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THE EARLY HABITAT OF THE AUCHENORRHYNCHA

C. W. Schaefer[1]

ABSTRACT

It is suggested that the first auchenorrhynchs lived on or in the ground, sometimes in association with ants. Feeding on trees, although perhaps not the original mode of feeding, arose early, in several evolutionary lines of Auchenorrhyncha.

KEY WORDS

Insecta, Homoptera, ant attendance, Cercopoidea, Fulgoroidea, Cicadoidea, Cicadelloidea, Membracoidea.

I

INTRODUCTION

I have suggested elsewhere (Schaefer, 1981) that the original habitat of the Hemipteroidea (Hennig's [1969] clade Acercaria) was on the ground. Many members of this group, and especially many evolutionarily older members, live in ground debris, or on or just below the surface of the ground, or associated with ground biota (such as roots, ants, burrowing mammals), or in groundlike habitats (e.g., in nests, under bark). This association with the ground is widespread throughout the Hemipteroidea, and throughout the order Hemiptera. The association may represent many independent acquisitions of a ground-living way of life, but it is easier--more parsimonious--to believe it represents the retention of an early way of life, a way of life retained in many groups which otherwise share few features except those shared by all hemipteroids.

From ground-dwelling hemipteran ancestors, which quite possibly were omnivorous scavengers, there arose two basic stocks. One became predacious and developed into the Heteroptera. The other, coming to suck plant juices (probably from roots), became the Homoptera. I discussed the Heteroptera briefly in 1981; I shall consider the Auchenorrhyncha (also briefly) here, and shall reserve for later an account of the Coleorrhyncha and Sternorrhyncha.

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[1] Department of Ecology and Evolutionary Biology, The University of Connecticut, Storrs CT 06268 U.S.A.

II

My premise is this. A character state may be found widespread throughout a large, diverse, and monophyletic group. (It is best if the cladistic relationships within the group be worked out <u>before</u> the following analysis is done, to avoid the "common=primitive" error.) The subgroups possessing this character state may have, as sistergroups, subgroups lacking the feature, which appears in a scattered fashion throughout the larger group. Two possibilities, or the two combined, may explain this distribution. The feature may have arisen independently many times in the several subgroups possessing it. Or the feature may have arisen once, in the ancestor of the large group, and been retained here and there by various of the descendent subgroups. Or both may have occurred, the first in some subgroups, the second (retention) in others. In the first instance, the feature is an apomorphy developed homoplastically. In the second, the feature is an autoplesiomorphy of the entire group. And in the third, the feature may be one or the other depending upon the phylogenetic history of the subgroups in which it occurs; moreover, in the third, reversals may have occurred.

How may one distinguish between the first two possibilities? One cannot, unequivocally; but two lines of argument may help. First, one may consider the condition of the alternative character state in the sistergroup of the subgroup possessing the state in question. Consider three distantly related groups, A, B, C, all members of a larger monophyletic group and each with two subgroups. A_1, B_1, and C_1 each have the same state of a character. A_2, B_2, and C_2 each have some other state. Is the state shown by A_1, B_1, and C_1 an autoplesiomorphy retained from the common ancestor, or has it since been independently acquired by A_1, B_1, and C_1? Look now at the alternative character states in A_2, B_2, and C_2. If these are all <u>different</u>, each from the other two, it is likely that the state in A_1, B_1, and C_1 is primitive, and was the state possessed by the ancestor of A_1 and A_2, by the ancestor of B_1 and B_2, and by the ancestor of C_1 and C_2. In each case, this plesiomorphic character state evolved to a different one--the states now possessed by A_2, B_2, and C_2. It is assumed here more likely that a primitive feature may evolve to several different advanced ones, than that several primitive features each evolve independently to the same advanced one. It is also more parsimonious.... If, however, the alternative states possessed by A_2, B_2, and C_2 are all the same, the problem cannot be resolved, because the character-state change could have gone in either direction.

The second line of argument asks if the subgroups themselves are recently or anciently evolved. A recent subgroup is likely to have had in its evolution from the group's common ancestor, many intermediate speciation events, and, therefore, many opportunities for change in the states of a character possessed by that common ancestor. A subgroup arisen from closer to the common ancestor (and therefore arisen longer ago) may have undergone in its evolutionary history fewer speciation events, and fewer opportunities for change of character states. One might therefore expect older groups to retain more of the group's ancestor's character states--which is why such subgroups are often (but confusingly) called "primitive."

A character state found more often among the older subgroups than among the more recent is more likely to be plesiomorphic, and less likely to be homoplastically apomorphic. This line of reasoning, of course, can appear circular, or at least elliptical. For often a group with many plesiomorphies (=few apomorphies) is considered to have arisen early. The reasoning is valid, however, if the character state scattered through the group is not a priori considered plesiomorphic and then used to judge the recency of its possessors' origins. This reasoning also ignores differing amounts of anagenetic change, and therefore assumes (often incorrectly) a constant rate of character change.

Neither of these lines of argument can be used blindly or blithely. In every case the group and subgroups, and the character and its various character states, must be carefully considered. A cladistic analysis, or at least a clear knowledge of the evolutionary history of the group and subgroups, is essential. Similarly, the complexity of the character must be considered, to determine how likely are repeated changes to the same state. For example, black and dark brown are common in the Heteroptera. Is this a retained autoplesiomorphy, or has the dark coloration been re-evolved many times? The biochemical pathways leading to dark color are relatively simple, and so must be their genetic bases. Therefore, dark coloration has probably been repeatedly acquired. In some cases, it may be an autoplesiomorphy retained from the dark, cryptically colored, ground-living heteropteran ancestor. But in many cases certainly, the brown or black has been more recently acquired.

III

Scattered throughout the Auchenorrhyncha are insects living on or near the ground, and occurring throughout too are insects feeding on trees. Also occurring fairly often is an association with ants, frequently on the ground but sometimes up on plants; I think it probable that the association with ants originated on the ground, and always preceded a life up on plants.

Here I shall trace these patterns through the Auchenorrhyncha. My taxonomic basis is the classification and phylogeny of Evans (1963, 1975, 1977; Fig. 4) which suggests that the Fulgoroidea is the earliest arisen of the five superfamilies, and is sistergroup to the common ancestor of the remaining four; and that the common ancestor of the Cicadoidea+Cercopoidea and of the Cicadelloidea+Membracoidea are sistergroups (the latter clade having arisen earlier in time than the former). I recognize that others have presented other systems, although these often do not differ substantially from Evans's.

My information comes from a general (but not exhaustive) survey of the literature; much comes from the superb volume edited by Nault & Rodrigues (1985). Unfortunately, I lack space to discuss the alternative habits, equivalent to character states of A_2, B_2, and C_2 in the first line of reasoning above. In general, they are sufficiently different from one another to justify the use of this line of reasoning.

In my survey I have not defined "tree" taxonomically--a "tree" is simply a large woody plant, or is the word used by my sources; I discuss the significance of tree-associations briefly at the end. Also, I have considered the associations of nymphs very important. This stage is the one most concerned with the getting of food. In addition, its habitat may be the most conservative (the one least likely to have changed over time, and therefore the most likely to reflect the original habitat). Eggs, vulnerable to predation and parasitism, are laid where most easily concealed, that is, on or in the ground, or in plant tissue; they may also be laid in the ground to protect them from seasonal adversity, the egg being the most resistant stage in hemimetabolans. Associations of eggs with the ground may therefore be secondary. The adult disperses and seeks mates and is, therefore, unlikely to live on or below the ground (where, among other things, sound production would be of little use). This is true today and was probably true in the past. Therefore when I maintain that early auchenorrhynchs lived on or in the ground, I usually refer to their nymphs: doubtless their adults (in many cases) lived above the ground.

Further, many planthoppers (and others) live near the bases of plants, particularly of grasses (Butler, 1907; O´Brien & Wilson, 1985). I believe this is not a primitive habitat but, rather, the insects are feeding on the growing portions of grasses, the nitrogen-rich meristematic tissue. Nevertheless, Cobben (1965, p. 66) has written, "the generalized mode of oviposition in leafhoppers [=Auchenorrhyncha] is to place the eggs freely on the soil-substrate"; and certainly some egg and adult ground associations are primitive.

IV

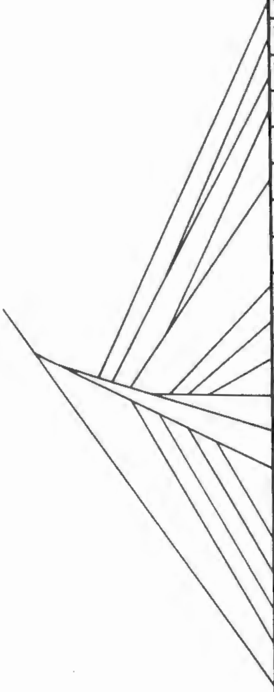
In his phylogeny of the Fulgoroidea, Muir (1923, Fig. 8) recognizes three lines: 1) Meenopliidae through Flatidae; to this may be added the monobasic Hypochthonellidae, which China & Fennah (1952) place near the ricaniid-lophopid-eurybrachyid-gengid group; this placement also suggests that the Gengidae, not treated by Muir, belongs in 1). 2) The Achilixiidae through Cixiidae. And 3) the Tettigometridae, the earliest arisen of these lines. To Muir´s list may be added the Kinnaridae, which resemble the Cixiidae (group 2), and the Nogodinidae, which resemble the Issidae (group 1) (O´Brien & Wilson, 1985).

Of the twenty fulgoroid families, members of ten are associated with the ground (Fig. 1). These ten include the most primitive line, the Tettigometridae; five of the thirteen families of group 1; and four of the six families of group 2. In addition, nymphs of the Derbidae, of group 2, feed on fungal hyphae on or under fallen trees, as do some achilids (Hepburn, 1967; Wilson, 1983). Immatures of three families, one in each group, are ant-attended, and some Achilidae are associated with termites (O´Brien & Wilson, 1985).

At least three cixiids (Fennah, 1973a, b), one kinnarid, and one meenopliid (Fennah, 1973a) are cavernicolous. Fennah (1973a) suggests this habitat has been attained by the movement of root-feeding nymphs down roots into caverns. It seems more likely that tree roots could penetrate thus than could those of smaller plants.

Several cixiids mentioned by Fennah are species of *Oliarus*, a large genus whose "nymphs are subterranean and feed on" roots (Mead & Kramer, 1982, p. 385). In Hawaii, nymphs occur in many ground habitats, from rotting vegetation to beneath tree bark and stones (Zimmerman, 1948), and--with their adults--in lava tubes (Fennah, 1973b). In North America, *O. vicarius* (Walker) may be associated with ants (Thompson, et al., 1979), and newly hatched nymphs of the Australian *P. felis* Kirkaldy work their way into the soil to feed on the roots of grass (Hacker, *fide* China, 1942). Although many species of *Oliarus* do not feed on roots of trees, some probably do (Thompson, et al., 1979). The genus is well adapted to an underground life (always of nymphs, often of adults as well), and its phylogenetic position in the family is therefore of interest.

Six families (five in the first group in Fig. 1, one in the second) contain members that feed on trees, and two of these are also associated with the ground. Three of the four not so associated are among the more recently evolved families.



	A	B	C	D	E	F	G		Reference
Flatidae							x		*, also Mead, 1965
Riconiidae									
Lophopidae									
Issidae (Hysteropterum)			x						*
Nogodinidae			x				x		*
Acanaloniidae									
Gengidae									
Hypochthonellidae	x	x							*, also China + Fennah, 1952
Achilidae			x			x	x		Hepburn, 1967; Wilson, 1983
Eurybrachidae							x		*
Fulgoridae							x		*
Dictyopharidae (Orgerini)		x							*
Meenopliidae									
Cixiidae	x			x					*, also China, 1942; Kramer, 1983
Kinnaridae				x		x			*
Delphacidae		x							*, also Butler, 1907
Tropiduchidae							x		*
Derbidae						x			*, also O'Brien *in* Wilson, 1972
Achilixiidae		x							*
Tettigometridae	x		x						*

* = O'Brien + Wilson 1985, unless stated otherwise

Fig. 1. Affinities and ecological associations of fulgoroid families (adapted from Muir, 1923, Fig. 7). A, ant associations; B, several stages on or in ground; C, eggs on or in ground; D, nymphs on or in ground; E, eggs in bark or dead wood, F, nymphs in bark or dead wood; G, feeding on trees.

This distribution suggests that the early fulgoroids lived on or in the ground. The evidence is less strong that they fed upon trees.

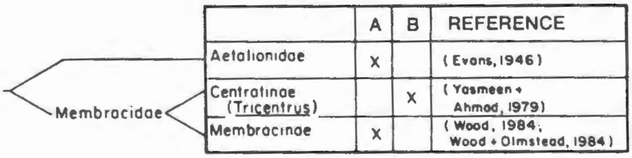
The association of the Cicadoidea with both the soil and with trees is well known (see White & Strehl, 1978). It is usually thought that cicadas need a long time to develop because they are large and feed on the xylem of tree roots. It seems likely that xylem feeding came first, and the consequent slow development permitted the larger size to be achieved. Slow development and large size are not inevitable consequences of xylem feeding, of course; but in many cicadoids these consequences were selected for, perhaps because both have advantages not usually considered (see Karban, 1986). It follows then that cicadoids require roots that will last a considerable time--those of trees.

I have little information on the Cercopoidea, the sistergroup of the Cicadoidea (Evans, 1977; Fig. 4). Imm´s textbook (Richards & Davies, 1977) says cercopid nymphs, and many aphrophorid nymphs, are subterranean; this has been well described for the sugarcane froghopper by King (1965). As is well known, many of these nymphs ("spittlebugs") live in masses of froth or in fluid-filled tubes. These occur also below ground, where perhaps they protect their inhabitants from predators and abrasion by soil particles. Froth and tubes are then a preadaptation to life above ground, where they protect nymphs from desiccation in the drier above-ground air.

Cercopoids do not appear to be closely associated with trees, although machaerotid nymphs, and some cercopid nymphs, "feed on woody dicotyledons" (Maa, 1963, pp. 145-6).

Maa agrees with Evans (1940, fide Maa, 1963) that cercopines (presumably their nymphs) were originally subterranean root feeders and, Maa continues, "the direct ancestor of the Cercopoidea was a general underground feeder on plant roots" (Maa, 1963, p. 146).

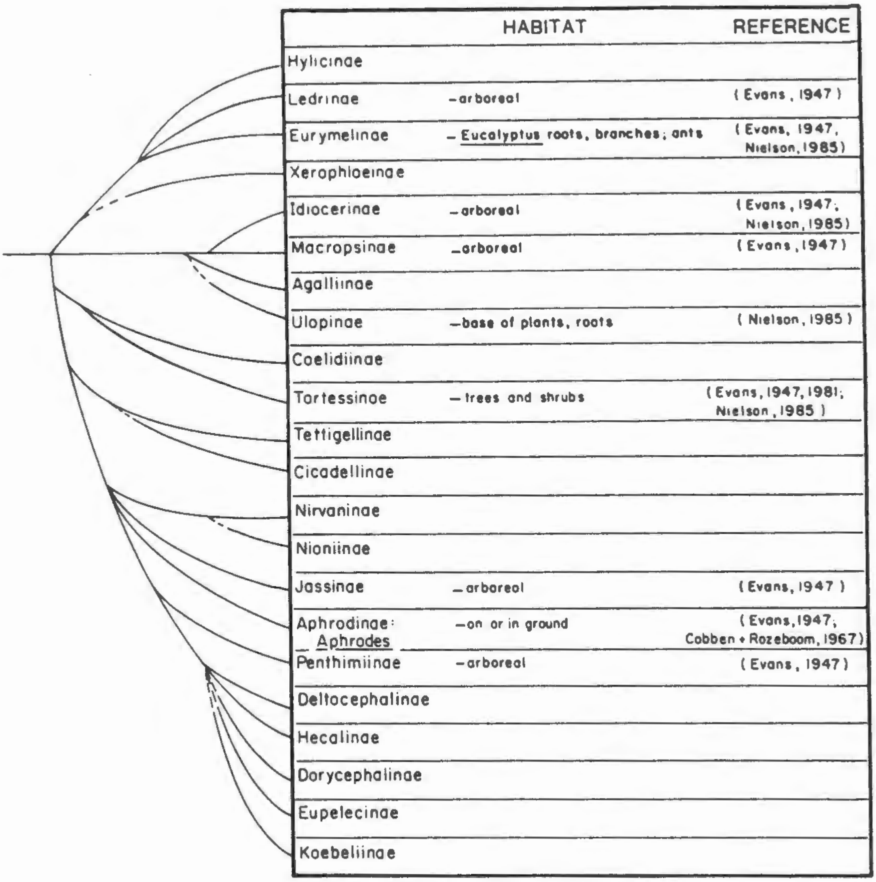
The Membracoidea-Cicadelloidea clade may be the most recently evolved of the major auchenorrhynch groups (Evans, 1977). Ant associations occur in the Aetalionidae, the more primitive (Strumpel, 1972) of the two membracoid families, as well as in one of the two membracid subfamilies (Fig. 2). These associations occur up on plants, but I believe it likely they originated earlier in the history of the Auchenorrhyncha, on the ground. Thus although ant-attended membracoids are up-on-plant insects, their associations with ants may betray an ancestral life on



	A	B	REFERENCE
Aetalionidae	X		(Evans, 1946)
Centratinae (*Tricentrus*)		X	(Yasmeen + Ahmad, 1979)
Membracinae	X		(Wood, 1984; Wood + Olmstead, 1984)

Fig. 2. Affinities and ecological associations of membracoid families (adapted from Strümpel, 1972, Fig. 164). A, ant associations; B, on or in ground.

the ground, where today lives an important genus in the other membracid subfamily (Yasmeen & Ahmad, 1979). These plants up on which membracids live, often with ants, are mostly trees. It is these associations, both with ants and with trees, whose evolutionary and ecological implications are being so well worked out by T. K. Wood.



	HABITAT	REFERENCE
Hylicinae		
Ledrinae	-arboreal	(Evans, 1947)
Eurymelinae	- *Eucalyptus* roots, branches; ants	(Evans, 1947, Nielson, 1985)
Xerophloeinae		
Idiocerinae	-arboreal	(Evans, 1947; Nielson, 1985)
Macropsinae	-arboreal	(Evans, 1947)
Agalliinae		
Ulopinae	-base of plants, roots	(Nielson, 1985)
Coelidiinae		
Tortessinae	- trees and shrubs	(Evans, 1947, 1981; Nielson, 1985)
Tettigellinae		
Cicadellinae		
Nirvaninae		
Nioniinae		
Jassinae	-arboreal	(Evans, 1947)
Aphrodinae: *Aphrodes*	-on or in ground	(Evans, 1947; Cobben + Rozeboom, 1967)
Penthimiinae	-arboreal	(Evans, 1947)
Deltocephalinae		
Hecalinae		
Dorycephalinae		
Eupelecinae		
Koebeliinae		

Fig. 3. Affinities and ecological associations of cicadellid subfamilies (adapted from Ross, 1957, Fig. 4).

Funkhauser (1917), discussing the host plants of New York Membracidae, divided them into four groups: hardwood trees, legumes, Rosaceae, and succulent composites; the first two groups are the most important. An examination of his host lists (pp. 387-390) shows that hardwoods harbor the most membracid species and that, moreover, those membracids on these trees are the least likely to be found also on other plants. Of 61 species of membracid listed, 32 (52%) are found only on one, or sometimes three, hardwoods; 8 (13%) are found on one or another member of the other three groups; and 13 (21%) are listed as "host unknown." This sample is somewhat biased because the number of genera is limited (21), and several large ones (e.g., Telamona, Cyrtolobus) are largely restricted to hardwoods. Nevertheless, the suggestion is strong that these insects ("treehoppers") are closely tied to hardwood trees.

The Cicadelloidea, recently evolved like its sistergroup the Membracoidea, has fewer ant and tree associations; most leafhoppers appear to feed on smaller, faster growing plants, and to have adapted their reproductive and dispersal habits accordingly; this is perhaps why leafhoppers do so much damage to crops.

Nevertheless, some subfamilies of the dominant family Cicadellidae do feed in trees, and several are on or in the ground (Fig. 3). Among the soil-inhabiting ones are the Eurymelinae, probably more primitive than Ross (1957; Fig. 3) suggests (Nielson, 1985); Aphrodes, whose tribe, Aphrodini, Evans (1946) considers the "least specialized" of the aphrodine tribes; and the Ulopinae, also considered a basal group by Evans (1946), and members of one of whose primitive tribes (Myerslopiini) occur in moss and litter on the forest floor (Evans, 1947).

Association with ants is infrequent here: some associations occur in the Eurymelinae; and a hecaline is tended, perhaps fortuitously, by several species of ants (Lavigne, 1966). And one ulopinae lives in termite nests (Poisson, 1938).

The tree-living groups also occur among the less advanced subfamilies (Fig. 3). Evans (1947, p. 108) writes, "The most primitive jassids feed on moss and reeds and live at the bases of woody plants.... Leafhoppers occupying a middle position in the evolutionary scale are largely arboreal, while those of most recent development feed on grasses and herbaceous plants." One may conclude that in the Cicadelloidea too, living on the ground and feeding on trees are likely to have been early ways of life.

V

I think the evidence so sketchily presented here supports the idea that the early auchenorrhynchs lived on or in the ground; some members of all groups (even Cicadelloidea), and many members of most groups, so live (Fig. 4), at least in their nondispersing stages. Associations with ants may have developed very early as well; they occur commonly in the Sternorrhyncha, and occur also in all auchenorrhynch superfamilies but the Cercopoidea and Cicadoidea. This association has been and is being lost in some subgroups of the Fulgoroidea and Cicadelloidea. It has been lost in the cercopoid-cicadoid clade, perhaps because the nymphs of these xylem-feeding insects do not produce a sufficiently rich honeydew. Members of the membracoid-cicadelloid clade live up on plants; and ant associations here suggest an ancestral life on the ground, where presumably such associations originate.

The Fulgoroidea and Cicadoidea exemplify the two evolutionary patterns (Fig. 4) of auchenorrhynchs´ associations with trees. Associations of the first with trees occur most frequently in the more recently evolved families, particularly the achilid-dictyopharid line (Fig. 1). It appears then that such associations occurred not in the ancestor of the Fulgoroidea, but have arisen since, within the superfamily. On the other hand, so widespread are the associations of Cicadoidea with trees that such associations surely characterized the superfamily´s ancestor.

Tree associations by cercopoids appear to fit the fulgoroid pattern. Such associations do not seem to be frequent, although in fact we simply do not know what most subterranean cercopoids feed upon.

Membracoids certainly, and cicadelloids possibly, were originally tree-associated. The former are now closely tied to trees. The latter are not, except for some of the earlier arisen subfamilies; however, if Evan´s (1947) statement, quoted above, is true, tree associations in the Cicadelloidea arose within the superfamily, and did not occur in its ancestor. The Cicadelloidea therefore may reflect either pattern.

Ant associations are scattered throughout the Auchenorrhyncha, and I consider them primitive. Tree associations are also scattered, but I have not considered them primitive, but as having arisen several times in the infra-order. The ant associations derive from--are a secondary consequence of--the early habitat of the Auchenorrhyncha, the ground. However, the associations with trees are not with trees that arose early. Very few auchenorrhynchs are associated with gymnosperms and, except for the Membracoidea (Funkhauser, 1917), few are associated with

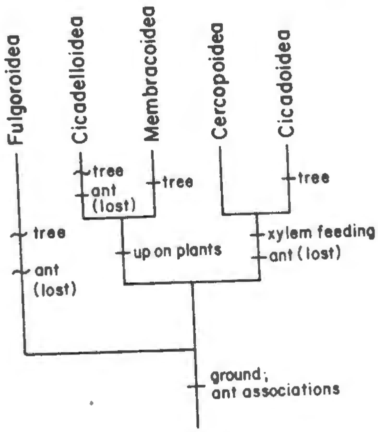


Fig. 4. Additions to phylogenetic tree of Evans (1977). — = character state arose in ancestor, occurs in all descendents (except where secondarily lost). ~ = character state not present in ancestor, but has arisen in one or more descendent lines.

the early (Cronquist, 1968) dicot subclasses Magnoliidae and Hamamelidae (in contrast to the Sternorrhyncha). Most auchenorrhynchs are associated with woody perennials, with *Eucalyptus*, or with trees of other recent groups; Costa Rican cicadas appear to prefer leguminous trees (Young, 1981). It is therefore unlikely the associations with trees are ancient; more probably, they have arisen--are still arising--independently in several lines of auchenorrhynch evolution.

Cicadoids and cercopoids feed on xylem fluid (Marshall & Cheung, 1973), and must pass much of it through the filter chamber to extract the scant nutrients. The excess fluid, excreted, becomes available for protecting the nymphs (the stage needing the most nutrients and therefore processing the most fluid) from soil abrasion and predators below ground (with froth, liquid-filled chambers), and from predators and desiccation above ground. Xylem feeding is not, I believe, widespread in other auchenorrhynch superfamilies. I suggest then that xylem feeding, with its attendant but secondary advantages, characterized the common ancestor of these two superfamilies (Fig. 4).

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