Re-evaluation of *Manduca blackburni* (Lepidoptera: Sphingidae)¹

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ABSTRACT

It is shown that Manduca blackburni is a species in its own right as originally described by Butler. It is related to M. quinquemaculata as well as M. sexta, a fact which escaped workers after Kirby (1892).

History of the species, Manduca blackburni (Butler): The first specimens were collected by the Rev. T. Blackburn on Oahu, near Honolulu, before 1880 (exact data as to place and date of capture unknown). The female type is in the British Museum (Nat. Hist.) and the remaining specimens, 2 males and 5 females, in the South Australian Museum, Adelaide, S.A. Recently one of these females was donated by the said Museum to Bishop Museum. Butler described the species in 1880, and, except for the mention in Kirby's catalogue (1892), it was not mentioned again until Meyrick, 1899.

Unfortunately Meyrick synonymized the species to "Sphinx celeus Hübner" = Manduca quinquemaculata (Haworth) without saying why. From his remark "widely distributed in America" can be deducted that he thought the Hawaiian entity was specifically the same as the well known continental one. He also saw only one specimen and therefore was not able to make observations on a series of specimens. The following taxonomic development resulted from this mistake.

In 1905 van Dine published his paper "The Tobacco Hornworm" in Bulletin #10 of the Hawaii Agricultural Experiment Station: Insect enemies of tobacco in Hawaii. He takes reference to Meyrick, illustrates with a very superficial drawing of the continental *M. quiquemaculata* as if this was without any doubt the same insect as the Hawaiian indigenous one. Would he have taken under consideration the widely used vernacular name he would not have mixed up a "Tobacco Worm" with a "Tomato Worm." As the "Tobacco Worm" is and always was used for *M. sexta* he probably would have had second thoughts about Meyrick's synonymization. Forbes (1923) rightly points out that the injurious limit of *M. sexta* and the commercial limit of tobacco nearly coincide.

Rothschild & Jordan (1903) also contribute to the accumulation of mistakes in their compendium of the Sphingidae of the world. They list the Hawaiian insect as a "subspecies," as was the widely followed use in those days with many not thoroughly researched species, of *M. quinquemaculata*. Their notes that *blackburni* was "not different in structure from the Nearctic form" and that the larva "described by Blackburn... agrees apparently perfectly with the Nearctic larva" shows just this missing research or missing material or both, because it is not so.

After 1905 mentioning of the species becomes more frequent in the Proceedings of the Hawaiian Entomological Society. It is mostly O.H. Swezey who reports

¹This paper is second in a series dealing with Sphingidae of the Hawaiian Islands. The first concerning the genus *Agrius* in the Pacific region was published in Intern. Jour. Entomol. 26,4:339-350.

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almost every adult and larva which were collected. In 1924 he calls the insect "The Tomato Hawk-Moth," otherwise uses the Rothschild & Jordan subspecific name and in 1931 finally calls it the "Hawaiian tobacco worm." As far as we were able to ascertain there are 10 notes in the Proceedings between 1923 and 1940. After this date nothing was reported further. However, there are a few specimens, reared or captured at light in collections after this year. The last known specimen was taken in 1975 on the island of Maui by Mr. Shishido and is in a "student collection" at the University of Hawaii at Manoa.

Since then we at Bishop Museum were trying to relocate the species without success for many years, notwithstanding the fact that the most reported foodplant of the larva, Nicotiana glauca, is still abundant in many places. Only very recently, Mrs. B. Gagné, field associate in Botany of Bishop Museum, reasoned that perhaps, M. blackburni being a native Hawaiian insect would be found on a native Hawaiian member of the Solanaceae. A native Hawaiian plant of this family is Nothocestrum, described in 1862 by Asa Gray. Working on a project in Maui she began to inspect plants of this tree genus and, one might say "of course," found a larva of our Manduca on N. latifolium Gray. On 14 September 1984 she had gone out to photograph N. latifolium in bloom and when lining up the flowers she was surprised to see right there a mature larva of Manduca which was photographed and is illustrated here (Fig. 1).

Not only this, she found still another larva high up in the tree with the purplish tint of near-to-pupating-larvae. Very probably there had been an entire colony of these larvae on this tree. On 26 September the collected larva pupated and on 26 October a female moth emerged. This compares favorably with 56 days of larval life from egg-hatching to adult (Williams, 1946). Nothocestrum is not too common and it may be that in times of higher population density Manduca then has the ability to freely choose other Solanaceae. The apparent rarity of our native Manduca may have been caused by the introduced egg-parasite Trichogramma (Williams, 1946). In 1985 Mrs. Gagné found on the same Nothocestrum tree again a Manduca larva on 20 December. The larva was ready to pupate but, taken home, was not able to produce the pupa. The mummified larva is in the collection of the Bishop Museum.

Zimmerman (1958) mistakenly listed 2 "subspecies" of "Phlegethontius" from the very same locality, namely quinquemaculata quinquemaculata and quiqquemaculata blackburni. About the first he says: "First reported from Hawaii by Meyrick (1899:193)." However, Meyrick did not do this but he synonymized Butler's blackburni to quinquemaculata, and this is something very other than to say that quinquemaculata (Haworth) was reported. Zimmerman also says that he has no records available at this writing, i.e. for quinquemaculata (Haworth). Of course not, because this species has never been captured on any of the Hawaiian Islands...

Zimmerman also mistakenly calls both "subspecies" "tomato (or tobacco) hornworm"; either they are one or the other, they cannot be both; and the Hawaiian species is evidently a "tobacco hornworm" while the continental quinquemaculata may be called rightly a "tomato hornworm."

Research into physiological and other properties of larvae and adults of the species involved in the problem would have easily shown that one has here indeed three related species of *Manduca: sexta* — feeding predominantly on tobacco, *blackburni* — feeding predominantly on tobacco and *quinquemaculata* — feeding predominantly on tomato. Nobody ever did this research, also Rothschild & Jordan were, as we saw, content with superficial statements. Therefore the following necessary data are now here presented.



FIGURE 1. Manduca blackburni larva, discovered 14 September 1984 by B. Gagné at SW slope of Haleakala, Maui, on Nathocestrum, photo Yvonne N.L.H. Ching-Paulson. First alive photographed larva ever. Enlarged 2 ×.

Manduca blackburni (Butler)

Protoparce blackburni Butler, 1880:6.

Phlegethontius blackburni Kirby, 1892:688.

Sphinx celeus Meyrick, 1899:193

Protoparce quinquemaculata blackburni Rothschild & Jordan, 1903:72; Wagner, 1913:36; Draudt, 1931:848.

Phlegethontius quinquemaculatus blackburni Zimmerman, 1958:442

ADULT (Figs. 2-5). Forewings: Outer margin straight (in quinquemaculata (Fig. 6) and sexta (Fig. 7) slightly convex); basic color grayish brown; light markings more or less white; 2 coherent arched double postmedial bands; the inner one

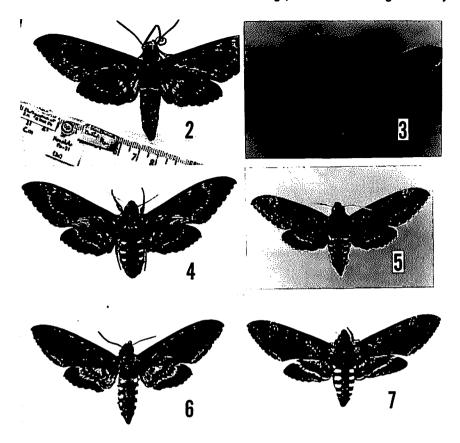


FIGURE 2. Manduca blackburni Q type, Honolulu, Oahu, before 1880, in BM.

FIGURE 3. Manduca blackburni & Spreckelsville, Maui, 6.IV.1928, Agr. HNL.

FIGURE 4. Manduca blackburni Q Spreckelsvill, Maui, 8.XII.1922, BPBM.

FIGURE 5. Manduca blackburni Q Makua, Oahu, 29.III.1931, Agr. HNL.

FIGURE 6. Manduca quinquemaculata Q Williamsport, Lycoming Co., PA, 9.IV.1927, BPBM.

FIGURE 7. Manduca sexta Q New York City, NY, 10.IX.1979, BPBM.

confluent, black edged, lunated white markings (in quinquemaculata and sexta no such; in the former interiorly of inner line only some grayish markings; in the latter interior line very weak); no white subterminal line as in quinquemaculata and sexta; instead a weak broken black line; fringes pure white and brown interchanging, very conspicuous as in sexta (in quinquemaculata brownish white interchanging with light brown); antemedial dark lines well perceptible, regularly oblique from inner to costal margin as in sexta, just touching white discal spot (in quinquemaculata these lines more parallel to outer margin, fading out before reaching discal cell). Hindwings: Basal blackish area; subbasal black band; 2 clear weavy black medial lines (in

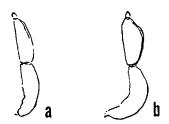


FIGURE 8. a, labial palpus of M. blackburni; b, of M. quinquemaculata.

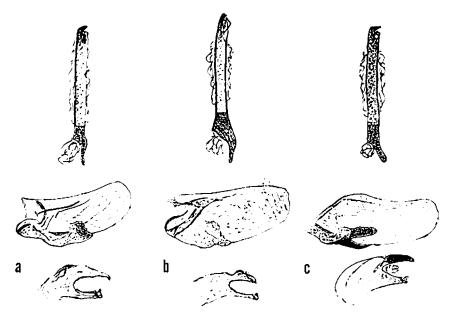


FIGURE 9. a, male genitalia of *M. blackburni*, right valve, aedoeagus, gnathos-uncus structure; spm. Sprecklsville, Maui, 8.XII.1922, gen. prep. 9-013 BPBM; b, same of *M. quinquemaculata*; spm. Chaffeys Locks, ONT, 1.VII.1964, gen. prep. 9-013 BPBM; c, same of *M. sexta*; spm. Ardmore, PA, VIII.1946, gen. prep. 9-155 BPBM.

quinquemaculata same; in sexta fused into one broader band); broad blackish postmarginal band, twice its width at costal margin (in quinquemaculata blackish brown, not much expanding, narrow; in sexta with the already mentioned black band in it and a very thin white line at margin). Body: Ventrally: grayish white with one to three black spots along the middle; dorsally: thorax light gray with a black band caudad, tegulae gray with black center-line; dorsum brownish-grayish with thin black medium line, laterally with five black (white bordered laterally) and five orange spots which decrease in size quite suddenly caudad (especially in the female), and more than even in sexta, towards anal extremity, the last spot being ¼ the size of that in quinquemaculata. Length of wing: male 50 mm; female 58 mm (quinquemaculata: male 46-50 mm; female 53-56 mm; sexta male 48 mm; female 54 mm). Labial palpi (Fig. 8): first and second segments of even width; the first only slightly

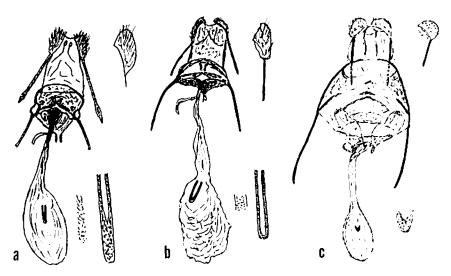


FIGURE 10. a, female genitalia of *M. blackburni*, entire line drawing, ovipositor lateral, signum bursae; spm. Spreckelsville, Maui, 17.VIII.1929, gen. prep. 9-160 BPBM; b, same of *M. quinque-maculata*; spm. Bowling Green, OH, gen. prep. 9-159 BPBM; c, same of *M. sexta*; spm. New York City, NY, 10.ix.1979, gen. prep. 9-167 BPBM.

curbed; the second straight (in quinquemaculata: segments not of even width; the first strongly curbed; the second much wider than the first). Abdominal spiny bands: the spines are short in both, quinquemaculata and blackburni, but in the latter somewhat more slender and longer. Genitalia: male (Fig. 9a-c): Valve of even width and curvature on both sides; process of sacculus narrow of 2 somewhat separated parts: aedoeagus straight, proximal end sigmoidally bent: gnathos-uncus structure wide, gnathos one half longer than uncus, gnathos dorsally slightly triangularly bent (in quinquemaculata (Fig. 9b) valve same; process of sacculus wide, not separated in 2 parts; aedoeagus straight, proximal end only slightly rounded; gnathus-uncus structure narrow, gnathos and uncus of equal length, gnathos dorsally straight with an invagination; in sexta by all similarity in pattern of wings and body the genitalia point for this species to another group of the genus, as Fig. 9c shows). Genitalia: female (Fig. 10a-c): The differences between quinquemaculata (Fig. 10b) and blackburni (Fig. 10a) are easily found in the antrum, the ovipositor valves, the form of the bursa copulatrix and the signum. The latter is in blackburni partially fused, in quinquemaculata wide open, and the granulation is different. The genitalia of the female of sexta (Fig. 10c) relate this species, as did the male genitalia, into another group of the genus.

EGG. Not yet described and not available for this study.

LARVA. This was described by Blackburn himself and his description is published by Butler (1881). This description was compared with 3 inflated larvae in the collection of Agr. HNL and found to be accurate. Color greenish, ashy green or pinkish; more or less sprinkled with well perceptible white dots; almost uninterrupted spiracular line white, emitting upwards and backwards (i.e. so that the stripes slant upwards in a backward direction) seven whitish stripes, the first of which is on the fourth segment, the last on the tenth, going up to the horn in the anal segment; on the anal segment is a small white stripe bent backwards over the spiracle, being

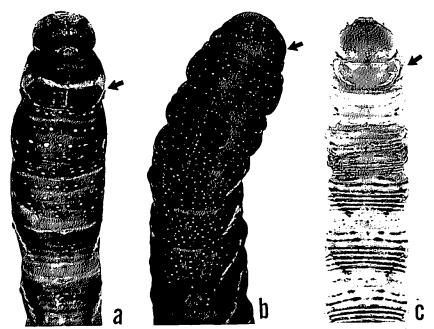


FIGURE 11. larvae: a, M. blackburni, Sprecklesville, 13.I.1926, Agr. HNL; b, M. quinquemaculata, no data, "North America," ex Rothschild bequest BMNH 1939-1, BPBM; c, M. sexta, Live Oak, FL, 24.VII.1976, BPBM.

much smaller than the white stripes on the other segments (Fig. 11a); head (Fig. 12a) orange-brown with 2 well defined blackish-brown longitudinal stripes, and clouded with blackish-brown laterally (compare headcapsule of quinquemaculata (Fig. 12b) and sexta (Fig. 12c)); spiracles black, surrounded with a bright blue ring; horn strong, shining blackish-brown, last third bent down almost rectangularly; prolegs of the groundcolor; prothorax with a very strongly developed cervical shield, the latter brownish with a big black spot on each side where it is bordered with whitish (in quinquemaculata (Fig. 11b) and sexta (Fig. 11c) not very distinctive and of body color), in the middle a twopartite vertical ecrescens (not observed in other Manduca larvae); thoracic legs blackish-brown at base, becoming red towards apex; mandibles strong as figured in Fig. 13a and different from those in quinquemaculata (Fig. 13b) and sexta (Fig. 13c); setae on headcapsule in blackburni (Fig. 12a) differently grouped on front and labrum than in quinquemaculata (Fig. 12b) and sexta (Fig. 12c). The available larvae were collected by O.H. Swezey from Nicotiana glauca at Spreckelsville, Maui, in 1926 and are preserved in Agr. HNL. Used also (for mandibles and headcapsule setae) was the larval skin of a larva collected by W. Meinecke from "Popolo" (Solanum sp.) at Waichinu, Hawaii, in 1955, and, of course, the larva collected by B. Gagné in 1984 and figured here, Fig. 1, as the first live photographed larva of the species. As foodplant is on the labels of reared specimens overwhelmingly mentioned Nicotiana glauca; twice we find tomato and once "popolo" (Solanum sp.). In the literature is also mentioned tobacco, eggplant and in Blackburn's larval description "a shrub growing some 6 feet high" which he was not able to name and which may have been the endimic Nothocestrum which was described by Gray in 1862.

It seems necessary to give for comparison also a description of the larva of M. quinquemaculata (Fig. 11b). Color mostly green also brown, even almost black.



FIGURE 12. larval headcapsules: a, M. blackburni; b, quinquemaculata; c, sexta.

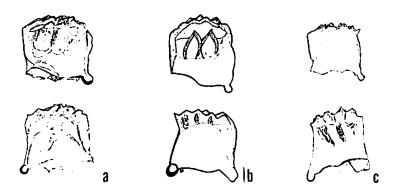


FIGURE 13. larval mandibles, lateral and mesal: a, M. blackburni; b, quinquemaculata; c, sexta.

This description is made from an inflated larva from the Rothschild Bequest BM 1939-1, now in the collection of Bishop Museum. This larva is green, covered with numerous small whitish dots; spiracular band whitish, infra-stigmatal, longitudinal, interrupted; on the abdomen and anal segments whitish lines (as in blackburni), however, in this species crossing the segmental incisions from segment to segment; the anal segment as in blackburni; spiracles testaceous, ringed with black (in very dark (blackish) larvae they are black, edged whitish; horn in this case black); head unicolorous like body, i.e., e.g., in green larvae green, in black ones blackish; horn bent upwards, thin, yellowish with blackish-brown apical third, prothorax without cervical shield (!); legs at base green, apex yellowish; prolegs green; mandibles as shown in Fig. 13b; headcapsule setae, as mentioned, differently arranged (Fig. 12b) from those in blackburni. For comparison was also used one larva in alcohol from the collection of Royal Ontario Museum, Toronto, Canada, collected on tomato in 1970 by B. Smith in Willowdale, Ontario. The mandibles used in the Fig. 13b are from this larva. There exists a description of the larva of quinquemaculata by B. Pickman Mann (1877) under the name of Macrosila [Sphinx] carolina. Rothschild & Jordan (1903:73) point out the mix-up of the name of carolina and quinquemaculata in this paper. Taken this under consideration the descriptions are appropriate.

PUPA. In the three species dark brown. According to Mosher (1918) the spiracular furrows are the main distinguishing character in the pupae of *Manudca*. The Figs. 14 and 15 show the differences between the three species: the spiracular furrow (Fig. 15a-c) extends ventrad of the spiracle in *blackburni* for 1.2 mm (Fig. 15a); in *quinquemaculata* for 1.6 mm (Fig. 15b); in *sexta* not at all (Fig. 15c). The overall length of the pupa is in *blackburni* 65 mm (Fig. 14a); in *quinquemaculata* 44 mm (Fig. 14b); in *sexta* 47 mm (Fig. 14c); the length of the proboscis is in *blackburni* 30 mm; in *quinquemaculata* 17 mm; in *sexta* 19 mm; the maxillary loop

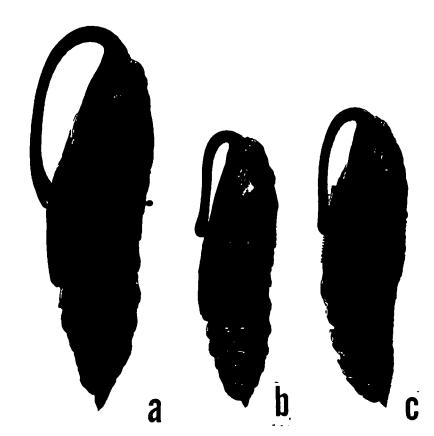


FIGURE 14. pupae: a, M. blackburnt, Molokai, 1946, Agr. HNL; b, quinquemaculata, Ottawa, ONT, 1954, CNC; c, sexta, Bedford, NY, 31.VII.1936, AMNH.

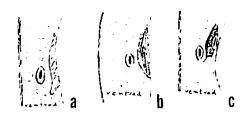


FIGURE 15. spiracular furrows of pupae in Fig. 14: a, M. blackburni; b, quinquemaculata; c, sexta.

arches in blackburni 6 mm; in quinquemaculata 2 mm; in sexta 3 mm; it reaches somewhat less than ¾ the distance between the cephalic end of the body and the caudal margin of the wings in blackburni; in quinquemaculata and in sexta somewhat more than ½. These data also confirm the difference between the species concerned, even when blackburni and quinquemaculata show some relationship (as in the genitalia).

TYPE MATERIAL. The holotype is a female specimen (Fig. 2), collected by Blackburn before 1880 near Honolulu, Oahu, Hawaiian Is., and is in the collection

of British Museum (Nat. Hist.), access. 80.31(30).

MATERIAL EXAMINED. The abbreviations for sites of specimen deposition are as follows:

Agr. HNL State Department of Agriculture Honolulu, HI

BM British Museum (National History)
BPBM Bishop Museum Honolulu, HI

CM Carnegie Museum of Natural History, Pittsburgh, PA
CNC Canadian National Collection of Insects, Ottawa, ONT
HSPA Hawaiian Sugarplanters Association, Honolulu, HI

ROM Royal Ontario Museum, Toronto, ONT SAM South Australian Museum, Adelaide, S.A.

UH University of Hawaii at Manoa, Entomology, Honolulu, HI

As there are only a few specimens of the species extant it was possible to examine all of them, except the ones in BM. The specimens are from the following islands in the Hawaiian chain, the following localities, collected mostly decades ago by "old time" collectors which makes them especially interesting.

Sandwich Islands: 13, BM access.99227, i.e., #227 ex 1899.

Hawaii: Hilo, 1Q, 7 July 1917, M. Newell, CM; Waichinu, 1Q ex larva on Solanum sp., 20 October 1955, W.H. Meinecke, BPBM; Kalaoa, 1Q, 23 February 1961, D.F. Hardwick, CNC.

Maui: Kahului, 1Q ex larva on N. glauca, 10 October 1919, O.H. Swezey, BM ex HSPA; Spreckelsville, 13, 1Q ex larva, 8 December 1922, O.H. Swezey, BPBM; 1Q, same data, Agr. HNL; 233, 25 March 1924, O.H. Swezey, CM; 1Q, 13 January 1925, O.H. Swezey, CM; 13, 6 April 1928, F.X. Williams, Agr. HNL; West Maui, 13 ex larva, 17 April 1929, F.X. Williams, UH; Spreckelsville, 1Q, 17 August 1929, O.H. Swezey; Wailuku, 1Q ex larva on tomato, 22 February 1937, F.X. Williams; Kula, 1Q, 28 November 1975, Shishido, UH; SW slope of Haleakala, 1Q ex larva on Nothocestrum latifolium, 14 September 1984, B. Gagné.

Molokai: Kamalo, 13, 13 January 1929, F.X. Williams; 13 ex larva, 27 January 1929, F.X. Williams.

Oahu: Blackburn specimens without specific data, Honolulu, before 1880, 19 holotype BM; 233, 499 SAM; 19 BPBM; Honolulu, 1 ex larva on tomato, 22 April 1924, G.P. Wilder, Agr. HNL; Makua, 19, 28 March 1931, O.H. Swezey, Agr. HNL.

There are also 3 inflated larvae in Agr. HNL from Sprecklesville, Maui, collected from N. glauca by O.H. Swezey 10 and 13 January and 27 February 1926.

Additionally specimens are mentioned in the literature which do not exist anymore or were not collected: van Dine (1905) from the experimental field at Hamakua, Hawaii, on tobacco; Browne (1940) reports larvae on Solanum melongena from Keopu, Molokai, and Nawiliwili, Kauai; Krauss (1940) reports eggs on N. glauca from Makena, Maui. Swezey (1924) reports some previous data: he saw in 1905 larvae which had been collected from cultivated tobacco at Pahala, Hawaii,

and in 1919 was told by J. Smith that the larvae were often found on cultivated tobacco at Kona, Hawaii. The first adult he saw was in a collection from C.W. Cockett of Lahaina, Maui, in 1916, and his first larva was obtained from N. glauca at Kahului, Maui, 10 October 1919. At Spreckelsville also J.A. Kusche collected larvae in 1919 or 1920 (the moths obtained, however, are not in the B.P. Clark collection (now in CM) as Swezey thinks).

FLIGHT PERIOD. From the data given above there seems to emerge a main flight period between January and April and a second one between July and October. This corresponds well to the flight periods of other lepidoptera in the Hawaijan Islands.

HOSTS. The main foodplant according to Swezey who did most of the work concerning the species is without doubt *Nicotiana glauca*. However, also other Solanaceae are frequented, among them cultivated tobacco on Hawaii at a time when there was the experiment to grow tobacco commercially; tomato in 2 isolated cases and eggplant also in 2 isolated cases; finally there is the rearing by Meinecke on the indigenous Popolo plant (*Solanum* sp.). Blackburn mentions a 6 feet high shrub which he did not know by name, which Swezey (1924) thinks may have been *Datura stramonium*, also in the Solanaceae, but what we now after the discovery of B. Gagné think might have been the indigenous *Nothocestrum latifolium*.

PARASITES. Williams (1946) notes 8 out of 11 eggs on N. glauca near Mapulehu, Molokai, parasitized by Trichogramma. One of these eggs produced 57 of the tiny wasps. In the same note he also contributes to the life history of our species: "One sphinx larva was reared to maturity, requiring 56 days from hatching to adult." (This adult specimen is not known from any collection.)

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