THE COCONUT LEAF-MINING BEETLE PROMECOTHECA PAPUANA*

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The severe depredations of the coconut leaf-mining beetle, "Promecotheca papuana", have been noted by many observers on coconut plantations in New Guinea. The author, Chairman of the Entomology Department of Bishop Museum, Honolulu, who made a detailed study of the ecology of the pest in 1956 *and* 1957, *draws attention to the "one-stage" nature of the infestation, when it reaches plague proportions. In this detailed review, Dr. Gressitt acknowledges published and unpublished material assembled by workers in New Guinea. He concludes that although much still remains to be learned about the factors leading to the outbreaks it is advantageous for planters to take steps to encourage predators of the beetle, such as lizards, birds and the kurukum ant.*

THE coconut leaf-mining hispine beetle, *Promecotheca papuana* Csiki (*P. antiqua* Weise, *P. biroi* Csiki) is a serious pest on coconut plantations in some parts of New Britain and Manus Island. This leaf beetle periodically attains plague proportions in these areas, when it exists in the "one-stage condition" as described below. Otherwise it is usually under good control by natural enemies.

In New Britain the areas principally affected are the Linga Linga area and some others on the north coast of central New Britain, west and east of the Willaumez Peninsula, the Lindenhafen area and others on the south coast of central New Britain, and parts of the Gazelle Peninsula at the north-east end of New Britain. Of the three areas, damage has been most severe at Lindenhafen Plantation, and generally least severe on the Gazelle Peninsula. A serious outbreak occurred on the Gazelle Peninsula in 1937, but was correlated with the great volcanic eruption of May, 1937, which caused damage to the palms and probably also seriously affected the native parasite populations.

Other lesser outbreaks have been reported from various parts of New Britain, the Duke of York Islands, and Manus Island. The species also occurs in New Ireland and north-east New Guinea, but has not been recorded as a pest from those areas.

Outbreaks of this leaf beetle appear to occur in cycles of about once every 10 to 15 years in some of the areas mentioned. Correlation with climatic cycles has been difficult because of insufficient records.

This beetle was recognized as a major pest in the period of German administration, and the kurukum ant (*Oecophylla smaragdina*) was used as a controlling agent (Friederichs, 1920).

In early 1937, G. H. Murray, Director of Agriculture, visited Lindenhafen and in his report (1937) includes the following paragraph :

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* This paper draws on published material by B. A. O'Connor, formerly Assistant Entomologist in the Territory of New Guinea and now Senior Entomologist, Department of Agriculture in Fiji, and unpublished material from C. S. Dun, Principal entomologist, and J. H. Ardley, Entomologist, of the Department of Agriculture, Stock and Fisheries, Territory of Papua and New Guinea. (Paper received for publication 15th June, 1959.)

" The estate presents a dreadful appearance and it is the worst infestation of *Promecotheca* of which there is any record in the Territory. When walking through the plantation one hears on all sides the continual drop of immature nuts which the palms can no longer sustain. Many of the trees have already succumbed, 370 dead palms having been cut down and destroyed, while there is not a single flower spathe on the whole plantation, so that no crop can be expected for two years, even from those trees that do eventually recover."

In 1938-1939 B. A. O'Connor studied the beetle, first in Manus and then at Lindenhafen Plantation in southern New Britain. His report (1940) was preceded by those of J. L. Froggatt (1936, 1937, 1939 and 1940). Summaries of this and other New Guinea coconut insects were published jointly by Froggatt and O'Connor (1941).

The parasite *Pediobius* ("*Pleurotropis*") *parvulus* which was so successful in controlling *Promecotheca caeruleipennis* ("*reichei*") in Fiji (Taylor, 1937), and to some extent *Promecotheca opacicollis* in the New Hebrides, was introduced into New Britain in October, 1938, from Fiji and became established and abundant. However, it has failed to prevent recurrence of outbreaks. In 1953-1954 simultaneous serious outbreaks occurred at Lindenhafen and Linga Linga Plantations. The outbreaks were observed by J. H. Ardley (1954) at these two plantations and at several others, mostly on the south coast.

After this I was asked by the Territory of Papua and New Guinea to study the ecology of the beetle. This I did for two months, April and May, 1956. The plan was to spend the time at Linga Linga and Lindenhafen Plantations. However, after about ten days at each a moderate outbreak was reported from Vunakanau Plantation on the Gazelle Peninsula. My second month was spent at Vunakanau and nearby plantations. In all I visited 20 plantations besides the three which were principally infested (Gressitt, 1958; 1959b). I had the opportunity to revisit Vunakanau three times (early and late July, 1956; October, 1957) after my month of study there. Mr. Ardley accompanied me during my visit to Linga Linga, and also during part of my stay at Vunakanau.

METHODS

O'Connor (1940) used the following methods in rearing and observing *P. papuana* :—

" One or more pairs of newly-emerged adults were placed in wire sleeves attached to a growing palm in such a way as to contain several leaflets. The wire sleeves were cylindrical, about 18 inches long and four inches in diameter, and at each end were continued into cloth cylinders about six inches long, which served to close the wire cylinder, and render it beetle-proof. Palms of from six months to a few years old were used, as their foliage is more easily accessible. When the palm used was only a few feet high, a stake was placed in the ground a few feet away and one end of the cylinder attached to a piece of twine coming from the end of the stake. Thus the weight of the cylinder was largely supported by the stake. When older palms were employed, a piece of tie-wire was passed along one side of the cylinder, and was attached to the midrib of the frond.

Cotton-wool wrappings were always used to ensure that the cloth fitted tightly over the leaflets, as otherwise the beetles were able to escape.

When food became exhausted, or when several egg-masses had been laid on the leaflets, the beetles were moved to fresh leaflets. Egg-masses were marked, and the development of the eggs and larvae followed up. Life histories of larvae were worked out also in the laboratory, where larvae could be carried through in leaflets kept in water, being put into mines in fresh leaflets whenever necessary."

O'Connor treated various aspects of the problem, but concentrated on working out the biology and determining the parasites, at Manus in 1938 and at Lindenhafen in 1938-1939.

Ardley (1954) spent the greater part of his effort on palm surveys at Linga Linga Plantation, determining severity of attack, density of population of the beetle, degree of parasitism and other aspects, by the spot-check, transect methods, sampling fronds cut down from palms climbed by plantation workers, and by comparative observation. He classified palms in eight categories relating to extent of damage by the beetle

(Table VI). Ardley also tabulated the correlation of presence of kurukum ants (*Oecophylla*) with degree of damage by the beetle, as discussed below.

I attempted to follow the methods and surveys of O'Connor and Ardley as far as possible to check facts and to obtain comparative data. I also tried to approach the problem from the broad ecological standpoint, taking into consideration all possible factors which might bear upon the problem. In the daily field work, the populations of *Promecotheca* and other insect inhabitants of individual palms were analyzed. Particular attempts were made to note the relationships of ants and various arthropod, or vertebrate predators of the beetle, as well as those of the beetle's parasites. Some observations differing from the conclusions of earlier workers were made.

To check data on the life-history of the beetle, daily observations were made by marking egg-cases or mines in the field, making measurements to determine periods of feeding and rest or transformation. Large numbers of the beetles, in various stages, were collected and caged in various ways to determine the nature of parasitism and other aspects. I used organdie sleeve bags instead of the wire sleeves used by O'Connor.

Certain palms were examined to determine changes in the beetle populations, and to evaluate predation. Mating pairs of beetles were caged with daily inserted fresh leaflets, supplied with water, to permit recording extent of oviposition. Adults were caged with various possible predators, such as lizards, ants, earwigs, spiders, and others. Observations were made upon nearly 600 palms, a number of them on several occasions.

THE GENUS *Promecotheca*

The chrysomelid genus *Promecotheca* contains at least 35 species, of which two are recorded from the mainland of East Asia (one questionable), one from Borneo, seven from the Philippines, one from Java, two from Celebes, one from the Moluccas, three (plus three new species) from New Guinea and nearby islands, three from northern Australia, two from the Bismarck Archipelago, ten (plus some new species) from the Solomon Islands (including Bougainville), one from New Hebrides, Santa Cruz and Banks Island, and two from Fiji, one of which, *caeruleipennis,* is also known from Tonga and Samoa. Thus the group has a predominantly Philippine-Papuan distribution. It is distinctly tropical, the species occurring mainly at low altitudes (Gressitt, 1959a).

All members of the genus are leaf-miners in monocotyledons. Seven of them feed upon coconuts, and all these have been recognized as pests. They occur in Malaya (Burkhill, 1918), Borneo *, Java, Celebes, Moluccas (Kalshoven, 1951; 1957), Philippines (Jones, 1913), parts of New Guinea, the Bismarcks, the New Hebrides (Kowalski, 1917; Risbec, 1935), Fiji, Tonga, and Samoa. No coconut *Promecotheca* has been recorded from the Solomons, except the Santa Cruz Group (Lever, 1933; Pagden and Lever, 1935), and none for certain from Australia (Froggatt, 1914) or most parts of the New Guinea Mainland. Some of the coconut species attack other palms as well, particularly other species such as nipa palm, sago palm and betel nut palm. About ten species mine only in leaves of palms other than *Cocos.* Most of these occur in the Solomons. About eleven species mine in leaves of *Pandanus* (one of them also is *Freycinetia*). Most of these are in New Guinea and the Philippines, with a few in the Bismarcks, Solomons and northern Australia. Two in the Solomons mine in ginger leaves. One species is known from *Flagellaria,* in Fiji, and one from sugar cane and other large grasses in the eastern Solomons (Gressitt, 1957, 1959a).

A Fiji member of the genus, *P. caeruleipennis* (*reichei*) was studied and reported in great detail (Taylor, 1937). This species differs, among other points, from *papuana,* in having only one egg per ootheca, and thus only one larva per mine, instead of three to five. The Fiji species was a serious pest of coconut, but was remarkably well controlled by the hymenopterous parasite *Pediobius* ("*Pleurotropis*") *parvulus* which was introduced to Fiji from Java for this purpose. Another species, *Promecotheca opacicollis* of the New Hebrides, also an important coconut pest, has been fairly-well controlled by the

* Gater [1924, Insect pests of Labuan and adjacent islands. Malayan Agric. Jour. 12 (11): 374-376] does not list *Promecotheca* from Labuan Island. However, on 24th October, 1957, at a small farm northeast of the airstrip on Labuan, I found *P. cumingi* very abundant and apparently in the one-stage condition, as adults and old mines were numerous, but no larvae could be found.

same wasp. Two species, *P. nuciferae* and *P. soror,* are coconut pests in Celebes and the Moluccas, but may represent a single species. The closely related *P. cumingi* is a serious pest of coconut in the Philippines, Borneo, Java and Malaya.

A second species in New Britain, *P. stramini-pennis,* was found during this study, at Vunakanau, to mine in the leaves of a tree-like *Pandanus* in the larval stage and to feed on the undersides of the same leaves in the adult stage (Gressitt, 1957). This species is much larger than *P. papuana* and appears not to share the same parasites. Another still larger species on Bougainville (*P. violacea*), mines in leaves of a large *Pandanus* and has up to at least seven larvae in a single mine.

In general, individuals of *Promecotheca* are very scarce on their native hosts under natural jungle conditions, but may become abundant under plantation circumstances or in village areas. I have noticed this for pandanus species as well as for palm species.

Copeland (1914), following Preuss (1911), states that in New Guinea *P. papuana* is specially liable to attack palms standing in grassy (*Imperata cylindrica*) areas, but that the beetles disappear when the grass is eradicated. This is probably a wrong deduction based on some coincidence.

BIONOMICS AND STAGES OF *Promecotheca papuana*

Host plants

The preferred food plant of this beetle is the coconut palm. The original native hosts, however, may have been the nipa palm and the sago palm. Of the latter two the nipa palm seems to be definitely preferred. O'Connor cited two species of palms as hosts in addition to the coconut palm : *Metroxylon sagu,* the sago palm, and *Elaeis guineensis,* the oil palm. The latter is not native to New Britain, and the larvae from eggs laid upon it (only in severe infestations) die after the first or second day of feeding. *Nipa fruticans,* the nipa palm, had been recorded as a host by Froggatt (1914) and others, and Ardley and I found ample evidence of the beetle developing and maturing in this palm at Linga Linga and westward on the north coast. Thirty-two adults and many larvae or pupae were taken from 24 mines in nipa.

At Vunakanau I found a population breeding in a group of betel-nut palms, *Areca catecu,* Interestingly enough, this group of betel-nut palms was surrounded by tall coconut palms which were almost unaffected by the beetle. The former, a group of six young to half-grown *Areca,* were quite densely populated by adult beetles, with much adult feeding damage (Plate 4A). Egg-cases and a number of larvae (Plate 4B), as well as mature mines from which adults had emerged, were also observed. A single adult was observed on a young betel-nut palm near a seriously affected part of the plantation, but betel palms in other parts of the plantation were not affected. It appears unlikely that outbreaks originate in native hosts, but they may occur concomitantly in hosts other than *Cocos,* adjacent to plantations.

Relationship to host

This beetle is very closely attached to the coconut palm, with all stages occurring in the palm crowns. Like other hispine beetles, it is destructive to the host both in larval and adult stages. It is a weak flyer, and rarely flies far at one time. If dislodged, or brought to the ground on a cut frond, an adult will almost always fly straight up to the palm crown again, or at most to the next nearest palm if the palms are tall. If part of the frond on which it was brought to the ground is projecting above the surroundings, the beetle may alight on leaflets of this higher portion. Thus the beetle is not a rapid spreader and is not known to migrate. Infestations apparently do not spread from one area to another to any great extent. If the beetle is widespread, it is apparently the result of a general local condition obtaining, such as factors working against the parasites or against most of the natural enemies.

The larvae spend their entire existence in the mine between upper and lower surfaces of a leaflet. After being mined, both surfaces of the leaflet turn pale brown, or dark brown when wet. The effect of this under conditions of dense population is to destroy all green tissue of the middle and lower fronds, rendering them dry and brown as if burned or killed by coconut blight. The adults spend their time on the undersides of the leaflets of the lower or middle fronds, going to newer fronds to feed or oviposit under crowded conditions. In serious outbreaks they complete the destruction of green tissue by

PLATE 1.—*Adult feeding on coconut fronds, Vunakanau, May, 1956.*

feeding on all the fronds not mined by larvae (Plate 1). Thus a plantation may turn completely brown.

In some cases the central shoot may be seriously damaged, leading to death of the palm. However, recovery is the general rule. Palms thought by Ardley to be dying during his 1954 survey proved to have revived by 1956, although they had not started bearing nuts again. Possibly some of the palms described in the quotation above from Murray as cut down at Lindenhafen might also have revived. At any rate, severe outbreaks set back nut production for at least two years.

Age of palms attacked

In general, *Promecotheca* appears to prefer mature palms. Actually the governing factor appears to be exposure to sunlight. Hispines are sun-loving insects, being strictly diurnal, although many spend much of their time hidden within plants. Younger palms, or palms lower than neighbouring ones, are usually less liable to attack than mature palms. Individually, isolated palms are particularly vulnerable. Young palms well away from the shade of mature palms or other shades are susceptible to attack, and all ages of palms are actually suitable for any stage of the beetle. However, new plantings of coconuts have not been observed to be seriously attacked.

During this survey, at Linga Linga and Lindenhafen, it was noted that almost all the *Promecotheca* of various stages were found on young palms. These young palms were largely within the shade of taller palms, which contradicts the above generalization. The reasons for this are not clear. I suspect that it was a reaction to some of the results of, and factors contributing to, the termination a short time before of the severe outbreaks at the two localities. These factors included the severe damage to the mature palms, which for some time eliminated plant tissue suitable for food or oviposition for the beetle, the great build-up of parasites and predators in the mature palms, also contributing to the elimination of the beetle population in those palms, and the general slowness of the beetle to move to new situations following the rejuvenation of the badly attacked palms. This explanation may not be completely satisfactory, and some other contributing factor may have been overlooked.

At Volupai where no serious outbreak had occurred, most of the population was also on young palms. As I went first to these three plantations, I concluded that the beetle preferred young palms, contrary to the case with the Fiji *Promecotheca*. However, this situation is apparently abnormal, and the New Britain species is normally sun-loving like the other species.

The eggs

The eggs (Plate 2 and Fig. II) are flattish, oval-elliptical, nearly white, with lower surfaces striate from attachment to the leaflet undersurface while soft. They are encased in a whitish buff ootheca, or egg-case, of partly digested fragments of coconut leaflet surface covered with a transparent mucilage. Both materials are ejected from the anus of the female. The egg is about 2 x 1 mm., and the ootheca is nearly round in outline, not very strongly convex, and 3-4 mm. in diameter. In the Lindenhafen area there are often five eggs per case, whereas on the Gazelle Peninsula and on Manus Island there are usually only three per case (2.97 average in 316 oothecae at Vunakanau).

The eggs are laid on the undersurfaces of the frond leaflets, sometimes one-tenth of them on the upper surfaces in overcrowded conditions. They are laid parallel, generally two beneath and one above, or three below and two above. After depositing the eggs the female covers them with the above-mentioned materials, taking at least half an hour for both processes together. She becomes rather active and excited towards completion of the process and at the end she

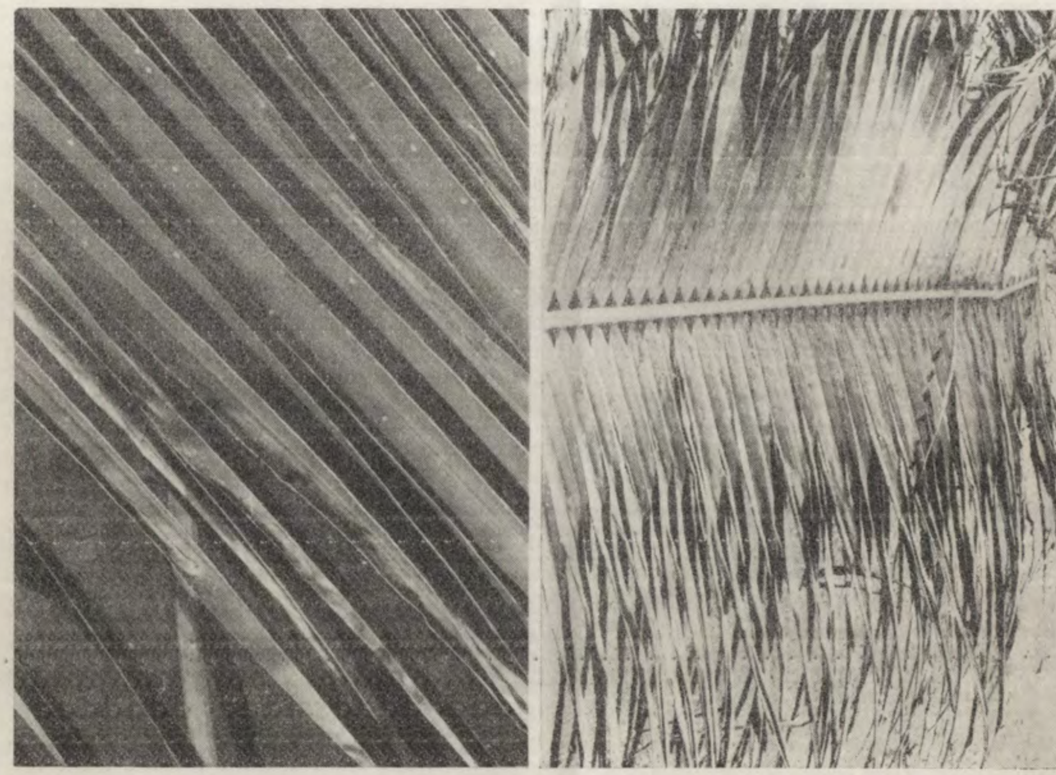

PLATE 2.—*Egg-cases on undersides of coconut fronds, Vunakanau, May, 1956.*

PLATE 3.—*Larval mines on coconut fronds, Vunakanau, May, 1956.*

reverses and pats the surfaces of the ootheca with her fore legs in a most ludicrous manner, moving all her legs and almost dancing about the sides of the egg case for nearly two minutes. The fresh case is pale green but turns straw-colour on drying.

Egg-laying generally takes place during the last hour of daylight but twice I observed it at Vunakanau in mid-morning. Before ovipositing, the female chews a slit in the leaf surface, over which the eggs are laid. On hatching, the young larvae enter directly into the inner leaf tissue by means of this slit. The larva, young or old, is unable to penetrate an undamaged leaf surface, as its mandibles point directly forward and work pincer-like in a horizontal plane.

In heavy infestations, and on young palms, eggs are laid on the new fronds, even the newest one before it is fully opened. The larvae from five or six egg cases (four for Lindenhafen) can mature in one large leaflet. But in the outbreak at Vunakanau the following numbers of cases were counted on single leaflets, indicating great waste of biotic potential : 14, 19 (two cases) ; 22, 23 (three cases) ; 24, 25 (three cases) ; 29, 31 and 32.

Larva

The larva (Figs. I and II) is a flattish, creamy white grub with heavily skerotinized head and mouth parts, from golden-brown to reddish-brown in colour anteriorly.

Technical description : Newly-hatched larva white with prothorax testaceous, but dark above front part of head, and occupying two-fifths length of body ; head capsule nearly parallel-sided, about as long as prothorax ; body length 1.6 mm. ; breadth 0.8 mm. Mature larva creamy whitish ; head capsule partly blackish anteriorly ; prothorax pale brown, transparent at side. Body about three-fifths as deep as wide, gradually tapered from mesothorax. Head capsule slightly broadened posteriorly, constricted between middle and apex, rounded at anterior and posterior angles, with four black dots at side behind antenna ; labrum obtusely emarginate apically ; antenna with second segment strongly oblique and third segment short with long setae. Prothorax strongly convex anteriorly and slightly convex posteriorly in dorsal outline, three-lobed, each lobe feebly convex, the lobes separated by narrow, deep emarginations, apical portion finely asperate-granulose, its margin slightly irregular ; lateral margin with fine setae, in particular anteriorly. Meso- and metaterga fairly smooth. Abdominal tergites one to eight each finely reticulate, with a transverse groove with raised borders, a short, longitudinally oblique groove just beyond end of this, and side rounded, with a low round spiracle followed by three setae and five or six setae arranged vertically but somewhat irregularly on lateral swelling ; ninth tergite plain, with a number of setae near posterior angle ; tenth tergite short, bearing an erect triangular process on middle and a pair of small nodes just above anal opening, all three slightly pigmented. Length 12 mm. ; breadth 2.8 mm.

The larvae always remain within the mine (Plate 3, Fig. II), and are thus never exposed. They may readily be seen while feeding by holding the leaflet against the light. They are then in the green, not yet dried terminal portion of the mine, whereas when moulting, or when badly disturbed, they retreat to the already dried, opaque portion of the mine. They feed upon the parenchyma tissue, cutting through it by the pincer-like action of the jaws, leaving upper and lower epidermis intact. Because of the structure of the coconut leaflet, the upper surface of a mine is thinner than the lower surface.

Generally the larvae in one mine feed side by side, and stop feeding at the same time to rest or moult. They work forward from the egg-slit where they entered the leaflet tissue, chewing a wide swathe and leaving behind common deposits of excrement of a sawdust-like

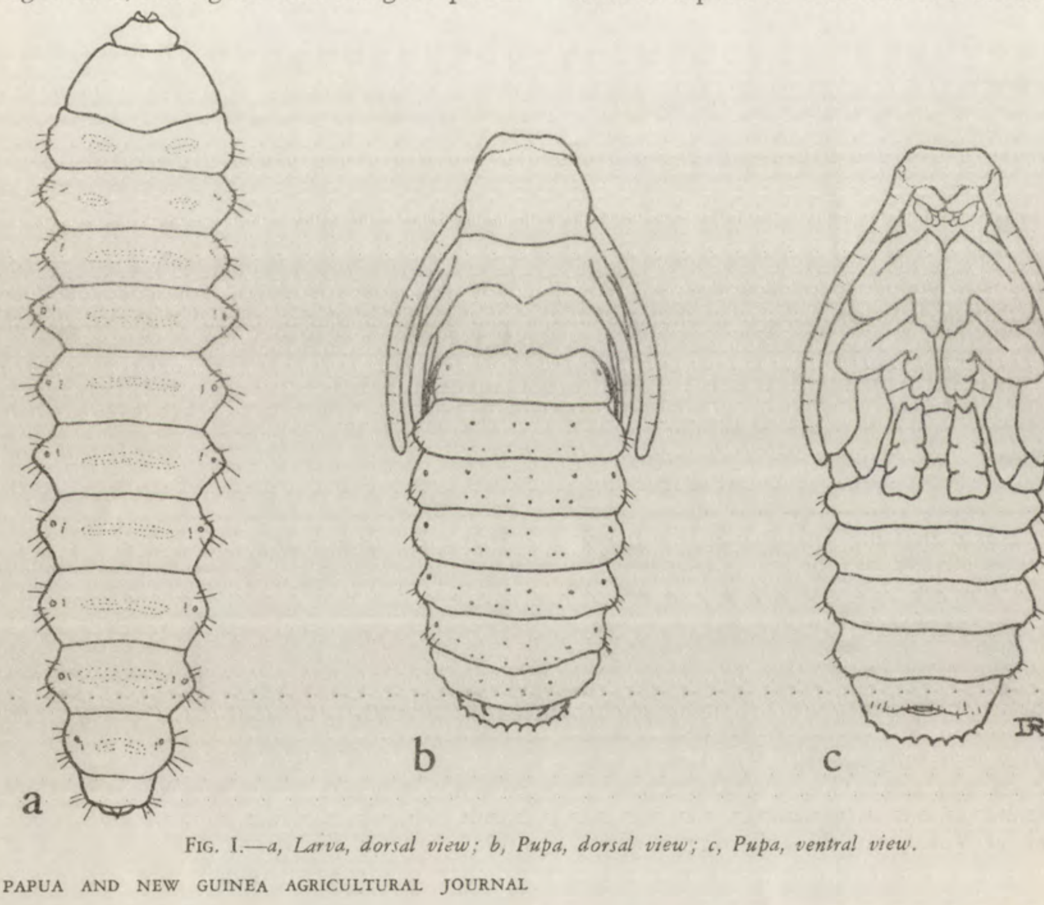

FIG. I.—*a, Larva, dorsal view; b, Pupa, dorsal view; c, Pupa, ventral view.*

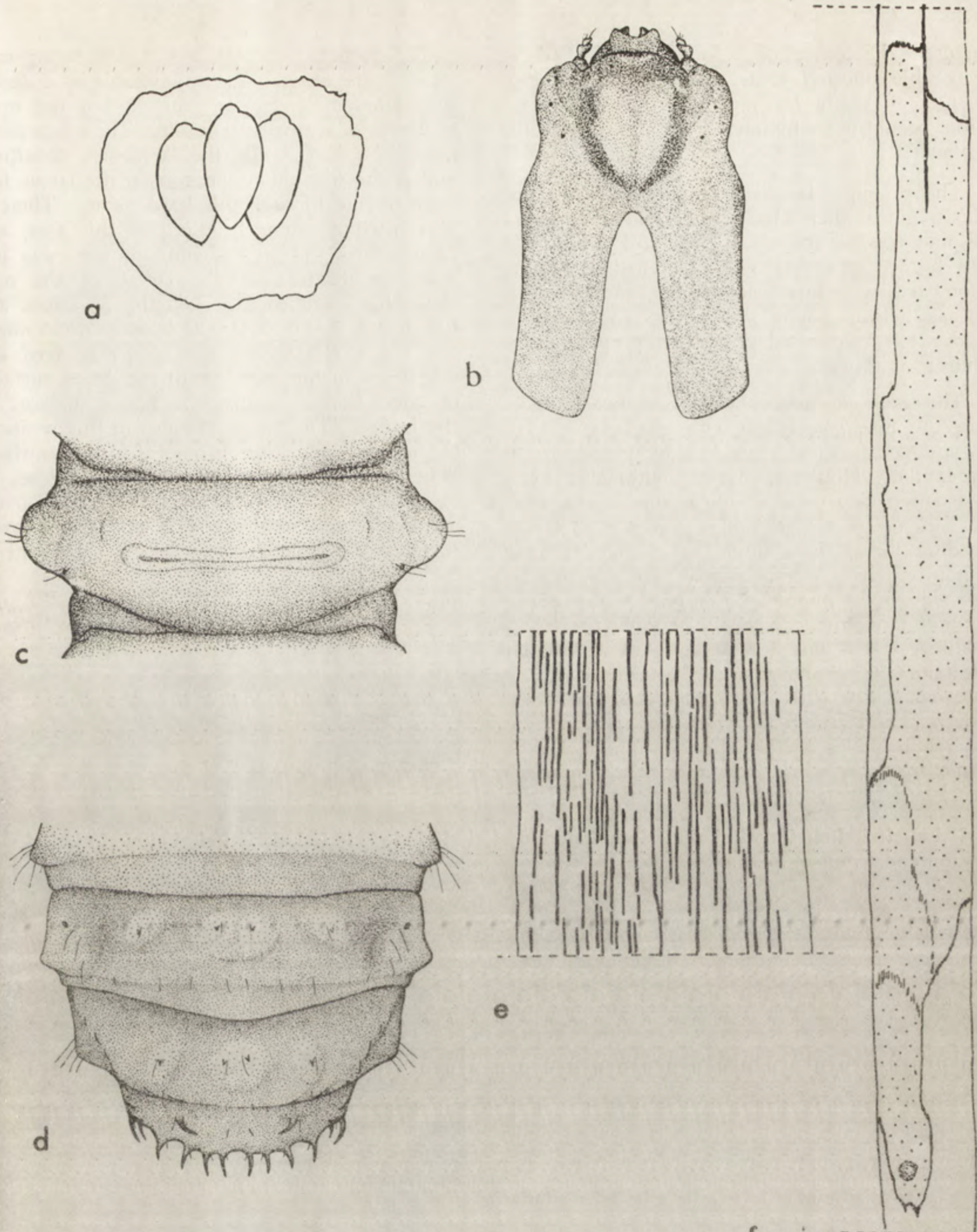

FIG. II.—*a, Ventral view of egg-case with 3 eggs; b, Dorsal view of head capsule of third instar larva; c, Dorsal surface of abdominal segment from middle of body of larva; d, Dorsal view of caudal end of pupa (mis-labelled larva in original publication); e, Adult feeding marks on underside of section of coconut leaflet; f, larval mine, from underside, on half of section of coconut leaflet, showing ootheca at bottom, and feeding areas of three larval instars; line at top is adult feeding scar. (Re-used from Gressitt, Nova Guinea, n. s., 8: 288).*

nature. Direction of mining is adjusted to accessible uneaten areas, and may be reversed Mines of moth leaf-miners are distinguished from beetle mines by having silk mixed with the excrement.

The principal beetle leaf-miners of palms of this region other than *Promecotheca* or other hispine beetles are small buprestid beetles, of which the larvae are more flattened and more elongated, with broadened thorax, and of which the adult beetles have shorter legs and antennae and a less constricted or less sculptured (never spiny) prothorax.

The average number of larvae per mine is three to five, correlating with numbers of eggs in the ootheca less eggs lost by parasitism or predation. However, during outbreaks, over-population may result in mines running together for lack of space. O'Connor once saw 13 larvae feeding abreast in a single mine. Under these conditions many cannot survive, for the area on one side of the midrib of a coconut leaflet cannot support more than about six or eight beetles to maturity. It is rare for larvae to mine through the midrib to the other side of a leaflet. At any rate, when one side is overpopulated, the other side is almost always likewise. As many as nine emergence holes were found in one leaflet at Vunakanau, but sometimes more than one beetle may emerge from one hole.

There are three larval instars, separated by resting and moulting periods. When the feeding period of one instar is completed, the larva recedes towards the middle of the mine, rests for two to three days, and then moults its skin, emerging from it with a larger new head capsule. Thus it is easy to recognize an instar by the size of its head capsule, which does not change its size as the body stretches during feeding in the course of one stadium.

Measurements of head capsules are :—

L_1 (1st instar)—0.54-0.6 x 0.78-0.84 mm.

L_2 (2nd instar)—0.72-0.81 x 1.28-1.40 mm.

L_3 (3rd instar)—1.15-1.30 x 1.95-2.05 mm.

Measurements of larvae :—

L_1—1.65-5.50 mm. (length).

L_2—5.5-7.5 mm.

L_3—7.0-13.2 mm.

Prepupa—12.0-13.0 mm.

The portions of the leaflet mined during each stadium are generally distinguishable by a darker pigmentation of the dry portion last fed upon by larvae of a particular instar. The green tissue here dries hard while the larvae are moulting, and at the start of the next instar the larvae first have to bite through this hard tissue. There is also often a slight shrinking of this area, and commonly a sudden widening of the mine just after the feeding of the larvae of the next instar has commenced. Lengths of mines are, first instar, 36-70 mm. ; 2nd instar 50-86 mm. ; 3rd instar, 84-394 mm. The larvae feed up-side-down in the mines, with the dorsal surfaces of their bodies against the lower surfaces of the leaflets. The pupae are also in this position, the adults thus exiting through the upper surface. When removed from a mine, a larva arches its body backwards, with the ventral surface convex, in attempting to contact both upper and lower surfaces of a mine in order to move forward or backward.

PLATE 4.—*Mines with larvae* (*a*) *and adult feeding* (*b*) *on betel-nut palm, Vunakanau, May,* 1956.

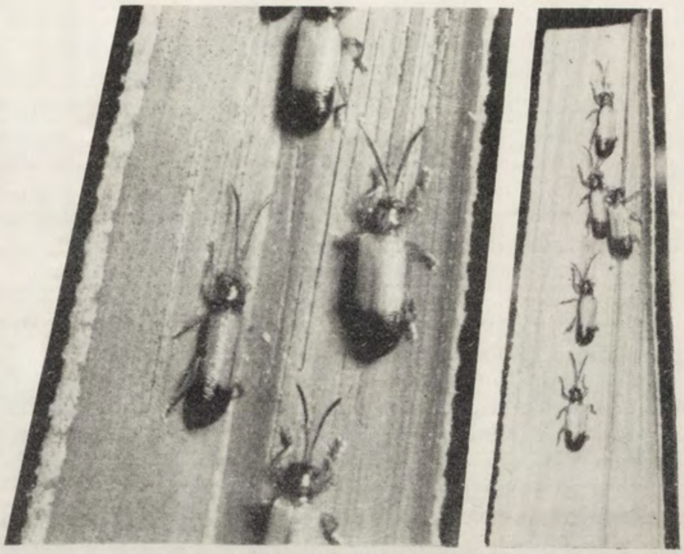

PLATE 5.—*a, Photograph of type specimen of Promecotheca papuana Csiki from Hungarian National Museum (Re-used from Gressitt, Nova Guinea, n.s., 8 : pl. 15 f) ; b, Adults resting after feeding on coconut leaflets (in captivity).*

Prepupa

The full-fed third instar larva recedes in the mine and undergoes a quiescent period called the prepupal stage, of about three days. Early in this stage the body shrinks slightly in length and becomes more swollen and pinker, while the internal transformation to pupa commences.

Pupa

(Figs. I*b* and II*d*)

At the end of the prepupal period, the larval skin splits along the mid-dorsal line of the thorax, and the pupa works its way out by a series of convulsive movements. The old skin is pushed backwards and shrinks into a dry mass at the posterior end of the abdomen, later detaching and remaining free in the mine. The fresh pupa is pale creamy-white, but soon becomes golden brown. As development proceeds, the mandibles and eyes turn black, and then the wing pads darken, shortly before emergence of the adult. The dorsal surfaces of the abdominal segments are armed with bristles which permit locomotion by an arching and extension of the abdomen.

Technical description : Pale reddish brown, slightly darker on setal insertions, tubercles and spines. Head with about nine setae on each side ; pronotum with about five on each side of anterior portion and more than ten along side, with a few subbasal setae ; mesothorax with a few setae on middle of elytral pad ; sides of legs and abdominal segments each with several setae of varying lengths. Thoracic terga and first abdominal tergum smooth to slightly rugose ; second to seventh abdominal terga each with four distinct tubercles in a transverse line anterior to middle, the inner two more closely spaced, followed by a subtransverse row of minute tubercles consisting of insertions of small setae ; last abdominal tergite with a pair of inward curving spines and outer margin armed with suberect slightly incurved spines. First five abdominal spiraches round, slightly projecting and tapering to opening; sixth similar but smaller; seventh vestigial, compressed. Abdominal sternites each with a postmedian transverse ridge bearing some setae, the insertions of which are larger and subtuberculiform on penultimate and antepenultimate segments. Length 8.5-10 mm.

Adult

(Plate 5)

On completion of the pupal stage the pupal skin splits down the back, and the adult emerges. At first it is pale, with some dark on posterior parts of elytra. It gradually hardens and becomes orange red with the head, prothorax, and ventral surfaces purplish-black and the posterior two-fifths of the elytra metallic blue to violet. Adults from Manus Island are paler than those from New Britain, and there is some variation in the proportion of blue on the hind parts of the elytra.

The new adult remains in the mine for about two days after emerging from the pupal stage. During this period it lies on its back, clutching the cast pupal skin with its feet. It then chews a crescentic slit through the upper surface of the leaflet, through which it emerges. The new adult generally flies away to another palm within a few minutes of emergence, and shortly afterwards starts to feed.

The adult beetles feed mainly on the undersurfaces of the palm leaflets, generally only on the terminal portions of terminal leaflets, unless the population is very dense. Sometimes the adults appear to prefer younger fronds and sometimes older fronds. They can feed upon both and when the population is at a high level they may go to the very nearest leaf shoot to feed. Since the adults are normally on the undersides of the pendant distal parts of leaflets, on the lower and middle fronds they are hidden from view from outside the crown, and are most easily seen on low palms by standing with back to the palm trunk and looking outward. It is easier to recognize the presence of the beetle by searching fronds with field glasses for evidence of mines or adult feeding. As shown below, there may be almost no adults present during part of the cycle of a "one-stage" epidemic.

The adults usually feed by facing upward with the body parallel to the leaflet. They turn their heads sideways to chew the surface by allowing the mandibles to penetrate between the main leaflet veins. This results in feeding marks consisting of straight narrow lines which turn brown and are visible from above or below. (Plates 1, 4.) When the beetles are abundant the entire ends, or entire leaflets, turn brown, and the whole palm may have a burned appearance. The damage caused by adult feeding is as extensive, or more so, as the damage by larval mining.

Copulation commences after a period of feeding lasting a few days, and is repeated frequently, sometimes daily over a period of two to three months. O'Connor noted copulation in captive beetles 135 days old. The copulating pairs appear to be gregarious. The females commence egg-laying 24 to 30 days after emergence, and may continue for some months if they survive that long. According to O'Connor the first eggs are laid seven to ten days after the first copulation, which he implied was more than two weeks after emergence. According to my observations, egg-laying commences at least two weeks after the first copulation, but the latter occurs just over a week after emergence. This is earlier than implied by O'Connor. After ovipositing for about a month, there is a resting period of about a month during which no eggs are laid.

The table of oviposition is after O'Connor.

The rate of egg-laying ranges between one ootheca every other day to two oothecae every three days and rarely one a day for a few days. One female at Vunakanau deposited five oothecae in one week. A female may lay at least 90 to 100 eggs, which is the equivalent of about 30 egg-cases at Manus and the Gazelle Peninsula and about 25 at Lindenhafen. Feeding, mating and oviposition take place only in the daytime, as far as known.

Sex ratio

Females are slightly more numerous than males. Of 500 reared adults, 217 were males and 283 were females, giving a ratio of about three males to four females. Of 179 collected adults, 84 were males and 95 were females, or nearly eight males to nine females. The higher ratio of collected males to collected females, as compared with reared individuals, probably reflects the tendency for females to go higher in the palm crowns to oviposit particularly when population is dense and undamaged leaflets for oviposition become scarce.

Life Cycle

The life cycle occupies about two months from egg-laying to adult, and less than three months from egg-laying to first egg-laying. Thus there may be four to five generations a year. The cycle at Vunakanau appeared to be more rapid than this, so the above preoviposition period is probably too long, reflecting the effect of caging or disturbance of the cycle.

The egg stage at Vunakanau lasted from 12.5 to 15 days, with an average of 13.6 days. For Manus, O'Connor reported 13.5 to 16 days (average 15 days), and for Lindenhafen 13 to 15 days (average 14 days).

The larval stage lasts 17 to 30 days. The first stadium has a feeding period of eight days (five to nine at Manus), followed by a resting period, including the moult, of two to three days. The second stadium has a feeding period of 2.5 to five days (eight to 13 at Lindenhafen according to O'Connor), followed by a resting period of two to three days, including moult. The third stadium has a feeding period averaging four to eight days (four to 10 at Manus, six to 12 at Lindenhafen—O'Connor). The prepupal period lasts three days, rarely four, and the

TABLE I.—Oviposition

Adult emergence from mine	Preoviposition period	First oviposition period	Non-laying period	Second oviposition period
A. 10th February	28 days	10th March-6th April 27 days : 16 oothecae	32 days	8th May-22nd May 14 days : 4 oothecae
B. 14th February	28 days	14th March-15th April 32 days : 13 oothecae	42 days	27th May-27th June 31 days : 11 oothecae

TABLE II.—Larval and pupal development, in days.

	Manus Island				Lindenhafen Plantation					Vunakanau	
	Palms				Palms						
	Mature		Young		Mature		Young			Young Palms	
	B	C	D	G	H	K	a	b	c	d	e
First stadium—											
feeding	8	8	5	5	6	6	4	4	3	4	5
rest	2	3	2½	3	3	3	2	3	3	3	3
Second stadium—											
feeding	5	5	3	3	8	13	3	4	3	5	4
rest	3	3	2½	2½	2	3	2	2	3	2	2
Third stadium—											
feeding	10	10	7½	4	6	12	4	5	4	5	5½
To emergence of adult	15	15	15	15	15	15	15	14½	15	15	15
Total, egg-hatching to adult	43	44	35½	32½	40	52	30	32½	31	34	34½

NOTE.—Individuals B-K were observed by O'Connor while I observed A-E. H and K were reared by O'Connor in the laboratory in leaflets kept in water. The others were observed from day to day on living palms under plantation conditions. Columns a-e are partly composited of different individuals because of shortness of stays.

pupal stage lasts 9.5 to 10 days. Following metamorphosis the adult beetle remains in the mine for two or, rarely, three days before cutting its way out. O'Connor showed that larval development was more rapid in very long palms (see Table II).

However, the period of 15 days from the end of the feeding portion of the third stadium to emergence of the adult from the mine is fairly uniform, consisting of three days as a prepupa, 10 days, or slightly less, as a pupa, and two days as a resting adult in the mine before emergence. My Lindenhafen figures were completed by taking caged material and dated pupae with me to Vunakanau.

The adult beetle can live as long as five months, and probably longer, according to O'Connor. Of those he kept in captivity, none was kept until it died of natural causes. "They either escaped, or were still living when observations had to be discontinued", O'Connor noted. "One female was kept at Lindenhafen for 160 days and a male and female for 140 days".

In nature adults probably never live this long. Predation and diseases must exact a very great toll. Otherwise the one-stage condition could not be maintained, as discussed below.

Potential reproductive capacity

On theoretical figures, without consideration of parasites, predators, diseases and starvation of larvae through over-crowding, the progeny of a single female during one year could be 2,160,000,000. This is worked out on the arbitrary basis of four generations per year, 100 eggs per female, and a sex ratio of 60 per cent. females. Under circumstances of the one-stage condition the number of generations per year is probably at least five, because the life of most adults is cut short and the mean point of the egg-laying period is much earlier than in caged beetles. Thus the number of eggs is much reduced.

Since only up to about 15 adults can develop from one large leaflet, not more than 3,000 beetles could come from a large frond, and about 35,000 from one palm, allowing half the fronds for adult feeding space.

NATURE OF *Promecotheca* OUTBREAKS

Outbreaks of this beetle are peculiar in that they seem generally to be restricted to a particular plantation or limited area, or two or more isolated areas, at one time and tend to recur at intervals in these areas. Meanwhile, the beetle may exist under normal biological control in nearby areas. Localities in New Britain which are known to have had repeated serious outbreaks are the Linga Linga-Talasea area on the north-central coast, the Lindenhafen area on the opposite south coast, and parts of the Gazelle Peninsula. Many small outbreaks have occurred at other places, particularly along the north and south coasts of New Britain, in part correlated with main outbreaks and in part independent, and others have been reported from Manus Island and the Duke of York Islands.

TABLE III.—Life cycle, in days.

——	Manus	Lindenhafen		Vunakanau
Incubation period	15	14	14	13.6
Larval period (to end of feeding)	28	30	15	19
Prepupal period	3	3	3	3
Pupal period	10	10	9.5	10
Adult in mine	2	2	2	2
Adult to egg-laying	28	28	24	25
TOTALS	86	87	67.5	72.6

NOTE.—First two columns after O'Connor, the last two are mine. O'Connor's reared specimens were evidently delayed by adverse conditions.

If the life cycle is counted from egg-laying to middle of maximum egg-laying period, then a figure of about 50 should be substituted for the 28 above for adult to egg-laying. However, as pointed out above, in nature adult life is much shorter. Also, the figures 24 and 28, arrived at by O'Connor and myself in different ways, are probably too high. Thus there could be more than five generations per year.

The reasons that certain areas are more affected than others are not clear. Abnormally long, dry seasons have been associated in literature (Taylor, 1937) with the development of *Promecotheca* outbreaks in Fiji, principally through the build-up of populations of the mites *Pyemotes* ("*Pediculoides*") *ventricosus* which is said to destroy the parasites and contribute to the development of the "one-stage condition", through destruction of young stages of the beetle at a given time.

However, it is difficult to connect dry weather with the development of the New Britain outbreaks, because of the differences in rainfall and seasonal occurrence of rain in the areas most susceptible to the occurrence of outbreaks. Lindenhafen, where the worst outbreaks have been reported, has the highest recorded rainfall in the Territory of Papua and New Guinea, whereas the Gazelle Peninsula coconut areas have a much lower rainfall. It might be that the heavy rainfall at Lindenhafen is detrimental to the parasites when combined with some other factors. But the last outbreak at Vunakanau correlated with an extremely dry period. Only one fully-fed *Pyemotes* mite was seen during my study. This was at Lindenhafen. In 1953, Ardley reported many in frond samples sent from Lindenhafen, but found very few on his visit. There seems to be a general widely-spaced periodicity in the occurrence of *Promecotheca* outbreaks in New Britain. From the incomplete records, it appears that outbreaks may occur at intervals of approximately every 11 to 15 years or longer. In the Linga Linga-Talasea area outbreaks were reported in 1923, 1940 and 1954, and at Lindenhafen in 1937 and 1954. Constrictions at subequally-spaced wide intervals on the trunks of the mature palms planted during the German regime are quite noticeable over much of Linga Linga Plantation and on parts of Lindenhafen. The intervals between the constrictions correlate with the time periods between the known or rumoured beetle outbreaks. On many palms four distinct constrictions are visible, the highest being at the base of the crown (not yet visible in 1956 where old pendant fronds were still adhering), and representing the then just-terminated 1953-1954 outbreak (see Copeland, 1914, or Gressitt, 1953, for summary of chronology of palm crowns). Information obtained elsewhere, including Vunakanau, indicates a recurrence of outbreaks at similar intervals. Possibly when more climatological data are accumulated, some correlation may become evident.

The "one-stage condition"

The "one-stage condition" obtains in a population when there is a single cycle or generation progressing at one time—in other words, when the population in a given area consists entirely of one stage, or two successive stages (such as adults and eggs, eggs and young larvae, mature larvae and pupae, or pupae and adults) at a given time. The one-stage condition seems to be characteristic of outbreaks in New Britain.

The main factors contributing to the development of the "one-stage condition" have not been determined. No concrete evidence has been demonstrated that it is caused by build-up of the harvest mite *Pyemotes* ("*Pediculoides*") *ventricosus,* as was proven in Fiji, although this mite is present in New Britain. It seems suggestive that some major upset of the parasite balance must take place, for the "one-stage condition" seems to be inseparably linked with the occurrence of outbreaks. For the development of such high populations as exist in outbreaks, the parasites must be rendered ineffective for a period.

Possibly the beetle population increases rapidly after mortality of certain stages has produced the "one-stage condition". The parasites then lack suitable host material for oviposition, as the life-cycle of the parasites is shorter than that of the beetle. Many beetle generations are apparently required before the parasites can gain the upper hand again and reduce the beetle population materially.

Once the "one-stage condition" is attained, it seems to be maintained for a long period—often up to two years. This seems to contradict knowledge of the egg-laying period of the female beetle, which theoretically should permit termination of the "one-stage condition" within a generation or two. However, my observations confirm O'Connor's suggestion that the adult population decreases much more rapidly than would be expected from the observed adult life-span and oviposition period in captivity.

Predators and diseases are probably mainly responsible for this rapid decline in adult population [very clearly observed at Vunakanau ; see diagrammatic graph (Fig. III)]. At the same time, the smaller number of eggs and larvae resulting from the small number of adults carrying over between one peak in adult population and the next, is undoubtedly completely parasitized by the parasites avidly searching for host material during the period of dearth between the peaks in larval population of two successive generations. Thus, between the predators and the parasites, the "one-stage condition" is perpetuated, to the continued disadvantage of the parasites. From the standpoint of the predators, the food supply (of course not an obligatory relationship) is irregular, particularly for those feeding only upon one stage of the beetle. O'Connor noted that the "one-stage condition" persisted during his eight-month study at Lindenhafen, which was two years after the outbreak started.

Further studies are required to prove whether the responsibility for the inception of the "one-stage condition" in New Britain lies with the mite *Pyemotes* or with some other factors. It also seems suggestive that climatic aberration is in some way involved. For several months preceding the discovery of the outbreak at Vunakanau at the end of 1955, the immediate area had suffered an unusually long period of drought.

The reason why the *Pediobius* ("*Pleurotropis*") parasite was so successful in Fiji, and much less so in New Britain, remains uncertain. The life-cycle of the New Britain *Promecotheca* is, however, slightly shorter than that of the Fiji species. Possibly some factors obtaining as a result of climatic cycles prove unfavourable to the *Pediobius*. The native parasite *Apleurotropis* ("*Derostenus*") definitely competes with *Pediobius*, and can win out over it when eggs of both are laid in the same mine. At Linga Linga the former was found to be more abundant than the introduced parasite in 1956. However, *Pediobius* is often more abundant than *Apleurotropis* in various parts of New Britain.

One interesting fact is that the beetle is often scarce in coconut plantings on off-shore islets near Linga Linga and Lindenhafen during outbreaks at these plantations.

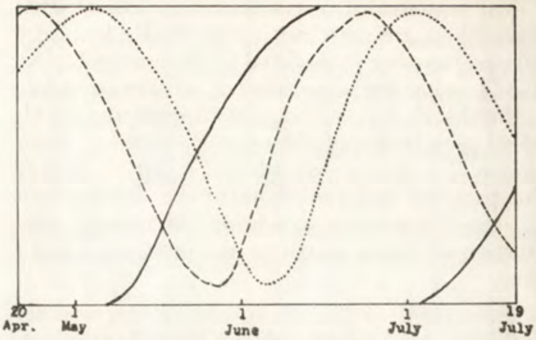

FIG. III.—*Diagrammatic graph showing a "one-stage condition" of generations of beetle at Vunakanau Plantation, Gazelle Peninsula,* 1956.

- - - - - - - Adults :—

Top of graph represents 200 or more adults per frond.

——— Mines :—

Top of graph represents completion of development, with complete area of majority of leaflets on older fronds mined, leaving no green tissue.

. . . . Eggs :—

Number newly laid. Top of graph represents super-oviposition on new fronds or remaining green tissue : up to 30 or more egg-cases per leaflet, which is many times the population which could develop from available food for larvae.

PARASITES

Much of this section is repeated from O'Connor's report (1940), as, during most of my period of study, hosts were extremely rare (Linga Linga in particular), or in the adult-egg-early larval phases of the "one-stage condition" (Vunakanau, Taliligap).

Pediobius parvulus (Ferriere).

This eulophid wasp, known in earlier *Promecotheca* reports as *Pleurotropis parvulus*, was introduced from Java to Fiji, and later to the New Hebrides, to control other species of *Promecotheca* and was outstandingly successful, particularly in Fiji where it is now difficult to find *Promecotheca* on the main island. In October, 1938, a colony of this wasp was received in Rabaul with the co-operation of R. J. A. W. Lever (1938), and Messrs. W. R. Carpenter & Co., Ltd. The parasites were bred up in Rabaul and distributed in the Rabaul district, Manus Island, Talasea, Pondo and other localities.

At the end of November, 1938, O'Connor was sent with a colony to Lindenhafen, where *P. papuana* was present in very large numbers at the time. Breeding and distribution of the parasite was carried on in the district until the end of July, 1939, by which time *P. parvulus* was firmly established at Lindenhafen. Daily collection of *Promecotheca* was carried out, so that a check could be kept on the progress of the parasites in the field. O'Connor found that two weeks after the initial liberations, parasitized larvae and pupae could be found on the site of liberation, and even as much as 200 yards away from this point. A gradual increase was discernible in percentage of parasitism in the field as shown by the figures below. Percentages were based only on mines which contained healthy larvae, pupae, or adults of *Promecotheca,* or larvae and pupae containing *P. parvulus,* all those from which *P. papuana* or *P. parvulus* had emerged being excluded.

TABLE IV.—Parasitism by *P. parvulus* at Lindenhafen six months after release (O'Connor).

	Total Mines.	Mines containing para-sitized individ.	Per cent. of mines containing para-sitized indivi-duals.
6th-22nd June, 1939	414	18	4.3
23rd-30th June, 1939	451	10	2.2
1st-14th July, 1939	872	33	3.8

Incomplete counts for the latter half of July indicated that the parasitism had jumped suddenly to about seven per cent. In October, 1939, counts of mines sent to Rabaul from Lindenhafen showed a 50 per cent. parasitism.

In the Rabaul District, possibly due to the generally drier and finer weather, *P. parvulus* seemed to have multiplied much more rapidly than at Lindenhafen. Most of the liberations around Rabaul and Kokopo were made early in 1939, and by August parasitized larvae and pupae could be found in numbers by casual inspection. At Wangaramut Plantation, for instance, between 200 and 300 mines were opened, and every one of these contained one or more parasitized larvae and pupae. Other plantations on which the parasites were by then well established were Ralabang, Ulatava, Keravat and Pondo, showing that their spread was rapid and wide.

In 1954 Ardley reported that *Pediobius* had re-established itself after the outbreaks at Linga Linga and Lindenhafen. He demonstrated a parasitism of 47.1 per cent. at Linga Linga, and noted 90 per cent. parasitism by *P. parvulus* on Boronga Island, just off Lindenhafen.

In 1956 I found low populations of both hosts and parasites at Linga Linga, where *Pediobius* was less abundant than *Apleurotropis* ("*Derostenus*"). Total larval parasitism appeared to be 13.3 per cent. At Lindenhafen it was 28 per cent., apparently all *Pediobius.* At Vunakanau, larval parasitism varied, going quite high, and consisting mostly of *Pediobius* (see Table V). In old mines it often proved to be at least 90 per cent.

Method of breeding

A satisfactory method for bulk breeding is as follows : Into a large mine, from 20 to 40 prepupae, or nearly-formed beetle pupae, are placed. The ends of the mine are cut and closed with wire clips, and the mine is then placed in a glass tube about eight inches by an inch and a half with 100 to 200 *P. parvulus* (i.e., five wasps per beetle) and left for two days. Food is provided in the form of honey very slightly diluted with water, which can be placed on a small piece of blotting paper stuck to the side of the tube, or on the upper surface of the mine in very small droplets.

At the end of two days, the prepupae and pupae are removed, and stored in a glass tube six inches by one inch.

If the climate is moist, the tube should be lined with blotting paper, and adult beetles emerging from unparasitized pupae should be removed daily, otherwise there is a risk of sweating, and consequent fungus attack on the parasitized individuals. The same individuals of *P. parvulus* can be used three or four times for oviposition in fresh lots of *Promecotheca.* Prepupae and pupae are preferred to larvae, as the latter have to be fed before and after parasitism, a process which occupies a great deal of time.

These methods were used at Lindenhafen, and produced from 1,000 to 1,500 well-grown wasps per day. Superparasitism was found to be negligible. The developmental period of *P. parvulus* from parasitism to emergence of wasps was found to be 16 days in Rabaul and 19 days at Lindenhafen, the difference being due to higher mean temperatures at Rabaul.

TABLE V.—Parasitism of immature stages, New Britain, 1954, 1956 and 1957.

———	Egg parasitism : "Closterocerus splendens"		Larval-pupal parasitism : "Pediobius parvulus" (unless otherwise noted)		
Data	Total oothecae	Per cent. parasitism	Larvae-pupae	Per cent. parasitism	Aborted mines
1954—					
Linga Linga (Ardley)			1,665	47.1	....
1956—					
Iboki (nipa palm ; Ardley), April	21	92	....	....	....
Linga Linga (*Apleurotropis, Pediobius* and *Eurytoma*), April	....		60	13.3	
Volupai, April			55 mines	95	40
Lindenhafen, April	151	58	129 mines	28	12
	177	24	32 mines	30	
Vunakanau :					
20th April (Ardley)	575 (old)	16.5	249	80.7	
5th May	362 (new)	7	233 mines (old)	25	32
	...		214 mines (old)	50	
15th May	40	86	....	....	
21st May	687	38	....	....	5
23rd May	809	63	....	....	
4th July	362 (old)	54	146	67	16
19th July	43	54	....	....	
1957—					
Vunakanau :					
10th October	56	55	....	....	
1956—					
Taliligap :					
25th May	244	49	....	....	
29th May	310	50	....	....	18
4th July	47	72	116	70	19

In this connection, it was calculated by O'Connor that the developmental zero for *P. parvulus* was approximately 55 degrees F. (12.8 degrees C.). To determine this figure, parasitized *P. papuana* were kept in a refrigerator and in the laboratory, and development of *P. parvulus* noted while taking temperatures at three-hourly intervals.

Description

The adult wasp is black, robust, about 1.6 mm. in length. The three proximal tarsal segments on each leg are white, the fourth segment, like the tibia and femur, being black. Males are smaller than females, and have a greenish sheen on the ventral portion of the thorax. The larva is white, slender, and tapering at each end.

Bionomics

The egg of the wasp is laid, from outside the mine, into the larva, prepupa or pupa of *Promecotheca*, the ovipositor of the female wasp penetrating the epidermis of the leaflet to reach the host. Oviposition is usually carried on from the under surface of the leaflet. Where the host is a well-grown, third-instar larva, a prepupa or a pupa, the developmental period of the parasite is shorter than when a first-instar or second-instar larva is the host. At Lindenhafen, 19 to 21 days was the usual period, but some individuals occupied as much as 27 days even in large third-instar larvae. In the second-instar larvae, the period was 21 to 23 days, with some individuals occupying up to 30 days. At Rabaul, 17 to 19 days was the usual period when large larvae were the hosts. When the life cycle covered 19 days, the larval period was about eight to nine days, and the pupal period 10 to 11 days.

The pupae, when first formed, are white, but darken quickly, until they finally become quite black. The skin of the host turns black about six or seven days after oviposition, in the case of third-instar larvae. When prepupae are attacked by the parasite, they almost invariably reach the pupal stage before dying and the pupa turns greyish brown, not black. Parasitized larvae always feed more voraciously after eggs of the parasite have been laid in them and in the case of first- or second-instar larvae, the subsequent feeding period may be as long as 14 days. Feeding by the parasite larvae goes on entirely within the host and when the prepupae form the pupae are packed inside the dried larval or pupal skin.

When fully developed, the adult parasites cut holes in the dry skin of the host, and emerge into the mine, where they then cut holes in the upper epidermis of the leaflet, and escape. If the portion of the host skin in which the hole is made is pressed against the epidermis, the parasites bite their way directly out, and do not enter the body of the mine. The number of holes made in host and mine varies from one to six.

Superparasitism

This has seldom been observed in nature, but in laboratory breeding, when parasites are placed in a tube with an insufficient number of hosts, it is of common occurrence. If the degree of superparasitism is moderate, the parasites complete their development, but emerge as stunted adults. If it is extreme, development is not completed, parasite larvae and host shrivelling up completely. In one shrivelled third-instar larva, 180 *P. parvulus* larvae were counted. It appears that up to 40 good-sized wasps can develop in a prepupa, pupa or mature larva.

Eurytoma promecothecae Ferriere

This parasite was described (1939) from specimens collected in the Rabaul and Lindenhafen areas. It is a black wasp, about 3 mm. in body length, with the distal ends of the tibiae yellow, and the tarsi white. The antennae of the male differ from those of the female, the funicle segments of the male being hairy and irregular in shape, while those of the female are smooth and rounded. This species has been recorded only from New Britain, and it appeared to be the main factor in controlling the outbreak of *P. papuana* which occurred along the north coast road in the Rabaul District subsequent to the volcanic eruption of May, 1937. It would appear that the outbreak was due largely to destruction of many of the local parasites by the deposits of ash which fell on the plantations in this area, followed by torrential downpours of rain. It was noticeable that those plantations which had suffered most from the ash and the cloudbursts were subsequently the most severely attacked by *Promecotheca.*

E. promecothecae is an external parasite of the larva of *P. papuana,* each of the three instars being attacked. The parasite larvae are voracious feeders and, attaching themselves to the sides of the host larva, they suck its body fluids. Feeding is especially heavy during the last day, when the host larva shrinks from almost normal size to a shrivelled husk. The host larvae are paralysed by the adult wasp when the latter lays its eggs and are unable to rid themselves of the parasite larvae.

When the larva of the parasite is fully fed, it moves along the mine and pupates, the pupa being attached to the wall of the mine by a drop of excreta and the cast larval skin. Its colour is at first pale yellow, later becoming black. The developmental period, from oviposition to emergence of the adult wasp, is 19 to 21 days at Lindenhafen and 17 to 20 days at Rabaul. The adult cuts a hole in the epidermis of the leaflet, usually on the upper surface, and emerges. Maximum longevity of adults in the laboratory was 60 days when not provided with hosts and 35 days when permitted to oviposit into larvae.

Apleurotropis lalori Girault ("*Derostenus* sp.")

This parasite (Girault, 1938) of the larvae of *P. papuana* occurs widely throughout the Territory, having been recorded from Lindenhafen, Rabaul and Manus. It belongs to the family Eulophidae. The adult is of a metallic-green colour, with coxae, tibiae and tarsi of all three pairs of legs white. Body length is about 1.6 mm. The adult has a very characteristic habit of running rapidly sideways and of standing on the leaf swaying its body to and fro.

This insect is an internal parasite of the larva of *P. papuana.* The host does not feed after oviposition by the parasite, and the parasite larvae develop inside the body of the host, which gradually assumes the appearance of the transparent envelope enclosing the parasite larvae. When fully fed, these latter bite their way out of the skin, and pupate in the mine, the pupae being attached to the walls of the mine by a drop of excreta and the cast larval skin. The skin of the host remains distended and transparent. The parasite pupae gradually become black in colour, and normally the adults emerge and bite their way out of the mine 18 to 21 days after oviposition by the parent generation. Larval and pupal periods at Lindenhafen were approximately equal. At Linga Linga the prepupal stage was three days and the pupal stage eight to nine days.

In the laboratory, *Apleurotropis* failed to oviposit in prepupae and pupae and no larvae parasitized by it ever reached the pupal stage. However, in the field it was not uncommon to find pupae parasitized by this species, their appearance being very similar to that of pupae attacked by *P. parvulus*. Three adult females, supplied regularly with food and host larvae for oviposition, lived 25, 26 and 32 days in the laboratory, laying eggs until a day or two before death. When *Apleurotropis* and *P. parvulus* females were allowed to oviposit into a host larva at the same time, *Apleurotropis* always won in the competition for food and only *Apleurotropis* adults later emerged from the parasitized larvae.

Closterocerus splendens Kowalski

This eulophid wasp is just over 1 mm. long, with brilliant metallic-green body and banded wings. It was originally described by Kowalski (1917) from the New Hebrides as a parasite of the larva of *Promecotheca opacicollis* Gestro, but in the Bismarcks, where it has been found in the Manus, Rabaul and Kandrian (Gasmata) districts, it is an egg-parasite. The bionomics of this species have not been extensively studied, but the developmental period from egg-laying to emergence of adult is about 21 days or less. One parasite develops in an egg of *P. papuana* and an ootheca may have one or more parasitized eggs. When the parasite is fully developed, it cuts a small hole through the covering of the egg case, through which it emerges.

C. splendens, and to a lesser degree the egg parasite *Anastatus* sp., are believed to be the main factors causing the break in overlapping of generations in the Lindenhafen and Rabaul areas. At the beginning of egg-laying in one generation of the beetle at Lindenhafen, an attempt was made to estimate the percentage of parasitism of the eggs at different periods. Egg cases were collected from widely separated portions of the plantation, and the leaflets on which they were laid were kept in water for 10 days to allow any parasites which might be in the eggs to develop to a point where they were easily distinguishable. Laying of eggs in the field by this generation of beetles began about 20th May, 1938, and hatching of parasites from these eggs began about 9th June. Results of the examinations of eggs collected at three different times are :—

6th June, 1938—30 per cent. of eggs parasitized.

20th June, 1938—80 per cent. of eggs parasitized.

3rd July, 1938—100 per cent. of eggs parasitized.

Hence we see that about six weeks after egg-laying began 100 per cent. of the eggs were parasitized, and this could explain the restriction of overlapping of generations to about that period.

In 1956 I followed some of the above steps taken by O'Connor, mainly at Vunakanau. My results are not quite as striking as his, but an increase in parasitism was clearly noted. My figures are shown in Table V.

Anastatus sp.

This encyrtid wasp is about the same size as *C. splendens*, and is of a brilliant blue-black colour. It has been reared from the eggs of *P. papuana* in the Manus and Lindenhafen areas.

Achrysocharella orientalis Ferriere

This species is apparently a hyperparasite, and therefore not beneficial. It was described (1933) from a *Promecotheca* from Java, taken by R. W. Paine. One was reared from a *P. papuana* larva at Lindenhafen, and another was taken on a first-instar larval mine at Vunakanau, both by me in 1956. This apparently constitutes a new record for New Britain (Burks identification).

Other internal parasites

One other parasite of the larva of *P. papuana*, whose habits are similar to those of *P. parvulus*, has been found in Manus by O'Connor. Two species of minute hyperparasites were found by O'Connor, one in Manus and one at Rabaul, both reared from the egg parasite *C. splendens*. I noted a possible dipteran parasite, but this was not adequately verified.

RELATIONSHIPS WITH ANTS

From my study it has become apparent that ants are of the greatest importance in relation to the population balance of *Promecotheca*, more so than earlier believed. Several species have been observed as predators, particularly of eggs of the beetle. Others are also larval or even adult predators, and at least one species is detrimental from the standpoint of preventing invasion by other ants useful in controlling the beetle.

Oecophylla smaragdina (Fabricius), (*the "Kurukum"*)

This ant has a very definite adverse relationship towards *Promecotheca.* There is fairly-general (often very distinct) correlation between the presence of kurukums and the absence of *Promecotheca.* This was observed repeatedly when searching for *Promecotheca* at Linga Linga and Lindenhafen. In May, 1954, Ardley correlated presence of kurukum ants on palm trunks at Linga Linga with palms not seriously affected, when nearly all other palms were badly affected (see Table VI) and this was further verified by Ardley and myself at Linga Linga in 1956.

At Vunakanau, where the area east of the manager's house in general was very badly affected to the extent of complete browning of all but the newly-emerging fronds, a number of palms were green and almost unaffected by the beetle. Of one group of six adjoining palms, all of which were green, four had kurukums in numbers going up and down the trunks. The other two were climbed and proved to be swarming with Kurukums. A few days later kurukums were noted on the trunks of these two palms also. The crowns of these palms were partly in contact, and presence of large numbers of kurukums in a palm crown cannot always be ascertained by merely examining the trunk.

Of another nearby group of five palms, which were largely green, all had numbers of kurukums running up and down the trunks or into a large cacao tree with leaves touching the trunks.

These cases, and those observed by Ardley, all involved mature palms. In the case of young palms, the correlation is not always so distinct. This I believe to be at least in part a result of the fact that kurukums observed in young palms may be there transitorily, or may have just recently established colonies and not yet evicted the *Promecotheca.* Small populations of kurukums obviously have a lesser effect on the occurrence of the beetle in palms.

TABLE VI.—Relationship of *Oecophylla* (kurukum) to *Promecotheca* damage, Linga Linga (after Ardley).

ANALYSIS OF 1,000 PALM SAMPLES, BASED ON TRANSECT TOTALS, MAY, 1954

Category	Degree of damage	Per cent. of palms	Per cent. of palms with kurukums
1	Palms unattacked by *Promecotheca*; full crown; full production; flowers to mature nuts	10.8	97.5
2	Palms partly damaged; full crown; 50 per cent. clean fronds; full production; flowers to mature nuts; production could be maintained if *Promecotheca* controlled	13.3	61.4
3	Palms severely damaged; full crown; 25 per cent. clean fronds; 75 per cent. production; flowers to mature nuts, but nuts will fall to nil	12.5	63.7
4	Palms partly defoliated; 50 per cent. crown; 25 per cent. clean fronds; 10 per cent. production, will fall to nil	19.2	30.4
5	Same as (4), but no nuts remaining	9.6	27.3
6	Palms more defoliated; 40 per cent. crown; 20 per cent. clean fronds; no nuts or flowers	17.0	17.1
7	Same as (6) but with signs of re-attack by *Promecotheca* on green fronds	1.7	0.0
8	Replantings and omissions	15.9	
		100.00	

NOTE.—It should be emphasized that the outbreak at Linga Linga was about over when Ardley's survey was made, and most of the palms contained no active *Promecotheca.* Thus the kurukums could have moved after the beetles were active.

Stanley (1938) failed to observe kurukums attacking beetles in infested palms, and O'Connor stated that he observed large numbers of kurukums passing along frond midribs while *Promecotheca* adults fed or oviposited undisturbed on the leaflets. I believe that such cases occur when the kurukums are migrating, or when they are busily engaged in tackling some major problem and are not carrying out general foraging. My data showing how seldom kurukums and *Promecotheca* are found in the same palms are presented in Table VII.

TABLE VII.—Relationship of *Oecophylla* (kurukum) to *Promecotheca,* 1956.

Plantation	Number of palms checked		Palms with............			
	Total	Young palms	Neither Promecotheca nor Oecophylla	Promecotheca, but no Oecophylla	Oecophylla, but no Promecotheca	Both Promecotheca and Oecophylla
Linga Linga	212	66	66	120	26*	0
Volupai	82	81	7	70	5	0
Lindenhafen	106	58	3	91	5	7*
Vunakanau	153	79	4	125	22	4

* The figures in next to last column include some cases where kurukums were present in palms with old adult *Promecotheca* feeding marks, or in a few cases with beetle eggs. The figures in last column in most cases represent palms with very few kurukums present.

Few positive observations have been made of kurukum predation upon *Promecotheca* yet the indirect evidence is strong and tests made in the field seem to add weight to these conclusions. In one instance, most of the egg cases, numbering hundreds, on a new frond of a young palm at Vunakanau were observed to be disappearing while under daily observation. Some new kurukum nests had just been established between a series of leaflets of the same frond. It is well recognized that few insects occur in numbers where kurukums are abundant.

Tests were made of reactions of kurukums to *Promecotheca* by releasing adult beetles on a coconut frond midrib, or near the bases of leaflets, where kurukums were going to and fro. Some of the beetles took immediate flight and escaped to a part of the palm lacking kurukums, while others flew into the presence of other kurukums and were caught and the remainder was caught by the ants before they could take flight. Several were caught by an antenna or leg by a single kurukum and held till other ants seized the other appendages. Then the beetle was simply held with its appendages stretched in all directions until it died. In one case the antennae were pulled with unequal force (Plate 6) so that the head was pulled off and promptly carried off while other ants later carried the body away.

I believe that kurukums both catch and chase away adult beetles, preventing them from laying many eggs in a palm well populated with the ants. They also chew away eggs when the ants invade beetle-inhabited palms. This ant is well known for its belligerency and will attack almost any invader. Once at Vunakanau I observed a large number of kurukums holding a dead rat on the midrib of a young palm. The rat remained there for several days, constantly held by many ants, as it gradually dwindled in size from being fed upon.

Kurukums were found at Linga Linga in palms of all conditions, from healthy to storm-felled, except for some of the very young or very unhealthy palms.

Monomorium floricola Jerdon

This minute, slender, black ant was several times observed singly or in small groups to be chewing in *Promecotheca* egg-cases. The cases, which were frequently found with small irregularly-chewed holes, were thought to be mainly the result of predation by this ant. *M. minutum* Mayr, *M. floricola,* and *Tetramorium guineense* Fabr. were reported by Froggatt and O'Connor (1941) to attack larvae in mines.

Technomyrmex albipes (Fr. Smith)

This very abundant, medium-small black ant was commonly found in palms infested by *Promecotheca.* It is probably one of the most important predators of *Promecotheca* eggs, and possibly also of the larvae. It may be the ant recorded by O'Connor as *T. detorquens* Walker.

Polyrhachis rastellata and P. sp.

These two large ants, shiny black and silvery grey-black respectively are often found in palms infested with *Promecotheca,* the ants making small nests of debris and silk on undersides of leaflets. Though insufficient positive observations were made, these may be predators of some importance. They are active and fairly belligerent ants. The latter species was particularly abundant at Linga Linga.

Camponotus papua Emery

These moderately large, shiny, reddish-brown ants, common in New Britain, are frequently found in coconut crowns, often nesting at the bases of leaflets. They are also thought to be *Promecotheca* predators.

Tapinoma melanocephalum Fabr.

This species was reported by Froggatt and O'Connor (1941) to attack larvae in mines.

Pheidole megacephala Fabr.

This medium-small, black ant was reported by Froggatt and O'Connor as being the most important local ant predator of larvae in mines. It also attacks the egg-cases, although I did not see as many as other workers have mentioned.

Cremastogaster sp.

This slender pale ant was occasionally found near *Promecotheca* egg-cases or mines, and is believed to be a minor predator.

The combined effect of predators, mostly ants, on egg-cases is shown in Table VIII.

Iridomyrmex aff. myrmecodiae

This small, reddish ant, a fierce biter, is common in coconut plantations. It builds long, slender nests of the grass-like pubescence on new palm petioles. The nests are often on the new leaf-shoots, or along the frond midribs. This ant is generally represented by large populations localized in certain palms and is often in the minority in New Britain. When *Iridomyrmex* is present, other ants are generally not found in the same palm.

The presence of *Iridomyrmex* does not seem greatly to affect the prevalence of *Promecotheca.* If this ant is not a predator of *Promecotheca* eggs or larvae, as are several of the common ants in the coconut plantations, then it is definitely not beneficial from the plantation standpoint, as far as *Promecotheca* is concerned, for it deters other ants, which are predators. *Iridomyrmex* is common in other palms, particularly on the

PLATE 6.—*Kurukum ants* (*Oecophylla*) *decapitating an adult beetle.*

TABLE VIII.—Predation upon oothecae and mines of *Promecotheca*

Data	Oothecae (egg cases) Number sampled	Per cent. predated (mostly by ants)	Mines predated	Agent
Vunakanau—				
14th May, 1956	135	33.3	6	earwig
14th May, 1956	385	57.1	22	miscellaneous
15th May, 1956	1,100	42.0	5	birds
19th May, 1956	250	40.0		
21st May, 1956	260	39.2		
22nd May, 1956	785	14.6		
26th May, 1956	157	7.0	2	?
19th July, 1956	125	23.2	1	bird
Taliligap—				
16th May, 1956	371	34.2		
4th July, 1956	80	27.5	3	?
Volupai—				
16th April, 1956			2	parrot
Lindenhafen—				
25th April, 1956			3	birds ?

NOTE.—In some cases new eggs were examined, and a more extended observation would have given higher counts of predation.

new leaf shoots. This ant in Bougainville and the British Solomons is responsible for coconut nutfall by deterring other ants, particularly the kurukum, which in turn deters the *Amblypelta* bugs, which cause the nutfall.

OTHER PREDATORS

Vertebrates

I believe the importance of vertebrate predators upon *Promecotheca* has been overlooked in New Britain. Various lizards, particularly skinks, and also geckos and others are abundant in the plantations, and those frequently seen in the crowns undoubtedly feed upon the adult beetles. Several lizards kept in captivity at Vunakanau fed upon adult beetles. Taylor (1937) reasoned that in Fiji mines were observed to be torn open with the larvae removed were the result of predation by a species of lizard, but similarly ravaged mines in New Britain I believe are at least partly the result of feeding by birds, probably parrots.

It was noted that at Linga Linga and Lindenhafen the malip parrot (*Domicella* sp.) was exceedingly abundant, whereas it was absent, or nearly so, from the Vunakanau area. At Volupai a pet malip tore open some mature larval mines I was observing, apparently eating the larvae. The marks left by this action—a doubt slit in the dorsal surface of the mine—were identical with those observed a number of times in central New Britain. Marks of this nature were seldom found at Vunakanau. Possibly some other birds may also be of importance as predators of the beetle.

Earwigs

Frequently, in examining old mines, living or dead earwigs were found inside. They had entered through roughly chewed, rounded holes on the undersides of the mines, quite different from the clean-cut crescentic dorsal emergence holes of the adult beetles. No observations were made that prove that the earwigs are actual predators upon larvae or pupae and they may be mainly scavengers. However, O'Connor believed they were predators, and this is probably true.. The same earwig is a known predator upon larvae and pupae of *Brontispa*. One adult earwig, confined with an adult *Promecotheca*, killed the beetle. Another may also have done so, though it first killed a young earwig in the same container. It is unlikely that earwigs often feed upon adult beetles, except possibly females ovipositing within a newly unfolding leaflet or in mines before emergence. An earwig catches living prey by seizing it with its caudal forceps and then chewing it while still holding it with the pincers.

Miscellaneous predators

A predatory pentatomid-bug, *Amyotea reciprocus*, was noted by Simmonds (1924) and others as a predator of adult beetles, but I did not observe it. A predaceous pyrrhocorid-bug, not yet identified, appears to be a general predator of adult insects (and also of snails) in this region, but it is more often found around logs and trunks of trees. One was seen feeding upon a cacao capsid. A fly of the genus *Drapetis* (Empididae) appeared to be sucking the body fluid of a first-instar *Promecotheca* larva through the epidermis, at Vunakanau. Another small fly, possibly a heleid, appeared to be feeding on an adult beetle. Dragon-flies undoubtedly catch some adults flying around palm crowns.

Mites

A trombidiiform mite, possibly a predator, was found in an ootheca. Mesostigmatid mites were found on adult beetles, but are probably of no particular harm unless occurring in large numbers. Oribatid and pterogasterine mites found in mines were probably scavengers or fungus feeders. *Pyemotes,* as discussed above, was rare.

Diseases

As noted by O'Connor, there are fungal, bacterial, and perhaps other diseases of larval or adult beetles. It is possible that a virus or other disease of the adult beetle may be partly responsible for the rapid diminution in adult populations during high population one-stage outbreaks. A disease of this nature becoming prevalent only at such times, however, would probably tend to maintain the one-stage condition, rather than reduce damage to palms. Under high population conditions the elimination of even a very high percentage of the adults will not greatly reduce the population of the next generation, as long as a small proportion of the eggs laid can develop to maturity. A fungus, *Synnematium jonesii,* is reported as attacking larvae in the mines (Lepesme, 1947).

ARTIFICIAL CONTROL MEASURES

No truly satisfactory artificial control measures against *Promecotheca* have been devised. The use of arsenicals, derris, D.D.T., etc., could be undertaken with high-power spraying equipment, but would most likely be uneconomic, except as a drastic measure to thwart an outbreak build-up. In general, it would be safe to assume that chemical treatment would do more harm to parasites than to the beetle. In the case of the build-up of a one-stage outbreak, the ineffectiveness of parasites might justify action.

Some control and purported offsetting of an outbreak has been attributed (Stanley, 1938; Froggatt, 1939) to the burning of infested leaflets by the use of burning oil in half coconut shells attached to the ends of long bamboos, with two ropes attached near the top to control operation from the ground.

STATUS OF POPULATIONS AND OUTBREAKS

To put on record data of possible historical or comparative value, brief sketches are here presented of the status of *Promecotheca* populations and damage at the five principal plantations in New Britain, where I observed *Promecotheca,* during April and May, 1956. Brief observations were also made at the last two in July, 1956, and October, 1957. Linga Linga and Volupai are on the north coast of New Britain, Lindenhafen is on the south coast, and Vunakanau and Taliligap are on the Gazelle Peninsula west of Rabaul Harbour.

Linga Linga

The outbreak, which started in 1953, must have ended in 1955. The effect was still evident in 1956 in copra production, visible gross effect on palms, and in the remaining old mines and adult feeding marks on the older fronds. Thus most of the palm crowns were green above and brown beneath. The beetle population in April, 1956, was exceedingly low, and in the normal multi-stage condition. Very little new evidence of the beetle was found on mature palms. Most of the new eggs, living larvae and adults were found on very young palms, most of which were near the manager's house and No. 1 drier. Four distinct constrictions are seen on many palms, representing four outbreaks. The previously-recorded one was in 1940 - 1941 (Richards), with an earlier one reported in 1923 (Simmonds, 1938). There must have been another one about 1910. Beetles were reported to be abundant in 1933 and gone again by 1935 (Richards). No egg parasites were noted in the few egg-cases seen. Of larval parasites, *Apleurotropis* was more abundant than *Pediobius,* with an apparent ratio of three to one. *Eurytoma* was found in smaller numbers. Ardley (1954) detailed the status of palms near the end of the outbreak.

Volupai

The beetle population at Volupai was larger, in April, 1956, than that at Linga Linga. Again, adults and mines were observed mostly on very young palms. Only one mature palm was sampled, but this was singled out by plantation workers as particularly infested. It showed considerable activity of some months earlier, with many old mines, old aborted mines, and adult feeding. There had been no noticeable outbreak. There seemed to be no distinct evidence of tendency towards the one-stage condition.

Lindenhafen

The outbreak here, like that of Linga Linga dating from 1953, had ended some months before my visit in April, 1956. Damage here was more complete than at Linga Linga. Copra production was just starting again in 1956, copra being worked every other month. As at Linga Linga and Volupai, *Promecotheca* was multi-stage, found principally on quite young palms, and as at Linga Linga almost none was found on mature palms, although plenty of evidence of old work remained on lower fronds. The active population was not localized, but spread in most areas with young palms. Often five to 20 adults, and similar numbers of active mines, were found in a single young palm, but they were not present in all of them. A recently-burned area near the manager's house seemed free of the beetle.

PLATE 7.—*Constrictions on coconut palm trunks at Lindenhafen, indicating former outbreak periods.*

The beetle was more abundant at the village, Lulakuni, across the mouth of the stream at the west end of the plantation, but was absent or nearly so on the offshore islands. This was apparently also true during the outbreak.

As at Linga Linga, marks of three outbreaks before the last existed as widely-spaced constrictions on palm trunks (Plate 7). These are not so general as at Linga Linga, but are quite evident in some areas, as near the beach at the point.

Pediobius seemed to be the most abundant parasite. Among submature and mature larvae, and pupae, parasitism was low. There was evidence of moderately high incidence of egg parasitism. The preceding documented outbreak was that of 1936-1938 (Murray, O'Connor). There was also said to have been one in 1928 and possibly one between 1941 and 1945. In December, 1956 (Dun, pers. comm.), a small outbreak in one-stage condition was reported for the first few rows of palms from the beach, both at Lindenhafen and Ring Ring Plantations, with adults up to 100 in number per frond.

Vunakanau

There was a serious outbreak here, with very dense population in limited parts of the plantation (Plate 8), but with very few beetles in other parts. The outbreak was obviously in the one-stage condition when first observed (20th April, 1956, Ardley and Dun ; 2nd May, Gressitt). It was noticed in late 1955, but not reported until April, 1956. In early May there were almost no active mines, but only adults and newly-laid eggs. At the end of May, the situation was not so distinct, as larvae of nearly all ages could be found and even a few pupae and a very few new adult emergence holes. During the month, the adult population fell off very rapidly. This proves that the average life-span of an adult in the field is much shorter than with caged individuals.

At the end of May it appeared as if the one-stage condition would have to break down rapidly, with new adults emerging and some adults from the previous generation still living.

PLATE 8.—*Badly damaged coconut palms at Vunakanau, Gazelle Peninsula.*

However, the old generation apparently began to die off even more rapidly, and egg-parasitism approached 100 per cent. Far more eggs had been laid on the newest fronds than could possibly develop on them. The beetles were more abundant on mature palms than on young palms. In late April there were a few hundred adult beetles in each of many young palms, while there were a few thousand in each of many infested mature palms, or 200 per frond. Figures for eggs, during May, and mines, at end of May, were analogous. According to Dun (pers. comm.) the damage was more marked in November, 1956, but by then most palms had a few new green fronds, and beetle population was reduced.

The one-stage condition probably terminated early in 1957, and the population had very markedly declined by June, 1957. In December, 1956, many aborted mines were noticed by Dun. In October, 1957, I noted a much reduced population, consisting of all stages, with the population somewhat differently distributed and a little more abundant in young palms at the upper edge of the plantation, near Malmalwan. In January, 1958, Dun noted that, except for some young palms, most palms had revived and were bearing well. Parasitism of larvae and pupae by *Pediobius* was more than 80 per cent. in late April, 1956, and of eggs by *Closterocerus* was fairly high in late May (see Table V). *Apleurotropis* was actively parasitizing young larvae, and *Eurytoma* was scarce.

Taliligap

The outbreak in this small plantation, a short distance from Vunakanau and slightly higher and wetter, was not noticed until May, 1956, during the study at Vunakanau. It was a little behind that of Vunakanau in intensity, but very slightly ahead in chronology of the one-stage condition. New adults appeared earlier at Taliligap and there were more mature mines before end of May. The rate of parasitism seemed slightly lower than at Vunakanau. This might suggest that the infestation started at Vunakanau and spread to Taliligap. However, the beetle's weak spreading potential also suggests that the two outbreaks started independently, from some general climatic change or upset of parasite or predator balance.

On 16th May, 1956, one frond of a 20-year-old palm bore 25 apparently healthy egg-cases, 20 cases with emergence holes of egg-parasites, two cases with hatched eggs, and 55 cases with eggs chewed up by predators, probably ants. Another frond had 36 apparently healthy egg-cases, 12 cases with emergence holes of parasites, three cases hatched and 16 cases chewed by predators. In November, 1956, Dun noted that browning of fronds was more marked, but there was little evidence of nutfall. The outbreak was still one-stage, but most eggs were predated or parasitized. In October, 1957, I noted that the palms looked better, that young palms had some mines, partly aborted, and some new egg-cases.

Other plantations

Witu Island is said to have had an outbreak in 1935 covering 50 hectares, with some nutfall. In 1937, Kabaira Plantation, on the north coast road, Gazelle Peninsula, was affected by the volcanic eruption. One-half the plantation was affected by ashes and this same half suffered from *Promecotheca* from six to nine months after the eruption. A small localized infestation exists by the road near the manager's house and this population is said to increase every one and a-half to two years. Mandras Plantation, Bainings, Gazelle Peninsula, is said to have had a small outbreak in 1956. Vuvu Plantation, Gazelle Peninsula, had one reported in 1955. Vunakambi Plantation, Gazelle Peninsula, was an area where, during German times, kurukum ants were used to control an outbreak of the beetle. Davuan, Gazelle Peninsula, is said to have had an outbreak in 1936. Bialla Plantation, north-central coast of New Britain, had a moderate outbreak in 1956, involving five per cent. of the plantation, with parasitism increasing rapidly in 1957. Worst-affected parts were near the beach and the wettest part over an underground river.

COPRA PRODUCTION

Reduction of copra production during and following *Promecotheca* outbreaks is conspicuous, although not always borne out clearly from the production statistics. Several factors are involved, such as premature nutfall, which sometimes temporarily increases production, more intense copra-cutting on non-infested off-shore islets or border areas and purchase of trade copra. Dun (1955) reported a 30 per cent. loss of copra production at Linga Linga, and a 50 per cent. loss for Lindenhafen at the start of the last outbreak period. However, as he predicted, the loss later increased.

CLIMATE

The average rainfall (for 17 years) for Lindenhafen is 258.55 inches per year, and for Talasea (near Linga Linga) is 168.28 inches.

TABLE IX.—Rainfall figures (inches) for main New Britain outbreak areas.

	17-year averages		
	Lindenhafen	Talasea (N. coast)	Malmalwan (Gazelle P.)
January	7.31	32.37	10.09
February	6.28	26.68	8.44
March	6.23	24.47	9.91
April	11.18	20.29	10.75
May	26.98	7.93	8.11
June	34.29	5.37	1.08
July	41.68	4.99	5.99
August	46.64	4.90	1.97
September	33.48	4.23	.69
October	21.32	7.26	1.52
November	14.53	8.89	6.95
December	8.63	19.90	8.26
Total annual	258.55	168.28	73.76

For Rabaul it is 89.73 and for Keravat it is 105.76. Vunakanau is between Rabaul and Keravat, but its rainfall is closer to that of Rabaul. In 1955, the rainfall at Malmalwan (very near Vunakanau) was 73.76 inches (see Table IX). This shows that a long, dry period preceded the outbreak at Vunakanau. However, the annual totals for Lindenhafen preceding the serious 1937 outbreak show a long, wet period, as indicated in Table X. Also, as shown in the table, the annual cycle of rainfall at Lindenhafen and Talasea is almost opposite. The 1956 rainfall total for Malmalwan (Vunakanau) was 85.85 inches. The 1957 rainfall was still higher. Humidity is slightly higher at Lindenhafen and Linga Linga than at Vunakanau, but all have a high humidity.

TABLE X.—Annual rainfall (inches) at Lindenhafen preceding 1937 outbreak :—

1934—214.32.

1935—298.62.

1936—268.48.

1937—308.60.

CONCLUSIONS

It is felt that until the main factors contributing to the development of an outbreak are understood, adequate steps to prevent outbreaks cannot be recommended. However, certain precautions, such as the encouragement and protection of lizards, birds, the kurukum ant, and most other ants, should be in order, and may at the same time help to curb other coconut and cacao pests.

Periodical examination of random palms in the plantations for detection of early stages of a developing outbreak could make it possible to effect control before serious damage is done, by using insecticides to kill the adults and cutting down of fronds bearing eggs and mines. It is undesirable to burn fronds bearing eggs or young mines, as the larvae cannot mature when the fronds die, and burning would only result in killing the parasites, most of which would emerge from these stages even after cutting of fronds. Fronds bearing mature mines should be burned or thrown into the sea, unless they can be put in screened containers permitting the escape of parasites but not beetles. Ardley suggested an itinerant extension worker to be on the look-out for incipient outbreaks while visiting plantations.

There is a need for information, which might be obtained during the build-up of an outbreak, to assist in the solution of the general problem.

Knowledge of the other species of *Promecotheca* in the New Guinea-Solomons area might bring to light parasites or predators in nearby areas which might be tried in New Britain to help prevent outbreaks. A better understanding of the general ecology of *Promecotheca papuana* will be required before effecting such introductions. New Guinea is the centre of distribution of the genus *Promecotheca.*

REFERENCES

ARDLEY, J. H. 1954. *Promecotheca* report. Typescript, 29 pp. (Copies in D.A.S.F., Port Moresby, and Bishop Museum, Honolulu.)

BURKHILL, I. H. 1918. *Promecotheca cumingii* Baly, another coconut hispid and pest in Malacca. The Gardens' Bull., Straits Settlements 2 (1) : 3-5.

COPELAND, E. B. 1914. The coconut. MacMillan. (1931, 3rd ed.).

DUN, G. S. 1955. Economic entomology in Papua and New Guinea 1948-1954. P.N.G. Agric. Jour. 9 (3) : 1-11.

DUN, G. S. 1956-1957. Personal communications.

DWYER, R. E. P. 1937. The diseases of coconuts (*Cocos nucifera*) in New Guinea. N. G. Agric. Gaz. 3 (1) : 28-93.

FERRIERE, C. 1933. Chalcidoid and proctotrupoid parasites of pests of the coconut palm. Stylops 2 (5) : 97-108.

FERRIERE, C. 1939. Chalcid flies attacking noxious beetles in India and New Guinea. Bull. Ent. Res. 30 (1) : 163-168.

FRIEDERICHS, K. 1920. Weberameisen und Pflanzenschutz. Tropenpflanzer 23 : 142-150.

FROGGATT, J. L. 1936. Entomological notes ; Some insect pests recorded from the Mandated Territory of New Guinea. N. G. Agric. Gaz. 2 (1) : 10-14, 15-18.

FROGGATT, J. L. 1937. *Promecotheca antiqua* Wse. Leaf pest of coconuts. N. G. Agric. Gaz. 3 (2) : 21-22.

FROGGATT, J. L. 1939. The coconut leaf-miner *Promecotheca papuana,* Csiki (*antiqua,* Wse.). N. G. Agric. Gaz. 5 (1) : 1-10.

FROGGATT, J. L. 1940. Entomologist's report. N. G. Agric. Gaz. 6 (2) : 9-13.

FROGGATT, J. L. AND B. A. O'CONNOR. 1941. Insects attacking the coconut palm in New Guinea, II. N. G. Agric. Gaz. 7 (2) : 125-133.

FROGGATT, W. W. 1914a. Pests and diseases of the coconut palm. New South Wales Dept. Agric., Sci. Bull. 3rd ed. 2 : 1-63 (1912, 2nd ed. 2 : 1-47).

FROGGATT, W. W. 1914b. Australasian Hispidae of the genera *Bronthispa* and *Promecotheca* which destroy coconut palm fronds. Bull. Ent. Res. 5 : 149-152.

GIRAULT, A. A. 1938. Descriptions of a few new parasites of pests, Australian mostly. Queensland Naturalist, Brisbane, 10 : 74-77.

GRESSITT, J. L. 1953. The coconut rhinoceros beetle, *Oryctes rhinoceros,* with particular reference to the Palau Islands. Bishop Mus., Bull. 212 : 1-157.

GRESSITT, J. L. 1957. Hispine beetles from the South Pacific. Nova Guinea 8 (2) : 205-324, 32 figs.

GRESSITT, J. L. 1957a. Hispine beetles of the coconut palm. Proc. 8th Pacific Sci. Congr. 3A : 1,539-1,545.

GRESSITT, J. L. 1958. The ecology of *Promecotheca papuana,* a coconut beetle. Proc. 10th Int. Congr. Ent. 2 : 747-753.

GRESSITT, J. L. 1959a. Host relations and distribution of New Guinea hispine beetles. Proc. Hawaiian Ent. Soc. 17 (1) (in press).

GRESSITT, J. L. 1959b. Beetle pests of the coconut palm in the New Guinea area. Proc. 9th Pacific Sci. Congr., Bangkok, 1957 (in press).

JONES, C. R. 1913. The coconut leaf-miner beetle (*Promecotheca cumingii,* Baly). Philippine Agric. Rev. 6 : 228-233 (also 6 : 105-106).

KALSHOVEN, L. G. E. 1951. De plagen van de cultuurgewessen in Indonesie. 2 : 356-359.

KALSHOVEN, L. G. E. 1957. An analysis of ethological, ecological and taxonomic data on Oriental Hispinae (Coleoptera, Chrysomelidae). Tijdschr. voor Entomologie 100 (1) : 5-24.

KOWALSKI, J. 1917. Un ennemi du cocotier aux Nouvelles-Hebrides. Ann. Service des Epiphytes, Paris 4 : 286-327.

LEPESME, P. 1947. Les insectes des palmiers. Paul Lechevalier, Paris. 903 pp. (see pp. 554-563).

LEVER, R. J. A. W. 1933. The coconut leaf-beetle of the Santa Cruz Group. British Solomon Is. Prot. Agric. Gaz. 1 (4).

LEVER, R. J. A. W. 1938. Entomological notes. Agric. Jour. Fiji 9 (4) : 12-18.

MURRAY, G. H. 1937. Outbreak *Promecotheca antiqua*—Lindenhafen Estate. N. G. Agric. Gaz. 3 (2) : 1-2.

O'CONNOR, B. A. 1940. The coconut leaf-miner *Promecotheca papuana,* Csiki, and its parasites. N. G. Agric. Gaz. 6 (2) : 20-30.

PAGDEN, H. T. AND R. J. A. W. LEVER, 1935. Insects of the coconut palm and the present position of the coconut problem in the British Solomon Islands Protectorate. B. Solomon Is. Prot. Agric. Gaz. 3 (1) : 2-22.

PREUSS, P. 1911. Uber Schadlinge der Kokospalme. Tropenpflanzer 15 (2) : 59-91 (see pp. 80, 81).

RICHARDS, A. 1956. Records of Custodian of Expropriated Property, Rabaul, 1932-1942 ; 1947. Typescript.

RISBEC, J. 1935. Note preliminaire sur les principaux parasites du cocotier aux Nouvelles-Hebrides. Ann. Soc. Ent. France 104 (2) : 159-173.

SIMMONDS, H. W. 1924. Report on mission to New Guinea, Bismarcks, Solomons and New Hebrides. Legislative Council, Fiji ; Council Paper, Suva, 13 pp.

SIMMONDS, H. W. 1938. Coconut pests and diseases in Melanesia and southern Polynesia. Dept. Agric., Fiji, Bull. 20 : 1-40.

STANLEY, G. W. 1938. Patrol notes. *Promecotheca* outbreak—Talasea. N. G. Agric. Gaz. 4 (1) : 37.

TAYLOR, T. H. C. 1937. The biological control of an insect in Fiji. Publ. Imp. Inst. Ent., London, 239 pp.

ZACHER, Fr. 1913. Die Schadlinge der Kokospalmen auf den Sudinsel. Arb. Kaiserl. Biol. Anstalt f. Land—und Forstwirtschaft 9 (1) : 73-119.

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