

The host range of *Aenetus virescens* (Lepidoptera: Hepialidae) and its evolution

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Abstract

The utilisation status of fungal and vascular plants as hosts for larvae of *Aenetus virescens* is presented. Larvae are recorded from the fruiting bodies of 8 wood-inhabiting fungi. Vascular plants are placed into categories of "terminal host", "marginal host", and "status unknown". The evolution of this host range is given an orthogenetic interpretation in relation to the origin and dispersal of angiosperms.

Keywords: Lepidoptera; Hepialidae; *Aenetus virescens* larva; plant; fungus; host; feeding; evolution; biogeography; coevolution.

INTRODUCTION

The insect host list of Spiller & Wise (1982) includes host records from the literature between 1860 and 1960. About 36 plant species are recorded as hosts for *Aenetus virescens* (Doubleday) larvae but no indication is given on the degree of utilisation. Information of this sort is valuable for the economic entomologist and of special interest for the interpretation of the insect/plant relationship. This paper provides an indication of the host status for some of the plants listed by Spiller & Wise (1982) along with additional records. The host range (with particular emphasis on terminal hosts) of *A. virescens* is discussed in relation to angiosperm phylogeny. This is followed by an evolutionary interpretation of the host range which considers 2 aspects—firstly the role of dispersal in bringing the insect into geographic contact with particular plants, and secondly the primary mechanism of interaction that allows *A. virescens* to utilise certain plants but not others. The former aspect is primarily one of biogeography since it involves the "spatial" aspect of evolution which determines the present distribution of the insect and its host plants.

The larval development of *Aenetus virescens* involves an initial period (litter phase) of feeding on fungal fruiting bodies or dead fungal-infested wood. This is followed by a longer period of feeding on live trees and shrubs (tree phase) where development is completed (Grehan 1981, 1983). The vascular plant hosts are classified as "terminal host" where larval development is known to be completed, and "marginal host" where attack has been recorded but observations by the author suggest that larvae do not reach maturity. For many plants the status as "terminal host" or "marginal host" is not known. No comparable distinction is made for the fungal hosts due to the transitory nature of the litter phase.

Table 1. Host records for tree phase larva of *Aenetus virescens* in New Zealand. (Symbols used: Host status: H, terminal host; M, marginal host; ★, attack frequent FRI records; ?, status unknown; +, probably a non-host. E, exotic plant; I, indigenous plant. Source of record: FRI, Forest Research Institute; G, communicated to or by author, Hu, Hudson (1898); SW, Spiller & Wise (1982); W, Winstanley (1982); Z, Zondag (1982).

<i>Acacia melanoxylon</i>	? E Z	<i>Litsea calicaris</i>	? I SW
<i>Acer</i> sp.	? E SW	<i>Liquidambar</i> sp.	? E G
<i>Acer palmatum</i>	? E FRI	<i>Malus sylvestris</i>	? E SW
<i>Alectryon excelsus</i>	H I SW	<i>Melicope simplex</i>	? I SW
<i>Aristotelia serrata</i>	H I SW	<i>Melicytus</i> sp.	+ I SW
<i>Astelia solandri</i>	+ I SW	<i>Melicytus ramiflorus</i>	+ I SW
<i>Betula pendula</i>	? E SW	<i>Metrosideros robusta</i>	? I FRI
<i>Carpodetus serratus</i>	H I SW	<i>M. scandens</i>	? I FRI
<i>Citrus</i> sp.	? E SW	<i>Myoporum laetum</i>	H I SW
<i>Citrus limon</i>	? E SW	<i>Nothofagus fusca</i>	H I SW
<i>Coprosma australis</i>	M I FRI	<i>N. menziesii</i>	H I SW
<i>Coriaria arborea</i>	M I G	<i>N. solandri</i>	H I SW
<i>Cornus capitata</i>	? E SW	<i>N. solandri</i> var. <i>cliffortioides</i>	?* I SW
<i>Cyathodes fasciculata</i>	H I SW	<i>N. truncata</i>	H I SW
<i>Cytisus proliferus</i>	? E SW	<i>Olearia rani</i>	M I G
<i>Dacrydium cupressinum</i>	+ I FRI	<i>Pennantia corymbosa</i>	M I G
<i>Dysoxylum spectabile</i>	? I FRI	<i>Persea americana</i>	? E FRI
<i>Elaeocarpus dentatus</i>	? I FRI	<i>Plagianthus betulinus</i>	? I SW
<i>Eucalyptus</i> sp.	— E FRI	<i>Populus</i> sp.	? E FRI
<i>E. delegatensis</i>	?* E FRI	<i>Populus nigra</i>	? E SW
<i>E. saligna</i>	H E FRI	<i>Prunus laurocerasus</i>	? E SW
<i>Fraxinus</i> sp.	?* E SW	<i>Prunus persica</i> var. <i>nectarina</i>	? E SW
<i>F. excelsior</i>	? E SW	<i>Pseudowintera colorata</i>	H I G
<i>Freycinetia banksii</i>	+ I SW	<i>Pyrus malus</i>	? E FRI
<i>Griselinia lucida</i>	? I SW	<i>Quercus</i> spp.	? E SW
<i>Gymnelea cunninghamii</i>	H I FRI	<i>Quercus robur</i>	? E SW
<i>G. apetala</i>	H I Hu	<i>Q. rubra</i>	H E G
<i>Hebe salicifolia</i>	? I FRI	<i>Quintinia acutifolia</i>	? E W
<i>Hoheria populnea</i>	H I G	<i>Salix babylonica</i>	? E SW
<i>H. sextylosa</i>	H I G	<i>S. fragilis</i>	? E SW
<i>Juglans regia</i>	? E SW	<i>Ulmus</i> sp.	? E SW
<i>Leptospermum</i> sp.	— I SW	<i>Vitex lucens</i>	H I SW
<i>L. ericoides</i>	H I SW	<i>Weigela</i> sp.	? E G
<i>L. scoparium</i>	H I SW	<i>Weinmannia racemosa</i>	M I SW

Table 2. Families and orders of terminal host-plants of *Aenetus virescens* tree phase larvae (classification from Allan 1961.)

Sapindaceae (Sapindales)	Malvaceae (Malvales)	Fagaceae (Fagales)
<i>Alectryon excelsus</i>	<i>Hoheria populnea</i>	<i>Nothofagus fusca</i>
Elaeocarpaceae (Tiliales)	<i>H. sextylosa</i>	<i>N. menziesii</i>
<i>Aristotelia serrata</i>	Myrtaceae (Myrtales)	<i>N. solandri</i>
Escalloniaceae (Cunoniales)	<i>Leptospermum ericoides</i>	<i>N. truncata</i>
<i>Carpodetus serratus</i>	<i>L. scoparium</i>	<i>Quercus rubra</i>
Ericaceae (Ericales)	<i>Eucalyptus saligna</i>	Winteraceae (Magnoliales)
<i>Cyathodes fasciculata</i>	Myoporaceae (Lamiales)	<i>Pseudowintera colorata</i>
Oleaceae (Loganiales)	<i>Myoporum laetum</i>	
<i>Gymnelea cunninghamii</i>	Verbenaceae (Lamiales)	
<i>G. apetala</i>	<i>Vitex lucens</i>	

TREE PHASE HOSTS

The utilisation of vascular host plants by *A. virescens* is summarised in Table 1. Although a total of about 64 plants is recorded only 19 are known to allow complete development, including only 2 out of 21 records for exotic species. These plants (including both exotic and indigenous) belong to 11 different families and orders (Table 2). Almost all the plants attacked are dicotyledonous woody angiosperms with the ex-

ceptions discussed below. The majority of indigenous records are plants having a growth form consisting of a single main stem and may be regarded as "trees" while a few have a stature that is more "shrub-like", such as *Coriaria arborea* and *Cyathodes fasciculata*.

Terminal host plants

Of the indigenous host plants, one new record is noted in this paper. Larvae and pupae of *A. virescens* were found in *Pseudowintera colorata* on the west facing slopes of the Rimutaka Range (41°21'7"S, 174°59'2"E; 600 m a.s.l.). However, above this site on the ridge top at 800 m a.s.l. *P. colorata* was free from attack as was *N. menziesii* which dominated the canopy. *N. menziesii* is recorded as a terminal host (as classified here) by Alma (1977). All other plants classified as terminal hosts in Table 1 have been confirmed by the author although for some this status may be also indicated in the literature, such as *Hoheria populnea* (Quail 1902) and *Aristotelia serrata* (Hudson 1884). For the 2 exotic hosts listed only one record of complete development is known for each. As well as the record for *E. salagna*, complete development is also known in *Eucalyptus* from 2 examples observed by the author but the specific identity of the hosts could not be determined. *A. virescens* does not usually "thrive" in *Eucalyptus* (Alma 1977).

Although no quantitative analysis has been made, host plants may be distinguished by subjective assessment into those which may have relatively high levels of attack (*Aristotelia serrata*, *Carpodetus serratus*, *Gymnelaea cunninghamii*, *G. apetala*, *Hoheria populnea*, *Nothofagus* spp., *Pseudowintera colorata*, *Vitex lucens*) and those with a comparatively low degree of attack (*Alectryon excelsus*, *Cyathodes fasciculata*, *Leptospermum ericoides*, *L. scoparium*, *M. laetum*). The attack frequency for *H. sexstylosa* is not known. This general assessment of host exploitation varies between sites. For instance the example given for *N. menziesii*, and the attack on *P. colorata* may be a localised phenomenon. Similarly at Lake Pounui Reserve in the southern Wairarapa at about 100 m a.s.l. *N. solandri* may exist as extensive hillside forest free from attack while in some gullies the trees are utilised by *A. virescens*. The significance of such localised ecology and geography on *A. virescens* attack is not known.

Marginal hosts

Only a small number of the records for indigenous plants have been observed sufficiently to reliably suggest that maturation of the larva does not occur or at least is very rare. On *Weinmannia racemosa* signs of attack (tunnel or feeding scar) can usually be found without difficulty in areas where *A. virescens* is known to be present. Tunnels were found to be common in *Coriaria arborea* at Te Karetā Inlet, Lake Waikaremoana, but I have not observed attack elsewhere on this plant. Attack on *Pennantia corymbosa* and *Olearia rani* is rare. In the last 5 years I have come across only 1 specimen of *P. corymbosa* with attack, the tunnels being of a size range suggesting that the larva did not continue its residence long after establishment as the 4 tunnels were only about 300 mm long and 3-4 mm diameter (c.f. Grehan 1983). Similarly, I have found only 3 vacant tunnels in 3 separate trees of *Olearia rani* at Wainuiomata and Lake Pounui Reserve. Two establishment sized tunnels were observed in *Coprosoma australis* by the author in Wainuiomata, and the records by the Forest Research Institute indicate that while this attack may be infrequent it is widespread.

Status unknown

This situation applies to most records and many may be only marginal hosts. It was difficult to obtain information on exotic species as it is necessary for the plants to be in relatively close proximity to "forested" situations. For example my observations on exotic plants with *A. virescens* attack were often made in gardens adjacent or close to a

forest. Away from a forest habitat even "favoured" hosts such as *Vitex lucens* are free from attack, as can be observed from trees planted along the roadside in Lower Hutt and Wellington. I have no detailed information on the record of attack for the gymnosperm *Dacrydium cupressinum* (Podocarpaceae).

I believe it very probable that *Nothofagus solandri* var. *cliffortioides* is a terminal host since attack of this plant is described as frequent in F.R.I. records and *Nothofagus solandri* var. *solandri* is recorded as a terminal host. Only a single tree of *Quintinia acutifolia* has been observed with *A. virescens* attack (Winstanley 1982) but the size of the tunnel diameters and feeding scars indicate that this is probably a terminal host (W. J. Winstanley pers. comm.).

Invalid or doubtful

The record of *Melicytus ramiflorus* (Table 1) is believed to be due to confusion of *A. virescens* tunnels with those of *Oemona hirta* F. (Coleoptera: Cerambycidae) (Grehan 1979). *A. virescens* larval attack on monocotyledons has been recorded for 2 species: *Astelia solandri* (herbaceous) and *Freycinetia banksii* ("woody" stems). I have examined both plants on many occasions and have found no indication of *A. virescens*. The herbaceous tissue of *A. solandri* would appear quite exceptional in comparison with all other hosts attacked by *A. virescens*. The only recorded attack on live herbaceous tissue by a wood-boring hepialid is for *Endoclita excrescens* and *E. signifer* in Japan where this is a transitory behaviour prior to the woodboring habit (Ueda 1979; Kondo 1961). The reference to *A. solandri* by Hudson (1898) gives the common name as "Kiki" which is like the name "kiekie" which refers to the plant *F. banksii*, and I therefore suggest that the reference to *A. solandri* is in error. In Hudson (1928: 358) *A. solandri* is recorded as a host (as kiki) but not in the appendix of plants (p. 373). The only information on the attack on *F. banksii* given by Hudson (1982) is the presence of *A. virescens* in the stems. I consider the attack of *A. solandri* to be extremely improbable and the attack on *F. banksii* to occur rarely, if at all.

LITTER PHASE HOSTS

Fungal hosts of *A. virescens* have been identified from fruiting bodies on which feeding was observed and are listed in Table 3. Fruiting bodies attacked by *A. virescens* are live, the tissue of healthy appearance, probably actively producing spores and therefore corresponding to the stage II classification for fruiting bodies given by

Table 3. Host records for *Aenetus virescens* litter phase larvae in New Zealand.

	Substrate	Growth form	Dr G. Stevenson Collection Catalogue Number
Polyporaceae: Aphyllophorales			
<i>Poria nothofagi</i> Cunningham	<i>Nothofagus</i> sp.	encrusting	80/14
<i>Poria correyana</i> (Berkeley ex Cooke)	<i>Carpodetus serratus</i> <i>Nothofagus</i> sp.	encrusting	80/16 —
<i>Chaetoporus eupotus</i> (Karsten) Bondazew and Singer	<i>Nothofagus</i> sp.	encrusting	80/15
<i>Fuscoporia ferra</i> (Person) Cunningham	<i>Nothofagus</i> sp. <i>Weinmannia racemosa</i>	encrusting	80/17 —
<i>Echinochaetae russiceps</i> Samuels	<i>Carpodetus serratus</i> <i>Pennantia corymbosa</i>	bracket	79/35 —
<i>Heterobasidion hemitephrum</i> (Berk. Cunn) 'Irpex' sp.	<i>Nothofagus</i> sp. <i>Leptospermum ericoides</i>	bracket encrusting	— 80/46
Tremallaceae: Tremellales			
<i>Tremella</i> sp.	<i>Carpodetus serratus</i>	encrusting	80/41

Graves (1960). Those fungi described as "bracket" in Table 3, have protruding fruiting bodies while those described as "encrusting" are entirely underlain by the substrate. Most of the host fruiting bodies have a woody texture but the tissue of *Echinochaeta russiceps* is comparatively soft and flexible while *Tremella* sp. has a gelatinous tissue.

Feeding on *Tremella* sp. appears to be incidental as only occasional larval activity has been noted on this species even though numerous larvae may be nearby on hosts such as *E. russiceps*. The actual host status of the fungi has not been determined against any specific criteria. The larvae are mobile and therefore potentially capable of changing food. Larvae also feed extensively on the surface of dead wood, either grazing on the surface growth of vegetative hyphae or ingesting wood tissue which contains fungal hyphae (Grehan 1979) so the fungal host range could be far more extensive than indicated by the fruiting body records. At Lake Pounui Reserve specimens of *E. russiceps* have been found with the entire hymenial layer removed by *A. virescens* feeding. Comparable feeding damage was observed on encrusting fungal hosts but not on other bracket species. *A. virescens* larvae were observed feeding on decayed wood of *Melicytus ramiflorus* at Lake Pounui Reserve. From regular observation over a period of 5 years the fungus which appears primarily responsible for this decay (and the initial death of the tissue) is *Pholiota* sp. (Agaricales). No feeding has been observed on the fruiting body of *Pholiota* sp. This may be partly due to the fruiting of this species in spring and autumn outside the main period of *A. virescens* litter phase development.

DISCUSSION

Although the absolute number of recorded host plants allowing complete development for *A. virescens* is relatively small, it includes plants from several families in different orders making this insect a "generalist" feeder in the sense of Slansky (1976). In comparison, the borer *Endoclita excrescens* (Lepidoptera: Hepialidae) is known to attack 103 species in 43 families (Matsuzawa et al. 1963) but for this insect the distinction between plants allowing complete development from other species is not recorded. For *A. virescens* there does not appear to be any greater range of exploitation for any particular plant group. In each plant family the terminal hosts are limited to 1 or 2 genera and only 1 or 2 species for each genus. Taxonomic relationship between various plants does not necessarily mean susceptibility to *A. virescens* attack. For example I have examined the non-host *Cyathodes juniperina* extensively at Lake Pounui Reserve and Wainuiomata where it was growing in association with the host *C. fasciculata* (Grehan 1982b). Similarly on the Rimutaka Range *Pseudowintera axilaris* growing at a lower altitude to *P. colorata* was not attacked although other plants present such as *C. serratus* and *Nothofagus* spp. were.

The range of host plants is not only broad in taxonomic groups but is also spread across the 3 main lines of angiosperm phylogeny recognised by Croizat (1961) who concluded from panbiogeographic and morphogenetic analysis that the origins of the angiosperms involve a "broad front" of evolution rather than being centred on any single plant group. Because of this, angiosperm plant groups may be represented in terms of their phylogeny in relation to 3 main groups considered to be representative of the transition to the angiosperm level of evolution. Two of these groups are only distantly associated with each other—Magnoliaceae/Nymphaeaceae and Betulaceae/Hamamelidaceae but both of these "pivot" around the Monimiaceae/Ulmaceae which constitute a "central" line of development.

This means that angiosperms did not "radiate" out from a single, fully angiospermous ancestor in a particular "centre of origin" but involved a wide range of forms and ancestral distributions. The indigenous host range of *A. virescens* is represented in the two extremes of the transition to angiospermy: *Pseudowintera colorata* being associated with the Magnoliaceae/Nymphaeaceae and *Nothofagus* spp. associated with

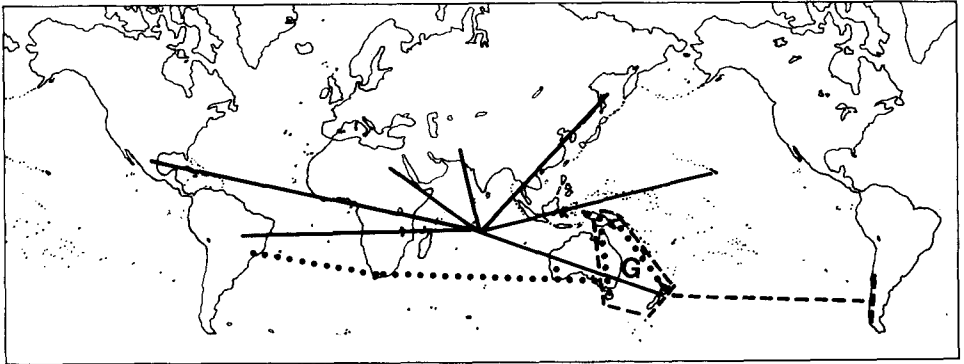


Fig. 1. Dispersal of *Aenetus* and related moths (dotted line), *Vitex* (solid line), and *Nothofagus* (dashed line). G, Western Polynesian Gate. This map is not intended to provide details of distribution but to give a summary of patterns of dispersal for the groups concerned. For further general explanation, refer to chapter 1 of Croizat (1964).

the Betulaceae/Hamamelidaceae. Other host plants (but not known to be terminal hosts) are associated with the central "node" of angiosperm phylogeny and include members of the genera *Litsea* (Lauraceae), *Ulmus* (Ulmaceae), *Pennantia* (Icacinaceae), and more distantly *Prunus*, *Pyrus*, and *Malus* (Rosaceae). Given such an association between the phylogeny of angiosperm plants and *A. virescens* the following discussion presents an interpretation of how this relationship arose.

If the evolution of angiosperms is over a broad front, how is it that the range of plants over the front became available to *A. virescens*? To interpret the host/plant relationship of *A. virescens* it is necessary to consider the process responsible for a particular range of plants being brought into geographic contact with the insect. Quite obviously an insect cannot feed on a "suitable" plant which does not exist within the geographic range of the insect. In conventional evolutionary terminology such plants are said to "escape" in space (Dethier 1954) but this is referred to here only in the descriptive sense for *A. virescens*. For example exotic hosts such as *Quercus rubra* are capable of supporting complete development but this potential has only been realised following artificial introduction. However, so far as the indigenous hosts are concerned, their distribution is considered to be the result of non-anthropogenic dispersal. Croizat (1952) made extensive studies of the patterns of dispersal for the higher plants by graphing out these patterns as lines (tracks) on a map. Interpretation of the tracks drew attention to particular biogeographic features he called "Gates" which were recognised by the confluence of tracks and the diversity of plant life involved. One such Gate which may be significant for the host range of *A. virescens* is the "Western Polynesian Gate of Angiospermy" (Fig. 1.). This is comprised of 2 biogeographic centres: the "Neocaledonian center" composed of lands involving New Guinea, Queensland, Lord Howe Island, Tonga, Samoa, and Fiji; and the "Macquarian Center" involving Tasmania and the islands to the south of New Zealand — Macquarie, Campbell, Auckland, and Antipodes (Croizat 1952: 543). This concept of a Western Polynesian Gate provides the background for interpretation of the evolution of the host range of *A. virescens*.

The patterns of dispersal are interpreted as the product of past geography (Croizat 1964: 712). The interpretation of dispersal given in reference to the Western Polynesian Gate is that there was a concentration of ancestral angiosperm dispersal occurring in the geographic range now occupied by the Pacific Ocean (Croizat 1958: 725) resulting in a primary centre of plant evolution during Triassic/Jurassic times and now represented by the Western Polynesian Gate (Croizat 1961: 725). This is not a "Center of origin" in the Darwinian sense (although it has been likened to such by Ball

1976: 420) since the Gate does not represent a process of "origin and subsequent dispersal and migration" as indicated by Ball (1976).

Understanding the Western Polynesian Gate as a focal point in the evolution of angiosperms means that *A. virescens* is able to avail itself of a wide array of plant groups because the dispersal of its ancestors brought this species into existence on land close to or intimately associated with the Polynesian Gate. However the pattern of dispersal for the ancestry of *A. virescens* is quite different to that of some of the insect's host plants. The ancestral evolution of *A. virescens* appears to be associated with the Indian Ocean (Fig. 1). According to Dumbleton (1966) there are no close relationships of New Zealand Hepialidae with South America. An apparent affinity of *Aenetus* with the monotypic genera *Zelotyphia* (Australia), *Leto* (South Africa), and *Tricophassus* (Brazil) (J. S. Dugdale pers. comm.) indicates an Indian Ocean (i.e., the palaeogeography that is now Indian Ocean) dispersal for the ancestry of these moths. In contrast, interpretation of dispersal patterns for some plants involved with the Western Polynesian Gate indicates that from the Jurassic to earliest Cretaceous some plants had a high concentration of ancestral dispersal in what is now the Pacific Ocean but this dispersal did not involve the Indian Ocean. Therefore, during the evolution of the *Aenetus* ancestry there may have been a marked change in host associations. Examples of hosts with a Pacific dispersal are *Nothofagus*, *Pseudowintera*, *Coprosma* (see for discussion Croizat 1952), and possibly *Aristotelia*. This is in contrast to the host *Vitex lucens* whose ancestral dispersal I interpret to be primarily involved with the Indian Ocean (Fig. 1). This is because the main evolutionary diversification is found on lands in or bordering the Indian and Atlantic oceans. For example, of about 114 present day species of *Vitex* recorded by Moldenke (1956, 1957, 1958a, b) the following general representations of species can be indicated: Africa, 36%; Madagascar, Mauritius, Seychelles, 18%; Asia, South East Asia, New Guinea, Australia, New Zealand, 25%; Brazil, Venezuela, Columbia, Argentina, 16%; Central America, Mexico, 11%; Florida, Texas, 1 species, also in the Caribbean, Venezuela and Asia—South East Asia. Pacific islands 1 species also in Asia and Indian Ocean. Therefore the evolution of *Aenetus* and its close relatives is understood here as a group which evolved in relation to a geography that is now the Indian Ocean but has been brought into contact with plants whose evolution centres on the Pacific.

Although the process of dispersal is responsible for the present distribution of a particular range of plants in geographic contact with *A. virescens*, the resulting pattern of the insect/plant interaction depends on the evolutionary "potential" of the insect to establish and/or maintain an association. Although *A. virescens* has demonstrated a generalised habit many other New Zealand insects are comparatively specialised (Dugdale 1977). Evolutionary interpretation of the insect/plant relationship has generally focused on a process called coevolution (Fox 1981; Eastop 1981; Gilbert 1982). Janzen (1980) defines this process as an evolutionary change in a trait of the individuals in one population in response to a trait of the individuals of a second population, followed by an evolutionary response in the second population to the change in the first, and Eastop (1981) refers to coevolution as an interactive adaptation between two organisms. Although *A. virescens* has certain qualities or characters which are compatible with a relationship existing to a greater or less extent with a particular range of plants can this be ascribed to coevolution? Janzen (1980) argues that utility itself is not a "proof" of coevolution since an animal may utilise a plant because of dietary preferences already established, and circumvent "defence traits" because of abilities carried at the time. This effectively excludes the pattern of utility as a necessary indicator of coevolution with respect to a particular existing relationship, although it might be argued that coevolution still underlies insect/plant evolution, the traits arising with respect to some other historical relationship (e.g. fruiting

characteristics of indigenous Central American plants, Janzen & Martin 1982).

Coevolution appears to be nothing more than a synonym for natural selection between 2 or more interacting organisms. As such natural selection is identified as the prime or exclusive factor orienting or directing evolution, the implication being that organisms have no inherent directional tendencies (explicit in Dethier 1970: 97). In this context orthodox evolutionary interpretations of insect/plant relationships often provide explanations for the origin of animal and plant features in terms of their functional role (Southwood 1972; Harborne 1977; Swain 1978; Rosenthal & Janzen 1979; Owen 1980).

However, coevolution cannot be the primary process underlying the evolution of insect/plant relationships because organisms do have inherent directionality in their evolution. The evolutionary change is directed not by natural selection but by the "structural state" of an organism at any point in time. This process is one of "orthogeny" and is indicated by the existence of "types of organisation" which maintain a structural integrity regardless of environment and manner of adaptation (Croizat 1964). This means that environment is secondary to the "types of organisation" and natural selection can only work within the limits of orthogenetically determined variation. The consequence of orthogeny for insect/plant evolution is that insects utilise what nature provides according to what utilisation is made possible by the insects structure (Croizat 1961). (The concept of orthogeny in relation to the orthodox evolutionary synthesis is discussed in Grehan in press.)

Given a particular orthogenetic potential *A. virescens* may be prone to varying levels of mortality with respect to host-plant density, forest structure and general climate. Within this orthogeny there is the potential to feed on both fungal and green plant tissues but only at distinct stages in larval development. The implication of this behaviour for interpretation of Lepidopteran feeding evolution is that the evolutionary "step" between fungal and green plant specialisation is not so large that it cannot be encompassed in the life cycle of a single species, in spite of the fact that the two plant groups exhibit totally different cell tissues (Martin 1979). The host plant survey of Powell (1980) indicates that for the Lepidoptera, fungal feeding does not normally occur in conjunction with live green plant feeding. The Mnesarchaeidae (closely related to the Hepialidae; Kristensen 1978) are known to ingest leaves of live and dead moss, liverwort leaves and rhizoids, fern sporangia, fungal spores and hyphae, and filamentous algae but it is not known to what extent these various food sources may be exploited (Gibbs 1979). A litter phase is probably generally present in the Hepialidae (Grehan 1979).

By drawing attention to the relationship between *A. virescens* and its hosts in terms of phylogeny and dispersal, I am not suggesting that there is necessarily anything unique about the features I have described. Only a brief outline of the insect/host evolution of *A. virescens* has been possible here and there remains considerable scope for the amateur entomologist to clarify the status for many of the plants listed in this paper. I believe that with future analysis of host/plant relationships by application of panbiogeography for other insects of the southwest Pacific, comparable patterns will be found. It is a truism, to say the least, that dispersal forever repeats (Croizat 1964: ii).

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