

## Morphological changes in the three-phase development of *Aenetus virescens* larvae (Lepidoptera: Hepialidae)

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A larval phase of *Aenetus virescens* (Doubleday) morphologically distinct from the young larvae found on dead wood and fungi (litter phase) and the older larvae in live trees (tree phase) is described, and designated the 'transfer phase'. It is characterised by expansion and fusion of the dorsal pinacula, which results in a darker overall coloration. The transfer phase is a single instar, but its exact position in larval development seems to vary. The 'transfer larva' migrates from the litter habitat to live tree hosts, where it establishes a tunnel. Chaetotaxy and other morphological features of *A. virescens* larvae are described and compared. The diagnostic value of certain features of a range of hepialid larvae is discussed.

**Keywords:** Lepidoptera; Hepialidae; *Aenetus virescens*; larva; developmental phases; morphology; chaetotaxy

### INTRODUCTION

The existence of two sequential colour morphs in the larval stage of *Aenetus virescens* (Doubleday) has long been known (Quail 1902), but it was not until the discovery of the two contrasting life styles of early larvae and later instars (Grehan 1979) that the significance of this change in form became apparent. After an initial development phase on fungi and dead wood, larvae ascend trees or shrubs of various species and bore into trunks, stems, and branches, where they complete their development. These two life history sub-stages are described as 'litter phase' and 'tree phase' respectively.

This paper draws attention to the distinctive morphology of the larva which transfers from the litter habitat to the final tunnel site in a live tree. I have called this substage the 'transfer phase'. For convenience, the parallel terms 'litter larva', 'transfer larva', and 'tree larva' are adopted in this report.

The tree larva of *A. virescens* has been described several times, either in general terms (Hudson 1898, 1928) or in comparison with other *Aenetus* species or other hepialids (Quail 1899, Hildige & Quail 1900, Quail 1902). Although adequate for identification, these descriptions were incomplete; only one species was involved, and its tunnel characters are reliably diagnostic. The occurrence of *A. virescens* larvae in the litter environment was not known to these entomologists (Grehan 1979). A number of Lepidoptera have superficially similar larvae in litter (pers. obs.), and hence there is a need for a more precise description of *A. virescens* larvae and a review of hepialid larval characteristics.

### IDENTIFICATION OF LARVA

*Aenetus virescens* belongs to the subfamily Hepialinae, which is also represented in New Zealand by the endemic genus *Aoria* (four species) (with subterranean larvae; Hudson 1928). Only *A. leonina* is recorded from the North Island, to which—apart from some offshore islands—*A. virescens* is confined (Dumbleton 1966). *A. leonina* occurs in the sub-alpine-alpine zone (J. S. Dugdale, pers. comm.), whereas *A. virescens* is a forest insect. However, an unidentified *Aoria* larva has been found in silver beech (*Nothofagus menziesii*) forest on a ridge top 800 m a.s.l. in the Rimutaka Range near Wellington (41°21'7"S, 174°59'2"E) (A. Moeed & M. J. Meads, pers. comm.), and larvae of this species might therefore be found with those of *A. virescens* in the litter.

Larvae of *A. virescens* and *Aoria* spp. can be distinguished from larvae of Oxycaninae by the arrangement of their ocelli (J. S. Dugdale, pers. comm.), as shown in Fig. 1. In the second and subsequent instars, the prothoracic sensory pit contains the setae SD1, SD2, and D2 in *A. virescens* (see Fig. 3) but only SD1 and D2 in *Aoria*. The chaetotaxy and morphology of *Aoria* first-instar larvae have not been recorded. Characters diagnostic of hepialid larvae are discussed below ('Larval chaetotaxy').

### TRANSFER LARVA

The transfer larva (Fig. 2A,C) was first recorded by Quail (1902), who observed a single specimen about 1½ inches (27 mm) long characterised by

"alternate brown and yellow dorsal lines with lateral and ventral brown spots, closer examination showing the elevated portions of segments, subsegments, and tubercle areas to be brown, hard and polished, the incisions and ground colour being yellow. The thoracic segments did not differ so from normal." Quail was at a loss to explain the significance of such a form, thinking that perhaps the larva had retained its juvenile characteristics until a later stage than usual, or was merely an exception. Neither Quail nor any subsequent worker made any further reference to this phenomenon.

I first encountered the transfer larva when sampling newly established tree larvae at monthly intervals on *Carpodetus serratus* at Lake Pounui Reserve (41°21'S, 175°07'E). Of 35 larvae established for 1 month or less, 26 were of the transfer morph; the remainder were 'normal' tree larvae. For these latter the feeding area around the tunnel was more extensive, indicating a longer period of occupation; moreover, head capsules found at the tunnel entrance of three specimens were evidence of a recent moult. I have found entire exuviae of the transfer larva at the tunnel entrance of a newly established tree larva twice at Lake Pounui Reserve and once at Wainuiomata (41°16'8"S, 174°59'7"E). New tunnels in which no feeding around the entrance had yet occurred were invariably occupied by transfer larvae. This supports the view that larvae of 'normal' appearance are not involved in the shift from litter to tree.

In February 1979 I caged four large (about 30 mm) litter larvae (Fig. 2B,D) on the surface of a live host tree. They did not tunnel until they had moulted into the transfer morph.

Monthly sampling of new tunnels indicates that the transfer larva assumes the pale colour of the tree larva at the first moult after establishment. This evidence is supported by examination of five transfer larvae induced to establish new tunnels. The larvae were extracted from *C. serratus* at Lake Pounui Reserve and caged on a fresh surface, where they excavated a tunnel. Following the first moult the larvae were again extracted, and all were found to have changed into the normal tree-phase morph.

From November 1979 to October 1980, Dr A. Moed and Mr M. J. Meads (pers. comm.) took 38 *A. virescens* larvae in specially designed insect traps operated in the Orongorongo Valley (41°21'S, 174°58'E). All were collected while ascending tree trunks, and all but two were transfer larvae (the exceptions were first instars). I have collected a further nine transfer larvae in similar circumstances in Wainuiomata.

Transfer larvae in the range 10–35 mm total length and 2.4–4.3 mm head width have been taken ( $n=25$ ), supporting the suggestion (Grehan 1979) that transfer is not a function of a particular instar. How-

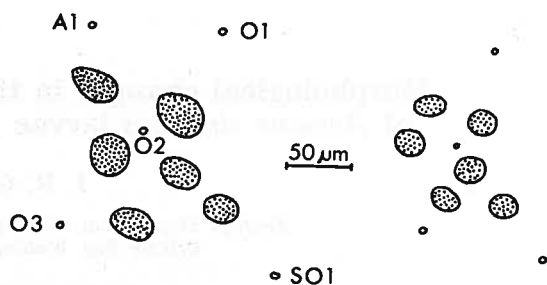


Fig. 1. Ocellar pattern in the larvae of *Aenetus virescens* (Heptaliinae) (left) and *Trioxycanus* sp. (Oxycaninae) (right). Small circles - insertions of adjacent head setae.

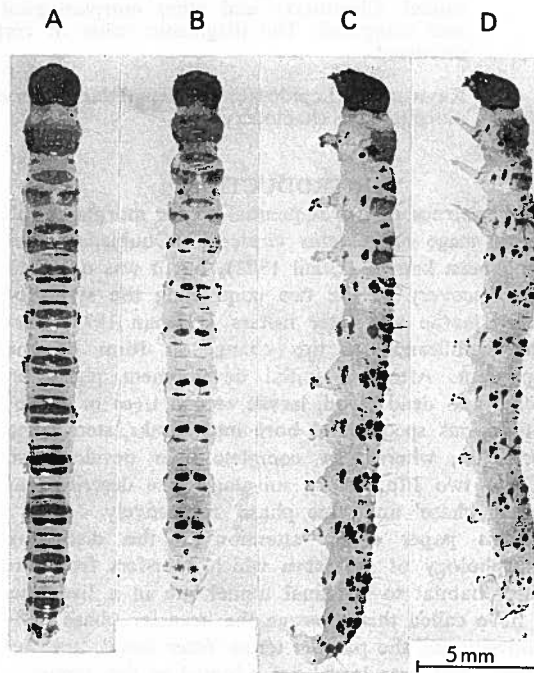


Fig. 2. *Aenetus virescens* larvae, dorsal and lateral aspects: A, C, transfer larva; B, D, litter larva.

ever, the range of instars over which transfer can be effected has not yet been determined. All that can be said is that transfer occurs relatively early in larval development, perhaps some 3 months after hatching in a life cycle that lasts as long as 5 years (Alma 1977).

Transfer larvae may occasionally be found in litter. For example, a single transfer larva was found in a sample of 50+ litter larvae taken in February 1979 in the Urewera National Park. Transfer larvae may be found at any time of the year, but appear to be most common from January to March.

**Table 1.** Major differences between the larval morphs of *Aenetus virescens*. Colour codes (Kornerup & Wanscher 1978) allocated by subjective assessment of hue

Character	First instar	Litter larva	Transfer larva	Tree larva
Head colour	black	reddish orange to brown (7A8-7E8)	reddish orange to brown (7A8-7E8)	reddish orange to brown (7A8-7E8)
Body colour	pale yellow to white	white; gut contents may be visible (black)	dull yellowish white to white	white; orange-white (5-A2); purple haemolymph (16-A5)
Thoracic pinacula colour	black	orange (5B-8); anterior margins sometimes greyish brown (6E-3)	orange (5B-8); anterior margins sometimes greyish brown (6E-3)	greyish yellow (4-B4)
Abdominal pinacula colour	black	pale to dark brown (6E-4-8 to 6F-4-8)	pale to dark brown or grey brown	greyish yellow (4-B4)
Fused dorsal pinacula	prothorax; anterior pinacula of meso- and meta-thorax; abdominal segment 10	prothorax; anterior pinacula of meso- and meta-thorax; abdominal segment 10	all segments	prothorax; anterior pinacula of meso- and meta-thorax; abdominal segment 10

**COLOUR MORPHS**

Variation in the colour pattern of *A. virescens* is expressed as differences in hue and in the extent of sclerotised areas (pinacula) and unsclerotised cuticle (Table 1). Pinacula containing setae are referred to here (after Mutuura 1980) as dorsal, subdorsal, lateral, subventral, and ventral; where two pinacula of one type are present on a body segment they are referred to as anterior or posterior, according to position. No attempt is made here to define the absolute limits of colour variation, but sufficient detail is given to distinguish the general features of litter, transfer, and tree larvae; these characters are summarised in Table 1.

The sclerotised areas of litter and transfer larvae tend to be dark relative to the tree larva, in which (apart from the head) they become very pale and often difficult to distinguish from the surrounding cuticle. The transfer larva is distinct in colour pattern because of fusion across the dorsal midline of the anterior and posterior dorsal pinacula and the intersegmental non-setaceous dorsal pinacula. This fusion results in the striped appearance of alternating yellow-white and dark bands (Fig. 2A) described by Quail (1902). Unsclerotised cuticle is colourless, and the body colour depends on the underlying tissue. Tree larvae may take on a purple coloration (due to haemolymph) not found in the litter or transfer larva. Hudson (1928) states that younger (tree phase) larvae differ in being an olive-green colour, but I have observed this in only a few specimens.

**CHAETOTAXY**

Chaetotaxy described here follows the nomenclature of Hinton (1946) and Aitkenhead & Baker (1964) for the head, thorax, and abdominal segments 1-9 (the

homology of setae on abdominal segment 10 was not described by Hinton). Descriptions are based on examination of whole specimens and of skins prepared by the method of Baker (1963). Chaetotaxy is shown in Fig. 3, 4, and 9 for body segments and in Fig. 7 for the head.

**FIRST INSTAR** (Fig. 3). Setae D1 and D2 occupy the same pinaculum as SD1 and SD2 on the prothorax. On the remaining segments D1 and D2 are on separate pinacula, D2 being slightly the lower. SD1 and SD2 occupy a single pinaculum on the mesothorax, metathorax, and abdominal segment 9. L1 and L2 on the prothorax are on a single pinaculum in juxtaposition to the dorsal pinaculum, but are on separate pinacula on abdominal segments 1-8. MV3 appears to function as a tactile seta on abdominal segments 3-7 but as a proprioceptor on other segments. Microtrichia are abundant on all segments, but not on the pinacula and parts of the intersegmental membranes.

**SECOND TO FINAL INSTAR** (excluding transfer larva) (Fig. 4). On the prothorax the pinaculum of setae L2 and L1 is fused completely with the dorsal pinaculum, and SD1, SD2, and D2 are grouped in a single sensory pit (absent in the first instar) which is covered with microtrichia (Fig. 5). On the mesothorax and metathorax D2 is on the same pinaculum as SD1 and SD2, and setae MD1, MSD1, and MSD2 are usually on a single pinaculum. L1 and L2 are usually on the same pinaculum on abdominal segments 1 and 2, but only sometimes on abdominal segments 3-8. Setae appearing at the second instar are: L3 on prothorax and abdominal segment 9; L2 on mesothorax, metathorax, and abdominal segment 9; SV2 on abdominal segments 8 and 9; and SV3 on abdominal segments 1-6.

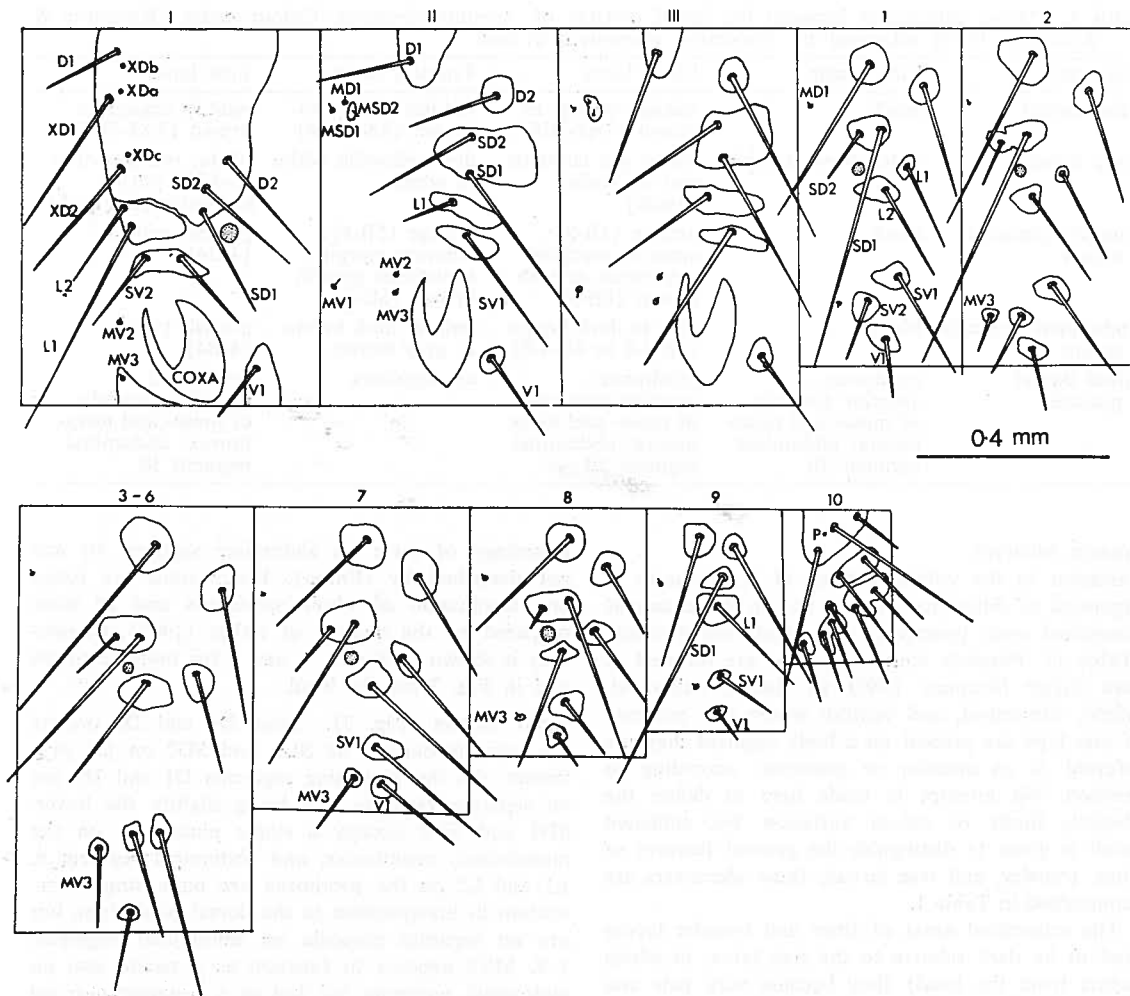


Fig. 3. Thoracic and abdominal chaetotaxy of *Aenetus virescens* first-instar larva (spiracle indicated by stippling; pinacula bounded by solid lines; p, pit).

There is an elongate pit just behind and below L1 on the mesothorax and metathorax. A further pit is located in front of and below D2 on the mesothorax and metathorax, on abdominal segments 1-9, and in a similar position with respect to an unidentified seta on abdominal segment 10. In the first and final larval instars the head has the same setae and pits, but these differ slightly in relative position owing to differences in head shape (Fig. 6).

The spiracles are circular in the first instar, but become oval in subsequent instars. There is one row of proleg crotchets in the first instar and two rows in subsequent instars (Fig. 7 and 8).

TRANSFER LARVA (Fig. 9). This instar has the same number and relative position of setae as other instars

after the first, but apparent differences in chaetotaxy arise through fusion of pinacula. Anterior and posterior dorsal pinacula fuse across the dorsal midline on the mesothorax, metathorax, and abdominal segments 1-8, so that each pair of dorsal setae occupy a single pinaculum. On abdominal segment 9 only the anterior dorsal pinacula fuse completely; the posterior dorsal pinacula tend to extend mainly forward to fuse with the single anterior dorsal pinaculum. The anterior dorsal pinacula also extend laterally to fuse with the pinacula of MD1 and SD1, and sometimes the pinaculum of L2 is included. The result is a single pinaculum covering most of the dorsal surface of abdominal segment 9. The pinacula of L1 and L2 are often fused on one or more abdominal segments subsequent to 1 and 2.

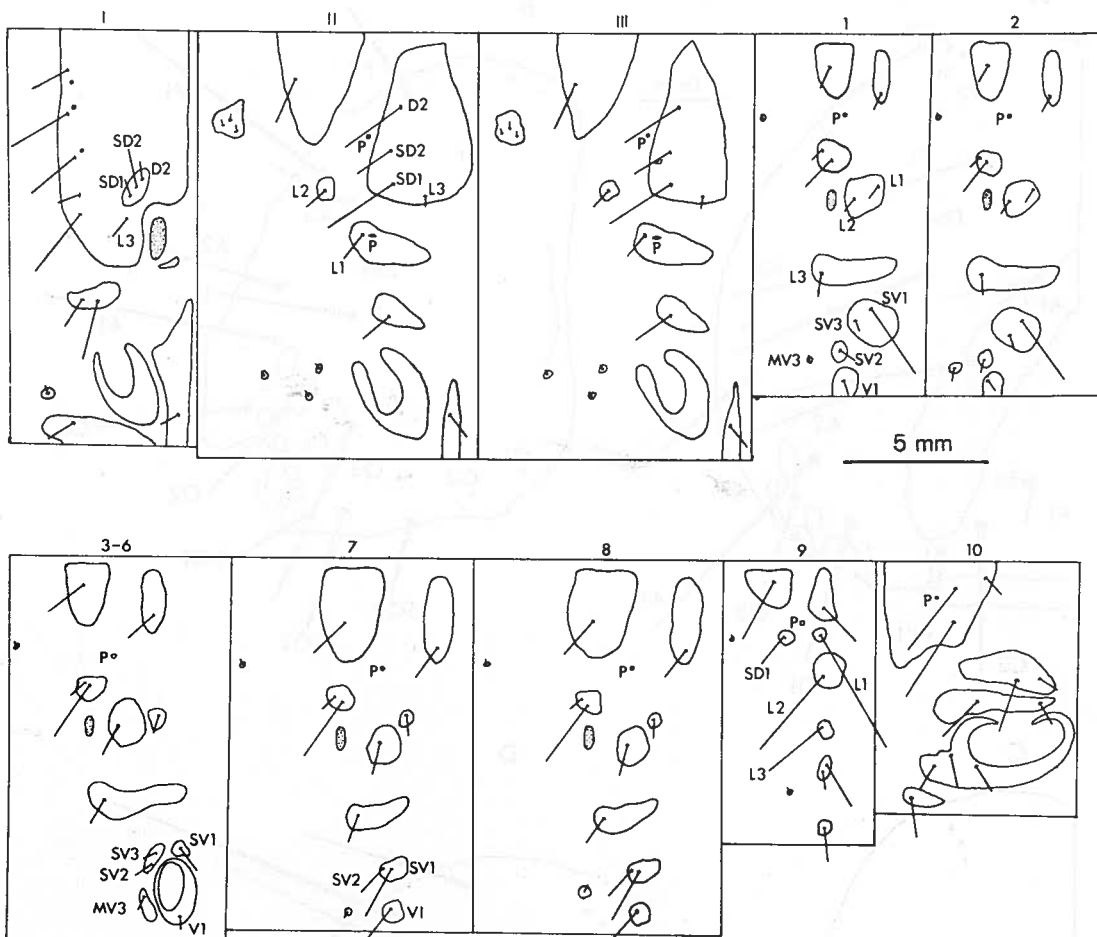


Fig. 4. Thoracic and abdominal chaetotaxy of *Aenetus virescens* final-instar larva (conventions as for Fig. 3).

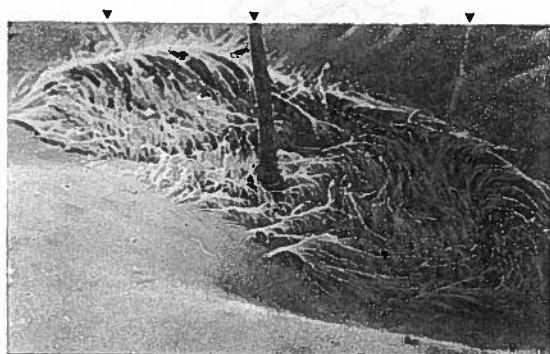


Fig. 5. Prothoracic sensory pit of *Aenetus virescens* larva (setae arrowed; the large central seta is SD2).

DIAGNOSTIC FEATURES OF HEPIALID LARVAE

Aitkenhead & Baker (1964) characterise larvae on the following criteria. On the head the pit Ga is absent (for certain other families Ga is located in the vicinity of G1; Hinton 1946) and the two Fa pits are lateral to the F1 setae. On the prothorax the lateral setae L1 and L3 are on the shield (dorsal pinaculum). On the mesothorax and metathorax D1 and D2 are arranged as on the abdomen. The proleg crochets are arranged in concentric circles. The anterior group of head setae is arranged in a line running roughly between the ocelli and seta P2, so that A3 is posterior to P1.

The position of L1 and L3 on the prothorax is applicable to the second and succeeding instars of

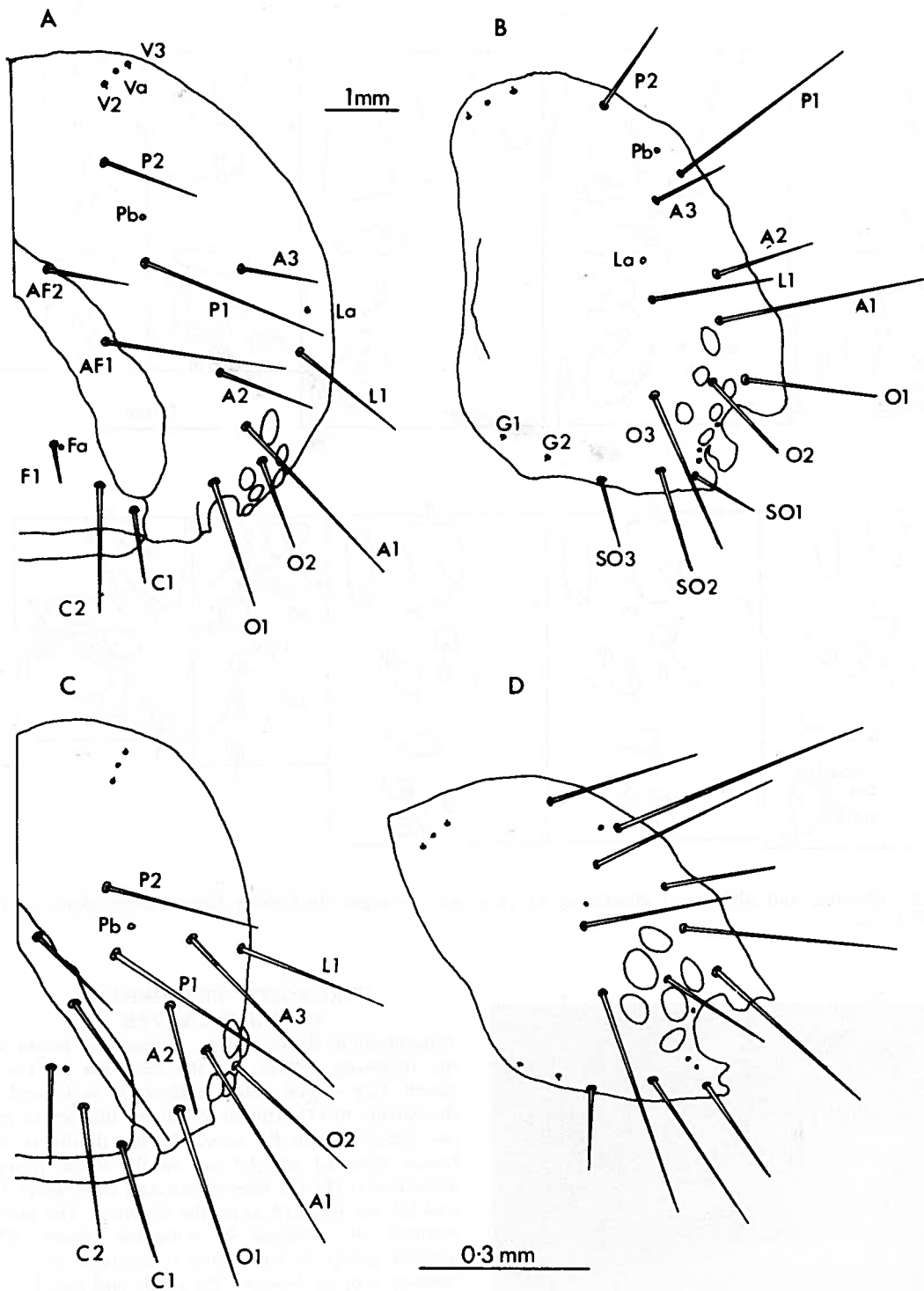


Fig. 6. Head chaetotaxy of *Aenetus virescens* larvae, dorsal (A,C) and right lateral (B,D) aspects. A,B, final instar; C,D, first instar.

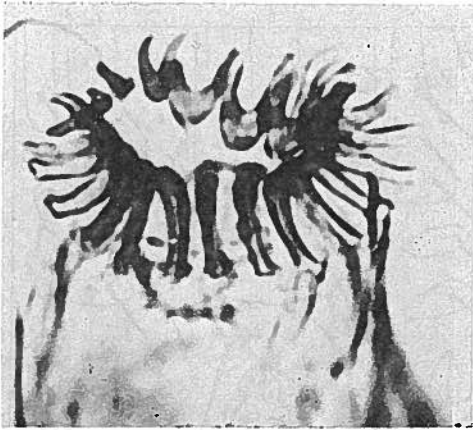


Fig. 7. Abdominal proleg of *Aenetus virescens* first-instar larva, ventrolateral view, showing single row of crotchets.

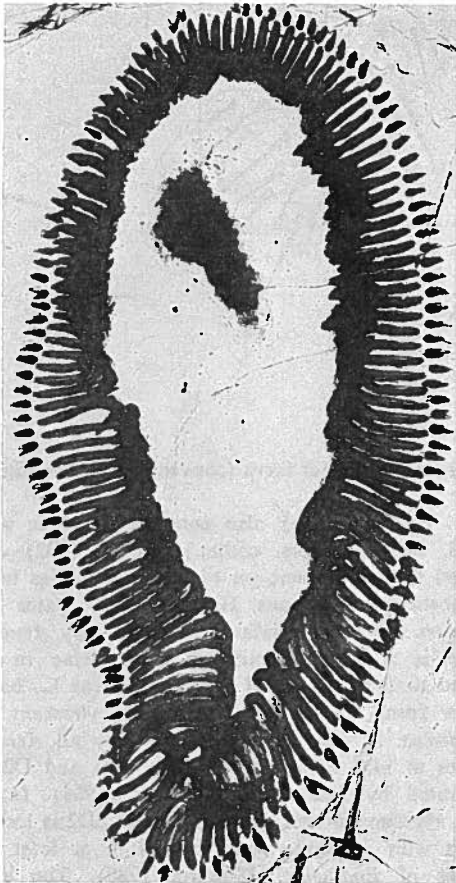


Fig. 8. Abdominal proleg of *Aenetus virescens* final-instar larva, ventral view, showing double row of crotchets.

*A. virescens*, but in the first instar a distinct pinaculum adjacent to the prothoracic shield bears L1 and L2. The only connection to the shield is a narrow band of lightly sclerotised tissue at the anterior margin. The same situation may apply to *Hepialus*; a line demarcates the prothoracic shield from the region with the lateral setae in fig. 9 of Aitkenhead & Baker (1964). Evans (1941) illustrates the first instar of *Oncopera intricata* Walker with the pinaculum of L1 and L2 completely separate from the prothoracic shield.

I have found the alignment of the anterior head setae in *A. virescens* difficult to assess, and not suitable for identification purposes. This feature is not considered further here.

Many of these distinguishing features of hepialid larvae noted by Aitkenhead & Baker (1964) also apply to the endemic New Zealand family Mnesarchaeidae. The only one which does not is the presence of setae L1, L2, and L3 on the prothoracic shield. In Mnesarchaeidae L3 does not lie on a pinaculum with L1 and L2 (G. W. Gibbs, pers. comm.). Mnesarchaeid larvae also differ from hepialids in the absence of seta V3 in the vertex group and the puncture La in the lateral group on the head (Gibbs 1979). Practical means of separating the two families could be important in New Zealand, since larvae of *Mnesarchaea acuta* Philp. occur in the layers of encrusting mosses and liverworts found on rotting logs (Gibbs 1979) where small *A. virescens* larvae might also be present.

Mutuura (1980) describes the hepialid arrangement of anterior dorsal pinacula for abdominal segments 1-8 as a united plate across the mid-dorsal line, but cites only *Phassus* sp. (= *Endoclita*; A. Mutuura, pers. comm.) as an example. This description fits the transfer larva of *A. virescens*, in which the posterior dorsal pinacula are fused also, but not other instars. There is no indication of dorsal pinacula fusion in *Hepialus* (Aitkenhead & Baker 1964) or in *Leto venus* Stoll (Janse 1939). In *Oncopera parva* Tindale the posterior dorsal pinacula are separate or in juxtaposition (Elder 1978). I have found no fusion of abdominal dorsal pinacula in larvae of *Aenetus paradiseus* var. *montanus* (Tindale) or *A. lignivorus* (Lewin). The fusion of anterior with posterior dorsal pinacula on abdominal segment 9 of the transfer larva of *A. virescens* is similar to the condition in *Endoclita signifer* Walker, as illustrated by Hattori (1969).

The sensory pit on the prothoracic shield is variable in the Hepialidae; it is considered here in its entirety, i.e., including the enclosed setae. Setae SD1, SD2, and D2 may variously have a sensory base lined with microtrichia, or two of them or all three may be grouped together in a sensory pit. In *A. virescens*



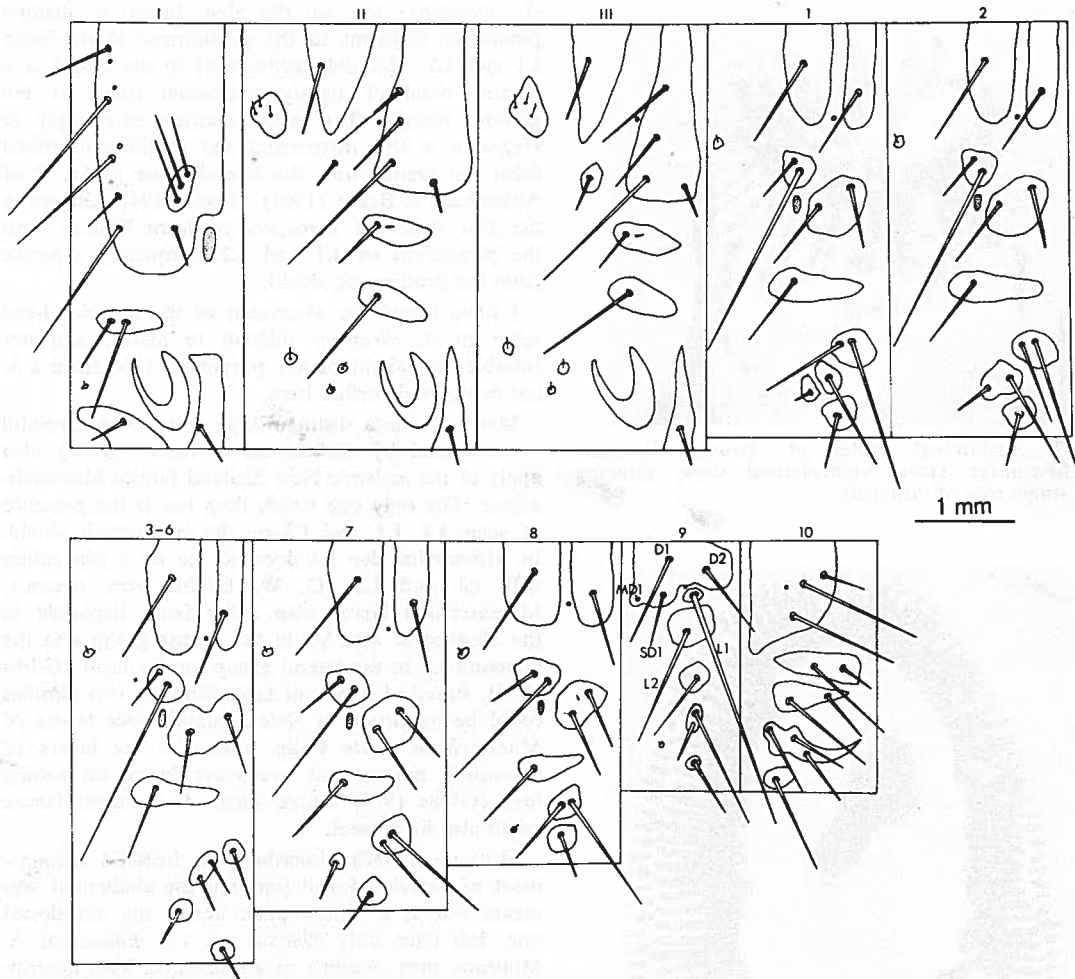


Fig. 9. Thoracic and abdominal chaetotaxy of *Aenetus virescens* transfer larva (conventions as for Fig. 3).

all three setae are included; in *Oncopera parva* the pit contains SD1 and SD2 (Elder 1978); and in *Fraus simulans* Walker SD1 and D2 each have a sensory base (Hardy 1973). Illidge & Quail (1901) referred to three setae in young (tree phase) *A. virescens* larvae and only one in mature larvae. My examination of final-instar exuviae revealed three setae, but the smaller SD1 and D2 setae are difficult to see against the dark background colour of the pit. Similarly, Illidge & Quail (1901) referred to only one seta in *A. eximia* Scott but three setae in *A. ramsayi* Scott and *A. scotti* Scott (*A. daphandrae* Lucas) (of unspecified age). I have examined the sensory pit of *A. paradiseus* var. *montanus* and *A. lignivorus*, and it appears to be superficially identical in structure to that of *A. virescens*. The sensory pit

of *A. cohici* (Viette) also contains all three setae (J. S. Dugdale, pers. comm.). Quail (1902) considered the prothoracic pit of *Aenetus* species to be diagnostic of the genus. Hinton (1948) states that it occurs in some Hepialidae, but cites only *Aenetus*. There is a pit containing all three setae in the second to final instars of *Hepialus hectus* L., but it differs from the sensory pit of *A. virescens*, *A. paradiseus*, *A. lignivorus*, and probably all *Aenetus* species in SD2 being shorter than SD1 and D2, as illustrated by Aitkenhead & Baker (1964). In the three abovementioned *Aenetus* species SD2 is longer. A pit with all three setae occurs in at least one species of *Endoclita* (Mutuura 1980). The larva illustrated by Mutuura (1980) was collected from Japan, and is either *Endoclita excrescens* Butl. or *E.*



signifier (A. Mutuura, pers. comm.). *Endoclista* is considered by Tindale (1957) to be quite closely related to *Aenetus*, but no evidence is presented. It is not known whether all *Endoclista* species have prothoracic sensory pits with three setae, or whether the pits' structure is the same as for *Aenetus*. Even so, the prothoracic sensory pit may be a useful diagnostic character at the generic level. The sensory pit may have evolved independently in *H. hectus*, since this is the only *Hepialus* species for which all three setae have been recorded as occurring together.

#### DISCUSSION

The easily recognisable transfer phase in the larval development of *A. virescens* has not been recorded for other Hepialidae, although two-phase larval development involving a change of microhabitat is known for the wood-borers *Endoclista sericeus* (Swinhoe) (Kalshoven 1950, 1965) and *E. gmelina* Tindale (Dhanarajan 1976). Some species with subterranean larvae are known to have a comparable pattern of development (Grehan 1979), but a morphologically distinctive transfer larva does not occur, at least in *Wiseana cervinata* (Walker) (Oxycaninae) (A. Carpenter, pers. comm.). Kalshoven (1950) states that the litter larvae of *E. sericeus* (as *Phassus damor* Mr; Kalshoven 1965) are cream-coloured, but when they move into bushes or trees they are then "mainly black with lighter coloured bumps" (as translated). This description lacks comparison with subsequent instars, and is too general for a morphologically distinct transfer larva to be inferred. It would be of particular interest to know if a transfer phase like that of *A. virescens* occurs in other *Aenetus* species.

The transfer larva is clearly associated with a change in habitat, and is characterised by the greater surface area covered by pinacula than in any other stage. Mutuura (1980) notes that many pyralid borers have pinacula united across the mid-dorsal line, and suggests that this may be an adaptation to the constant friction generated by the tunnel wall. He further suggests that there is an evolutionary trend towards increase in the size, number, and fusion of pinacula as larvae become more adapted to living in a tunnel. However, in *A. virescens* the most extensive pinacular covering occurs at the one phase of the life cycle when the larva must be exposed, although it may occupy a tunnel for several years following transfer.

The prothoracic shield, anal plate, and pinacula bear many points of muscle attachment, and Mutuura (1980) suggests that the prothoracic shield and anal plate may have developed as an expansion of sclerotised cuticle resulting from strongly developed muscle bases in these areas. If this is so,

it is possible that the fused thoracic and abdominal pinacula in the transfer larva of *A. virescens* support a musculature more robust than in the other larval phases.

In general, white or pale-coloured lepidopteran larvae are tunneling insects, and this is true of *A. virescens* in its litter and tree phases. In the transfer larva the predominantly dark colour pattern appears to be cryptic, and the transverse dorsal bands of fused pinacula may serve to disrupt the outlines of the body.

#### ACKNOWLEDGMENTS

My grateful thanks to Dr G. W. Gibbs (Zoology Department, Victoria University of Wellington) for liberal help and for constructive criticism of the draft manuscript and photo of larvae; Mr J. S. Dugdale (Entomology Division, DSIR) for advice and comments on the draft; Dr A. Moeed and Mr M. J. Meads (Ecology Division, DSIR) for supplying specimens of transfer larvae; Mr P. Aitkenhead (Department of Agriculture, Fisheries & Food, U.K.) for providing mounted skins of *Hepialus hecta*; Mr A. Carpenter (Ministry of Agriculture and Fisheries) for information on *Wiseana*; Mr D. Gilliver for help with field equipment; and the Wellington Regional Council for allowing access to the Wainuiomata Water Supply Catchment.

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