Larval feeding habits of the Hepialidae (Lepidoptera)

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The host–plant relationships of the Hepialidae are discussed in relation to host range and larval tunnelling behaviour. Larvae are mostly phytophagous on live angiosperms, gymnosperms, pteridophytes and mosses. Generally they specialize as feeders of leaf, stem/branch or root tissue, but dietary transitions from leaf to stem and root to stem occur in some species. An early period of mycophagy where larvae feed on fungi or dead decaying plant tissue is recorded in a wide range of species that feed on live embryophytes in later instars. Feeding patterns of the Hepialidae are compared with those of other major lepidopteran taxa and the evolutionary implications of hepialid feeding habits for the origin and derivation of larval host–plant relationships in Lepidoptera are discussed. It is suggested that the developmental transition from mycophagy to phytophagy in the Hepialidae is the result of partial 'suppression' of mycophagy in the generalist feeding ancestor of Lepidoptera.

KEYWORDS: Lepidoptera, Hepialidae, Evolution, Larvae, Feeding, Host-plant, Phytophagy, Mycophagy, Fungivory, Tunnelling.

The Hepialidae comprise about 80 genera and 500 species (Kristensen, 1978; Nielsen and Robinson, 1983; Nielsen, 1985) and represent the largest of 6 families in the sub-order Exoporia (Kristensen, 1984; Nielsen and Scoble, 1986). The Exoporia is the sister group of the Heteroneura which includes about 99% of all Lepidoptera species (Kristensen, 1984). Traditionally the Hepialidae have been defined by the absence of tibial spurs (Kristensen, 1984; Nielsen and Robinson, 1983), but this has been recently revised and some genera, such as Gazoryctra, are now excluded from Hepialidae sensu stricto (Nielsen and Scoble, 1986). They are included in this paper as Hepialidae sensu lato because of their close affinity with Hepialidae sensu stricto and the absence of revised higher taxonomy for alternative allocation (Nielsen and Scoble, 1986). Hepialids occur in most parts of the world (Madagascar being a notable exception) ranging from tropic to sub-arctic/antarctic climates and ranging in altitude from sea level to alpine. The moths are found in most vegetation types including forest, shrubland, grassland, tundra, swamp and bog (Tindale, 1938, 1981; Dumbleton, 1966; Dugdale, 1975a). The main centers of taxonomic diversity appear to be Australasia (Dumbleton, 1966; Common, 1970; Tindale, 1938, 1981) and South America (Nielsen and Robinson, 1983).

Adult Hepialidae have reduced mouthparts and are non-feeding, but larvae have generalized, biting mouthparts with well-developed mandibles and spinneret (Viete, 1946, 1948; Common, 1970). Larvae may feed on roots, stems or leaves (Powell, 1980; Tindale, 1981; Mitter and Brooks, 1983; Rawlins, 1984). Most detailed descriptions of
larval development and feeding refer to major pest species feeding on roots or ground herbage where the life cycle is generally of one or two years duration (Barrett, 1895; Perrott, 1974; Joubert, 1975; Heath, 1976; Pottinger, 1980). The stem borers are generally poorly known and some species may have a comparatively long period of larval development. The larval period of the wood borer Aenetus virescens (Doubleday) lasts from one to at least four years (Grehan, 1987).

This paper reviews the current knowledge on larval feeding in the Hepialidae with respect to live embryophyte hosts (phytophagy) and fungi or plant detritus (mycophagy) (terms from Rawlins, 1984). The host-plant relationship of the Hepialidae has been widely portrayed as exclusively phytophagous with larvae feeding on 'higher' plants such as angiosperms and, to a lesser extent, gymnosperms and pteridophytes (Powell, 1980; Mitter and Brooks, 1983; Rawlins, 1984). Several studies, however, have shown that some phytophagous species of Hepialidae also feed on fungi or detritus (see Grehan, 1979). Mycophagy in the Hepialidae occurs either as a specialist feeding stage during the early instars or it is combined with phytophagy for all or part of larval development. Some species may be exclusively phytophagous throughout development, but this needs detailed corroboration. Records of first instar phytophagy in Hepialus humuli (Edwards, 1964) and Palpifer sordida (Snellen) (Kalshoven, 1965), for example, were obtained from studies under laboratory conditions only (C. A. Edwards, 1982 personal communication, Kalshoven, 1965) and may not be directly related to the field situation. Young larvae of some species with mycophagous habits can be 'induced' to feed on vascular plants under laboratory conditions (Slachsevskii, 1929; Grehan, 1979). Hill (1929) specifically referred to phytophagy in the first instar larvae of Oncopera intricata, in the field, but he did not preclude mycophagy.

Phytophagy

Phytophagy in the Hepialidae may be sub-divided into three descriptive categories with respect to the leaf, root and stem of the host plant. These divisions do not refer to natural units of plant structure (Heads, 1984), but provide reference to the principal tissue substrates of larval diet. Most genera are characterized by only one feeding category (Table 1). Hepialid larvae are primarily borers with tunnelling and feeding closely integrated. Some root and stem borers feed by ingesting host tissue during tunnel construction while other species feed in particular parts of the tunnel such as the tunnel entrance where callus tissue is grazed. Leaf-feeding species that bore tunnels down into the soil below ground herbage, use the tunnel for shelter, food storage and access to the host plant. Hepialid tunnels are partly or completely lined by a thin layer of silk (Evans, 1941; Milyanovskii and Mitrofanov, 1952; Edwards, 1964; Hardy, 1973, 1974; Joubert, 1975: 14; Kile et al., 1979; Wagner, 1985; Grehan, 1988 a). The silk may not always be easily visible, perhaps leading Robson (1892) to question its existence for Hepialus (sensu lato). The tunnel entrance of many stem- and leaf-feeding species is closed over by a web comprising silk and debris and some leaf feeders construct the entire tunnel from silk and debris.

Leaf feeders

Tunnels are excavated in soil or constructed from silk and debris among ground litter and vegetation. Tunnels in the soil are more or less vertical and are open to the ground surface where the larva feeds. Tunnel length increases during larval development, but is generally less than about 50 cm with variation according to the species and soil structure or density (c.f. Evans, 1941; Hardy, 1974; Joubert, 1975). The
Table 1. Generic list of larval feeding in the Hepialidae. The species are listed as the number of species in each genus (approximate) and the number in which larval feeding has been described (approximate). The references cited are not exhaustive but provide most details. Refer to text for further citation. Locations for genera are intended for general geographic reference and have no biogeographic significance. Locations are as follows: A—Australia, As—Asia, Aus—Australia, New Zealand, New Guinea, New Caledonia, Br—Brazil, Ca—Caucasus, C—China, E—Europe, J—Japan, I—India, M—Malaysia, NAf—North Africa, NAm—North America, N—Nepal, NZ—New Zealand, SAf—South Africa, SAm—South America, SEA—South East Asia. *—some root feeding also recorded. **—no specific information. ?—number not known.

<table>
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structure of the web over the tunnel entrance varies from a simple silk roof (Fig. 1 a) which may incorporate debris (Fig. 1 b) to a complex canopy with 'feeder tunnels' reaching nearby plants, and specific sites for deposition of debris and faecal material respectively (Fig. 1 c). At pupation the entrance web may be partially or completely dismantled. In Eudalaca rufescens (Hampson) it is replaced by an upraised silk cap or 'operculum' (Fig. 1 d) (term from Quail, 1902).

Foraging by leaf feeders is usually limited to the immediate vicinity of the tunnel entrance. Larvae of Wiseana spp. usually remain partly within the entrance web when foraging (Esson, 1970: 203) but Wiseana sp. reared on artificially prepared swards of selected plants foraged in a circular feeding zone with a radius up to 8 cm. Feeding by Wiseana sp. was concentrated on particular plants until all the readily accessible and/or palatable plant material was removed (Harris, 1969). Most species probably forage during the night (c.f. Evans, 1941; Martyn, 1960; Esson, 1970; Farrell, 1972: 882; Hardy, 1973: 118, 1974). Larvae of Eudalaca rufescens forage day and night when temperatures range from 15–45°C (Joubert, 1975). Larvae of O. fuscomaculatus have sometimes been observed crawling over pasture during the day but they were not feeding (Hardy, 1974).
French and Pearson (1981) found in a population of *Wiseana* larvae that an average of only 50 per cent were feeding on any one night and feeding was suspended by individual larvae for periods that sometimes exceeded 10 consecutive nights. Food storage sites may be constructed in the tunnel (Fig. 1 a) or the entrance web (Fig. 1 c). Larvae of *Eudalaca rufescens* drag leaves and stalks through the feeder tunnels to the central web where they are eaten or cut into shorter lengths and stored to one side of the tunnel (Joubert, 1975: 3). Larvae of *Wiseana* sp. sometimes pull leaves into the tunnel and store them about 5–8 cm below ground (Harris, 1969).

Pest species of *Dalaca, Eudalaca, Oncopera, Osycanus*, and *Wiseana* are polyphagous feeders on both mono- and dicotyledonous angiosperms. Important hosts in sown or 'improved' pasture include grasses and herbaceous dicotyledons (Evans, 1941; Madge, 1956 a, 1957; Martyn, 1960; Lloyd and Blackman, 1966; Hardy 1973, 1974; Farrell 1972; Farrell et al., 1974; Joubert, 1975; Carrillo, 1974). Some pasture species include a variety of horticultural crop plants. Larvae of *Oncopera intricata*, may feed on wheat, onion, carrot, strawberry, barley, pean vine, tomato and crucifer seedlings (Martyn, 1960). Several studies on feeding by *Wiseana* show that larvae exhibit different host preferences in relation to species diversity and combination of host-plants (Harris, 1969; Harris and Brock, 1972; Farrell et al., 1974). Larvae of *Eudalaca refescens* will ignore certain plants if other 'preferred' hosts are present (Joubert, 1975). Mosses are included in the diets of some grassland species (Hill, 1929; Madge, 1954, 1956; Martyn, 1960; Evans, 1941; Joubert, 1975), but they are the principal hosts only for some swamp-living hepialids (Grehan and Patrick, 1984). Some 'typical' leaf-feeding species also feed on roots of a different range of plants. Larvae of *Wiseana* eat the fleshy roots *Phormium tenax* (Agavaceae) (Miller, 1971) and possibly *Muilenbeckia australis* (Polygonaceae) (Grehan, 1983 a). The grassland species *Oncopera fuscoculatus* Walker may feed on potato tubers (Tindale, 1935: 282) and roots of the tussock grass *Poa* sp. (Poaceae) (Martyn, 1940). *Oncopera intricata* and *O. rufobrunnea* larvae will not eat roots unless leaves are unavailable (Evans, 1941: 14). Some records of root feeding may be erroneous or over-emphasized. Larvae of *Oncopera intricata* were commonly believed to feed on roots until a detailed study by Hill (1929) showed them to be leaf feeders. Generalized records of feeding such as *Hepialiscus nepalensis* Hampson on roots (Hampson, 1892: 317) need confirmation.

Larvae of *Dioxycanus oreas* (Hudson) construct tunnels of silk and debris among the sward/litter layer of host-plants and other vegetation. The tunnel takes the form of a 'horizontal' winding tube from which the larva forages at the base of host-plants such as *Poa* spp. (J. S. Dugdale, personal communication; J. R. Grehan, personal observation). Several species of Hepialidae construct inclined silk tunnels in the sward and litter of moss and cushion bogs. Three species, *Wiseana umbraculata* (Guénée), *Cladoxycanus minos* (Hudson) and an undescribed species of a new genus (*Oxycaninae sensu* Dumbleton, 1966) feed within moss swards (Fig. 2) (Grehan and Patrick, 1984). The tunnels extend down through the moss without reaching any soil if there is a sufficiently high water table. The lower part of the tunnel may penetrate the water table, but it is not known to what extent the larvae can or do remain submerged. *W. umbraculata* is also known to inhabit wet grassland (Perrott, 1974; Ferro, 1976) and this is probably true of *Cladoxycanus minos* since adults have been collected over pasture (B. H. Patrick personal communication). The undescribed species is limited in distribution to bogs or soil on bog margins where it feeds on plants such as *Poa colensoi* (Grehan and Patrick, 1984). An undescribed species of *Aoraria* is restricted to bogs where the larva feeds on the hard cushion plant *Oreobolus pectinatus* (Cyperaceae) (Fig. 3). The larva emerges at
night to feed on the cushion surface resulting in a meandering channel partly filled with dead leaves. The tunnel reaches a depth of about 200 mm and one or two lateral chambers are constructed at 20 mm where faecal pellets are stored (Fig. 4) (J. R. Grehan and B. H. Patrick, personal observation). Tindale (1935: 278) observed newly emerged adults of *Elhamma australasiae* (Walker) 'clinging to wet sward grass and to reed stems
in swampy places' and he suggested that the larvae may feed on the roots of swamp grasses and weeds, but the species is also known from drier locations (E. S. Nielsen personal communication).

Root feeders

Many descriptions of root feeding are brief or generalized and this may be due to the difficulty of directly observing the subterranean habit of Hesperididae (Edwards, 1964: 147). For example, larvae of *Gazoryctra fuscoargentatus* were found feeding on *Betula nana* (Betulaceae) only when Tham et al. (1985) were digging rainwater channels around their tents! Nevertheless, root feeding has been emphasized in some general accounts as a major characteristic of hepsialid feeding (Forbes, 1923; Janse, 1942; Gerasimov, 1952; Pinhey, 1975; c.f. Tindale, 1932) and it may prove to be the most common host-plant association of the Hesperididae (c.f. Nielsen 1985: 6).

Root-feeding larvae tunnel into soil, the host root or a combination of both. The larvae of *H. lupulinus* and *T. sylvestra* (L) first tunnel into soil and later into host plants (Edwards, 1964; Perju and Ghizdavu, 1977). Feeding by *Hepialus lupulinus* varies from biting completely through the basal part of plants such as lettuce, to constructing semicircular cavities in plants with a fleshy or woody base. Tunnels of *H. lupulinus* were described by Edwards (1964) as open ended galleries where larvae fed at either end. Larvae of *T. sylvestra* excavate 'short', almost vertical galleries in and around host roots and when feeding on hops they remove the cortex at the juncture of the shoot and main roots. Sometimes this feeding results in the complete separation of shoot and root (Perju and Ghizdavu, 1977) Barrett (1895) described the tunnel of *T. sylvestra* in *Echium vulgare* as a spiral which begins at the root surface with the entry hole closed over by tissue fragments bound together by silk. Larvae of *Thitarodes armoricanus* Oberthür feeding on *Polygonum viviparum* (Polygonaceae) construct vertically inclined tunnels in the soil which may include lateral connecting burrows and chambers. The tunnels are

![Diagram of a generalized longitudinal section of tunnel of *Aoraha* nsp. in cushion bog of *Oreobolus pectinatus*. Chambers contain faecal pellets. Structure of cushion surface outlined by dotted line.](image-url)
5–20 cm below ground in the summer, but in the winter this depth is increased to 10–20 cm below a 3–8 cm upper layer of frozen soil (Ch’en et al., 1973). Phylmatopus hectar larvae may feed externally on the roots of the fern Pteris aquilinum for the first season, but after overwintering they excavate oval-shaped depressions in the base of the stem (Buckler, 1887; Barrett, 1895; South, 1908). The woody roots of Acacia (Leguminosae) trees are host to Oxyccamus direptus (Walker) (Tindale, 1935: 292) and O. australis (Tindale, 1938) while O. roseusus Tindale may feed externally on the roots of Eucalyptus sp. (Myrtaceae) (Tindale, 1964: 665). The genera Trictena and Abadiades are external root feeders of Eucalyptus and possibly other trees and shrubs (Pescott, 1934; Tindale, 1935, 1938; Kile et al., 1979; McQuillan and Forrest, 1985). Tunnels of Trictena argentata (Herrich-Schaeffer) around the roots of Eucalyptus rostrata extend from 15 cm below the ground to a depth of 2 m (Tindale, 1938). Larvae of Abantiades latipennis feeding on roots of Eucalyptus regnana and E. obliqua excavate near vertical tunnels (± 30°) 12–35 cm in depth and 6–10 mm in diameter. Tunnels may branch 3–5 cm below ground and are almost horizontal when in contact with surface litter. Larvae cause localized lesions and feed on the resulting callus, generally at a depth of 5–20 cm. The feeding area is sometimes enveloped by callus growth and larvae continue feeding inside the cavity (Kile et al., 1979).

At least three genera include species that may feed in both roots and stems. Larvae of Hepialus lupulinus sometimes tunnel up from the roots into the stem of Chrysanthemum (Edwards and Dennis, 1960). The tunnels of Stenopis begin in the root and later extend up into the stem where the adult emerges (Kellicott, 1888; Lyman, 1893; Packard, 1895; Forbes, 1923; Vallée and Béique, 1979). The tunnels of S. quadrangulatus Grt. in Populus balsamifera (Salicaceae) are oval shaped, about 15 cm in length and have a basal chamber with a 1–2 cm opening in the root surface (Fig. 5). Droppings are evacuated from the stem through 1–2 cm wide holes which are sealed by a loose plug of frass bound together with silk (Vallée and Béique (1979). According to Forbes (1923: 67) the larvae of Stenopis are virtually aquatic and usually tunnel below the water level in trunks of trees and shrubs growing partially submerged. The description by Vallée and Béique (1979) suggests that larvae are not always submerged and it is not known to what extent Stenopis may be aquatic in comparison with hepialids in moss bogs. The closely related Zenocphassus schamyl (Chr.) (Robinson, 1977) is recorded from grape vines, European hawthorn (Corylus avellana, Corylaceae) and blackberry (Rubus, Rosaceae) (Milyanovskii and Mitrofano, 1952; Zagainyi and Iurchenko, 1955). The larva does not always tunnel up into the stem but may mature within the roots and the adult emerges directly from the soil (Zagainyi and Iurchenko, 1955).

Detailed records of the host-range of root feeders is confined mainly to pest species of agricultural and horticultural crops in Europe. Pest species may feed on a wide range of angiosperms including both herbaceous and woody perennials (Buckler, 1886, South, 1908; Balachowsky and Mensil, 1936; MacDougall, 1914; Stokoe, 1948; Viette, 1948; Cameron, 1960; Edwards and Dennis, 1960; Edwards, 1964; Heath, 1976; Perju and Ghizdavu, 1977). The larva of Hepialus humuli (L.), for example, is recorded from about 26 angiosperm genera and families (Table 2) and it has been suggested that the species will attack any plant with a woody or fleshy base (Barrett, 1895; Edwards and Dennis, 1960; Edwards, 1964). The host range of T. sylvina includes a wide range of angiosperms such as Rumex, Taraxacum officinale, (Compositae) Echium vulgare (Boraginaceae) (Edwards, 1964), Agropyron repens (Poaceae), Symphytum officinale (Boraginaceae) and Equisetum arvense (Sphenophyta) (Edwards, 1964; Perju and
Fig. 5. Larval tunnels of *Sthenopis quadriguttatus* in subterranean portion of main stem of poplar (*Populus balsamifera*) (R. Béique personal communication).

Table 2. Host range of *Hepialus lupulinus* (Lepidoptera: Hepialidae). From Edwards (1964), Cameron (1960) and Edwards and Dennis (1960).

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<tr>
<td>Lettuce</td>
<td>(<em>Lactuca</em>, Asteraceae)</td>
</tr>
<tr>
<td>Lilies</td>
<td>(<em>Lilium</em>, Liliaceae)</td>
</tr>
<tr>
<td>Lily of the Valley</td>
<td>(<em>Convallaria</em>, Liliaceae)</td>
</tr>
<tr>
<td>Oats</td>
<td>(<em>Avena</em>, Gramineae)</td>
</tr>
<tr>
<td>Peas</td>
<td>(<em>Pisum</em>, Leguminosae)</td>
</tr>
<tr>
<td>Potatoes</td>
<td>(<em>Solanum</em>, Solanaceae)</td>
</tr>
<tr>
<td>Parsley</td>
<td>(<em>Petroselinum</em>, Umbelliferae)</td>
</tr>
<tr>
<td>Parsnips</td>
<td>(<em>Pastinaca</em>, Umbelliferae)</td>
</tr>
<tr>
<td>Peonies</td>
<td>(<em>Peonia</em>, Ranunculaceae)</td>
</tr>
<tr>
<td>Raspberries</td>
<td>(<em>Rubus</em>, Rosaceae)</td>
</tr>
<tr>
<td>Snowdrops</td>
<td>(<em>Galanthus</em>, Amaranthaceae)</td>
</tr>
<tr>
<td>Strawberries</td>
<td>(<em>Fragaria</em>, Rosaceae)</td>
</tr>
<tr>
<td>Wheat</td>
<td>(<em>Triticum</em>, Gramineae)</td>
</tr>
</tbody>
</table>
Ghizdauv 1977). Pteridophytes may be important hosts for some Hepialidae and have been recorded as the only host (generally Pteridium aquilinum) of Korscheltellus fusconebulosus (De Geer) (Vielle, 1948; Edwards, 1964) and Phymatopus hectar (L.) (Edwards, 1964; Heath, 1976). Other host plants are implicated however, since the moths occur where P. aquilinum is absent or unrecorded (Blackie, 1956; Edelsten, 1957; Heath, 1976).

**Stem/branch borers**

Larvae enter the host plant from above ground and the tunnel entrance is closed off by a web of silk and debris. Most species (e.g. of Endocrita, Aenetus, Zelotypia) probably feed on callus tissue growing around the tunnel entrance whereas Leto venus (Stoll) and Hepialus californicus (Bdv.) feed on wood tissue during tunnel excavation (Grehan 1988 a; Wagner, 1985). The tunnel is first excavated toward the stem centre (radial tunnel), usually at a slightly inclined angle, and then turns to follow the wood grain (longitudinal tunnel). The longitudinal tunnel of genera such as Aenetus and Zelotypia extends downwards only (Fig. 6) while in some Endocrita species it may be excavated both up and down (Fig. 7). The longitudinal tunnel of 'Hepialus' may be in either direction (Wagner 1985: 35). There is considerable variation in tunnel shape and structure between hepialid species or genera, but very little attention has been given to this aspect of larval biology (Grehan, 1988 a).

Some arboreal species have an extensive host range and this is particularly true of Endocrita exrescens and E. signifer which are important forest and agricultural pests in Japan. E. exrescens may feed on at least 103 species in 43 families, including Equisetum (Sphenophyta) and the gymnosperm genera Pinus, Cryptomeria and Chamaecyparis (Matsuzawa et al. 1963). E. signifer (Walker) is recorded from 72 plants, including 22 gymnosperms in the genera Cycas, Ginkgo, Podocarpus, Cephalotaxus, Abies, Picea, Tsuga, Cedrus, Pinus, Cryptomeria, Biota, and Thujaos (Kondo, 1961). The host range of these two hepialids is further extended by the young larvae which feed for about one month on stems of herbaceous plants such as annual and perennial grasses, Asteraceae

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**Fig. 6.** Tunnel of the wood borer Aenetus virescens in Carpodetus serratus. Longitudinal section. c, cover; p, plug blocking initial longitudinal tunnel; o, pupal operculum (from Grehan 1988a).
Fig. 7. Tunnel of the wood borer *Endoclita excrescens*. Longitudinal section. Upper longitudinal tunnel filled with frass. c, cover; dashed line, feeding surface (from Grehan 1988a).

(e.g. *Chrysanthemum*) and major crops such as *Triticum* and *Zea* (Gramineae) (Kondo, 1961; Toyomura and Matsuzawa, 1965; Matsuzawa et al., 1963; Ueda, 1979; Nishi and Yoshii, 1979). Host records may not always refer to plants that support complete larval development. *Aenetus virescens* is recorded from about 68 angiosperm species but only 19 are known to support larvae to maturity and the only gymnosperm record is of a single abortive feeding attempt (Grehan, 1984). Host records for other *Aenetus* species suggest angiosperms as the primary host group and most species appear to have a wide range of host plants (Grehan, 1988a). A generalist host range occurs in ‘*Hepialus*’ hektoides (Bdv.) and *californicus* which bore into stems or roots of woody Compositae and perennial Rosaceae (Wagner, 1985). *Aenetus paradiseus* var *montanus* Tindale and *Leto venus* (Stoll) may be species specific monophages (Grehan, 1988a; Duke and Taylor, 1964).

*Mycophagy*

Specialist mycophagy was first recorded in the Hepialidae by Slashchevskii (1929) who discovered third and fourth instar larvae of *Phassus schamyl* Chr. (transferred to *Zenophassus* by Tindale, 1941; c.f. Robinson, 1977) in decaying leaf litter in the Caucasus National Park (U.S.S.R.). He believed that dead plant tissue comprised the principal diet of young larvae although they could be reared in the laboratory on both live and dead plant leaves. The third instar larvae could also be fed on various fungi growing from wood but Slashchevskii (1929) was unable to locate older larvae in the leaf litter and suggested that they burrowed into the soil and fed on roots. This habit was later confirmed by Milyanoskii and Mitrofanov (1952).
Since the observations by Slashchevskii (1929; 1930a, b) mycophagy has been recorded in the early instars of a wide range of species. Gerassimov (1952) noted that the younger larvae of Hepialidae apparently live on the soil surface and feed on withered or even fresh leaves, but he did not provide any details. The only other confirmed record of mycophagy in a root feeding species is for Trictena argentata (Herrick-Schaeffer) whose larvae feed in dead leaf litter for at least the first instar (Tindale, 1981). The young larvae of Korscheltellus lupulinus (L.) (Sankey, 1948) and Triodia sylvisa (Perju and Ghizdavu, 1977) may be mycophagous during their occupation of upper soil layer before tunnelling down to the roots of host plants.

A complete physical and behavioural separation of mycophagy and phytophagy occurs where older larvae feed on the stems and branches of trees and shrubs. Mycophagy has been confirmed for only four species, but the early larval stages have yet to be observed in detail for the remainder (Grehan 1988a). The newly hatched larvae of Aenetus virescens (Doubleday) and A. cohici Viette feed on dead wood and fungal fruiting bodies growing from logs and twigs on the forest floor (Grehan, 1988a). Young larvae of Endoclita sericeus (Swinhoe) feed on decaying twigs (Kalshoven, 1965) while those of E. chalybeatus Moore are recorded in forest litter (Barlow, 1983). The transition from mycophagy to phytophagy in Aenetus virescens occurs through a specialized morph characterized by the fusion and darkening of pinacula. The morph is ‘lost’ at the first moult after larvae tunnel into vascular plants (Grehan, 1981). It has been recorded in three other species of Aenetus, (Grehan, 1988a) but remains unconfirmed outside the genus (Wagner, 1985). Mycophagy has not been recorded in the early instars of Japanese Endoclita species, but newly hatched larvae may live under the bark of large trees or damaged wood at the site of an old tunnel as well as on herbaceous plants (Toyomura and Matsuzawa, 1965; Matsuzawa, et al., 1963).

An early mycophagous stage is known or inferred for several leaf feeding species. A distinct mycophagous stage occurs up to the sixth instar Eusalaca rufescens (Hampson) in South Africa where young larvae feed on dead, dry leaves and stalks of grasses on the soil surface. Newly hatched larvae of Oncopera brachyphylla Turner and O. mitocera (Turner) may feed on fungal mycelia, and Elder (1970) concluded that the food of larvae in rain-forest areas, and of young larvae in pastures, must consist mainly of debris rich in micro-organisms. In the laboratory, young larvae were fed with lawn debris and fresh grass leaves while older larvae were given both fresh leaves and dead, decayed leaves and twigs from the forest floor (Elder, 1970). Mycophagy is not unlikely for those species in which the early instars are known to live and feed in the litter and upper soil (e.g. Oncopera intricata (Walker) [Hill, 1929; Evans, 1941; Martyn, 1960], Dalaca paliens (Blanchard) [Lloyd and Blackman, 1966] and Oxycanus fuscomaculatus [Hardy, 1974: 323]). Young instars of Wiseana spp. live in litter on the ground surface for about the first 6–8 weeks (Dumbleton, 1945; Taylor, 1964, Helson, 1967; Perrott, 1974; Potter, 1980; Dugdale, 1975b; French and Pearson, 1981) and probably feed on dead plant tissue (Dugdale, 1975b).

In pasture and grassland live and dead plant tissues are in close physical proximity and it would not be surprising to find extensive overlap between mycophagy and phytophagy throughout the larval development of some species. Hardy (1974: 324) found fungal hyphae to be common on most of the plant material consumed by about 25 per cent of the larvae of Oxycanus fuscomaculatus Walker. The larvae of Oncopera fasciculata (Walker) can ‘apparently’ feed on young grass, decayed organic matter, soil, fungi and moulds under laboratory conditions (Madge, 1954) and larvae in the pasture overwinter on herbage or straw from the preceding year, consuming new growth as it
appears (Madge, 1956: 315). From the sixth instar the main diet of *Eudalaca rufescens* consists of growing green leaves and stalks, but larvae will also consume dry leaves, sheaths, or stalks throughout the summer (Joubert, 1975). The larvae of pasture blackworms (probably *Dalaca* spp. c.f. Cabellero, 1955; Carrillo, 1974) are recorded by Castillo (1975) feeding at the soil surface on debris, leaves and tender shoots. When live plants are scarce, larvae of *Oncopeira intricata* Walker will eat rotten wood, surface vegetable debris and cow dung (Hill, 1929). Soil is ingested along with host plants by the larvae of *Oncopeira brachyphylla* (Elder, 1971), *Fraus simulans* (Hardy, 1973), *Oxyeucanus fuscomaculatus* (Hardy, 1974) and *Eudalaca rufescens* (Joubert, 1975). Joubert (1975) was unable to rear larvae beyond 6 or 7 instars on plants without soil.

At least two species may be specialist mycophages throughout larval development. Elder (1978: 6) suggested that larvae of *Oncopeira parva* Tindale feed exclusively on leaf debris although they could be artificially fed on fresh leaves (mixed with rain forest leaf debris). Larvae of *Trioxycanus enysii* (Butler) live in subterranean tunnels where the ground surface lacks any surface vegetation (Grehan et al. 1983; J. S. Dugdale personal communication) and excavation of tunnels has not revealed any evidence of root feeding (A. Moeed, M. J. Meads personal communication). I have reared larvae of *T. enysii* from first to second instar on a diet of dead leaf material taken from the forest floor; and larvae were reared by J. S. Dugdale (personal communication) on a diet of dead *Agathis* leaves for 3 months during which time the larvae grew in length from 10 to 25 mm.

Comparison with other Lepidoptera

Angiosperms comprise the major host group of the Hepialidae and in this respect hepialid feeding is similar to most of the other lepidopteran families. However, host records for many species of Hepialidae are either generalized, incomplete or entirely unknown and non-angiosperm hosts may yet prove to be more important than currently recognised (c.f. Wagner, 1985). Mosses may be important host-plants for many of the pasture or grassland species, but liverworts appear to be excluded from the diet. In contrast, the Micropterygidae feed mainly on liverworts and although moss host-plants are recorded (e.g. Gerson, 1969; Heath 1958), they have not been confirmed (G. W. Gibs, J. Heath personal communication).

Unlike most angiosperm feeding families in the Lepidoptera, the Hepialidae do not include leaf-feeders of trees or shrubs. Leaf-feeding on trees and shrubs does occur in other non-Ditrysian groups, including the ‘primitive’ Heterobathmiina (Kristensen and Nielsen, 1983), and larvae of some of the Zeugloptera feed on the leaves of angiosperm seedlings (Lorenz, 1961). The absence of hepialids feeding in tree or shrub canopies is not constrained by the tunnelling habit since canopy leaf-feeding occurs, for example, in the ditrysian wood-boring family Xyloryctidae (Common, 1970). The Cossidae (Ditrysia) represent a close ‘parallel’ to the feeding behaviour of the Hepialidae by tunnelling in soil, roots or stems, but there is no leaf-feeding or mycophagous stage (Common, 1970, Grehan, 1983 b).

Larval transition between diets is a major feature of the Hepialidae. In the phytophagous stage dietary transitions involve root/stem or leaf/stem changes (Fig. 8), but it is most apparent in the mycophagous/phytophagous relationship (Fig. 9). Dietary transitions involving fungal and higher plant feeding are comparatively rare in other Lepidoptera (Fig. 10) and fungal and higher plant feeding are mutually exclusive in the Ditrysia (possible ‘exceptions’ notwithstanding). Obligate ditrysian mycophages are common in only a limited number of species, principally within the superfamilies
FIG. 8. Changes in phytophagous diet during larval development of some Hepialidae. Arrows represent direction of change during larval development. No sequential pattern is known to involve leaves and roots although both tissues may be included as a single diet.

FIG. 9. Developmental relationship between obligate mycophagy and obligate phytophagy in the Hepialidae. Arrows represent direction of change during larval development. ‘Litter’ refers to feeding on dead plant tissue (leaf, wood) or fungi.

Tineoidea, Tortricoidea, Gelechioidae, Pyraloidea, Geometroidea, Papilionoidae and Noctuoidea (Rawlins 1984). The Hepialidae represents the only non-ditrysian group where obligate fungivory is currently recognised, but mycophagy is implicated for the non-ditrysian subfamilies Adelinae and Incurvariinae (Incurvariidae). Young instars are phytophagous while older instars are associated with fallen leaves and debris (Powell, 1969: 214, 1980: 141; Rawlins, 1984: 383). Although the Micropterygidae are generally characterized as bryophyte feeders (Powell, 1980), mycophagy may also be important (Mitter and Brooks, 1983) since some species are associated with litter (Mitter and Brooks, 1983; Carter and Dugdale, 1982) and may feed on dead or dying plant tissue (Carter and Dugdale, 1982). Larval feeding is unrecorded in the families most closely related to the Hepialidae—the Neotheoridae, Anomosetidae, Prototheoridae, and Palaeosretidae (Kristensen, 1978), but larvae of Mnesarchaeidae (the sister group of all these) ingest a range of plants including bryophytes, angiosperms and fungi (Gibbs, 1979).
Larval feeding habits of the Hepialidae

Fig. 10. Distribution of mycophagy in the major Lepidopteran taxa. The lepidopteran groups are not treated here as terminal 'taxa' and the cladogram does not, therefore, suggest that the Zeugloptera-Neopseustina Lepidoptera comprise a monophyletic group. Larval development is represented as vertical rectangles. Phytophagy as vertical lines, mycophagy as horizontal lines and generalist feeding as cross hatched.

Discussion

Accounts of the possible evolutionary history of larval feeding in the Lepidoptera by Powell (1980) and Rawlins (1984) have been constructed in the context of obligate mycophagy and phytophagy being mutually exclusive where highly specialized mycophagy is confined to the Ditrysia. Powell (1980) carried out a general survey of host records for 'microlepidoptera' comprising the non-ditrysian Lepidoptera and the ditrysian superfamilies Tineoidea, Gelechioidea, Copromorphoidea, Yponomeutoidea, Sesioidea, Cossoidea, and Tortricoidea. He found that each superfamiliy and major family uses a wide diversity of Angiospermae. He suggested (p. 152) that the 'fundamental evolutionary radiation' of Monotrysia (Nepticuloidea, Incurvarioidae) and Ditrysia occurred through specialised larval feeding in niches or horizons within communities rather than along botanical evolutionary lines (Fig. 11). He concluded (p. 154) that the ancestral branches of Lepidoptera mostly did not survive and all that remains is an 'anomalous guild of relics associated with certain lower plants'. Rawlins (1984) focused on the origin and evolution of mycophagy. The apparent absence of obligate mycophagy in the 'primitive' Zeugloptera (Micropterigidae), Aglossata (Agathiphagidae), Dacnonypha (Eriocranioidae), Neopseustina, Exoporia (Hepialoidea and Mnesarchaeoidea) and Monotrysia (Nepticuloidea and Incurvarioidae) led Rawlins (1984) to suggest that fungal feeding was a derived trait that evolved several times within the Ditrysia from phytophagous ancestors. The evolution of mycophagy was linked to phytophagy via several 'adaptive' pathways (Fig. 12).

In the Hepialidae obligate feeding associations with the most 'primitive' multinucleate plants (fungi) are juxtaposed by larval development with the most 'advanced' (angiosperms). The presence of mutually exclusive stages of mycophagy and phytophagy within single life-cycles of Hepialidae suggests that the two feeding modes
Fig. 11. Evolution of Lepidopteran feeding according to Powell (1980). Reproduced with permission from Annual Review of Entomology Vol. 25 © 1980 by Annual Reviews Inc.

TRENDS TOWARD MYCOPHAGY IN LEPIDOPTERA

Fig. 12. Evolution of larval feeding from a phytophagous ancestor by 'adaptive' pathways. (From Rawlins, 1984). Copyright © 1984 Columbia University Press. By permission of the publisher.

are not necessarily incompatible components of the evolutionary biology of Lepidoptera, despite major biochemical differences between fungi and higher plants (Martin, 1979). Preliminary biochemical analysis of polysaccharide digestion for larvae of A. virescens has demonstrated the ability of both mycophagous and phytophagous stages to degrade starch, a fungal and higher-plant storage compound, and laminarin, a
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major fungal cell wall component comparatively rare in higher plants (Grehan, 1988b). The duality of hepal lid feeding removes the need to assume a specialist ancestral feeding habit for the Lepidoptera and highlights the potential importance of developmental processes affecting the evolution of specialist feeding. A generalist feeding ancestor may have differentiated into specialist feeders in different descendants by a developmental 'suppression' of the mycophagy or phytophagy present in the ancestral diet (Fig. 13). Within lineages the process of suppression would be expressed as specialist feeding during different stages of larval development (Fig. 13). This hypothesis suggests that the evolution of obligate phytophagy has been the major evolutionary trend in both 'primitive' and 'advanced' Lepidoptera. The evolution of

![Diagram](image)

**Fig. 13.** Evolution of mycophagy and phytophagy from a generalised ancestor through developmental transition. This model suggests that a generalist ancestral lepidoperan fed on fungal and higher plant tissue. Specialisation into obligate phytophages (ob. phyt.) and mycophages (ob. myc.) may have taken place to relative suppression of one dietary component. In the Hepialidae, Adelinae (Adel.) and Incurvariinae (Inc.) this suppression has resulted in a differential expression of combined obligate phytophagy and mycophagy during larval development.
feeding in the Hepialidae could be interpreted as having an 'intermediate' position relative to specialist feeders. In the Hepialidae the evolution of mycophagy and phytophagy has resulted in temporal isolation through larval development in contrast to the phylogenetic isolation between different taxa as found in most Lepidoptera. The evolution of obligate phytophagy and mycophagy may represent 'parallelisms' or 'convergences' in the systematic sense (i.e., show character incongruence with the most 'parsimonious' character association), and yet involve a single evolutionary trend from generalist ancestor to specialist descendants. This view is not incompatible with ecological interpretations as attempted by Powell (1980) and Rawlins (1984), but suggests that research into the evolutionary biology of Lepidoptera could benefit from a closer look at the evolutionary relationship between larval development and feeding in lepidopteran phylogeny.

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