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Feeding Behaviour and Enemies of Rhaphidophoridae (Orthoptera) from Waitomo Caves, New Zealand

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Abstract

RHAPHIDOPHORIDS are scavengers and omnivorous in their diet, as their gut content always includes both plant and animal remains. Fungi and animal food can be obtained inside caves; but mosses, liverworts and angiosperms are also eaten, and in many cases Rhaphidophorids must seek these in the epigean region. However, where a river flows through a cave, plant debris is washed inside and left stranded on the walls or the surface of the water. Where electricity has been installed in caves, mosses and ferns are able to grow near the light source. In both cases they form a food supply for the insects making it unnecessary for them to go outside the cave. In other parts of the world, Trichoptera and Lepidoptera form most of the animal portion of the diet of Rhaphidophoridae, but they have never been found in the faeces of New Zealand members of the family, where the hemipteran *Scolypopa australis* Walker, the dipteran *Anatopynia debilis* (Hutton) and Rhaphidophorids themselves are eaten instead. Rat faeces also form a part of their food supply. In the bush, Rhaphidophorids show a preference for ferns and rata. The main enemies of Rhaphidophorids are glow-worms, spiders and opiliones.

INTRODUCTION

DURING 1955 a study was made of the biology, habits and ecology of two species of cave-wetas, *Gymnoplectron waitomoensis* (Richards) and *Pallidoplectron turneri* Richards, living in limestone caves at Waitomo. The paper is concerned with the feeding behaviour and enemies of *G. waitomoensis* and *P. turneri* in these caves. Previous findings by the author and overseas workers (Richards, 1954a; Remy, 1931; Jeannel, 1926 and Chopard, 1938) have shown that the Rhaphidophoridae are primarily scavengers.

FEEDING BEHAVIOUR

Until this study was commenced very little was known about the feeding behaviour and habits of cave-wetas in New Zealand. Information obtained from examination of faecal material led to a more detailed study of the feeding habits of these insects.

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Examination of Faecal Material

In November, 1954, faeces of *Pallidoplectron turneri* from the Grotto of Waitomo Cave were found to contain the remains of a liverwort leaf, with chloroplasts still distinguishable; a whole moss leaf and stem; and other remains of mosses and liverworts. As no moss or liverwort grows inside the Grotto, it was assumed that they must have been eaten outside the cave entrance. Also found in the faeces were green algae, which grow on the walls of the cave; angiosperm remains, consisting mostly of leaves showing spiral, scalariform and pitted vessels; Capnodiaceae hyphae; and chitinous animal tissues covered with setae.

The faeces of *Gymnoplectron waitomoensis* from the Side Branch of Ruakuri Cave were also studied. They consisted primarily of moss, with a few pieces of angiosperm leaf, recognisable by irregular stomata and pitted vessels. *G. waitomoensis* do not occur near the stream in this cave, so it was assumed they fed on the numerous trees and shrubs growing around the cave entrance (Plate 1, fig. 2).

During May and June, 1955, the Grotto of Waitomo Cave (Text-fig. 1) was flooded several times for considerable periods. Each time the water subsided sufficiently to permit inspection of the tunnel, all the debris which the stream had washed into the cave was found stranded on the walls or floating on the surface of the water, and *P. turneri* could always be observed feeding on this. In particular, they seemed to prefer grass, as was the case with all *Gymnoplectron edwardsii* (Scudder) collected from Stephens Island (Richards, 1954a). This suggested that the presence of angiosperm remains in the wetas' alimentary tracts was due to the wetas eating twigs, leaves and flowers swept into the cave by the stream, rather than through the wetas climbing trees outside the cave at night in search of them.

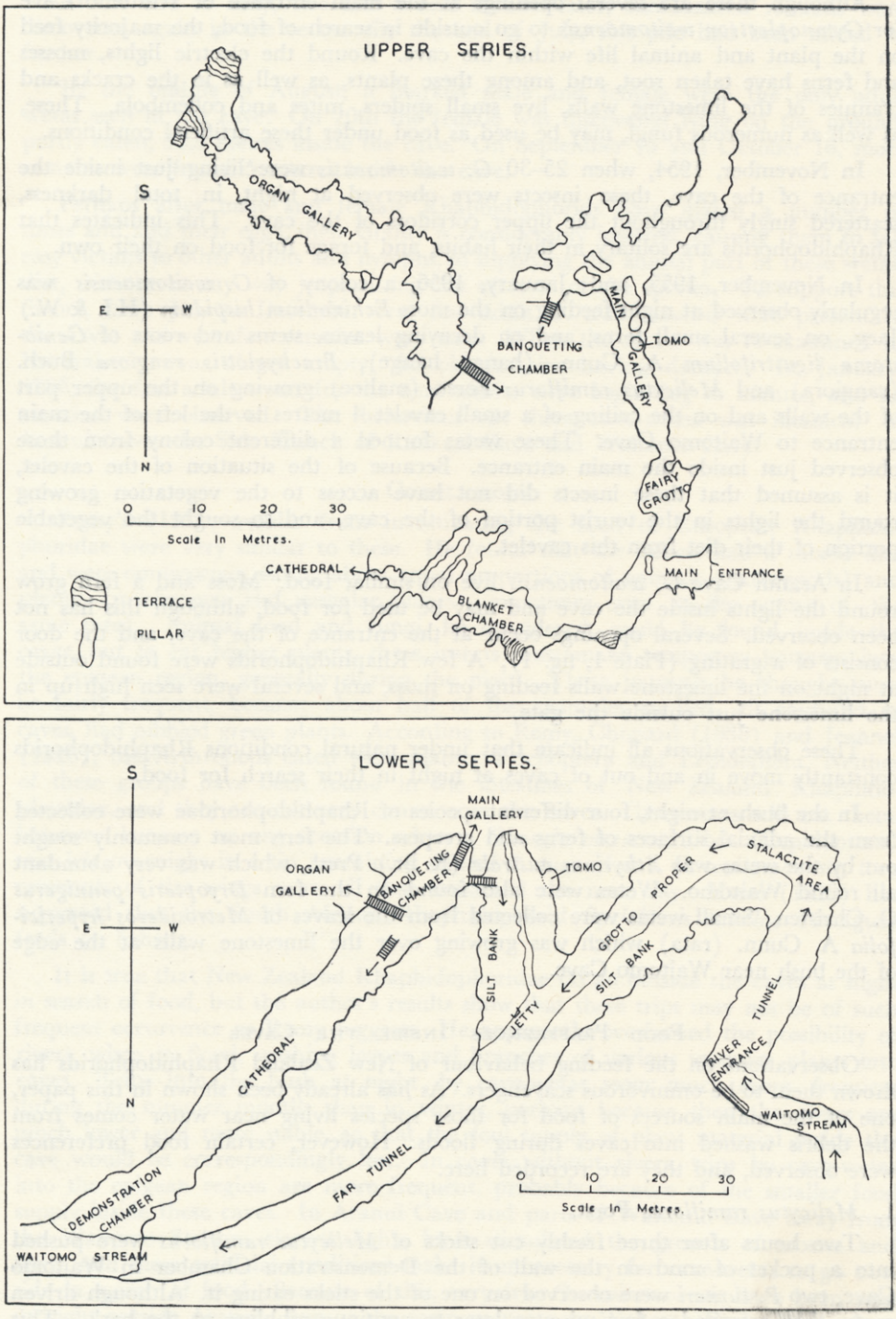
At the end of February, 1955, the stomach-content of three *P. turneri* collected from the far tunnel, about 160 metres from the river entrance, yielded only a little fresh-water algae. The alimentary tracts in all cases were flat and empty, showing that the wetas had not eaten for some time. There had been no floods for over four months to wash fresh debris into the cave, so the insects must have remained in that particular part of the cave.

Examination of Saliva

On being captured, several of the *Gymnoplectron waitomoensis* from Aranui Cave emitted from their mouths large quantities of either a dark brown or a colourless fluid. In nearly all cases the wetas were males. They kicked furiously, seemed very agitated, and their jaws moved continuously. Examination of a smear under the microscope showed numerous fungus spores and septate mycelia of a basidiomycete. The results from examining this fluid were very different from those obtained from specimens of *G. edwardsii* where the fluid was full of actively swimming flagellates (Richards, 1954b). It seems that when annoyed, Rhaphidophorids regurgitate a fluid which consists partly of saliva and partly of their last meal.

Feeding Behaviour Outside the Caves

Through capturing, individually marking and releasing over 300 *Pallidoplectron turneri* in the Grotto of Waitomo Cave, it was conclusively shown that at dusk the wetas moved towards the river entrance. They could be observed feeding on the thick growth of liverwort, mainly *Marchantia* sp., growing on the lower parts of the wall just outside the cave (Plate 1, fig. 3). They also fed on the associated bog mosses *Philonotis tenuis* (Tayl.) Jaeg. and *Breutelia pendula* (Hook.) Mitt. and the water moss *Fissidens asplenioides* Hedw.



Map of Waitomo Cave. (From the map drawn by Thomas Humphries in 1889.)

Although there are several openings at the main entrance of Waitomo Cave for *Gymnoplectron waitomoensis* to go outside in search of food, the majority feed on the plant and animal life within the cave. Round the electric lights, mosses and ferns have taken root, and among these plants, as well as in the cracks and crannies of the limestone walls, live small spiders, mites and collembola. These, as well as numerous fungi, may be used as food under these artificial conditions.

In November, 1954, when 25–30 *G. waitomoensis* were living just inside the entrance of the cave, these insects were observed at night, in total darkness, scattered singly throughout the upper corridors of the cave. This indicates that Rhaphidophorids are solitary in their habits, and forage for food on their own.

In November, 1955, and January, 1956, a colony of *G. waitomoensis* was regularly observed at night feeding on the moss *Echinodium hispidum* (H.f. & W.) Jaeg., on several small ferns, and on decaying leaves, stems and roots of *Geniostoma ligustrifolium* A. Cunn. (hange hange), *Brachyglottis rangiora* Buch. (rangiora) and *Melicytus ramiflorus* Forst. (mahoe) growing on the upper part of the walls and on the ceiling of a small cavelet 4 metres to the left of the main entrance to Waitomo Cave. These wetas formed a different colony from those observed just inside the main entrance. Because of the situation of the cavelet, it is assumed that these insects did not have access to the vegetation growing round the lights in the tourist portion of the cave, and so sought the vegetable portion of their diet from this cavelet.

In Aranui Cave *G. waitomoensis* live on similar food. Moss and a fern grow round the lights inside the cave and may be used for food, although this has not been observed. Several openings occur at the entrance of the cave, and the door consists of a grating (Plate 1, fig. 1). A few Rhaphidophorids were found outside at night on the limestone walls feeding on moss, and several were seen high up in the limestone just outside the gate.

These observations all indicate that under natural conditions Rhaphidophorids constantly move in and out of caves at night in their search for food.

In the bush at night, four different species of Rhaphidophoridae were collected from the adaxial surfaces of ferns and creepers. The fern most commonly sought out by the wetas was *Athyrium australe* (R. Br.) Presl., which was very abundant all round Waitomo. Wetas were also found on the fern *Dryopteris pennigerus* C. Christen. Small wetas were collected from the leaves of *Metrosideros hypericifolia* A. Cunn. (rata) which was growing over the limestone walls at the edge of the bush near Waitomo Cave.

Food Preferences Inside the Caves

Observations on the feeding behaviour of New Zealand Rhaphidophorids has shown them to be omnivorous scavengers. As has already been shown in this paper, one of the main sources of food for those species living near water comes from the debris washed into caves during floods. However, certain food preferences were observed, and they are recorded here.

1. *Melicytus ramiflorus* Forst.

Two hours after three freshly cut sticks of *Melicytus ramiflorus* were pushed into a pocket of mud on the wall of the Demonstration Chamber in Waitomo Cave, two *P. turneri* were observed on one of the sticks eating it. Although driven away, they returned a few minutes later to continue nibbling at the bark. This points to the keen olfactory sense possessed by these insects, as normally wetas are seldom seen in that part of the cave. Experiments on feeding Rhaphidophorids

FIG. 1.—(Upper left): Main entrance and smaller entrances to Aranui Cave.

Photo: A. M. Richards.

FIG. 2.—(Upper right): Vegetation around the entrance to the Side Branch of Ruakuri cave.

Photo: A. M. Richards.

FIG. 3.—(Lower): *Pallidoplectron turneri* Richards feeding on bryophytes outside the river entrance of Waitomo Cave.

Photo: S. A. Rumsey.

in the laboratory had already shown that the common Wellington cave-weta, *Gymnoplectron edwardsii,* had preferred *M. ramiflorous* to any other plant offered it (Richards, 1954a), so it was interesting to observe similar behaviour in a species of Rhaphidophoridae belonging to a different genus.

2. *Fungi*

Two different types of fungi were observed in the Grotto of Waitomo Cave.

One fungus was a waxy, fawn-coloured ascomycete, *Peziza* sp. (Pezizales). One specimen was discovered on the side of a large stalactite at the far end of the tunnel. Serrations left by mandibles were clearly visible on it, and it is assumed that it had been eaten by *P. turneri.* A number of other specimens of this fungus were observed in the upper parts of the cave near the Tomo.

The other fungus, a white, sausage-shaped fungus, about 3.5 cm long, was very common, especially in the tunnel, occurring on the ceiling and on some of the stalactites, where it attacked *Arachnocampa luminosa* (Skuse) larvae (Mycetophilidae). It has been identified as *Beauveria* sp. (Fam. Moniliaceae). To see if Rhaphidophorids would eat this fungus, several samples were collected and placed in a box with five *P. turneri.* Two days later a small portion of one sample was observed to have been nibbled. More samples of this fungus were then placed in the box for a *G. waitomoensis* nymph, and again a small part of the fungus was nibbled. These results indicate that if food were scarce in the Grotto it would be highly probable that Rhaphidophorids would eat this fungus.

A large unidentified fungus mycelium, known locally as fan fungus, grows over large areas on the walls of the Cathedral and near the jetty. It is usually associated with rotten wood, and both the wood and the fungus probably supply the wetas with a part of their diet.

Two different species of basidiomycetes grow on the duckboards in the Cathedral. Groups of one of these species also occur on the wall of the Tomo, 13 metres above the stream. These fungi had their tops eaten during the night, so that only the stalks remained the following morning. Because of the fungi found in the wetas' faeces, it is possible that the tops were eaten by wetas when wandering about the cave at night in search of food.

3. *Cork*

In May, 1955, in a high corridor about 12.5 metres inside the Side Branch of Ruakuri Cave, a small phial of yellow paint was found on the ground. It had been accidentally dropped there by the author three and a half months earlier. No cave-wetas had been seen in the tunnel, but a large portion of the cork had been eaten, and the mandible marks left in the cork were those made by cave-wetas and not by rats. This is further proof that Rhaphidophorids roam about caves in search of food. Similar behaviour had been noted when cave-wetas had been kept in test tubes overnight in the laboratory. Eating of the cork in this case had always been interpreted as an attempt by the cave-weta to escape from the tube.

4. *Rat Faeces.*

P. turneri was observed several times feeding on fresh water-rat faeces. This was the first time the author had observed any New Zealand Rhaphidophoridae feeding on mammalian faeces. In North America, bat guano forms an important part of the food supply of cave crickets. In New Zealand, however, bats are found very rarely in caves. Judging from the large number of rat droppings in the

caves around Waitomo, they could form quite a large portion of the wetas' diet, and could perhaps explain the large quantity of unidentifiable brown material present in the alimentary tract of these insects.

5. *Insects*

On a number of occasions *P. turneri* were observed in the Grotto feeding on *Scolypopa australis* Walker (Hemiptera), which were very common during the summer and autumn periods. They also fed on the remains of *Anatopynia debilis* (Hutton) (Chironomidae) ejected by *Arachnocampa luminosa* larvae, or on dead *A. debilis* lying on the mud banks.

Whether in captivity or in their natural surroundings, cannibalism is frequently practised by cave-wetas. The main reasons for this arise from their sexual behaviour and a liking for animal tissue (Richards, 1954a). While studying these insects at Waitomo, a number of different cases of cannibalism were observed.

In June, 1955, three male *Pallidoplectron turneri* and two *Gymnoplectron waitomoensis* nymphs were kept together in an observation box for ten days on a diet of raw meat and fungus. By the eleventh day, one of the male *P. turneri* had been completely eaten except for two tibiae. This weta had had its tarsi amputated, and was easily trapped by the other wetas. Twelve days later the other two male *P. turneri* were eaten by the two *G. waitomoensis* nymphs. Whether by chance or design, one species had eaten all members of the other species. Three days later the smaller *G. waitomoensis* nymph died, but was not eaten by the remaining nymph, which survived for another fortnight.

In no instances were the cave-wetas observed to kill and devour their own kind in their natural habitat. Fighting between male *P. turneri* has, however, been observed, and the actions suggested that the object was to obtain food. In one instance two male *P. turneri* were observed fighting on the wall of the tunnel in Waitomo Cave. They faced each other, waving their antennae about, with both hind legs lifted off the wall and stretched out straight behind them. Each kept snapping at the head of the other. It is unlikely that these actions were associated with sexual activity, since no females were observed near these males.

In early February, 1955, the remains of a female *G. waitomoensis* were found lying on the ground in the Side Branch of Ruakuri Cave. The side of the body had been eaten. At the end of May, a large number of remains of *G. waitomoensis* and *P. turneri*, consisting of legs, ovipositors and antennae, were found scattered throughout the whole cave. Mandible marks could still be seen on two or three hind femora, and it was clear that these marks were produced by other wetas. It is not known, however, whether the wetas were killed and eaten, or had died naturally and then been eaten by other wetas wandering about the cave in search of food.

In a small recess to the right of the entrance to Aranui Cave, the remains of a male and two female *G. waitomoensis* were found. Two hind legs, part of the thorax and the middle legs belonged to the male, two ovipositors and the remains of fore and middle legs belonged to the females. Just beyond these were the hind and fore legs of another male. The high humidity could have caused their decay, but as the hind femora of both male wetas had mandible marks round the edges of the chitin, it is possible that all the wetas had been eaten. In captivity, where cases of cannibalism are of common occurrence, the legs, antennae and ovipositor are usually all that are left (Richards, 1954a).

At the end of May, two and a half months later, cannibalised remains were discovered again in the recess. By the end of July, this pile had been added to further.

By the middle of August, a marked male and female were the only adult wetas seen in the cave. On 20th the female was discovered lying on the ground, partly eaten, 15.3 metres inside the cave. On September 15 and October 16, more remains were found 5 metres inside the cave.

Perhaps after male and female Rhaphidophorids have mated a number of times and laid their eggs, their vitality is considerably lowered, causing them to fall easy victims to other adults and nymphs, so supplying the animal part of these wetas' diet, without in any way jeopardising the survival of the species. To support this theory, from July to December very few adult *G. waitomoensis* were present in the cave, and very few remains were seen. When the recess was re-examined in November it was almost empty, the old remains having decayed. In January, 1956, the first adult wetas for the next season were beginning to mature, and no remains were observed. The behaviour of these cave-wetas was identical in Aranui Cave, the Side Branch of Ruakuri Cave and Waitomo Cave.

CONCLUSIONS

Remy's (1931) results from investigating the food of European Rhaphidophoridae were very similar to these. He found that the insects had a mixed diet and were omnivorous, eating about equal proportions of animals (Arthropods) and plants (mushrooms and vascular plants), sometimes even in the course of the same meal. Animal food and fungi, he considered, could be found inside the caves, but to eat higher plants, these insects must make temporary journeys into the epigean region, generally during the night. These journeys he thought must be fairly frequent, because about half of the examples studied, all captured in caves, had nibbled green plants. According to Remy, Chopard (1938) and Jeannel (1926), the Arthropods eaten were mainly Trichoptera and Lepidoptera. Neither of these groups have been found in the intestines of New Zealand Rhaphidophoridae, and they are not very common in the caves. Cave-wetas will eat them, however, because on one occasion when a *Chargia virescens* Dbd. (Lepidoptera) was left overnight in a tin containing several *P. turneri* and *G. waitomoensis*, torn remnants of the wings were all that remained the next day. Hesse (1929) has suggested that the South African Rhaphidophorid *Speleiacris tabulae* Péringuey feeds on lichens.

It is true that New Zealand Rhaphidophoridae do go outside the caves at night in search of food, but the author's results show that these trips may not be of such frequent occurrence as Remy suggests. He apparently overlooked the possibility of rivers, when in flood, washing leaves and branches of various vascular plants into caves. Trips into the bush at night by cave-wetas seem much more frequent during the summer months than in winter, perhaps because then the rivers are much lower and more stable, so that the fool supply of plant material inside the cave would be correspondingly low. In caves without rivers, trips by cave-wetas into the epigean region are more frequent, probably because of the smaller food supply inside these caves. In Aranui Cave and parts of Waitomo Cave away from the Waitomo Stream, electric lights have stimulated the growth of mosses and ferns, and these artificial conditions make it unnecessary for cave-wetas to go outside in search of food. Because of this, very few *G. waitomoensis* have been seen at night outside Aranui Cave or the main entrance to Waitomo Cave. The colony of *G. waitomoensis* observed 4 metres outside Waitomo Cave came from a different part of the cave where green vegetation was lacking.

ENEMIES OF RHAPHIDOPHORIDAE

In the grotto of Waitomo Cave the natural enemies of *Pallidoplectron turneri* are *Arachnocampa luminosa* larva, several species of large spiders and opiliones.

The long, sticky threads of the *A. luminosa* larvae have a great tensile strength, so that any wetas caught in them easily become entangled (Richards, 1960). *P. turneri* are usually confined to the lower walls of the cave up to about 1.5 metres above the level of the water. Thus they keep out of the range of the glow-worms, which occur on the upper parts of the walls and on the ceiling. After marking over 300 wetas on the left wall of the tunnel, on six occasions only from February to the end of June, 1955, was a cave-weta which had been marked observed on the right wall. It is possible that the cave-wetas may have crossed over to the other wall at, or near, the cave entrance where the *A. luminosa* density is much lower; the guiding wires for the boat may have provided an alternative route; or the wetas may have been carried across on the surface of the stream. Thus the glow-worms appear to form an effective barrier to the distribution of the wetas.

Cave-wetas probably form a source of food for spiders, although this has not been observed. Large hunting spiders occur on the lower parts of the walls in the Grotto, while higher up the walls several *Porrhothele* sp. have built nests in cracks in the limestone; and, between outjutting edges of stalactites, a few large spiders have spun big, thick, intricate webs covered with masses of sticky globules. On one occasion a *P. turneri* was observed caught in the threads of one of these webs. They probably form another barrier confining cave-wetas to the lower parts of the walls.

Opiliones are quite common in the Grotto, and *Megalopsalis tumida* Forster was observed on several different occasions eating *P. turneri.* Opiliones have a carnivorous diet, for Jeannel (1926) has also recorded members of the genus *Phalangodes* in the Pyrenees as, in one night, eating up to 30 individuals of a troglobite silphid (Coleoptera). In the Grotto of Waitomo Cave, opiliones have been observed eating larvae and adults of *Arachnocampa luminosa,* adult *Scolypopa australis* Walker, as well as *P. turneri.*

No predators of *Gymnoplectron waitomoensis* were observed. In Aranui Cave, where the walls are 11–12.5 metres high, the average height to which *G. waitomoensis* occurs is 4–5 metres, although a few have been seen on the ceiling. No spiders, except for one or two specimens of *Porrhothele* sp., occur in the cave; and no opiliones, except for a very occasional *Hendea myersi* (Phillipps and Grimmett). Here light appears to be the main factor influencing the distribution of the cave-wetas.

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LITERATURE CITED

CHOPARD, L., 1938. *La Biologie des Orthoptères.* Paul Lechevalier. Paris. pp. 541.

HESSE, A. J., 1929. Appendix to *Speleiacris tabulae* Pér. *Ann. S. Afr. Mus. 29* (1): 273–275.

JEANNEL, R., 1926. Faune cavernicole de la France, avec une étude des conditions d'existence dans le domaine souterain. Paul Lechevalier. Paris. *Encycl. Ent. Ser. A* 7 pp. 334.

REMY, P., 1931. Observations sur les Moeurs de quelques Orthoptères Cavernicoles. *Ann. Sci. Nat.-Zool.* (10) *14*: 263–274.

RICHARDS, AOLA M., 1954a. Notes on Food and Cannibalism in *Macropathus filifer* Walker, 1869 (Rhaphidophoridae, Orthoptera). *Trans. Roy. Soc. N.Z. 82*: 733–737.

——— 1954b. Notes on Behaviour and Parasitism in *Macropathus filifer* Walker, 1869. *Trans. Roy. Soc. N.Z. 82*: 821–822.

——— 1960. Observations on the New Zealand Glow-worm, *Arachnocampa luminosa* (Skuse) 1890. *Trans. Roy. Soc. N.Z. 88*: 559–574.

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