

## Evolution of arboreal tunnelling by larvae of *Aenetus* (Lepidoptera: Hepialidae)

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**Abstract** Aspects of larval feeding and tunnelling were described for seven species of the wood-boring genus *Aenetus*. The species were studied in Australia, New Caledonia, and New Zealand. A sequential pattern of larval feeding involving transfer from a fungal based diet to callus tissue in live trees, previously known for *A. virescens*, was confirmed for *A. cohici* and inferred for *A. dulcis* and *A. paradiseus*. A specialised "transfer" morph linking the two feeding stages in *A. virescens* was also confirmed for *A. cohici* and two unidentified species. The wood-boring habit involved entry into the host above ground level and the construction of a tunnel which extends into and then down the stem. Tunnels were often located on the lower surface of leaning branches or stems. Tunnel entrances were open to the host surface, but overlain by a silk/frass web. Bark and underlying tissue were removed from around the tunnel entrance and a callus growth resulted, which the larva consumed. The evolutionary history of arboreal tunnelling in the Hepialidae was investigated using biogeographic analysis of generic distribution. It is argued that evolution and variation in arboreal tunnelling resulted from specialised recombinations of generalised ancestral characters. It is suggested that the study of arboreal tunnelling can provide a source of useful characters for systematic analysis of phylogenetic relationships within *Aenetus*. The potential systematic value of tunnel characters is illustrated for *A. virescens*.

**Keywords** Lepidoptera; Hepialidae; *Aenetus*; larvae; wood-boring; feeding; tunnelling; host plant; evolution; biogeography

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### INTRODUCTION

The larvae of most species of Hepialidae occupy tunnels excavated in soil and feed on roots or ground vegetation (Tindale 1938, 1981; Common 1970), but a few genera include species which spend most of their larval development tunnelling and feeding in the stems and branches of trees and shrubs. The tunnels of these arboreal species may extend down into the roots, but they have no direct contact with the soil. Genera with arboreal species include *Aenetus* (Common 1963, 1970), *Endoclyta* (Beeson 1941), *Sahyadrassus* (Beeson 1941; Nair 1982), *Zelotypia* (Common 1963), *Leto* (Janse 1945), *Trichophassus* (Briquetot 1956), *Aepytus* (Winder & Harley 1983), and *Hepialus* (Wagner 1985). *Zelotypia*, *Leto*, and *Trichophassus* are monotypic. Although the larval habits are not known for all species of the remaining arboreal genera, non-arboreal feeding has been recorded only for *Hepialus*, where the arboreal species (*Hepialus californicus* Bdv. and *H. hectoides* Bdv.) are to be placed in a separate genus in a forthcoming revision (Wagner 1985). Stem boring has been recorded for the chinese species of *Palpifer* by Chu & Wang (1985), but the larval habits were not described. Their classification may be incorrect because the larvae of *P. sexnotatus* Moore are definitely known to be root borers (Sonan 1938; Kalshoven 1965; Baker 1983).

The arboreal habit is known for about 13 species of *Aenetus* (Table 1, Grehan 1984). Several species are known from New Guinea, (Pfitzner & Gaede 1933; Viette 1956), but the larval habit is known for only one species which was found in *Nothofagus* sp. (E. S. Nielsen pers. comm.). The larval stages of *Aenetus* were of interest to a number of biologists during the late 19th and early 20th century in Australia (Lewin 1822; Scott 1864, 1869; Olliff 1887; Froggatt 1894, 1907, 1923; Illidge 1899, 1900; Illidge & Quail 1901; Gallard 1915; Pescott 1934; McKeown 1935; King 1962) and New Zealand (see Grehan 1979, 1987 for references), but descriptions were generalised and fragmentary, particularly with respect to the mode of larval tunnelling and early larval development. Scott (1864) described the habits and metamorphoses of the then known *Aenetus* species as "remarkably consistent" and a single description was regarded sufficient for all members. Illidge & Quail (1901) observed variation in larval tunnelling by *Aenetus*, but they did

not undertake detailed comparison. Recent observations on the biology of *A. virescens*, have indicated that the relationship between larval development and feeding is more complex and diverse than suggested in earlier accounts on the genus (Grehan 1979, 1983a, 1987).

In this paper, I combine the results of previous studies on *A. virescens* with further field observations on this and other species of *Aenetus*. The evolutionary history and significance of arboreal tunnelling and tunnel characters is investigated in a biogeographic context by analysing the distribution of *Aenetus* and individual tunnel characters. This approach does not require a priori assertions of selective (e.g., Mayr 1984: 352) or functional advantage (e.g., Savile 1984) as explanations of biological patterns (cf. Croizat 1964; Cheverud et al. 1985; Gray 1987). Biogeographic analysis is used in this paper to interpret the phylogenetic significance of arboreal feeding and the potential value of tunnel characters for systematic studies of arboreal Hepialidae.

## SPECIES AND STUDY AREAS

### *A. virescens* (Doubleday)

Observations were primarily at Wainuiomata (41°16'S; 174°59'E) and Lake Pounui Reserve (41°21'S; 175°07'E), New Zealand. The survey of tunnel location was carried out on the property of Mr and Mrs D. B. A. Innes (41°15'S, 174°59'E; 100 m a.s.l.). The host surveyed was *Carpodetus serratus* growing in hillside broadleaf forest regeneration.

### *A. paradiseus montanus* (Tindale)

Ginini Gap (1 620 m, 35.31 S, 148.46 E) and Mount Franklin Chalet (1 494 m, 35.30 S, 148.4 E: Australian Series R 502, 1:2 500 000 Map S.I. 55-16 Canberra). Both sites were located on ridge tops of the Brindabella Range where seedlings and saplings of *Eucalyptus pauciflora* (Sieb) grew beneath a canopy of mature trees of about 17 m height. Tindale (1953) referred to this host as *E. niphophila* (Maiden & Blakely) which was later synonymised with *E. pauciflora* by Pryor (1957). The study was confined to regenerating *E. pauciflora* where *A. paradiseus montanus* was accessible for a short-term study.

### *A. paradiseus paradiseus* (Tindale)

Australia, Tasmania near Geevston (43°9'S, 147°10'E; 23-24/11/82) in forest regeneration of *Eucalyptus obliqua* L'Herit. with a canopy of about 8 m. The vegetation was previously logged and burned before oversowing.

### *A. cohici* Viette

New Caledonia at Forêt du Thy (22°10'S, 166°35'E) in a forest about 400 m a.s.l. on a north facing hillside where *Nothofagus discoidea* (Baumann-Bodenheim) van Steenis formed part of the canopy, and at Montanes Koeanonoa (22°14'S, 166°40'E; 400 m a.s.l.) in a gully with a forest remnant with a canopy of *Nothofagus*.

### *A. eximius* (Scott)

Australia, New South Wales: Mount Kembla (34°25'S, 150°49'E) on the eastern, coastal facing escarpment behind Wollongong. Larvae were observed in *Cassinia* sp. in a gully with a small, almost dry, stream bed where the host trees formed a 6 m high canopy under *Eucalyptus* trees about 20 m high and with basal diameters up to 121 mm. Victoria: 3 km from Erica (37°58'S, 146°22'E) larvae were found in *Pomaderris aspersa* trees growing up to a height of 6 m and basal diameter of 133 mm in a forest dominated by *Eucalyptus* sp.

### *A. ligniveren* (Lewin)

Australia, Tasmania: Snug Tiers (43°2'S, 147°14'E; 350 m a.s.l.) on 25 November 1983 and alongside Highway 8 (42°12'S, 145°59'E). The vegetation at the Snug Tiers site comprised a wet sclerophyll forest dominated by *Eucalyptus obliqua* whereas the Highway 8 site was a "rainforest" of *Nothofagus cunninghamii* (Hook.) Oerst and other species.

### *A. dulcis* (Swinhoe)

Australia, Western Australia: Karridale, on the property of Mr and Mrs Shenstone (34°12'S, 115°6'E), Point D'Entrecasteaux (34°50'S, 116°05'E) and Torndirrub National Park (35°06'S, 117°55'E). Larval feeding by *Aenetus* was observed in *Agonis flexuosa* (Spreng.) Schauer which formed a 6-7 m high sub-canopy under a forest of *Eucalyptus diversicolor* F. Muell. on the Shenstone property. In coastal areas such as Windy Harbour and Torndirrub National Park, *A. flexuosa* formed part of the vegetation canopy. Larval tunnels in *Agonis juniperina* were observed at at Sir James Mitchel National Park (34°18'S, 116°31'E), Walpole (34°59'S, 116°40'E), Ocean Beach, and alongside the road between Collie and Dwellingup. In these localities, *A. juniperina* was generally a sub-canopy plant growing next to, or close to small streams. It could also occur in exposed conditions where previous forest cover had been destroyed.

### *A. mirabilis* (Rothschild)

Information and samples of tunnelling were sent to me by Mr N. Quick who examined the species at Kuranda, Queensland.

## METHODS

Larvae were identified by known host association supplemented by rearing to adult or through previous locality records. *A. virescens* and *A. cohici*, are the sole representatives of *Aenetus* in New Zealand and New Caledonia respectively (Dumbleton 1966; Viette 1961), whereas *A. paradiseus montanus* is the only species present on the summits of the Brindabella Ranges (I. F. B. Common, E. D. Edwards pers. comm.). The two species in Tasmania are *A. paradiseus paradiseus* and *A. ligniveren* which tend to occur in different situations and host plants (P. B. McQuillan, H. J. Elliott pers. comm.). Other species, identified through rearing of larvae or pupae, included *A. ligniveren* (in *Acacia delbata* and *Pomadereis apetala* Labill), *A. eximius* (*Antherosperma moschatum* Labill., *Pomadereis aspersa* Sieb.), *A. dulcis* (*Agonis flexuosa*, *A. juniperina*), and *A. cohici* (*Nothofagus discoidea*, *Hibbertia brongnartii* Gilg. ex Gilg. et Werdermann [Dilleniaceae]). Larval stages of *A. cohici* were also recorded from *Nothofagus codonandra* (Baill.) Steen (Fagaceae) at Mount Do (21°45' S, 166°66' E) by Mr J. S. Dugdale, and *Hibbertia paucheri* (Pauch. et Sebert) by Mr W. J. Winstanley. Vacant larval tunnels of *A. cohici* in *Nothofagus aequilateralis* (B.-B.) Steen, were shown to the author at Pic du Pin (22°15' S, 166°15' E) by Mr T. Azais and Mr M. Boulet (Service Territoriale des Eaux et Forêts).

At each locality a survey was made of entire trees or shrubs in which larvae were found. Since the survey was specifically directed towards locating and recording occupied tunnels no assessment was made of overall larval density in the habitat. Larval occupation was determined by the presence of an entire cover or a relatively "fresh" feeding surface in the case of tunnels containing pupae. Measurements were of insect or plant features (tunnel dimensions, host size) and tunnel location in relation to host plant, but it was not always possible to record every feature for all tunnels surveyed.

### Tunnel structure

In this paper, tunnel structure will include the tunnel "proper" (as excavated wood) and associated features related to other aspects of larval occupation such as feeding and pupation. The tunnel is described in terms of a penetration ("radial tunnel") and a downward "longitudinal tunnel" which is approximately in line with the wood grain. Details of tunnel structure are presented in the section on the tree phase.

The radial tunnel diameter was measured at right angles to the wood grain, radial tunnel length measured from a line flush with the limb surface

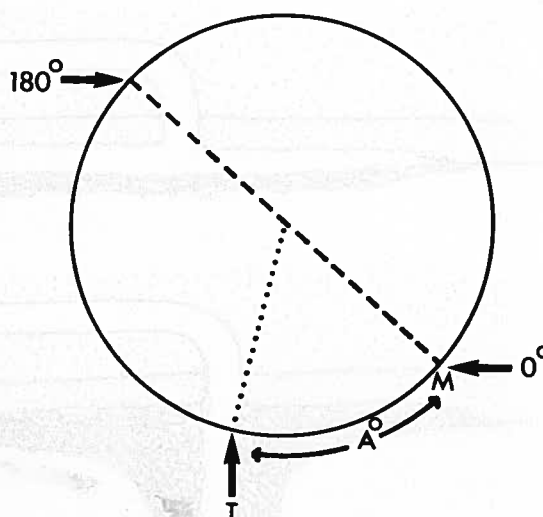


Fig. 1 Diagrammatic transverse section of stem to show the measured position of the tunnel entrance (T) in relation to the position of maximum lean (M). The tunnel position is given as the number of degrees (A°) from the point of maximum lean for the stem or branch which is given an arbitrary position of 0°. The maximum distance to either side of maximum lean is 180° which is located on the opposite, upper side of the limb.

to the innermost side of the longitudinal tunnel; longitudinal tunnel length was measured from where it meets with the lower surface of the radial tunnel. The extent of feeding surface cover was measured at the line of greatest lateral and vertical width. All species have a single longitudinal tunnel and feeding surface cover unless otherwise stated.

### Tunnel position

The lean of limb at a tunnel site was recorded in degrees, from 0° where the limb is vertical, to a maximum of 90° for a horizontal limb. The lean was recorded for a length of 100 mm above and below the tunnel entrance to compensate for any distortion resulting from any localised limb swelling. The lean was designated positive and negative for a tunnel on the under and upperside, respectively.

The position of the tunnel entrance relative to the point of maximum lean (the lean at any particular height varies because of limb curvature) was recorded in degrees using a compass (Fig. 1). The point of maximum lean was designated as having a position of 0° and the position of the tunnel away from this point was indicated by the number of degrees to a maximum of 180 where the tunnel

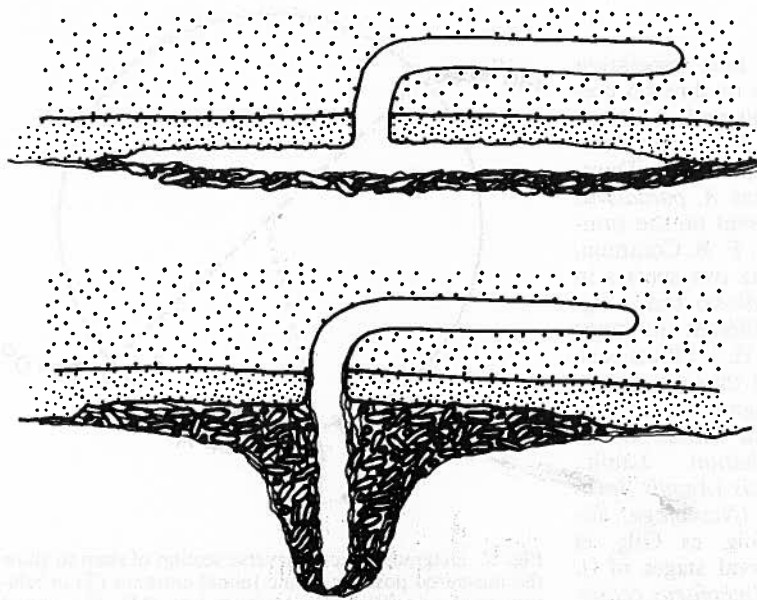


Fig. 2 Generalised longitudinal section of *Aenetus virescens* litter-phase larval tunnel. Top, simple feeding surface cover. Bottom, feeding surface cover extended as cone-like protrusion. Coarse stippling, dead wood; fine stippling, fungal tissue.

would be positioned on the opposite side. Where the limb is vertical (i.e., lean of  $0^\circ$ ) at the tunnel site, both maximum lean and tunnel site were given a compass position of  $0^\circ$ .

#### Host features

An indication of host size was recorded by height and both basal and standard (1.25 m) diameters. The limb diameter for a tunnel site was estimated as the diameter below the tunnel surface where there was no observable swelling of the limb.

#### RESULTS

Each of the following accounts begin with *A. virescens* for which more information is available. Host records from the literature and this study for Australian and New Caledonian species are recorded in Table 1. A detailed host list for *A. virescens* is provided in Grehan (1984). An indication of relative size of the larval tunnel structures are recorded in Table 2, but no statistical comparison is attempted because of the small size of most samples.

#### Litter phase

Larvae of *A. virescens* litter-phase feed on fungal fruiting bodies or dead, fungal-infested wood of hosts and non-hosts of the tree-phase larvae. Larvae inhabit the underside of the substrate (whether

fungus or wood) where the host surface is exposed to air (Grehan 1984). Larvae feed beneath a canopy of faecal pellets bound with silk and, after the first instar, may reside in tunnels excavated in the substrate. The tunnel consists of a radial section which penetrates the host, and a longitudinal section following the wood grain, more or less parallel to the surface (Fig. 2). The longitudinal section is usually horizontal, but may occasionally extend up or downwards. The tunnel entrance is surrounded by a feeding surface formed by a shallow (about 1 mm or less) excavation of the wood or fungal substrate. The feeding area is overlain by the cover of faecal pellets and uningested wood fragments bound together by silk. The web is attached loosely to the substrate compared with the tree phase and may become entirely packed with faecal pellets. Older litter-phase larvae sometimes build the web into a downward projecting cone filled with faecal pellets (Fig. 2). Enzyme analysis of polysaccharide digestion suggests that fungi comprise the main food source for larvae feeding on dead wood (Grehan 1988).

In New Caledonia, the first, second, and possibly older instars of *A. cohici* were found feeding on dead wood and polypore fungi. The pattern of web and tunnel construction appeared to be no different from *A. virescens* although there were no conical projections of the web. The presence of cylindrical *Aenetus*-like faecal pellets bound with silk under dead wood were observed under dead wood in Western

**Table 1** Food-plant records for *Aenetus* in Australia and New Caledonia. (Compiled in cooperation with E. D. Edwards.)

<i>A. astathes</i>	<i>Casuarina</i> sp. (Tillyard 1926)
<i>A. cohici</i>	<i>Nothofagus aequilateralis</i> (J. R. Grehan) <i>N. codonandra</i> (J. S. Dugdale unpub.) <i>N. discoidea</i> (J. R. Grehan) <i>Hibbertia brongnartii</i> (J. R. Grehan) <i>H. paucheri</i> (J. R. Grehan)
<i>A. cyanochlorus</i>	<i>Glochidion disparipes</i> (Edwards unpub.) <i>Macaranga involucreta</i> (Common unpub.)
<i>A. dulcis</i>	<i>Agonis flexuosa</i> (Common & Upton unpub.) <i>A. juniperina</i> (J. R. Grehan)
<i>A. eximius</i>	<i>Acacia binervata</i> (J. R. Grehan) <i>Acmena smithii</i> (Lillipilli) (Froggatt 1907) <i>Antherosperma moschatum</i> (J. R. Grehan) <i>Cassinia</i> sp. (J. R. Grehan) <i>Daphanandra micrantha</i> (Common & Upton unpub.) <i>Dendrocide exelsa</i> (Robinson unpub.) <i>Diploglottis australis</i> (Robinson unpub.) <i>Dodonea viscosa</i> (Scott 1869, 1890) <i>Doryphora sassafras</i> (Common & Upton unpub.) <i>Eucalyptus</i> sp. (Robinson unpub.) <i>E. grandis</i> (King 1962) <i>Glochidion</i> (Common 1970) <i>G. ferdinandi</i> (Common unpub.) <i>Lantana camara</i> (Robinson unpub.) <i>Melaleuca</i> (Illidge 1900) <i>Pomaderis aspersa</i> (J. R. Grehan) <i>Prostanthera lassianthos</i> (Common unpub.) <i>Tristania</i> sp. (Froggatt 1907)
<i>A. lewinii</i>	<i>Acalypha</i> sp.? (King 1962) <i>Casuarina</i> sp. (Scott 1869) <i>Leptospermum flavescens</i> (King 1962)
<i>A. ligniveren</i>	<i>Acacia</i> sp. (Tillyard 1926) <i>Acacia delbata</i> (J. R. Grehan) <i>Acmena</i> sp. (Scott 1864) <i>Callistemon</i> sp. (Scott 1864) <i>Cassinia aculeata</i> (Edwards unpub.) <i>Casuarina</i> sp. (Lewin 1805) <i>Dodonaea</i> sp. (Scott 1864) <i>Eucalyptus globulus</i> (Froggatt 1923) <i>E. regnans</i> (Hardy unpub.) <i>Eucalyptus</i> sp. (Scott 1864) <i>Eugenia</i> sp. (Lillipilli) (Tillyard 1926) <i>Lantana camara</i> (Common unpub.) <i>Leptospermum</i> sp. (Froggatt 1923) <i>Melaleuca</i> sp. (Froggatt 1923) <i>Olearia lirata</i> (Edwards unpub.) <i>Pomoderis apetala</i> (J. R. Grehan) <i>Prostanthera</i> sp. (Prescott 1934) <i>Prostanthera nivea</i> (Tas. Ins. Pest Surv. 11) <i>Pyrus</i> sp. (Apple) (French 1909) <i>Rubus</i> sp. (Raspberry) (Tas. Ins. Pest surv 13) <i>Tristania</i> sp. (Froggatt 1923) <i>Ulmus</i> sp. (Golden Elm) (Tas. Ins. Pest Surv. 13)



**Table 1 (Continued)** Food-plant records for *Aenetus* in Australia and New Caledonia. (Compiled in cooperation with E. D. Edwards.)

<i>A. mirabilis</i>	<i>Alphitonia excelsa</i> (N. Quick unpub.) <i>Trema aspersa</i> (N. Quick unpub.)
<i>A. paradiseus paradiseus</i>	<i>Eucalyptus regnans</i> (Elliott unpub.) <i>Eucalyptus</i> sp. (Tindale 1953)
<i>A. paradiseus montanus</i>	<i>Eucalyptus pauciflora</i> (Tindale 1953)
<i>A. ramsayi</i>	<i>Acmena</i> sp. (Scott 1869) <i>Alectryon</i> sp. (Scott 1869)
<i>A. scotti</i>	<i>Dendrocnide excelsa</i> (Stinging tree) (Scott 1869) <i>Diploglottis australis</i> (Robinson unpub.) <i>Milletia megasperma</i> (Native wisteria) (Scott 1864) <i>Wistaria</i> sp. (Meyrick 1889)
<i>A. splendens</i>	<i>Acmena</i> sp. (Scott 1864) <i>Callicoma serratifolia</i> (NSW Ins. Pest Surv. 1960) <i>Callistemon</i> sp. (Scott 1869) <i>Casuarina</i> sp. (Scott 1869) <i>Eucalyptus</i> sp. (Scott 1869) <i>Dodonea</i> sp. (Scott 1869) <i>Lantana camara</i> (Robinson unpub.) <i>Pandorea pandorana</i> (Tecoma) (Scott 1864) <i>Rubus</i> sp. (Blackberry) (Robinson unpub.) <i>Trema aspersa?</i> (King 1962) <i>Trema cannabina</i> (Robinson unpub.)

Australia at Karridale and Napier River. Similar pellets were found in Tasmania at Mount Wellington (42°54'S, 147°14'E) along with a head capsule whose chaetotaxy conformed to Hepialidae and eyes positioned in two more or less parallel rows like those of *Aenetus* (Grehan 1981).

#### Transfer phase

The transfer phase of *A. virescens* occurs in one of several possible instars (Grehan 1981). The transfer larva vacates the litter-phase tunnel and establishes itself in a vascular plant by excavating a tunnel which is very similar to that of the litter-phase but the longitudinal tunnel is always directed downwards. The larva removes bark around the tunnel entrance which results in callus growth on the exposed surface. The cover over the feeding surface is more robust than that of the litter-phase and does not normally include faecal pellets (Grehan 1983a).

A single transfer larva of *A. cohici* was located in a tunnel with no bark removed from around the tunnel entrance. This indicated that feeding had not begun and the larva was therefore considered to have become established recently (cf. Grehan 1983a). The larva measured about 28 mm long with a head-width of 3.3 mm. Unidentified records of

transfer larvae were made at Snug Tiers (*A. lignivoren* or *A. paradiseus*) and Napier Bridge, respectively.

#### Tree phase

**Tunnel structure.** Tunnel structure varies in number, relative size, and shape of the feeding surface, cover, and tunnel proper (Grehan 1983a). Expansion of the tunnel during larval development involves an elaboration of the tunnel initiated by the litter-phase. In general, all species exhibit a radial and longitudinal tunnel, but the larva of *A. virescens* usually (84%  $n=29$ ) extends the radial tunnel further into the host and a new longitudinal tunnel is constructed (Fig. 3, 4). Occasionally this process is repeated, resulting in three longitudinal tunnels. The vacated tunnels are blocked by an approximately 5 mm thick plug of silk and wood fibre. Near the top of the longitudinal tunnels of *A. eximius*, *A. dulcis*, and *A. mirabilis*, wood tissue is removed on the "outer" edge (Fig. 6, 7) and replaced by a pad of silk and fibre up to about 10 mm thick and 20 mm long.

At the junction of the radial and longitudinal tunnel, *A. virescens* extends the radial tunnel deeper into the limb. This extension varies from a barely

Table 2 Dimensions (mm) of tunnel and associated structures for *Aenetus* larvae.  $\bar{X}$  = mean,  $n$  = sample size,  $l$  = length.

	Radial tunnel diameter		Radial tunnel (l)		Longitudinal tunnel (l)		Cover width		Cover height	
	range	$\bar{X}$	range	$\bar{X}$	range	$\bar{X}$	range	$\bar{X}$	range	$\bar{X}$
<i>A. virescens</i>	3.8-13.6	9.5	19-70	51	37-153	114	22-95	53	28-53	27
<i>A. p. montanus</i>	1.8-8.5	4.0	6-75	20	10-70	30	16-155	62	10-34	19
<i>A. p. paradiseus</i>	2.7-7.3	4.1	8-28	15	10-58	36	17-80	40	12-39	29
<i>A. cohici</i>	2.8-14.6	7.3	6-56	34	24-145	98	10-180	39	17-79	41
<i>A. eximius</i>	2.8-11.5	6.8	12-34	22	12-600	311	22-110	50	20-36	52
<i>A. ligniveren</i>	2.5-7.8	5.3	8-12	10	64-68	66	10-58	27	16-52	33
<i>A. dulcis</i>	4.4-15.6	8.9	9-40	28	17-300	134	34-270	113	19-56	34

perceptible 1 mm deep shelf to one or more blind ending tunnels (Fig. 3, 4) which may coalesce into a chamber (Fig. 10a). In *Aristotelia serrata* (J. R. et G. Forst.) W. B. Oliver, the chamber may occupy as much as 50% of the cross sectional area of a limb. The radial tunnel can be almost non-existent in limb diameters of about 20 mm. The radial tunnel of *A. cohici* (Fig. 8) has a distinctly sigmoid shape, penetrating first directly into the host before turning upwards and then leveling off to meet with the longitudinal tunnel. At the junction of the radial and longitudinal tunnel there is a shallow 1-3 mm shelf. In the other *Aenetus* species there is a curved junction between the radial and longitudinal tunnels (Fig. 5-7).

Length of the longitudinal tunnel length varies between species (Table 2), but this does not appear to be closely related to larval size. Two species with comparatively long tunnels are *A. eximius* and *A. dulcis*. The longitudinal tunnel of *A. eximius* has been recorded as up to 1.52 m by Froggatt (1894: 318). The longitudinal tunnel of *A. virescens*, *A. dulcis*, and *A. eximius* may penetrate the root zone.

The feeding surface is covered by a web of silk and wood chips (Fig. 4, 6, 7, 8), or a combination of web and outer wood and bark where a "feeding chamber" is formed (Fig. 3, 5, 10a, 13). Both types of feeding surface may occur in the same host, but in others only one is present. For example, a feeding chamber never occurs in the *A. virescens* hosts *Carpodetus serratus* and *Cyathodes fasciculata*. Conversely, a chamber always forms over the feeding surface of *A. paradiseus montanus* in *E. obliqua*. The web over the feeding chamber of *A. paradiseus* differs from other *Aenetus* species by having two superimposed covers (Fig. 5, 9a). The outer cover (Fig. 11) is positioned over the entrance to the feeding chamber (Fig. 13) whereas the less robust inner cover fills the chamber opening (Fig. 12). The outer cover is reddish-brown and is often distinct against the relatively pale bark of the host.

A distinct lateral extension (Fig. 14) of the cover may occur in some species and it may encircle smaller limbs (10-40 mm). One or more translucent "windows" (areas of thin silk) have been observed approximately in line with the tunnel entrance in the cover of *A. virescens*, *A. cohici*, and *A. eximius*. Near the base of the *A. virescens* cover there is a "valve" through which faecal pellets, exuviae, and other particles are ejected (Grehan & Winstanley 1980). The valve consists of a narrow slit in the cover near the lower margin and it is closed off by loosely woven silk when not in use. Both valve and window might be present in other species, but they are difficult to detect because they are less well "defined" where the cover is of a relatively loose construction.

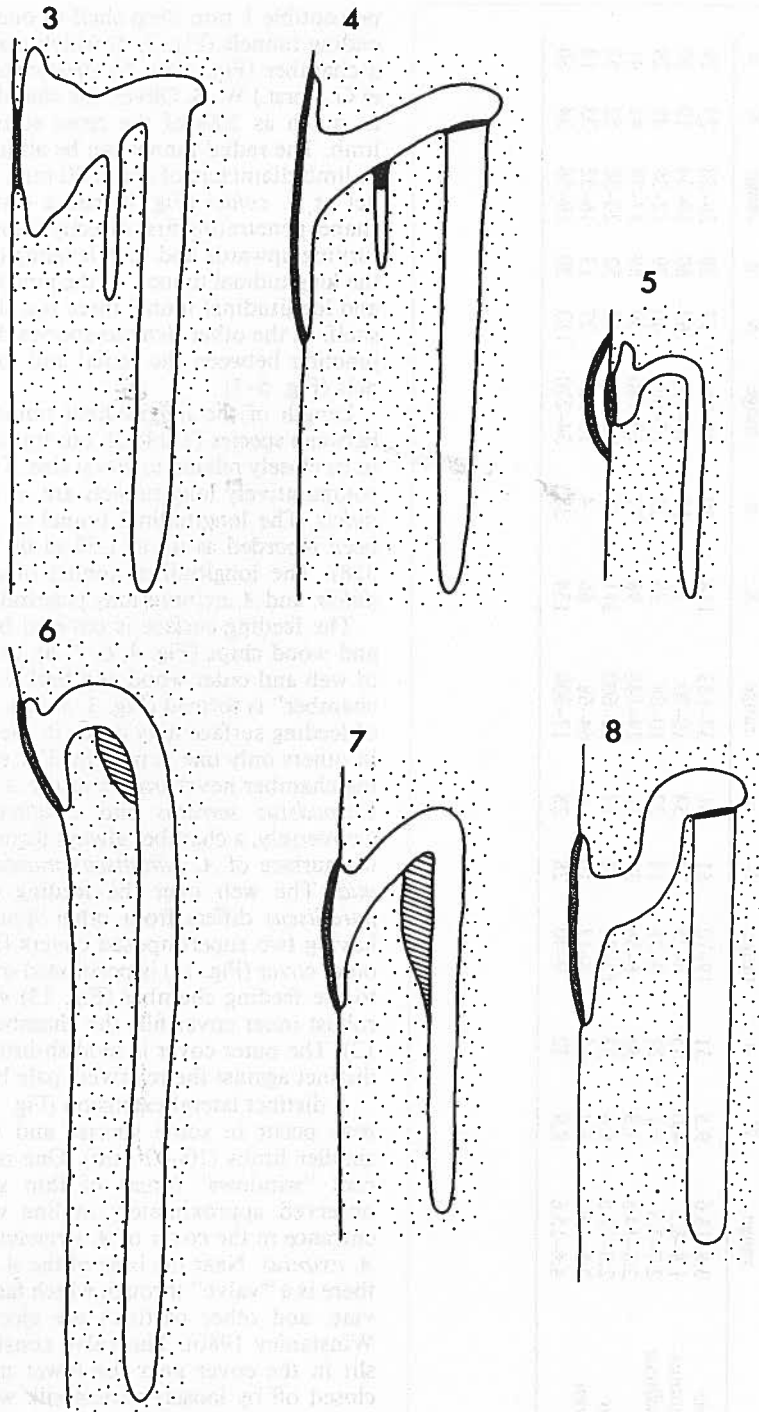


Fig. 3-8 Generalised longitudinal section of larval tunnels of *Aenetus* species: (3) *A. virescens* in *Aristotelia serrata*; (4) *A. virescens* in *Carpodetus serratus* showing establishment tunnel blocked by frass, and longitudinal tunnel closed by pupal operculum; (5) *A. paradiseus montanus* in *Eucalyptus pauciflora*; (6) *A. dulcis* in *Agonis flexuosa*; (7) *A. mirabilis* in *Trema aspersa*; (8) *A. cohici* in *Nothofagus discoidea*. L = longitudinal tunnel. R = radial tunnel. E = establishment tunnel. P = plug of establishment tunnel. PO = pupal operculum. Fine stipple over tunnel entrance = cover. Oblique lines = pad of silk and fine wood frass. Scale line, 30  $\mu$ m.



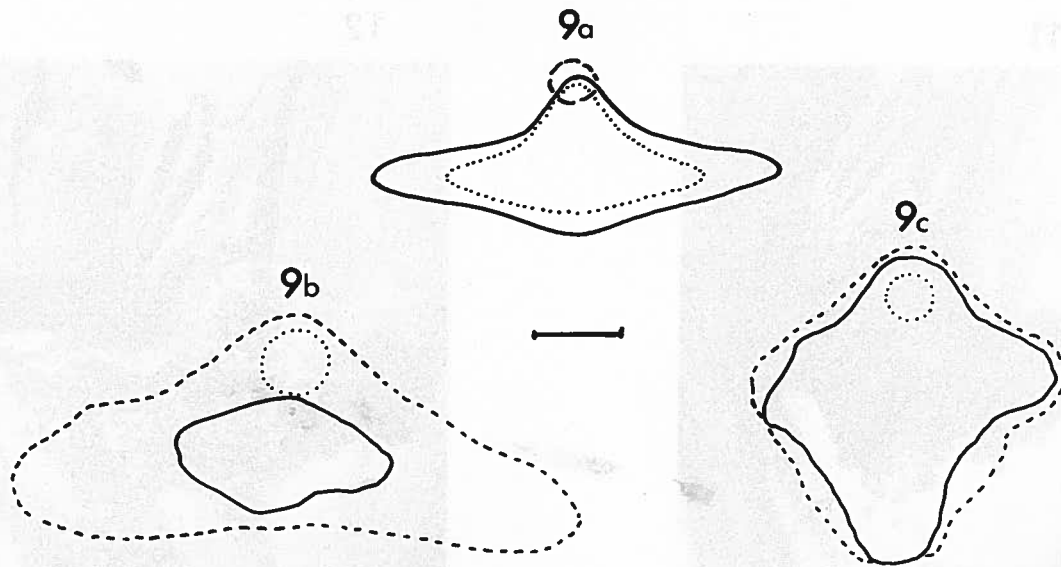


Fig. 9 External view of relative position of radial tunnel and cover. (a) *Aenetus paradiseus montanus* in *Eucalyptus pauciflora*. Dotted line, inner cover. Solid line, external cover. Dashed circle, radial tunnel. (b) *Aenetus virescens* in *Nothofagus solandri*. Solid line, external cover. Dashed line, extent of feeding surface beneath tree bark. Dotted circle, radial tunnel. (c) *Aenetus cohici* in *Nothofagus discoidea*, conventions as for (b). Scale line, 10 mm.

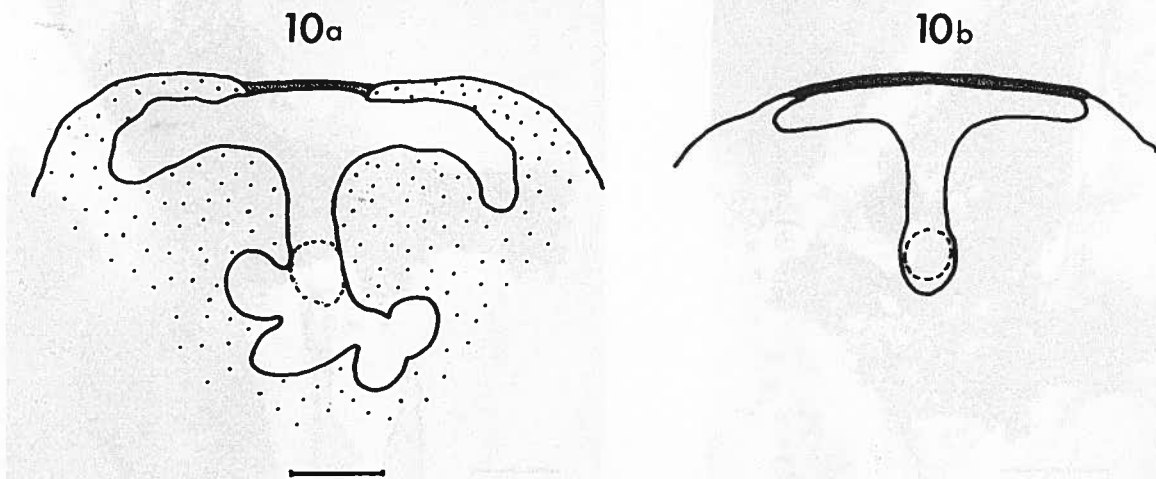


Fig. 10 Transverse section of feeding chamber and radial tunnel. (a) *Aenetus virescens* in *Nothofagus solandri*. (b) *Aenetus cohici* in *Nothofagus discoidea*. Dotted circle, longitudinal tunnel. R, radial tunnel. E, radial extension of radial tunnel. Hatched line, feeding surface. Cover, fine stipple. Scale line, 10 mm.

Before pupation, the feeding surface cover is perforated or removed entirely, although sometimes it may be left hanging from the lower margin of the feeding surface. The larvae of Australian species also apply a thin layer of pale or white silk to the wood surface of the feeding area and the tunnel entrance (Table 3). The longitudinal tunnel forms

a pupal chamber which is sealed by a silk "operculum" at the junction of the radial and longitudinal tunnels (Fig. 4, 8). With cessation of feeding, callus continues to grow over the feeding surface (Fig. 15a) and eventually may seal the tunnel entrance after the adult has emerged (Fig. 15b).

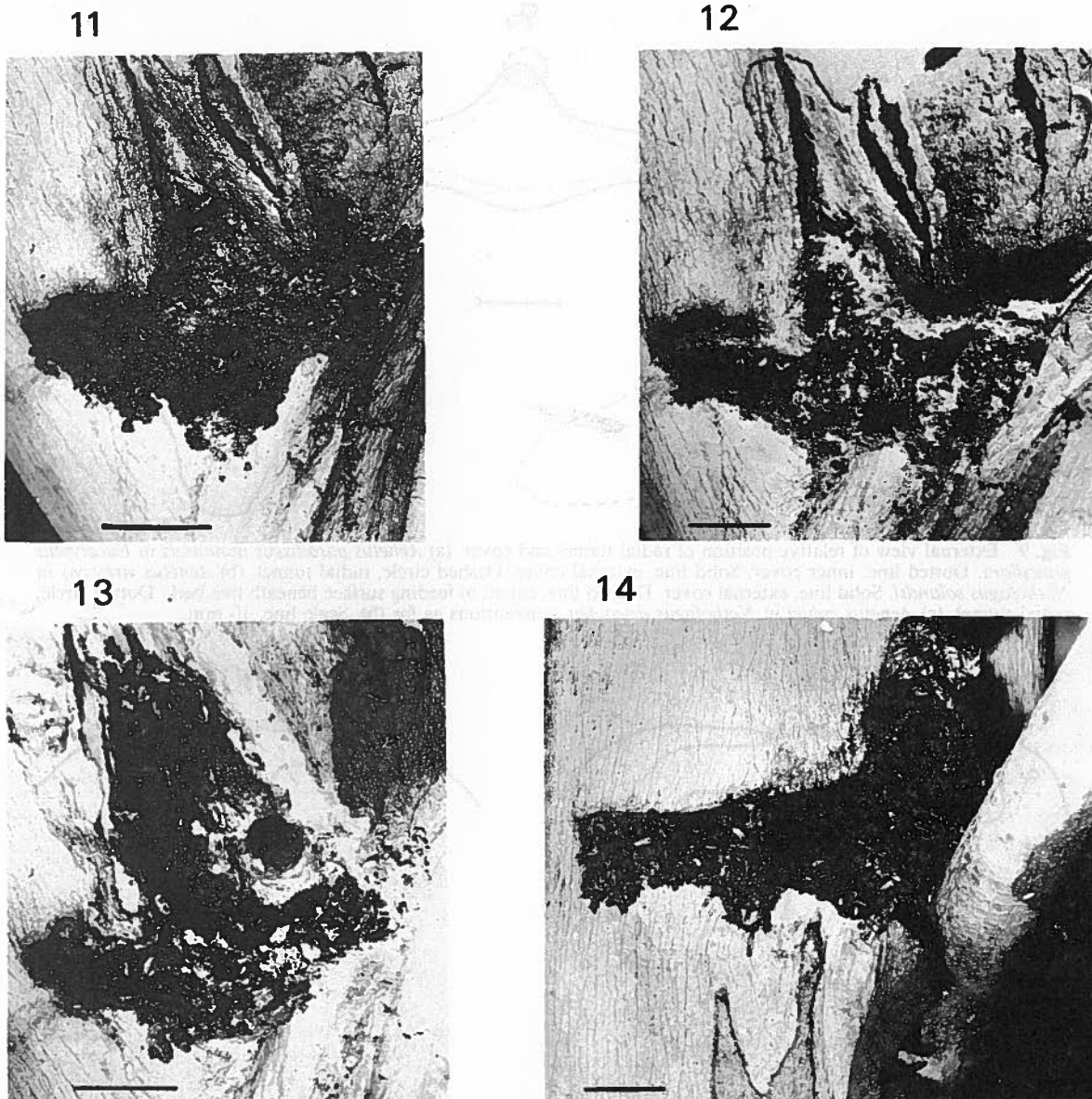


Fig. 11-14 Tunnel entrance of *Aenetus paradiseus montanus* in relation to feeding chamber and cover. (11) Outer cover. (12) Inner cover. (13) Feeding chamber exposed by removal of bark. Radial tunnel visible and part of inner cover intact. (14) Tunnel of *Aenetus paradiseus montanus* in branch axil of *Eucalyptus pauciflora*. Scale line, 10 mm.

#### Tunnel position

The relative location of tunnels with respect to the stem diameter and height of the host is summarised in Table 4. *Aenetus* species appear to be limited to the smaller diameter stems and branches, but it was not possible to define the absolute limits within the scope of this study. The only species

which were found in limb diameters large enough to be called "trunks" were *A. virescens* and *A. cohici*. Larvae of *A. virescens* may complete development in limbs as small as 20 mm diameter in *Nothofagus truncata* (Col.) Ckn., *Carpodetus serratus* and *Cyathodes fasciculata*. Its upper diameter limit is about 180 mm in *Nothofagus solandri* var.

**Fig. 15** Entry site for vacated tunnels of *Aenetus cohici* in *Nothofagus discoidea*. (A) vacated previous season. Extensive tissue growth from feeding surface but tunnel entrance is still visible. (B) Scar formed by closing over of the tunnel entrance. Scale line, 20 mm.

15a



15b



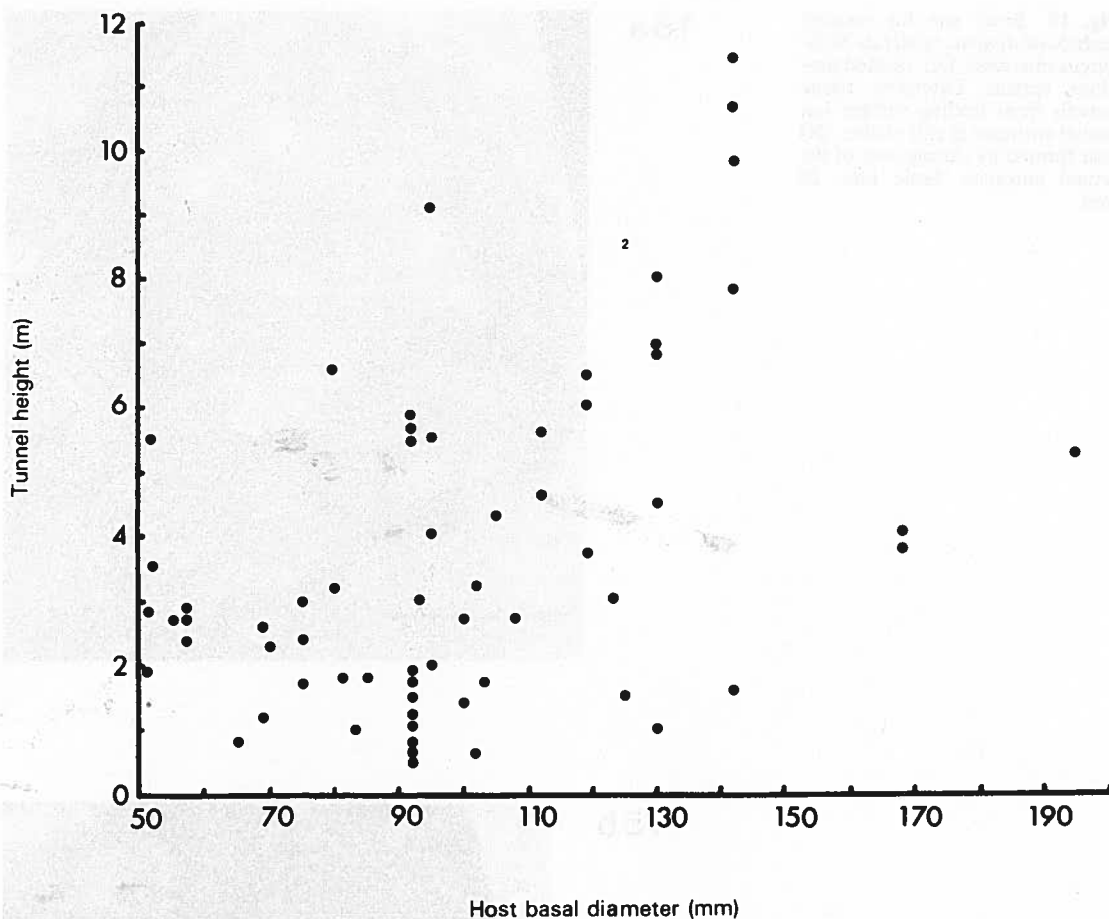


Fig. 16 The relationship between the vertical distribution of *Aenetus cohici* tunnels (at tunnel entrance) and basal diameter of *Nothofagus discoidea*.

*solandri* (Hook. f.) Oerst., but newly established tunnels have been observed in trunks of *Vitex lucens* Kirk. with diameters up to 1500 mm. In *Nothofagus*, larval tunnels of *A. virescens* are found higher up on the main stem or on the branches as the girth of the trunk increases. A similar pattern was observed for tunnels of *A. cohici* (Fig. 16) although it was not practical to carry out the survey on relatively large trees. Only five tunnels (8%,  $n=64$ ) of *A. cohici* were found below a height of 1 m and all were in trees with a basal diameter less than 100 mm.

Larvae of *A. virescens*, *A. cohici*, and probably other *Aenetus* species, establish within a wide range

Table 3 Variation in tunnel structure of *Aenetus* species (+) character present, (-) absent, (?) unrecorded.

	Tunnel characters				Tunnel no.
	Shelf	Pupal silk	Cover Pad	no.	
<i>A. virescens</i>	+	-	-	1	1-3
<i>A. cohici</i>	+	-	-	1	1
<i>A. paradiseus montanus</i>	-	+	-	2	1
<i>A. paradiseus paradiseus</i>	-	+	-	2	1
<i>A. lignivorus</i>	-	+	-	1	1
<i>A. eximius</i>	-	+	+	1	1
<i>A. dulcis</i>	-	+	+	1	1
<i>A. mirabilis</i>	-	?	+	1	1

Fig. 17 The relationship between *Aenetus paradiseus montanus* radial tunnel diameter (Fig. 9a) and *Eucalyptus pauciflora* limb diameter.

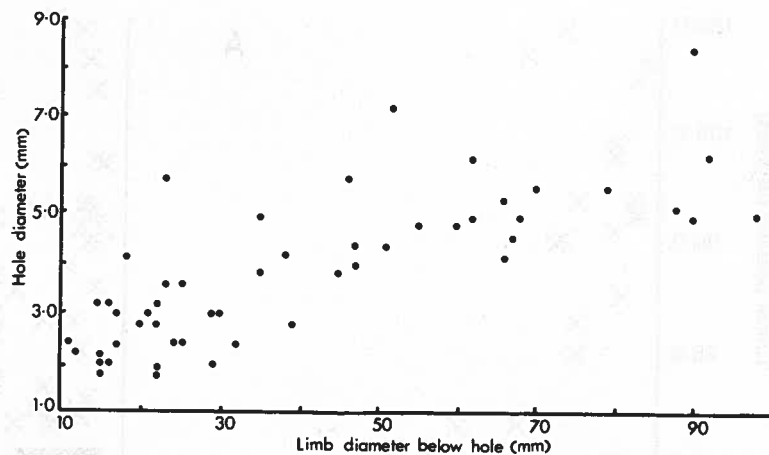


Table 4 Position of *Aenetus* tunnels relative to host size (diameter and height).  $n$  = number of hosts.  $\emptyset$  = diameter. Basal diameter as maximum for sample size.

Species	Tunnel position		$n$	Host	Height (m)	Basal $\emptyset$ (mm)	$n$
	Height (m)	Limb diameter (mm)					
<i>A. virescens</i>	0.21–4.4	24–150	12	<i>Aristotelia serrata</i>	7.3	163	12
<i>A. p. montanus</i>	0.55–4.95	11–111	43	<i>Eucalyptus pauciflora</i>	7.8	262	43
<i>A. p. paradiseus</i>	0.16–7.3	14–67	32	<i>Eucalyptus regnans</i>	8.3	101	32
<i>A. cohici</i>	0.36–11.4	41–140	28	<i>Nothofagus discoidea</i>	13.0	168	28
<i>A. eximius</i>	0.16–2.64	19–134	26	<i>Pomoderis aspersa</i>	7.5	143	26
<i>A. ligniveren</i>	0.70–2.54	17–42	11	<i>Acacia delbata</i>	5.0	61	11
<i>A. dulcis</i>	0.12–4.1	23–94	26	<i>Agonis flexuosa</i>	6.8	125	26

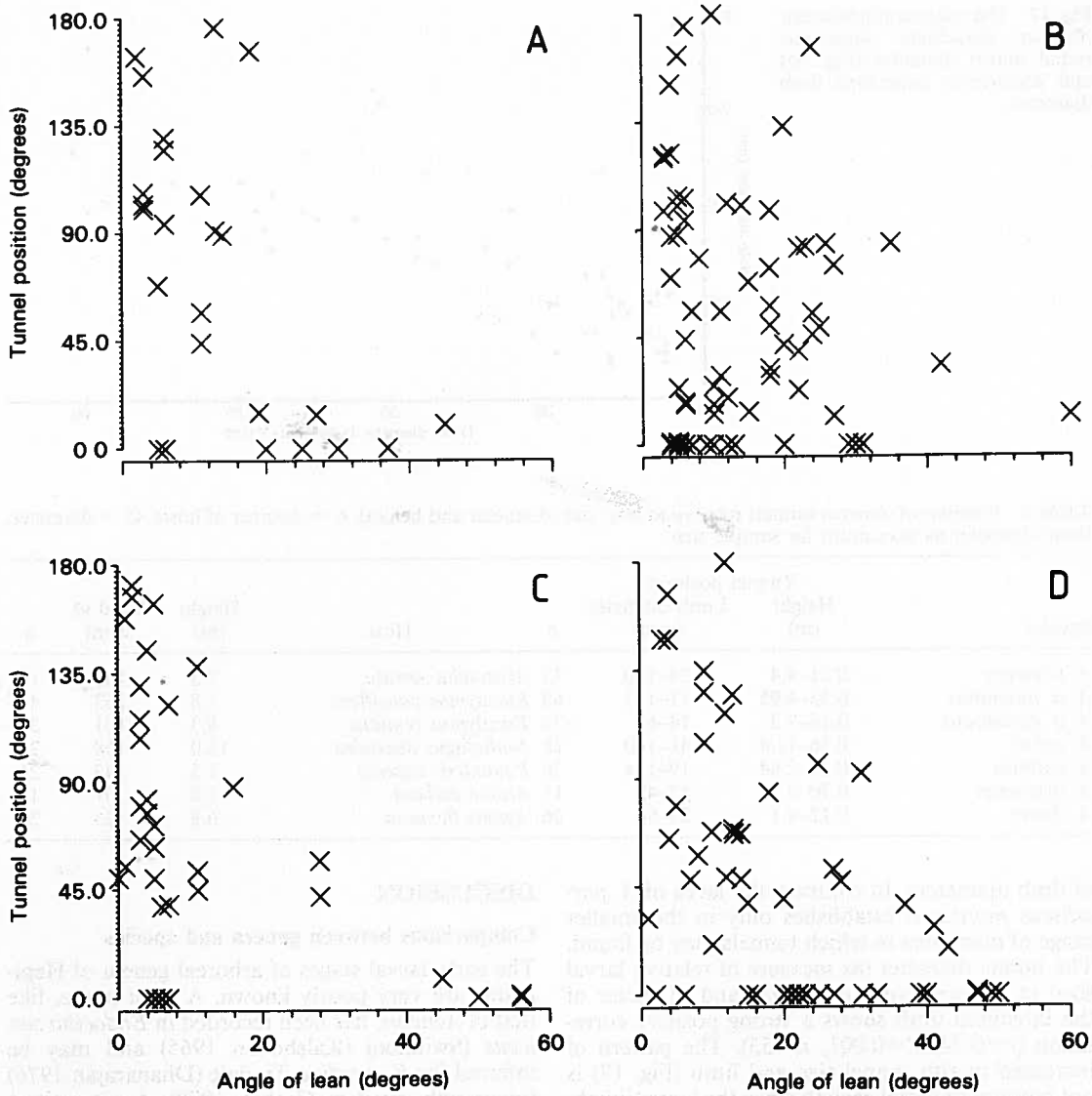
of limb diameters. In contrast, the larva of *A. paradiseus montanus* establishes only in the smaller range of diameters in which tunnels may be found. The tunnel diameter (as measure of relative larval size) of *A. paradiseus montanus* and diameter of the inhabited limb shows a strong positive correlation ( $r=0.74$ ,  $P=0.001$ ,  $n=53$ ). The pattern of increased in situ tunnel size and limb (Fig. 17) is not because of larval growth since the larger inhabited limbs were up to 15 years old, whereas the development period of the larva is only about 3 years (Tindale 1953). I therefore suggest that the larva may re-establish itself one or more times in larger diameter limbs.

The distribution of tunnels around the limb in relation to the lean of the limb is illustrated in Fig. 18. In this study no larvae were found on the upper side when the lean exceeded 25°. Dr I. F. B. Common (in Tindale 1953) noted that *A. paradiseus montanus* often commences tunnel excavation in a branch axil (Fig. 14) and in this study 75% of the tunnel sites examined were found in or below a branch axil.

## DISCUSSION

### Comparisons between genera and species

The early larval stages of arboreal genera of Hepialidae are very poorly known. A litter-phase, like that of *Aenetus*, has been recorded in *Endoclita sericeus* (Swinhoe) (Kalshoven 1965) and may be inferred for *E. gmelina* Tindale (Dhanarajan 1976) (incorrectly cited in Grehan 1979). A litter-phase has not been recorded for *E. excrescens* (Butler) and *E. signifer* (Walker) where the young larvae feed on live herbaceous plants before the wood-boring stage (Kondo 1961; Toyomura & Matsuzawa 1965; Matsuzawa et al. 1963; Ueda 1979; Nishi & Yoshii 1979). The larvae of *Trichophassus giganteus* (Briquet 1956), *Sahyadrassus malabaricus* Moore (Nair 1982), and *Phassus* spp. (now *Endoclita* and other genera, Gardner 1941) are already well grown when they first tunnel into trees; a similar observation was made for *A. virescens* before discovery of the litter-phase (Milligan 1974). The early larval stages of *Leto venus* (Stoll) are unknown (cf. Janse 1945). The larvae are relatively small when first entering the host tree (tunnel diameter only about



**Fig. 18** Location of tunnels relative to lean of host limbs. Y axis refers to relative position of tunnel entrance in degrees away from the underside.  $0^\circ$  refers to the underside,  $90^\circ$  to either side and  $180^\circ$  the opposite side (top side) of a stem or branch. X axis, lean of limb from vertical at  $0^\circ$  to horizontal at  $90^\circ$ . (A) *Aenetus dulcis*, (B) *A. virescens*, (C) *A. eximius*, (D) *A. paradiseus montanus*.

1 mm, G. W. Gibbs pers. comm.) and if a litter-phase is present it would appear to be relatively of short duration. The litter-phase is known from a wide range of different feeding associations in the Hepialidae (cf. Slashchevskii 1929; Joubert 1975; Grehan 1979; Tindale 1981) and it may well be

common in most, if not all, arboreal species. The transfer morph, however, is unknown outside *Aenetus* and may be a diagnostic character for this genus (Grehan 1981).

Inter-generic comparisons of tunnelling habits are limited by the lack of detailed information for many



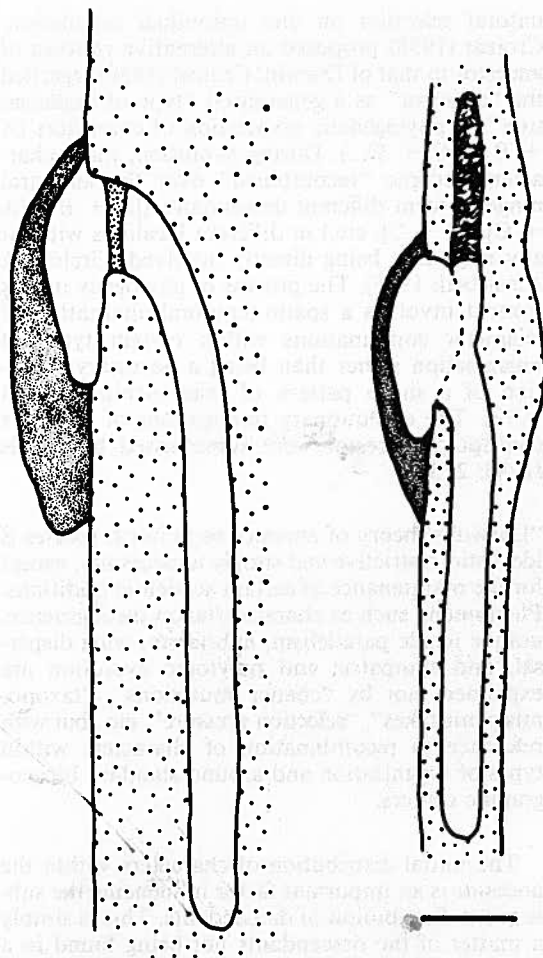


Fig. 19 Two generalised longitudinal sections of the larval tunnels of *Endoclita excrescens*. The tunnel may extend downwards only (a) or both up and down (b). The upward longitudinal tunnel illustrated in b is filled with wood particles. Cover over tunnel entrance as fine stipple, Pupal operculum in (a) as coarse stipple.

species, but some differences appear to be present although they are not necessarily characteristic of all species. The longitudinal tunnel of *Aenetus* extends downwards only, and this may also be true of *Zelotypia*, *Leto*, *Trichophassus*, and *Sahyadrasus malabaricus* (Olliff 1887; Froggatt 1894, 1907; Gallard 1915; Janse 1945; Briquelot 1956; Duke & Taylor 1964; Nair 1982). Some species of *Endoclita* have a downward longitudinal tunnel only (Atkinson 1931); in others, however, an upward longitudinal tunnel may also be present (Fig. 19)

(Dhanarajan 1976; Ueda 1979). The upward longitudinal tunnel of *E. gmelina* Tindale is constructed first (Dhanarajan 1976: 216), and in *E. excrescens* (Fig. 19), may be abandoned and blocked by frass in a similar manner to the establishment tunnel of *A. virescens*. Both upward and downward longitudinal tunnels occur in arboreal species of *Hepialus* (Wagner 1985).

The tunnel of *Leto venus* is confined to the host *Virgilia oroboides* (Berg.) Salter (Duke & Taylor 1964) distributed in the cape region of South Africa (van Wyk 1986). The tunnels occur in the lower 150 mm of the stem and probably extend into the roots. The tunnel is located only a few millimetres below the bark. Near the time of pupation the stem may split longitudinally between the tunnel and stem surface and the exposed portion of tunnel is sealed over with silk by the larva. At pupation the tunnel entrance is blocked by a dome-shaped cap of silk and wood fibre (Janse 1945; G. W. Gibbs pers. comm.) which protrudes from the tunnel in contrast to the operculum of *Endoclita* and *Aenetus*. The larva of *L. venus* appears to feed on wood rather than callus tissue (G. W. Gibbs pers. comm.); a habit is shared by the stem-boring species of *Aepytus* (Winder & Harley 1983) and *Hepialus* (Wagner 1985). A heavy layer of silk lines the tunnel of *L. venus* and arboreal *Hepialus*.

The precise structure and position of the pupal operculum is rarely described in detail. In this study the operculum of *Aenetus* was found to be "horizontal", but Illidge & Quail (1901) and Tindale (1953) recorded a vertical position for *A. eximius*, *A. splendens*, *A. lewinii*, *A. ligniveren*, and *A. paradiseus*. However, where the radial tunnel curves into the longitudinal tunnel without a distinct angle, the operculum could vary in position sufficiently to appear "vertical" in some instances. The operculum of *Zelotypia* is horizontal, but differs from that of *Aenetus* by consisting of a thick (10 mm) "plug" (V. J. Robinson pers. comm.). The operculum of *Endoclita excrescens* is about 3 mm thick (Ueda 1979) and placed vertically across the radial tunnel (Fig. 19).

A cover over the tunnel entrance is present in all arboreal tunnelling Hepialidae. The cover of *Aenetus* is relatively thin but that of *E. excrescens* is "padded" with faecal pellets and wood fragments (Fig. 19), in a manner similar to the temporary condition found with *A. virescens* at establishment of the tree-phase (Grehan 1983a). A distinct "window" was observed in only some species of *Aenetus*, but it may occur in other arboreal Hepialidae where the cover is densely woven. This feature has been recorded also in the Cossidae (Plaut 1973: 241).

## EVOLUTION

Evolutionary interpretations depend on what is understood of the phylogenetic history of a group. It is commonly assumed that character diversity arises from an ancestor with a limited or uniform range of variation (Heads 1985). To explain this process in terms of distribution (evolution in space and time) it was necessary for Darwin (1861: 382), in his theory of evolution by natural selection, to propose a single centre of origin:

"We are thus brought to the question which has been largely discussed by naturalists, namely, whether the species have been created at one or more points of the earth's surface. Undoubtedly there are very many cases of extreme difficulty in understanding how the same species could possibly have migrated from some one point to several distant and isolated points, where now found. Nevertheless the simplicity of the view that each species was first produced within a single region captivates the mind. He who rejects it rejects the *vera causa* of ordinary generation and subsequent migration, and calls in the agency of a miracle."

This kind of reasoning provided the foundation for "dispersalist" biogeography where distributions are explained by identifying a common centre of origin and the migratory abilities ("means of dispersal") by which the descendant taxa spread to the localities they now occupy (Craw 1988).

Darwin's theories on centres of origin and casual migration were extensively tested in a comprehensive and global study of biotic distribution using the track method of biogeography (panbiogeography) (e.g., Croizat 1952, 1958, 1961, 1964, 1968, 1975). Distributions were transformed into graphs of biogeography by linking localities together as a line or "track" (Craw 1978, 1985) which can then be compared on a repetitive or statistical basis (Croizat 1964: 707; Page 1987; Craw 1988). Croizat (1952, 1958) found that distributions were not characterised by either current geography or means of dispersal but by the ocean basins they crossed. Different tracks intersected at precise geographic locations called "nodes". The standard, repetitive pattern of transoceanic distributions suggest that oceans are not barriers to distribution but represent distinct biogeographic regions from which modern distributions evolved (Craw 1983, 1987).

Croizat (1958) argued that the standard patterns of global distribution did not conform to single centres of origin followed by migration, but involved an ancestor, already widely distributed, which subsequently evolved into different descendants in different localities over the ancestral range. The process of evolutionary differentiation was, therefore, not confined to the unique effects of

natural selection on one individual population. Croizat (1958) proposed an alternative concept of ancestor to that of Darwin. Croizat (1958) regarded the "ancestor" as a generalised "type of organisation" or phylogenetic association of characters (A + B + C + D...). During evolution, these characters become "recombined" over the ancestral range to form different descendants ([A + B], [A + C], [B + C], etc.) in different localities without any migration being directly involved (Grehan & Ainsworth 1985). The process of phylogeny in this context involves a spatio-temporal alternation of character combinations within certain types of organisation rather than being a necessary reflection of a single pattern of relationship (Croizat 1978). The evolutionary implications of Croizat's concept of ancestor were summarised by Heads (1985: 213):

"Darwin's theory of ancestor as uniform species is idealistic, restrictive and simply unnecessary, except for the maintenance of certain academic traditions. Phenomena such as character/taxon incongruence, unique inside parallelism, hybridism, wing dispersal, and sympatric and polytopic evolution are explained, not by "chance mutations", "taxonomists' mistakes", "selection pressure", etc., but with reference to recombination of characters within types of organisation and around standard biogeographic centers."

The initial distribution of characters within the ancestor is an important factor influencing the subsequent distribution of descendants. This is simply a matter of the descendants not being found in a range which the progenitor has never entered (Croizat 1968: 108). This aspect of evolution is described as a "main massing" and may be expressed as the numerical, genetical, or morphological center of diversity for a particular taxon or group of taxa (Craw 1985). The role of the ancestral type of organisation in the evolution of arboreal tunnelling can be examined in reference to the distribution of two major arboreal genera: *Endoclyta* (40 species, Tindale 1941, 1942), and *Aenetus* (25 species, E. S. Nielsen pers. comm.). Although their respective distributions are in close contact they show little, if any, geographic overlap (Fig. 20). They are spatially vicariant to each other with a common boundary in the vicinity of the Banda sea where *Aenetus* occurs along the eastern parts of the Lesser Sunda (Damar, Aru, Ambon, Misool, E. S. Nielsen pers. comm.) and *Endoclyta* is present in the Celebes and Greater Sunda (Java, Sumatra). The presence of *Endoclyta* in the Lesser Sunda (islands east of Java) has yet to be confirmed (K. Ueda pers. comm.).

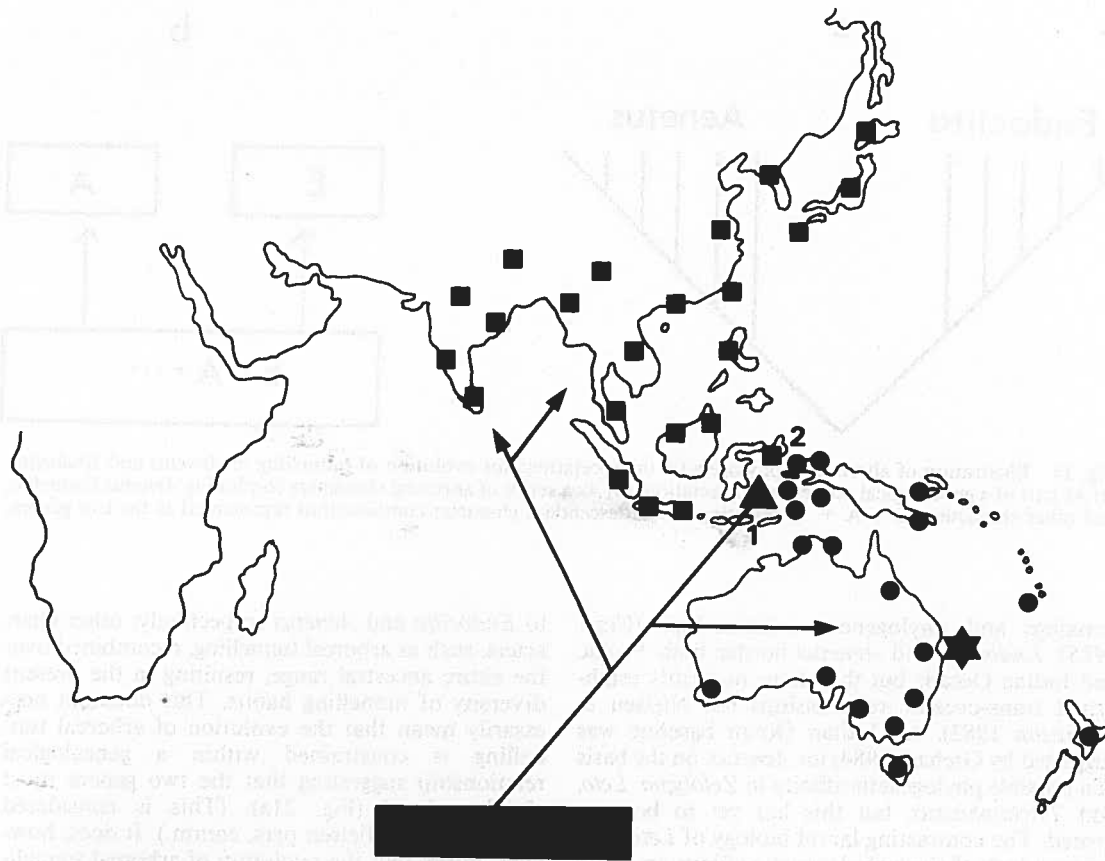


Fig. 20 Dispersal of *Endoclita* (■) and *Aenetus* (●) with an Indian Ocean baseline (■). Banda Sea as full triangle with Flores Soemba (1) and Two Moluccas (2) nodes offset slightly. McPherson/McCleay overlap as ★. Arrowed lines from baseline refer to alternative character recombinations represented by the vicariant form-making of *Endoclita* and *Aenetus* respectively. Distribution data from Tindale (1941, 1942) and E. S. Nielsen (pers. comm.).

Tindale (1958) suggested that the two genera replaced each other (i.e., vicariated) west and east of "Wallace's Line", one of several phytozoogeographic boundaries widely interpreted as barriers to migration from alternative centres of origin such as the "Palearctic" or "Australasia" (Keast et al. 1959; Keast 1981; Archer & Fox 1984). The role of centres of origin and casual migration is ruled out, however, by the presence of the Flores Soemba and Two Moluccas nodes at the distributional boundary (Fig. 20). These nodes represent two points of overlap or intersection between animal and plant distributions which are not centered on current geographic centres to the north or south, but one or more ocean basins (Croizat 1958, 1968). The focus of distributions on these (and other) points is the result of tectonic convergence (Craw & Weston 1984). Vicariism of *Endoclita* and *Aene-*

*tus* in relation to the Flores/Soemba and Two Moluccas nodes is a consequence of the historical relationship between the ancestral range of the genera and the tectonic origins of the present-day distributional boundary.

The biogeographic history of the Flores Soemba/Two Moluccas nodes directly involves two major ocean basins — the Indian and the Pacific (Croizat 1958, 1968). Each of these oceans are natural biogeographic regions which provided the palaeogeographies upon which the modern plant and animal distributions of islands and continents are formed (Craw 1988). The biogeographic relationship between ocean basins and the ancestral range of a group is suggested by the hypothesis of a "baseline" (Craw 1983). A baseline is assigned according to the relative distance of plant and animal distributions to ocean basins, in terms of main

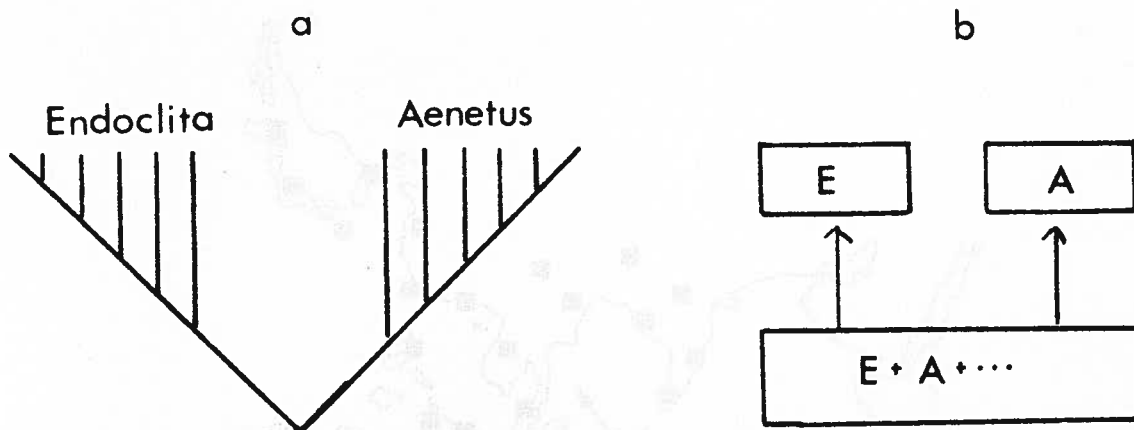


Fig. 21 Illustration of alternative phylogenetic interpretations for evolution of tunnelling in *Aenetus* and *Endoclita*. (a) As part of a genealogical sequence of speciation. (b) As a series of ancestral characters combining *Aenetus*, *Endoclita*, and other characters ( $E + A + \dots$ ) resulting in the descendant character combinations represented as the two genera.

massings and phylogenetic relationships (Craw 1985). *Endoclita* and *Aenetus* border both Pacific and Indian Oceans but they have no firmly established trans-oceanic relationships (cf. Nielsen & Robinson 1983). An Indian Ocean baseline was suggested by Grehan (1984) for *Aenetus*, on the basis of a possible phylogenetic affinity to *Zelotypia*, *Leto*, and *Trichophassus*, but this has yet to be confirmed. The contrasting larval biology of *Leto* may reflect a lack of close phylogenetic affinity to either *Aenetus* or *Endoclita*. The larval habits of *Trichophassus*, appear to indicate that its mode of wood-boring is similar to *Endoclita* and *Aenetus* and its occurrence in eastern Brazil may indicate trans-Atlantic relationships with other Hepialidae. The distribution of *Endoclita*, along with the related *Sahyadrassus* (Tindale 1942) is quite strongly represented by the Indian ocean, being present in India, Sri Lanka, and South-east Asia. The western limits of *Aenetus* distribution is western Australia where four endemic species are found. The absence of any close trans-Pacific hepialid relationships and the presence of Hepialidae in Africa (Janse 1942) may suggest that the evolutionary origins of the vicarism of *Endoclita* and *Aenetus* are to be found with the Indian Ocean (Fig. 20). The baseline (Fig. 20) may approximate Gondwanaland, but only insofar as it relates to the biogeographic sector defined by the Indian Ocean basin (Croizat 1961: 1246).

I suggest that the biogeography of *Endoclita* and *Aenetus* indicates that they did not each evolve at a single point or centre of origin, but by recombination of ancestral characters over a broad geographic front. Some characters recombined out in a manner that was mutually exclusive, giving rise

to *Endoclita* and *Aenetus* respectively; other characters, such as arboreal tunnelling, recombined over the entire ancestral range, resulting in the present diversity of tunnelling habits. This does not necessarily mean that the evolution of arboreal tunnelling is constrained within a genealogical relationship suggesting that the two genera most closely related (Fig. 21a). (This is considered unlikely, E. S. Nielsen pers. comm.). It does, however, imply that the evolution of arboreal tunnelling over a standard biogeographic range is a function of an ancestral type of organisation preceding both genera (Fig. 21b). The evolution of arboreal tunnelling is not, therefore, a "chance" event but an integral part of hepialid phylogeny in relation to the biogeographical massing of ancestral characters.

The phylogeny of arboreal tunnelling may be represented by two potential main massings. One represents the geographic range of *Endoclita* and *Aenetus* (also includes *Sahyadrassus* (seven species) in western India (Tindale 1942) and *Zelotypia* in Australia). *Zelotypia* has a localised distribution in the vicinity of Sydney, (New South Wales), south of the McPherson/Mcleay node which is one of the major biogeographic centres in Australia (Fig. 20) and may be significant for understanding the origins of *Aenetus* as a whole. A second potential massing may occur in Central and South America where the genus *Aepytyus* is represented by at least 50 species (Nielsen & Robinson 1983). The remaining diversity of arboreal tunnelling is limited to the monotypic genera *Leto* and *Trichophassus* in South Africa and southern Brazil, respectively (Janse 1945; Briquelot 1956), and two species of

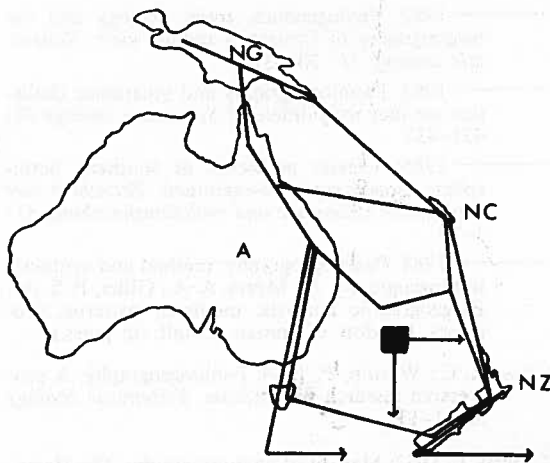


Fig. 22 Network of tracks (patterns of dispersal) in an around the Tasman sea (from Craw 1979). The baseline (■) represents the hypothesis of *A. virescens* characters being "inherited" along different tracks, but oriented to a common baseline (ancestral combination) in a Tasman Sea palaeogeography. A, Australia; NC, New Caledonia. NG, New Guinea. NZ, New Zealand.

*Hepialus sensu lat.* in North America (Wagner 1985). The origin of arboreal tunnelling on the western Pacific appears to be an ancient feature of hepialid evolution since it coincides with the recognised centre of taxonomic diversity for the Hepialidae (Meyrick 1889; Forbes 1923: 67; Tindale 1932: 497, 1981; Dumbleton 1966; Common 1970).

#### Implications for systematic analysis

Evolution of characters over a broad geographic front suggests that evolutionary relationships may be expressed spatially in more than one direction. The recombination of characters also provides for a situation of reticulate character evolution, where a number of phylogenetic affinities may be involved in the evolution of a group (Croizat 1978; Henderson 1985). There is no current, comprehensive systematic analysis of *Aenetus* by which the tunnel characters could be "tested", but it is possible to introduce the potential of biogeography to provide phylogenetic information on the evolution of arboreal hepialids. For example, the tunnel characters of *Aenetus virescens* show greater similarity to *A. cohici* of New Caledonia than to species of south western and eastern Australia (Table 4). This relationship is paralleled by the common exploitation of *Nothofagus* as a host, but morphological features of the genitalia and coremata may indicate a greater affinity between *A. cohici* and Australian species than to *A. virescens* (Holloway 1979; Grehan 1983b).

In and around the Tasman Sea there is a network of tracks (dispersal patterns), two of which link New Zealand and Australia (Craw 1979) (Fig. 22). With reference to these tracks, the character relationships of *A. virescens* could involve ancestral connections directly to Australia or alternatively, to Australia via New Caledonia and New Guinea. The two tracks have a common baseline in the Tasman sea (Fig. 22) and *both*, therefore, may be responsible for the evolution of *A. virescens*; each having "independently" (not really independent since they have a common baseline) contributed to the present juxtaposition of tunnel and genitalic characters in New Zealand. In systematics there is often an emphasis on conflicting characters to be resolved by classifying one set as "right" or informative (true phylogenetic homology) and the other being "wrong" or uninformative (homeoplasy, parallelism, or convergence). The biogeography of tunnel characters suggests that more than one phylogenetic relationship is possible with at least two standard tracks being involved in the evolution of *Aenetus virescens*. This means that the phylogenetic origin of *A. virescens* is "polyphyletic" in space but "monophyletic" in form, which is consistent with the concept of New Zealand as a biogeographic and geological composite (cf. Craw 1982, 1985, 1988).

The relationship of tunnel structure between New Zealand and New Caledonia is of particular interest since this pattern forms part of two major trends in trans-Tasman dispersal involving two major channels ("beams"), one extending from Queensland to Tasmania, the other from New Britain to New Zealand (Croizat 1968: 34). It is possible that the northern affinities of *A. virescens* may bypass New Caledonia and connect directly with New Guinea in a manner comparable to other plants and animals such as *Carpodetus* (Escalloniaceae) (Croizat 1968: 372-374) and some lepidopteran genera (Holloway 1979: 225). Evaluation of the latter possibility will require study of the New Guinean *Aenetus* species. This analysis suggests that a full appreciation of the systematic relationships and evolutionary origin of characters can be reached only in reference to the biogeographic history of taxa. It is this type of analysis which may prove to be useful to future systematic studies of tunnelling in the arboreal Hepialidae.

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