GHOST MOTH (LEPIDOPTERA: HEPIALIDAE) RESEARCH AND DISCOVERY IN THE SOUTHWEST PACIFIC

John R. Grehan
Buffalo Museum of Science, 1020 Humboldt Parkway, Buffalo New York 14211
jgrehan@sciencebuff.org

ABSTRACT - A personal history on entomology and ghost moth (Hepialidae) research in New Zealand with particular focus on the life history study of the endemic tree-boring species *Aenetus virescens*. Comparative studies of other Hepialidae are also described for research projects or expeditions within New Zealand and overseas in Australia, New Caledonia and Fiji.

INTRODUCTION

Ghost moths were one of many insects that attracted my interest from an early age while growing up in the small town of Wainuiomata, New Zealand. I was born with an interest in creepy crawlies and when two years old I was already collecting worms and isopods (pill bugs) in my pockets. By the time I went to school I was collecting caterpillars and trying to keep them alive with leaves in boxes. Not long after that I had figured out how to mount specimens and make a collection. I was fortunate that my parents, Valarie and Walter Grehan, were not averse to these proclivities and did everything possible to encourage my fascination with natural history. Family vacations were often in New Zealand's volcanic region which was a rock collector's paradise and I always returned home with weighty objects in the back of the car. Other vacations were at the beach and I would collect anything that looked interesting such as crabs, stones, fish skeletons, and I was also always on the lookout for fossils.

At about eight years of age I became an avid frog collector and I would return home with frogs (an Australian species that had been introduced into New Zealand) and tadpoles from the nearby local swamps. I would keep them in aquaria in my bedroom where I would watch the tadpoles turn into miniature frogs. Sometimes frogs would escape. One laid eggs all over the kitchen floor (which I had to clean up), and another spent a week in a shoe and fortunately dropped out before my father put the shoe on. But it was winter and on his way to work the dampness of the shoe became apparent and his foot became very cold and uncomfortable. Only at work was he able to dry it out on a heater and suffer the amusement of his colleagues. The sea was never far distant and for a while I tried maintaining marine aquaria, but there were always technical problems and I gave it up. In the early 1960's there was little available in the way of collecting and storage equipment and for many years I relied on my mother to bring home empty cardboard paper boxes for keeping my insect collection.

First collection box, March 1958 at two years, five months of age.

Insects remained a constant interest even as other aspects of natural history caught my attention at different times. I was especially fascinated by the night life that congregated at our front door light and then largely disappeared by morning. On the way to the primary (elementary) school after a cloudy and damp spring night, I would sometimes find the occasional large green moth on the ground below one of the street lights. These moths were about five cm (two inches) long with bright mottled green and white wings. At closer inspection I would notice

that the moth was still alive, but usually injured as if it had hit a hard object. They were an exciting find, although I do not think I quite knew what they were at that time. But I did realize that they were unusual compared with the usual smaller and less spectacular brown moths. I was to later learn that the roadside moths were *Aenetus virescens*, a ghost moth and the sole member of its genus in New Zealand, and that the injuries were probably incurred during clumsy landings on the road. The moth is widely known as the puriri moth because many puriri trees are infested in the North Island, but I will refer to the species here as *A. virescens*.

Ready to collect frogs. About 10 years of age.

Ghost moths comprise the family Hepialidae and are found in most temperate and tropical regions of the world, with the noticeable exceptions of Madagascar and the Caribbean, as well as western Africa and much of the midwestern and southeastern coastal United States. Species diversity is comparatively low in Europe and North America north of Mexico, but much higher in eastern-southeastern Asia, Australasia, and Latin America. There are only about 500 described species and 80 genera worldwide so the family is not as diverse as many other moth and butterfly groups. But the Hepialidae stand out as the largest family in the suborder Exoporia that also includes five other small families. Together the exoporian moths are the sister-group of the Ditrysia comprising the butterflies and the great majority of all moth species. In this respect the ghost moths are characterized as 'primitive' compared with the more specialized characteristics of most Lepidoptera. All ghost moth caterpillars live within tunnels in the soil, roots, or stems of plants. In New Zealand, ghost moths were represented by the stem-boring *A. virescens* and a variety of other species found in the soil of pastures and forests.

By the time I was about 10 years of age I was an avid insect collector and observer. But there was very little in the way of accessible information on insects for the beginner such as myself. I had no knowledge of the research world of entomology. Luckily, a local cub-scout leader, Tom Grant-Taylor, was a geologist and amateur entomologist and from him I was able to learn some of the techniques of insect collecting. With literature I had to rely mostly on books about the northern hemisphere that helped in my general understanding of insects, but not of the local fauna. In 1966 David Gaskin published *The Butterflies and Common Moths of New Zealand*, and for the first time I had access to a source of local information on a major insect group. This book included plates of various species as well as biological notes on *A. virescens* and other ghost moths. I learned about the tunneling habits of caterpillars and how the adults, unlike most moths, lacked functional mouthparts. I also remember being intrigued by how ghost moths had a different body form and pattern of color compared with other Lepidoptera.

Over the next decade I continued to build up a broad insect collection comprising specimens collected within and around Wainuiomata, or various parts of New Zealand during family vacations. This collecting covered all manner of insects, although I continued to have a strong interest in the night life world of moths. I was also fortunate to live in a town that was surrounded by forested hills and low mountains supporting an immense diversity of insect life. By 11 or 12 years of age I was making regular trips into forested gullies to observe and collect. I discovered that if I went before sunrise it was possible to find many emerging insects that were later invisible among the vegetation. Even when it rained collecting could be worthwhile as many insects would shelter under leaves where they could be easily found.

A nearby shopping center also provided a source for moth collecting at the well lit window displays. I would periodically roam along the storefronts to find interesting specimens

which included *A. virescens* and other ghost moths. I would bring with me some alcohol and a syringe to immobilize the moths so they would not be damaged. A couple of times a police patrol stopped by to check on my roaming along the storefronts but they had no problem with the insect collecting.

About eight or nine years of age my mother took me to the natural history museum in Wellington to identify moths I collected. One of the floor staff noticed our attempts to use display specimens in the public gallery and suggested we try to get some help from Ron Ordish, the museum entomologist. He kindly identified the specimens despite the fact some were found in spider webs and wrapped up in silk. When I was about 15 I started visiting the museum regularly and Ron kindly answered my many questions and also entrusted me to identify my specimens using the research collection including a reference collection of Lepidoptera made by the pioneering New Zealand lepidopterist George Vernon Hudson. At that time there were also very few resources for developing insect collections. Through the kind support of the local high school wood work teacher Don Gilliver I was able to attend his night class and build as many insect boxes as I needed.

My natural history interest was also shared by my childhood friend Mark James who became fascinated by the diversity of New Zealand's land snail fauna as well as mollusks in general. We would often search for snails in forest leaf litter and visit the museum together where Mark would consult the resident conchologist Frank Climo. While we were looking for fossil shells in the Wairarapa mudstones near Wellington, Mark discovered the third fossil whale barnacle recorded in New Zealand up to that time (Beu, 1971).

THE UNIVERSITY EXPERIENCE

I always knew I wanted to be an entomologist although I had no idea about what direction that would take and I knew little about entomology as a career even when I enrolled at the local university (Victoria University of Wellington). In my final year of high school I used my insect collection to present an exhibit on Hymenoptera diversity at the annual Science Fair and this was brought to the attention of Tony Harris, a graduate student working on his Master's thesis at Victoria University. Tony was interested in my inclusion of some spider hunting wasps (Pompilidae) since these were the subject of his Master's thesis. I found Tony to be a very intensely focused individual with a wry sense of humor about science and about life, and he was enthusiastic about my interest in helping to collect specimens.

Pompilids are impressive wasps. Two species frequented urbanized areas and they were often seen around my home. One was a brilliant reddish-brown with a patch of gold on the thorax, while another was a large iridescent purplish-black wasp that was sometimes seen dragging a hapless and paralyzed funnel-web spider to its nest where it would be later eaten by the wasp larva. The spider was equally impressive with black, hairy legs and abdomen surrounding a bright orange cephalothorax. I would sometimes crawl under the house to collect these spiders from their funnel webs while managing not to get bitten - which would have surely been painful, although not deadly.

Tony was dedicated and single minded in his research. I joined him in several field studies collecting and identifying the species and learning to recognize current and new species. We would travel on his off-road bike hurtling along precipitous and rocky fire breaks on the ridges of the southern Tararua Ranges north of Wellington where he had established malaise traps to collect wasps. With help from my mother I constructed and placed traps in strategic locations in Wainuiomata to provide Tony with additional specimens as well as greatly expanding my personal collection. From Tony I learned for the first time how it is often easy to distinguish between superficially similar species. This experience gave me a new appreciation of the importance of detailed observation. Tony also introduced me to Robin Craw who was then a postgraduate student of botany. Robin was to later become a leading New Zealand researcher in biogeography and systematics.

Over the next three years I continued to collect at every opportunity, especially during undergraduate botany field trips where my wandering attention was kindly tolerated while bota-

nist Ross McQueen was expounding on some critical point about plant ecology. In my final undergraduate year I met George Gibbs who supervised an introductory entomology course. By that time I had developed a general interest in how plants and insects interacted. With the support of George and Ross, I attempted to combine these interests in a small research project at the university's Lake Pounui field station; about two hours drive from Wellington.

I was curious about the long-term impacts of wood boring beetles and *A. virescens* on tree health at different stages of forest succession. The study was superficial because it was not possible to survey the insects in detail. I became intrigued by the detailed effects on host plant growth (Grehan, 1982a), and for the first time I had the opportunity to see that the larvae of *A. virescens* maintained a tunnel that opened to the tree surface under a web cover. Trunks of one host tree, *Carpodentus serratus*, were often riddled with old, vacated tunnels that were later occupied by the tree weta (a wingless cricket). This feature is reflected in the Maori name puta-putaweta for the tree, referring to the many weta holes.

Recently emerged male *Aenetus virescens* at tunnel entrance with empty pupa.

My general interest in plants and insects connected with ecology, but I felt uncomfortable with the vagaries of ecological theory which seemed to lack the kind of pragmatic empirical experience that appealed to my interests. Systematics, on the other hand, should have been an obvious fit. All through my life I had focused on insect diversity and classification and for this reason I chose a systematics course during my fourth year. But I was in for a deep disappointment. I received the impression that systematics was even more diffuse and muddled than ecology and I failed to comprehend any consistent empirical foundation. Against all personal experience to the contrary I decided systematics was not for me.

I spent nearly a year deciding on an alternative that would suit my inclinations. Insect pollination of forest or alpine plants looked promising, but was rejected on the advice of Botany faculty. I then looked back at my interest in wood boring forest insects which continued to attract my attention. In collaboration with another student I had recorded bark beetle infestations of cabbage trees, a previously unknown host species (Grehan & Nixon, 1978).

I consulted with New Zealand Forest Service entomologist Robert Milligan who had written most of what was then documented about forest tree borers. With time running out, my attention was once again drawn to *A. virescens*. This moth was classified as a forest pest but there was surprisingly little known about its ecology or biology. Most information was documented by 19th century entomologists such as Ambrose Quail, George Vernon Hudson, and Rowland Illidge. After that, there was almost nothing new in the literature.

DISCOVERING LIFE HISTORY

I began with a purely descriptive investigation of *A. virescens* ecology. Population studies were impractical because the insect was scattered through the forest and it could not be surveyed up into the forest canopy. I was mostly interested in finding about the missing details of life history and behavior. I managed to convince the PhD committee that a descriptive approach would yield something productive and George Gibbs agreed to be my project supervisor. George was a very cautious and thorough researcher who studied the systematics and biology of New Zealand butterflies and two obscure families of tiny moths - the Micropterigidae and the Mnesarchaeidae. Micropterigids look superficially like miniature caddisflies and are related

to all other Lepidoptera. Mnesarchaeids are similar in appearance to micropterigids but are most closely related to ghost moths and several other small families in the superfamily Hepialoidea. Both micropterigids and mnesarchaeids usually escape notice, but they are locally abundant along forest trails if one knows where and what to look for.

This was going to be an extended project as the literature already indicated that larval development of *A. virescens* may last five years. I initiated a field survey at the Lake Pounui research station by tracking larval development using color coded pins to first mark tunnels already present and then any new tunnels each succeeding month. Termination of larval development could also be recorded by observing a partially dismantled web and the emergence of adults was manifest by empty pupal skins protruding from the tunnel. The most immediate challenge, however, was to solve the great mystery of early larval development. It was well-known that the female moths fly and drop their eggs while flying over the forest floor. Entomologist Mike Meads at the Water and Soil Division said that sometimes so many eggs were being dropped in the forest that the sound of their impact on the leaves and ground sounded like rain. The eggs are small, about one millimeter in diameter, so the emergent caterpillars had to be similarly small. New tunnels on trees were about four millimeters in diameter suggesting considerable growth had already occurred before tunneling in trees.

A dense population of tree tunneling larvae would suggest a correspondingly large population of younger caterpillars living in some other part of the habitat, but none had been reported. Earlier experiments by Forest Service entomologists based on eggs placed with caged seedlings suggested that newly hatched larvae feed on the fine terminal twigs, but this had never been observed in nature. The only other obvious possibility was the forest litter, but after meticulously sorting through large amounts of leaf litter I only found a few tiny caterpillars of other lepidopteran families. I was confronted with a seemingly simple and yet intractable problem. The solution came, as it does all too often in science, by accident and circumstance.

The circumstance was the result of the initiative of Bill Winstanley, an enterprising individual who had left his former career to start over as a student in a university program. Bill was working on a PhD study of an obscure (at least to me) crepuscular forest dragonfly and he was concurrently developing a broad interest in dragonfly diversity and classification. In pursuit of his research Bill proposed a field excursion to the Urewera National Park in February of 1979. The expedition also included fellow students Ian Henderson, Tony Beauchamp, and Alicia Scott.

The park comprises an upland forested region of the North Island comprising extensive forests dominated by the southern beech (*Nothofagus*) which was a favored host plant of *A. virescens*. I was easily able to find a sufficiently dense population to survey the abundance and distribution of tunnels. And for the first time I also saw tunnels exposed when sections of trunk were ripped off by the kaka, a forest parrot, as it extracted caterpillars for food.

After many repetitive measurements of tunnel distribution, I took a break and engaged in one of my favorite pastimes – turning over dead logs and stones to look for ground beetles (Carabidae) and other insects. I found one large beech log partially suspended above ground gave me the surprise of my life. I was surprised to find that the exposed underside was lined with a polypore fungus covered by a loose web of silk and droppings that extended along the surface for about two meters. Cliché notwithstanding, I could not believe my eyes when I found beneath the web dozens of pale, grayish-white caterpillars with reddish-brown heads. The caterpillars had every appearance of being *A. virescens*. This find demonstrated that the early stages of *A. virescens* lived in gregarious fungal feeding communities, a biological pattern that was unprecedented in New Zealand natural history. From this one log I collected about 50 caterpillars ranging in size from newly hatched larvae to some that were 20 mm long (Grehan, 1979).

This finding established the principal theme for my research – the developmental relationship between the early fungal feeding stages and the subsequent tree boring behavior that dominated much of the life cycle. As is often the

case in science my discovery was not unprecedented. Checking Forest Service files, entomologist John Bain found sketches of a caterpillar found on a bracket fungus that was labeled *Aenetus virescens*. The record was made by entomologist John Dugdale who was currently the Lepidoptera systematist of the Systematics Section in the Department of Scientific and Industrial Research. John had an encyclopedic knowledge of New Zealand Lepidoptera and over the succeeding years he became an invaluable source of insight and assistance as he kindly endured all manner of questions about ghost moths and Lepidoptera in general. One of his major projects was to revise the classification status of all New Zealand ghost moths that later resulted in a comprehensive systematics treatment of the New Zealand Hepialidae (Dugdale, 1994).

John Dudgale (left) and John Grehan at Dugdale's Nelson office, New Zealand in January 2002.

I spent the next six years collecting information on *A. virescens* growth and development. I concluded that female moths dropped their eggs over the forest and the first instar larvae would locate decaying wood or fungi where they would remain for up to three months. Caterpillars would then transfer themselves to one of about eight host plants where they would complete development by feeding on continuously regenerating callus tissue around the tunnel entrance (Grehan, 1983; Grehan, 1984a). I found that caterpillar preferred to excavate tunnels on the lee side of a leaning trunk or branch.

Most caterpillars in my study site developed to the adult within three years, but a few matured within nine months and some took four years It is possible that in other host plants and habitats development could last even longer (Grehan, 1988a). Most moths emerged from the pupa in the spring months of September through early December. This season featured many more warm wet nights than other times of the year. I also found that pupation could take place up to six months before emergence, and the later the pupation the shorter the duration of the pupal period.

I never observed any evidence of parasitoid mortality by either wasps or flies, but several fungal diseases were observed with the kind assistance and support of insect pathologist Peter Wigley who enthusiastically lent his talents to the identification of fungal diseases. He was able to confirm *A. virescens* as a new host record for the fungus *Beauveria bassiana* and of a bacterium of uncertain taxonomic status. The bacteria-infected caterpillars would emerge from their tunnels before dying and turn into a black gelatinous mass (Grehan, 1982b; Grehan & Wigley, 1984).

I was unable to observe the mating behavior of *A. virescens* in small cages, and the construction of large cages was beyond my resources. I thought mating might occur on the host tree after the female first emerged. Moths emerge in the mid to late afternoon and by three or four o'clock they could be found at rest on the tree trunk near their former tunnel. This afternoon emergence may be characteristic of other wood boring hepialids as it has also been recorded for *Phassus* and *Zelotypia* (Chadwick, 1989). But as I watched several emergent moths during the evening and into the night I was disappointed to see the moths fly up into the forest canopy at sundown or within about an hour after dark.

Male moths have scent hairs (androconia) on the hind legs and this structure is found only in a comparatively few ghost moth genera. In an English species, *Hepialus hectus*, the males fly in groups (leks) at dusk above grassland vegetation and the females would fly up into this cluster and meet up with a male before mating on the ground. In contrast, the North

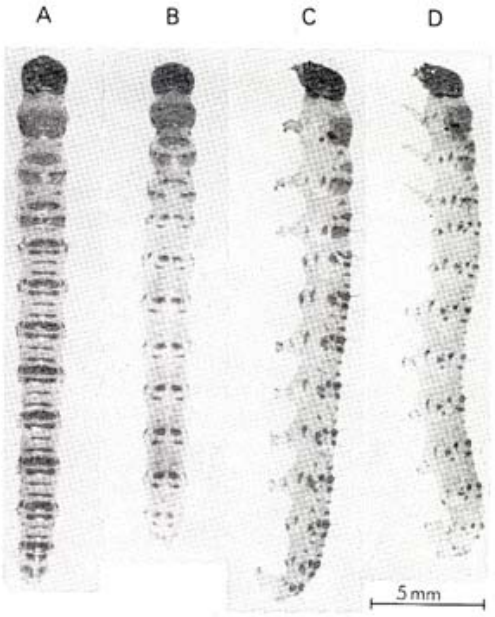
American *Sthenopis auratus* male perches on a plant and fans its wings until a female is attracted and mates with the resting male (Wagner & Rosovsky, 1991). Either process might apply to *A. virescens*, but this aspect of their life history remains unknown.

DEVELOPMENTAL BIOLOGY

It was clear to me that *A. virescens* larvae have two different biological stages, but I did not expect this to also show up in their anatomy. I noticed that some caterpillars were darker and had a banded appearance. A combination of evidence led me to the conclusion that they were a transitional form between fungal feeding and plant feedings stages of development. A major clue came from a study of insect ecology by ecologists Mike Meads and Abdul Moeed who designed traps to distinguish between insects moving up or down tree trunks (Moeed and Meads, 1983). They found numerous *A. virescens* caterpillars in the upward traps and all were of the banded form. Caterpillars in new tunnels were also the banded form. Discovery of the fungal feeding stage, along with a transitional morph led me to produce a detailed description of larval morphology (Grehan, 1981) which brought me back to my original interests in the diversity and classification of insects.

The separation of fungal and plant feeding stages contrasted with most other Lepidoptera that feed on one or the other only, with most being plant feeders. Here was a case where a single insect specialized on each food source at different stages of development. A literature search revealed that fungal and plant feeding involved some similarities and differences in host carbohydrate biochemistry. I had little background in biochemistry so I contacted Bill Jordan of the biochemistry department who helped design a biochemical test based on published research for other insects.

I spent many months placing gut tissues with various fungal and plant carbohydrates and testing for enzyme activity. This required the collection of many caterpillars, especially for the early instars where the body is small. Caterpillars within trees had to be extracted by cutting down the tree or shrub, or by adding water and detergent to a tunnel so the caterpillar would crawl out – a modification of a technique used by the Maori to extract caterpillars for food. I was partially successful in showing that both stages could digest starch which was present in fungi and plants while the ability to digest major structural compounds in fungi and plants appeared to be low or absent. Both stages could also digest laminarin, a compound common in fungi. Although laminarin is generally rare in plants, it is present in regenerating tissue such as the callus formation grazed by *A. virescens* caterpillars (Grehan, 1988a).



Banded (A, C) and non banded morphs of young *Aenetus virescens* caterpillars.

EXPEDITION TO AUSTRALIA

Aenetus comprises about 25 species, with about 16 in Australia, seven in New Guinea and nearby islands, and one in New Zealand and New Caledonia respectively. I was curious about how much of the development and behavior in *Aenetus* also occurred in other members of the genus. Again, my inclination for comparing insects influenced my study by extending the research beyond the single species. There was little information on other *Aenetus* species so it was up to me to find out for myself. Australia was a natural choice, particularly with my father's relatives living there. For advice I contacted lepidopterist Ian Common at the Commonwealth Scientific and Industrial Research

Organization (CSIRO) in Canberra. He suggested I come to Canberra as there were two or three accessible species in the nearby Brindabella Ranges.

I arrived in Canberra in February 1980 and with the kind assistance of Ted Edwards I was transported to the mountain habitat of *Aenetus paradiseus montanus* that was relatively abundant on snow gum trees. A ski chalet was also available at the site for accommodation and I remained there for several days taking measurements and obtaining larval and tunnel specimens. I was interested to observe that in most cases the larvae were able to excavate a tunnel without being flooded by gum exudates. I was also intrigued to find that in addition to the web over the feeding area, there was also a smaller loose web or plug over the tunnel entrance during the day.

To locate caterpillars at different heights on the trunks I designed a portable ladder comprising a set of aluminum angles that could be bolted together in pairs. With a climbing belt my hands free to take measurements. It was disconcerting to see ants running down the tree while I was climbing up. It gave me the uneasy sense that I was going in the wrong direction. But I was happy not to run into any nasty biting or stinging insects, although the fastest and aggressive mosquitoes I ever encountered managed to make washing outside almost impossible. I was interested to view nocturnal insects on the vegetation, but I quickly found there were many large bull ants on the foliage and decided otherwise.

EXPEDITION TO NEW CALEDONIA

The Australian trip gave me the experience to take advantage of a proposal by Bill Winstanley to visit New Caledonia. This island was loaded with dragonflies as well as having *Aenetus cohici* which was known from only two female specimens collected from the mountains of Koghi by M. F. Cohic in November 1960 (Viette, 1961). No other specimens or biological information had since been recorded. Partial support for our expedition was provided by the university and the New Zealand Entomological Society. A cooperative research agreement between the university and the New Caledonian *Office de la Recherche Scientifique et Technique Outre-Mer* (ORSTOM) provided us with facilities and interested support by ORSTOM entomologists Jean Gutteriez and Jean Chazeau. We also benefited from assistance from the Service Territoriale des Eaux et Forêts.

We arranged for a two week visit with an initial focus on the region around the capital of Noumea in the south. We then made a trip around the entire island to survey other habitats. We first obtained forest permits to collect in various forests and during this process the Director offered to show me habitats where he had possibly seen evidence of *A. cohici*. We examined some forest remnants with a few old tunnels but no active population. A few days later, however, I located a small forested gully dominated by *Nothofagus* next to the main highway. There was a sufficient density of caterpillar feeding to survey the tunnels and I was also able to extract several specimens. I was surprised to find that some contained pupae that were close to emergence and I succeeded in rearing one female and four males, the latter having two color forms – one yellowish green and the other grayish-blue. These specimens were used in the first published description of the male (Grehan, 1984b).

Bill and I traveled around the island along the main highway, either camping in abandoned roadside quarries, on the seashore, or in small hotels. We were unfortunately unable to access to some of the northern forests, but we were very successful in collecting many dragonflies, including species that came out in large numbers only after sundown. We would set ourselves up along their flight path to search for the dark dragonflies flying back and forth a few inches above the ground. We had about 20 minutes of dusk in which to frantically sweep up as many specimens as possible, each time transferring them to envelopes before proceeding to the next specimen. All this time we endured stifling heat and humidity while beset by thousands of mosquitoes that would try to collect as much as they could from us. Not the most pleasant experience.


New Caledonia collecting: field staff (Claude Ihilly center) from ORSTOM, and Bill Winstanley.

BACK TO AUSTRALIA AND THEN TO FIJI

After my initial single-species expeditions, I decided in 1982 on a much more ambitious project to survey several Australian species. I began with a survey of *Aenetus paradiseus*, a close relative of *A. montanus* that I examined in the Brindabella Ranges. This was kindly facilitated by lepidopterist Peter McQuillan who provided accommodation and access to a field site near Hobart. Unlike the high elevation habitat of *A. montanus*, these moths were located in a regenerating stand of eucalyptus interspersed with high sedges and streams that was also residence for many tiger snakes. These could be seen crossing the logging trails. I was told that they were highly poisonous, and if I were bitten the best thing to do would be to relax and sit things out as I would be more likely to survive than if I attempted to move. As I was totally isolated during this time I was very much on my own with respect to any accidents. Early one morning I heard a snake slithering across the ground near my tent while having breakfast, and I did get close enough to attempt a photo. Apparently a rather stupid thing to do as the snakes were apparently bad tempered at that time of the year. I was otherwise able to complete my survey over several days, although at the time I was unable to understand why the work went so slowly. I later learned that the temperatures were well into the 40's Celsius (90's F) and the lack of acclimatization resulted in a much reduced rate of work.

I drove north through central Tasmania to the northern coastal town of Burnie. On the way I visited a roadside locality from which micropterigids had been collected, but I had no luck finding anything. I camped overnight along the roadside and experienced temperatures that dropped from the daytime summer heat to near freezing. It was so cold that I had to use my propane stove to keep warm (fortunately without burning the tent down in the process). I was able to locate some *Aenetus* tunnels in some small shrubs at one roadside location and later reared *A. lignivorus* from stems. At Burnie I stayed with an aunt and uncle who allowed me to dig up their lawn to collect ghost moth caterpillars burrowing in the soil. From there I flew to Melbourne where I stayed with my father's sister Joyce and her husband Alan. I used their home as a research base to rear moths from stems and explore the surrounding foothills east of Melbourne. I found a stand of small trees in a roadside gully where I camped for several days to collect specimens and measure tunnels.

I next flew 2,000 miles (3,219 kilometers) west to Perth. After making inquiries at the local university and being told I was crazy to go rummaging about in the snake-infested bush, I drove north and then south of Perth in search of suitable habitats. I was disappointed to find much of the western forests were converted to farmland and or reduced to shrubbery. On other areas much of the forest understory was burnt out from forest fires.

When I reached Karridale about 200 miles south of Perth I found a thick growth of *Agonis flexuosa* shrubs under a canopy of large eucalyptus trees that were clearly supporting a good population of an *Aenetus* species. The owners gave me permission to survey and collect specimens, and they also provided accommodation for the night. I next continued south to Point D'Entrecasteaux before heading north again further inland. I found a couple of localities with occasional larval damage, but I was learning that dense populations of *Aenetus* were harder to find in the dryer habitats of Western Australia compared with New Zealand.

From Melbourne I flew to Sydney and caught a bus south to the coastal city of Wollongong at the base of a large escarpment with patches of 'rain forest' supported by groundwater seepage while the top of the escarpment is dominated by the dryer eucalyptus forests.

I quickly located a fairly dense population of *Aenetus* tunnels, but after a short time I noticed a small crimson-colored leech on the ground inching its way in my direction. I was unconcerned until I noticed some others and then realized I was in the center of a circle of leeches all making their way to me, and more leeches on the surrounding foliage. Forest leeches are thankfully absent in New Zealand and I did not like them at all. Exiting the forest I quickly took off all my clothes and was relieved to find no leeches until I took off my socks and boots and found several in each. Although none had attached themselves to me, I was sufficiently creeped out by these worms that I was unable to continue working in that habitat.

I also an effort to find the ghost moth *Zelotypia stacii* known to bore only into the trunks of eucalyptus trees in central eastern Australia. Its occurrence in the Wollongong region was recorded by the local entomologist Victor Robinson. I planed to meet him in Wollongong, and although he had suffered a fall and required a hip replacement not long before, he was well enough for me to visit and see his extensive collection of ghost moths and other insects. I explained to him my interest in locating tunnels and obtaining specimens of the tunnels and larvae, but he felt that the insect was becoming rare and asked that I not collect any specimens. Out of respect for his concern I agreed, although this was very hard for me as I had come such a long way to obtain this kind of information. But my searches on the escarpment resulted in one tunnel that may have been of this species and so I made no attempt to collect it.

BIOLOGYAND EVOLUTION

As my research progressed I also became more interested in the biology of ghost moths in general. In New Zealand there were a number of species in the genus *Wiseana* that were major agricultural pests. The caterpillars occupied a vertical tunnel in the soil and they would partially emerge at night under a surface webbing to feed on leaves of grass or herbs. I found that one of the grass-feeding species also fed on tubers growing in sand dunes (Grehan, 1984c). There was considerable entomological interest in *Wiseana* because several species were involved and there was considerable uncertainty about their taxonomic status. John Dugdale was working on this group along with other New Zealand Hepialidae. A Masters project was initiated at Victoria University to investigate possible amino acid differences between species and this was carried out by Gordon McArthur who took to the project with dedicated deliberation, spending many hours on laboratory analysis and also extensive field collecting which coincided with my interest in collecting specimens of *A. virescens* and other ghost moths. After collecting from a portable light trap we would sometimes cruise along the deserted main streets of small towns picking moths from the display windows of stores – only inviting polite police interest on one occasion.

I continued to expand my interest in other Hepialidae and collaborated with Mike and Abdul Moeed on describing the larvae of a forest floor species (Grehan, Moeed & Meads, 1984). Another major New Zealand genus was *Aoraia* with habitats ranging from forests to high elevation tussock grasslands. In mid April of 1983 (early autumn) I joined John Dugdale and Brian Patrick to observe ghost moths in the tussock grasslands and swamps of the Rock and Pillar Range. Brian was an extremely enthusiastic lepidopterist with seemingly unlimited energy and enthusiasm for Lepidoptera and other insects. Among his many accomplishments was the discovery of many new species, localities and biological information in the southern South Island. One of his major discoveries was *Heloxycanus*, a new genus of sphagnum inhabiting ghost moths that now includes a species (*H. patricki*) named after Brian (Dugdale, 1994).

The day we arrived at the Rock and Pillar Range the weather was moderately warm and clear with a slight breeze. From our vehicle we could see what looked like fast-flying bumble bees. These were day-flying males of *Aoraria* that were rapidly searching for the pheromones of flightless females. Occasionally a male would be seen to instantly drop to the ground. If the spot could be marked, a female would be found on the ground within the grass surrounded by one or more males attempting to mate. I managed to locate and excavate the larval tunnels to describe their characteristics, but my major interest was in the moss-feeding *Heloxycanus*. It was easy to find caterpillars by shifting away surface moss and exposing the characteristically

pale bodies and dark brown heads. They were instantly obvious, yet in spite of more than a century of entomological collecting, neither adult nor larva had been previously discovered. Brian said that this was in part due to the late flight of the moth which flew after most collectors had retired from the mountain habitats. Presumably the larvae had been observed, but did not attract attention. They were of interest to me as the first record of ghost moths feeding entirely on a moss species (Grehan & Patrick, 1984). At night the temperatures plummeted to near freezing, but this did not dissuade the moths and over 50 specimens congregated around an ultraviolet tube and a pressure lantern – quite amazing for such a recently discovered species.

Bran Patrick walking over moss bog habitat of *Heloxycanus* ghost moths.

At this time I was also using the literature to compare *Aenetus* tunneling with other wood borers (Grehan, 1988c) and ghost moth development and feeding. I came to the conclusion that most, if not all, ghost moth species begins their life cycle with a period of feeding on fungi or plant detritus followed by plant feeding for the majority of their development. The separation of fungal and plant feeding between different development stages could also be regarded as an alternative evolutionary pathway to that of separating fungal and plant feeding between different phylogenetic lineages. I suggested that the two forms of separation were evolutionarily homologous and derived from a generalist feeding ancestral lepidopteran that combed fungal and plant tissues in its diet, perhaps sometime prior to the Triassic (Grehan, 1989).

I had been fortunate to experience research under many different conditions both within and outside New Zealand. In all of these activities I had managed to avoid any major accidents. Camping in Australia I always slept with a machete – in case of what I don't quite know. I managed to nearly chop my thumb off while holding a small stem and using a foot long blade and five foot handle to extract a tiny beetle larva at Lake Pounui. But the nearest thing to life on the edge occurred when I became lost among tussock grass covered hills in the South Island in the autumn. With temperatures not much above freezing and soaking wet after hiking to a ridge to find *Aoraria* caterpillars, I realized I was lost as it was getting dark. With light rain falling I decided to stay put and with only a pack and a ground sheet and the lee slope of a tussock for shelter I shivered through the night until dawn. By then I had to move and decided to follow a fence line that appeared familiar. Twenty minutes later I found my rental car and was able to return to Dunedin, just in time to catch the plane home.

END OF A CHAPTER

By 1987 I was finalizing my PhD thesis. This project had transformed from a purely ecological study to a comparative approach on the biological evolution of *Aenetus* (Grehan, 1987). This departure entailed some detours into unorthodox areas of evolutionary biology that complicated my academic career, but this provided a coherent evolutionary context for interpreting the biology and ecology of ghost moths.

But 1987 was not a good time to complete a research work that had little direct application to the applied sciences. I knew a lot about ghost moths, but little else that was then in demand. My dilemma was further apparent when I met Niels Kristensen from the Zoological Museum of the University of Copenhagen, and his student Ebbe Schmidt Nielsen who was to soon succeed Ian Common's position in Canberra. Over the last decade these two researchers had made tremendous progress in clarifying the systematic relationships of various primitive Lepidoptera, including the ghost moths (Nielsen & Robinson, 1983; Kristensen, 1984). When I asked about the possibility of opportunities to work more in the systematics field, particularly on *Aenetus*, they pointed out that since the main

focus of my research was not in systematics I would not find anyone to support that goal. I was naturally disappointed at finding my options limited this way, but I did have a great time with Niels driving across the North Island to collect high elevation moths on the Taranaki and Ruapehu volcanoes.

In the same year of my PhD completion there was a major stock market crash and a new government policy lead to a 30% reduction in government support for science. Many established science positions in the natural sciences were being terminated. New Zealand science was in turmoil and I was facing the prospect of leaving science altogether as some of my colleagues had already. But I continued to live in denial about the future and focused on publishing my research. The Zoology Department kindly allowed me continued use of my office and university facilities for an extended period during which Robert Wear kindly contracted me to conduct an invertebrate survey on a nearby island (Grehan, 1991).

The International Entomology Congress was holding its 1988 conference in Vancouver, Canada, and it would include a session on primitive moths. Since there was nothing else on my career horizon I decided to experience an international meeting and also visit Venezuela in connection with my evolutionary biology interests. In early July I made what I expected to be a short visit to the New World. But one action leads to another and in consequence this would open up unexpected opportunities for continuing ghost moth research and expand my research horizons into other fields that continue to this day.

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John Grehan collecting in the Rock and Pillar Range, New Zealand, 1983