in the male and female genitalia but differing in the forewing color and markings. Their larvae feed exclusively on the endemic *Capparis sandwichiana* but those of the O'ahu form (*P. xylostella* host-race 1) seem to prefer, in contrast to those of the *capparidis*-subgroup, the fruits rather than the leaves. However, the sparse observations on the Hawai'i form (*P. xylostella* host-race 2) suggest that its larvae feed on the leaves and co-exist with those of *P. noholio*. Regrettably, such detail is rarely, if ever, recorded on the specimen labels. We assume that these populations represent local host-plant races as a result of 1 (or 2) independent natural, pre-European and possibly pre-Polynesian, immigrations in conjunction with a host-plant shift from Brassicaceae to Capparaceae followed by modest evolution of the forewing pattern.

In their study of mitochondrial DNA sequence variation in the diamondback moth, Chang et al. also investigated 2 of these races (UPA, (Nāpō'opo'o) and UPB (Kaloko)) from the island of Hawai'i, finding that sequence variation in cytochrome oxidase I (COI) between them and typical *xylostella* was substantially greater (5% and 10% respectively) than between *xylostella* populations from Hawai'i, the Philippines and Pennsylvania (< 1%). It should be noted that the identity of UPB (Kaloko) is uncertain (see Material and Methods). The preservation in future of well-prepared and accurately labelled voucher material from all molecular, biological and other studies is of vital importance.

1. While this paper was in press, Montgomery informed us that he had reared 5 adults of a *Capparis*-feeding host-race of *Plutella xylostella* from Polihale, Kaua'i.

A parallel example of rapidly evolving host-plant forms in Hawai'i is found in the genus *Omiodes* Guenée (Pyrallidae: Pyraustinae). Five closely related taxa, which are currently recognized as separate species, are believed to have evolved from a common palm-feeding ancestor since bananas were first introduced into Hawai'i about 1000 years ago by Polynesian immigrants (Zimmerman, 1958: 67; as *Hedylepta* Lederer; Zimmerman, 1960).

If at all possible, laboratory cultures of the endangered *Plutella xylostella* host-races 1 (O'ahu) and 2 (Hawai'i) should be established before they become extinct. In view of the uniqueness of the *Capparis*-feeding races, experimental rearing of typical *xylostella* on *Capparis* would also be of considerable interest, as would the converse – rearing of *Capparis* host-races on *Brassica*.

ACKNOWLEDGMENTS

We thank Scott Miller (USNM, Washington) and Neal Evenhuis (BPBM, Honolulu) for first suggesting this project to us. Bernarr Kumashiro (HDOA, Honolulu) and Neal Evenhuis made painstaking searches of the collections in their care and provided loans and documentation. Special thanks go to Steve Montgomery (BPBM Research Associate, Honolulu) for his crucial recent collecting and rearing of *Capparis*-feeding *Plutella*. Mikhail Kozlov (University of Turku, Finland) drew to our attention the true identity of *Plutella continentalis* Zagulajev. Campbell Smith (BMNH) provided invaluable assistance in teaching us to drive the *Synoptics* system and advised on digital processing of images. Peter York (BMNH) was responsible for the genitalia photographs. This project was funded in part by BPBM and the USFWS in partial fulfillment of USFWS Agreement 14481220097J155. We thank Malcom Scoble, Frank Howarth and Steve Montgomery for critical review of the manuscript.

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APPENDIX: Checklist of world Plutellidae *sensu stricto*

<i>EIDOPHASIA</i> Stephens, 1842	
= <i>PARASEMIA</i> Stephens, 1841	
= <i>SPANIA</i> Guenée, 1845	
= <i>HUFNAGELIA</i> Reutti, 1853	
= <i>EUODOPHASIA</i> Herrich-Schäffer, 1853	
<i>messingiella</i> (Fischer von Röslerstamm, 1840) (<i>Plutella</i>)	Europe
<i>transversella</i> (Stephens, 1841) (<i>Parasemia</i>)	Britain
<i>infuscata</i> Staudinger, 1870 (<i>Eidophasia</i>)	Greece
addenda Doets, 1950 (<i>Eidophasia</i>); infrasubsp.	Netherlands
triangulella Schille, 1905 (<i>Eidophasia</i>); infrasubsp.	Poland
dorsana Caradja, 1920 (<i>Eidophasia</i>); infrasubsp.	Germany
dorsomaculata Doets, 1950 (<i>Eidophasia</i>); infrasubsp.	Netherlands
interrupta Doets, 1950 (<i>Eidophasia</i>); infrasubsp.	Netherlands
reducta Doets, 1950 (<i>Eidophasia</i>); infrasubsp.	Netherlands
<i>aereoella</i> Lhomme, 1949 (<i>Eidophasia</i>)	France
<i>syenitella</i> Herrich-Schäffer, 1854 (<i>Eudophasia</i> [sic])	Europe
<i>concinella</i> Christoph, 1888 (<i>Eidophasia</i>)	Caucasus: Borshom
<i>zukowskyi</i> Amsel, 1939 (<i>Eidophasia</i>)	Greece
<i>tauricella</i> Staudinger, 1880 (<i>Eidophasia</i>)	Turkey
<i>albifasciata</i> Issiki, 1930 (<i>Eidophasia</i>)	Japan
<i>dammersi</i> (Busck, 1934) (<i>Plutella</i>)	USA: California
<i>albidorsella</i> (Walsingham, 1881) (<i>Plutella</i>), comb. n.	USA: California
<i>vanella</i> (Walsingham, 1881) (<i>Plutella</i>), comb. n.	USA: California
<i>hufnagelii</i> (Zeller, 1839) (<i>Plutella</i>)	Europe
<i>insulella</i> (Walsingham, 1900) (<i>Caunaca</i>)	Corsica
<i>peristigma</i> Diakonoff, 1955 (<i>Eidophasia</i>)	New Guinea
<i>LUNAKIA</i> Klimesch, 1941	
<i>alyssella</i> Klimesch, 1941 (<i>Lunakia</i>)	Austria
<i>PLUTELLA</i> Schrank, 1802	
= <i>ANADETIA</i> Hübner, [1825]	
= <i>EUOTA</i> Hübner, [1825]	
= <i>CREAGRIA</i> Sodoffsky, 1837	
[Group 1 – <i>geniatella</i> -group]	
<i>notabilis</i> Busck, 1904 (<i>Plutella</i>)	USA: Washington
<i>omissa</i> Walsingham, 1889 (<i>Plutella</i>)	USA: California
<i>armoraciae</i> Busck, 1913 (<i>Plutella</i>)	USA: Colorado
<i>monochlora</i> Meyrick, 1914 (<i>Plutella</i>)	USA: Colorado
<i>geniatella</i> Zeller, 1839 (<i>Plutella</i>)	Switzerland
<i>polaris</i> Zeller, 1880 (<i>Plutella</i>)	Norway: Spitzbergen
<i>hyperboreella</i> Strand, 1902 (<i>Plutella</i>), syn. n.	Finland
<i>haasi</i> Staudinger, 1883 (<i>Plutella</i>)	Norway
<i>mariae</i> Rebel, 1923 (<i>Plutella</i>)	Russia

[Group 2 – *xylostella*-group]

<i>porrectella</i> Linnaeus, 1758 (<i>Phalaena</i>)	Europe
<i>hesperidella</i> (Hübner, 1796) (<i>Tinea</i>)	Europe
<i>vigilaciella</i> Clemens, 1860 (<i>Plutella</i>)	USA: Pennsylvania
<i>capparidis</i> Swezey, 1920 (<i>Plutella</i>)	USA: Hawai'i (O'ahu)
<i>noholio</i> Robinson & Sattler, sp. n.	USA: Hawai'i (Hawai'i)
<i>kahakaha</i> Robinson & Sattler, sp. n.	USA: Hawai'i (Kaua'i)
<i>xylostella</i> (Linnaeus, 1758) (<i>Phalaena</i>)	Europe
<i>cinerea</i> (Geoffroy, 1785) (<i>Tinea</i>)	Europe
<i>maculipennis</i> (Curtis, 1832) (<i>Cerostoma</i>)	Britain
<i>cruciferarum</i> Zeller, 1843 (<i>Plutella</i>)	Germany
<i>brassicella</i> Fitch, 1856 (<i>Plutella</i>)	USA: New York
<i>limbipennella</i> Clemens, 1860 (<i>Plutella</i>)	USA: Pennsylvania
<i>mollipedella</i> Clemens, 1860 (<i>Plutella</i>)	USA: Pennsylvania
<i>cicerella</i> (Rondani, 1876) (<i>Gelechia</i>)	Italy
<i>dubiosella</i> (Beutenmüller, 1889) (<i>Cerostoma</i>)	USA: Alaska
<i>albovenosa</i> Walsingham, 1907 (<i>Plutella</i>)	Hawai'i
<i>butalidella</i> Turati, 1926 (<i>Plutella</i>), syn. n.	Libya
<i>megapterella</i> Bentinck, 1934 (<i>Plutella</i>)	Netherlands
<i>continentalis</i> Zagulajev, 1981 (<i>Plutella</i>), syn. n.	USSR

PLUTELLA sensu lato

[Neotropical]

<i>acrodelta</i> Meyrick, 1931 (<i>Plutella</i>)	Argentina
<i>deltodoma</i> Meyrick, 1931 (<i>Plutella</i>)	Chile
<i>diluta</i> Meyrick, 1931 (<i>Plutella</i>)	Chile
<i>nephelaegis</i> Meyrick, 1931 (<i>Plutella</i>)	Argentina
<i>rectivittella</i> Zeller, 1877 (<i>Plutella</i>)	Colombia

[New Zealand]

<i>antiphona</i> Meyrick, 1901 (<i>Plutella</i>)	New Zealand
<i>psammochroa</i> Meyrick, 1886 (<i>Plutella</i>)	New Zealand

[Incertae sedis]

<i>balanopsis</i> Meyrick, 1909 (<i>Plutella</i>)	South Africa
<i>canaella</i> (Costa, 1836) (<i>Tinea</i>)	Italy
<i>formicatella</i> Legrand, 1965 (<i>Plutella</i>)	Seychelles

LEUOPERNA Clarke, 1965

<i>sera</i> (Meyrick, 1886) (<i>Plutella</i>)	New Zealand
<i>leioptera</i> Clarke, 1965 (<i>Leuoperna</i>)	Juan Fernandez Is.

RHIGOGNOSTIS Zeller, 1857

= <i>CAUNACA</i> Wallengren, 1880	
= <i>EUMACHAERISTIS</i> Meyrick, 1938	
= <i>SUBEIDOPHASIA</i> Weber, 1938; unavailable	
= <i>SUBEIDOPHASIA</i> Moriuti, 1977	
<i>annulatella</i> (Curtis, 1832) (<i>Cerostoma</i>)	Europe
<i>bicungulata</i> (Zeller, 1839) (<i>Plutella</i>)	Germany/Poland

<i>erysiphaea</i> (Meyrick, 1938) (<i>Plutella</i>), comb. n.	China: Yunnan
<i>senilella</i> (Zetterstedt, 1839) (<i>Plutella</i>)	Greenland
<i>dalella</i> (Stainton, 1849) (<i>Plutella</i>)	Britain
<i>marmorosella</i> (Wocke, 1850) (<i>Plutella</i>)	Poland: Silesia
<i>septentrionum</i> (Zeller in Staudinger, 1857) (<i>Plutella</i>)	Iceland
<i>incarnatella</i> (Steudel, 1873) (<i>Plutella</i>)	Europe
<i>wolfschlaegeri</i> (Rebel, 1940) (<i>Cerostoma</i>)	Greece
<i>sibirica</i> Kyrki, 1989 (<i>Rhigognostis</i>)	Russia: Siberia
<i>japonica</i> (Moriuti, 1977) (<i>Caunaca</i>)	Japan
<i>interrupta</i> (Walsingham, 1881) (<i>Plutella</i>)	USA: Oregon
<i>poulella</i> (Busck, 1904) (<i>Plutella</i>)	Canada: British Columbia
<i>schmaltzella</i> (Zetterstedt, 1839) (<i>Plutella</i>)	Sweden
<i>immaculicornella</i> (Guenée, 1845) (<i>Plutella</i>)	Finland
<i>horticola</i> (Tengström, 1847) (<i>Plutella</i>)	Finland
<i>norvegicella</i> (Strand, 1920) (<i>Plutella</i>)	Norway
<i>incarnatella</i> (Steudel, 1873) (<i>Plutella</i>)	Europe
<i>kuusamoensis</i> (Kyrki, 1989) (<i>Plutella</i>)	Finland
<i>kovacsi</i> (Gozmány, 1952) (<i>Subeidophasia</i>)	Hungary
<i>viatica</i> (Durrant, 1906) (<i>Plutella</i>)	Tibet
<i>taenias</i> (Meyrick, 1938) (<i>Eumachaeristis</i>)	China: Yunnan
<i>dryoxyla</i> (Meyrick, 1932) (<i>Plutella</i>), comb. n.	Abyssinia
<i>stichocentra</i> (Meyrick, 1932) (<i>Plutella</i>), comb. n.	Abyssinia
<i>symmorpha</i> (Bradley, 1965) (<i>Plutella</i>), comb. n.	Uganda
<i>orosema</i> (Meyrick, 1932) (<i>Plutella</i>), comb. n.	Uganda
<i>orosoma</i> ; Bradley, 1965, misspelling	
<i>oxylopha</i> (Meyrick, 1932) (<i>Plutella</i>), comb. n.	Abyssinia
<i>fornicata</i> (Meyrick, 1920) (<i>Genostele</i>), comb. n.	Malawi
<i>culminata</i> (Meyrick, 1931) (<i>Plutella</i>), comb. n.	Argentina

Species transferred from Plutellidae to Ypsolophidae:

<i>YPSOLOPHA</i> Latreille, [1796]	
<i>bigraphella</i> (Turati, 1929) (<i>Plutella</i>), comb. n.	Libya

