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#### The Biology and Taxonomy of the Aphids Transmitting Barley Yellow Dwarf Virus

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##### Abstract

*All the cereal-feeding aphids are potential vectors of cereal viruses, as indeed are aphids feeding on other Gramineae and Cyperaceae. At least 24 species of aphids belonging to 15 different genera have been shown experimentally to transmit viruses of the barley yellow dwarf group. This paper reviews the biologies of the main Gramineae-feeding genera, with more detailed consideration of the principal vectors of barley yellow dwarf virus. Several of the vectors belong to complexes of species that are difficult to separate, for example Melanaphis sacchari/sorghii, Rhopalosiphum maidis and Sitobion fragariae/miscanthi. These problems of species recognition and their agricultural implications are discussed.*

The objective of this paper is to summarize present knowledge of those aspects of the biology and taxonomy of cereal aphids that influence their ability to transmit barley yellow dwarf virus. Many aspects of aphid biology are relevant to virus transmission. We shall be mainly concerned with updating and filling any gaps in previous reviews (Plumb 1983; Gildow 1984). About the taxonomy of cereal aphids we will have more to say, as we wish to draw particular attention to the problems and uncertainties that exist in both the conceptual and the practical recognition of "meaningful taxonomic units" in most cereal aphids. By "meaningful taxonomic units" we mean groups of individuals or populations that have in common a set of correlated traits, such that the knowledge of one trait enables one to predict others. In those aphids that have an obligatory annual sexual phase, the smallest meaningful taxonomic units may be the species. On the other hand, in those aphids that reproduce continuously throughout the year by parthenogenesis, the smallest meaningful taxonomic unit may be a single clonal lineage, or a set of clonal lineages derived from a single clonal lineage, or a set of clonal lineages derived from a common ancestor and therefore having shared properties.

The term "biotype," as applied to aphids by economic entomologists, cannot be regarded as a meaningful taxonomic unit, because biotypes are recognized by only the single trait that happens to be of interest to the observer, such as the

ability to colonize a certain crop variety. A biotype may be a single clone, but on the other hand, it might consist of any number of clones with just the single trait in common, especially if the trait in question is determined at a single genetic locus. The designation of a population as "biotype A" does not necessarily imply any relationship with other populations of "biotype A," nor does it enable one to predict any other properties for the population, other than the one by which it was recognized. Studies on biotypes, if they fail to give full consideration to this limitation, can result in endless confusion in the literature.

We will deal first, in alphabetical order, with the aphid genera containing the principal vectors of barley yellow dwarf virus (BYDV), and then discuss the other aphids that may possibly bring virus into the crop.

##### Cereal Aphids Transmitting BYDV Within the Crop

###### **Anoecia (and other root aphids)**

Some species of the main aphid subfamily Aphidinae colonize Gramineae at or below soil level (e.g., *Rhopalosiphum insertum* (Walker), *R. rufiabdominalis* (Sasaki), *Aphis maidiradicis* Forbes), but the true root-feeding groups are in two other subfamilies, the Anoeciinae (*Anoecia* spp) and the Pemphiginae (e.g., *Tetraneura*, *Forda*, *Aploneura*, *Geoica*). Aphids of these subfamilies can be recognized by

their very short antennal terminal process (much shorter than the base of the last antennal segment) and siphunculi reduced to small cones, pores, or even absent.

*Anoecia* species have a sexual phase on *Cornus* in Europe and North America, but anholocycly (overwintering of parthogenetic morphs) on roots of Gramineae is common and probably predominates in the Mediterranean region and in South America. The apterae on roots are more active than Pemphiginae, with longer legs and antennae, and usually have a dark dorsal shield. The alatae migrating to and from *Cornus* have a conspicuously large dark pterostigmal spot on the forewing. The species are difficult to differentiate. *Anoecia corni* (F.), the only species shown to be a BYDV vector (A'Brook and Dewar 1980, Conti and Casetta 1983), occurs in Europe eastward to Iran and the Himalayas, and in North America. Similar aphids also occur in Korea and Japan.

*Tetraneura* have *Ulmus* spp. as primary hosts, and the Fordini (*Forda*, *Geoica*, *Aploneura*) have a two-year life cycle with a sexual phase on *Pistacia* in the Mediterranean region and the Middle East. The apterae of all these genera are plump, sluggish aphids with short legs and antennae. Anholocycly on the roots of Gramineae is common, especially where the primary hosts are unavailable. The migrations to and from the primary hosts are probably of little importance in BYDV transmission, and it is not known whether the alatae produced by anholocyclic populations transmit virus.

### **Diuraphis**

*Diuraphis* is a genus of about 10 species of small, elongate, wax-covered aphids with inconspicuous siphunculi, living in the rolled leaves of Gramineae in Europe and North America. The subgenus *Diuraphis* bears a conspicuous backwardly directed supracaudal process (Figure 1), which is barely indicated or lacking in the subgenus *Holcaphis*. Only three species occur on crop plants, and only one (*D. noxia* (Mordvilko)) is recorded as a virus vector.

*Diuraphis (Holcaphis) frequens* (Walker), widespread on *Agropyron repens* (L.) Beauvois in Europe and eastward to Turkey, was introduced into North America, where it has been collected on wheat (*Triticum aestivum* L.) and *Echinochloa crus-galli* (L.) Beauvois as well as on *Agropyron*, and it perhaps occurs also on other grasses. It was found in Quebec in 1956, New Brunswick in 1964, Manitoba in 1965, Washington in 1983 and Idaho in 1985.

*Diuraphis (Holcaphis) tritici* (Gillette) is the only *Diuraphis* known only from North America, and can be distinguished from *D. frequens* by its longer last rostral segment and other morphological features (see key below). It occurs on wheat, but is also recorded from *Agropyron occidentale* (Scribn.), which is possibly its native host.

*Diuraphis (Diuraphis) noxia* (Mordvilko), Russian wheat aphid, occurs mainly on barley (*Hordeum vulgare* L.) and wheat and more rarely on other cereals and grasses. First described from Russia, it is now found in southern Europe, Spain to Turkey, North and South Africa, the Middle East, Pakistan, and Argentina,

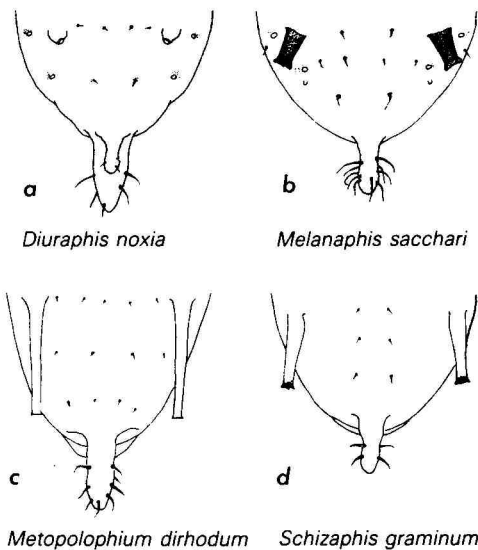


Figure 1. Rear of abdomen in dorsal view of aptera of four cereal aphids.

and has recently extended its range into Mexico and the USA. *D. noxia* has been reported as a vector of brome mosaic virus, barley stripe mosaic virus, cucumber mosaic virus, and BYDV. (von Wechmar and Rybicki 1981; von Wechmar et al. 1984). Walters (1984) reviews information about *D. noxia* and provides many references. Gilchrist et al. (1984) give an account of the problems associated with *D. noxia* in Mexico.

Key to the *Diuraphis* found on wheat:

1. Supracaudal process well-developed. Siphunculi about as long as broad. Lateral abdominal tubercles present on segments 3-5. Short-haired aphid, even the postero-dorsal cephalic and 8th abdominal tergite hairs only 8-12  $\mu\text{m}$  long ... *D. noxia*.
- Supracaudal process absent or only slightly indicated. Siphunculi little more than pores on pigmented bases. Lateral abdominal tubercles absent. Longer-haired aphids, hairs on 8th abdominal tergite 20-35  $\mu\text{m}$  long... 2
2. Ultimate rostral segment 0.85-1.15 times as long as 2nd segment of hind tarsus. Eighth abdominal tergite bearing 7-11 hairs, the spinal (median) hairs about 20  $\mu\text{m}$  long ... *D. tritici*.
- Ultimate rostral segment 0.55-0.75 times as long as second segment of hind tarsus. Eighth abdominal tergite bearing 4-6 (occasionally 7) hairs, the spinal ones being 25-35  $\mu\text{m}$  long ... *D. frequens*.

### **Melanaphis**

*Melanaphis* is an Old World genus of about 20 species of small, broadly oval aphids with short siphunculi (Figure 1), mostly associated with *Arundinaria* and the other bamboos in the Far East. A few species have Pyroidea as primary host plants, like members of the related genera *Rhopalosiphum* and *Schizaphis*. *Melanaphis* (= *Longiunguis*) *sorghii* (Theobald) has usually been regarded as a synonym of *M. sacchari* (Zehntner), but aphids from sorghum generally have a shorter antennal terminal process relative to length of hind tibia than those from

sugar cane (Figure 2), and it now seems more likely that the two are distinct taxa, although not absolutely specific to the hosts indicated by their names. The separation needs to be confirmed by experimental studies. The true situation may well be more complicated, as this group, like *Rhopalosiphum maidis* (Fitch) discussed below, is mainly or entirely anholocyclic. Color, general size, hair lengths, and numbers of lateral abdominal tubercles are very variable and probably subject to environmental conditions, particularly nutrition. *M. indosacchari* David appears to be one such environmental form (of *M. sacchari*).

*Melanaphis sacchari* (Zehntner) lives on sugar cane (*Saccharum*) in South Africa, Asia, Australia, and Central and South America. It seems to have arrived in Central America (Guyana) about 1932 and spread south gradually, reaching Uruguay and Argentina only recently (Delfino 1985). Apart from sugar cane, it sometimes colonizes *E. crus-galli* and rice (*Oryza sativa* L.), and specimens from sorghum in Brazil in the British Museum (Natural History) collection seem to be this aphid rather than *M. sorghi*.

*Melanaphis sorghi* (Theobald) is common on *Sorghum halepense* Pers. in the Middle East and on *S. vulgare* Pers. in Africa and Asia, also sometimes colonizing sugar cane in Africa and maize in Southeast Asia.

### **Metopolophium**

Species of *Metopolophium* are readily distinguished from other aphids on cereals by their pale tapering siphunculi, relatively long antennae, and rather slender body shape. The affinities of this genus are in some doubt. Morphologically the species are very like *Acyrtosiphon*, but biologically and karyologically they resemble *Sitobion*. Of the 18 described species, 15 have Gramineae as either their secondary or only host plants. The host-alternating species overwinter as eggs on *Rosa*. The few species without graminaceous hosts perhaps do not really belong in *Metopolophium*. The genus is predominantly European, and Stroyan (1982, 1984) and Heie (1986) have

comprehensively reviewed the European species so far recognized, including the important cereal pest *M. dirhodum* (Walker), which now has a worldwide distribution. The only other species regularly infesting cereal crops is *M. festucae cerealium* Stroyan. The non-pest species are morphologically very hard to distinguish from these two, but each restrict their feeding to one or two grass

species in particular habitats. *M. friscum* Hille Ris Lambers, which lives on *Poa* spp. in damp places, and *M. albidum* Hille Ris Lambers, which is specific to *Arrhenatherum elatius* Mert. and Koch, can transmit BYDV (A'Brook and Dewar 1980), and there is no reason to suppose that other species of *Metopolophium* are not also potential vectors wherever they occur.

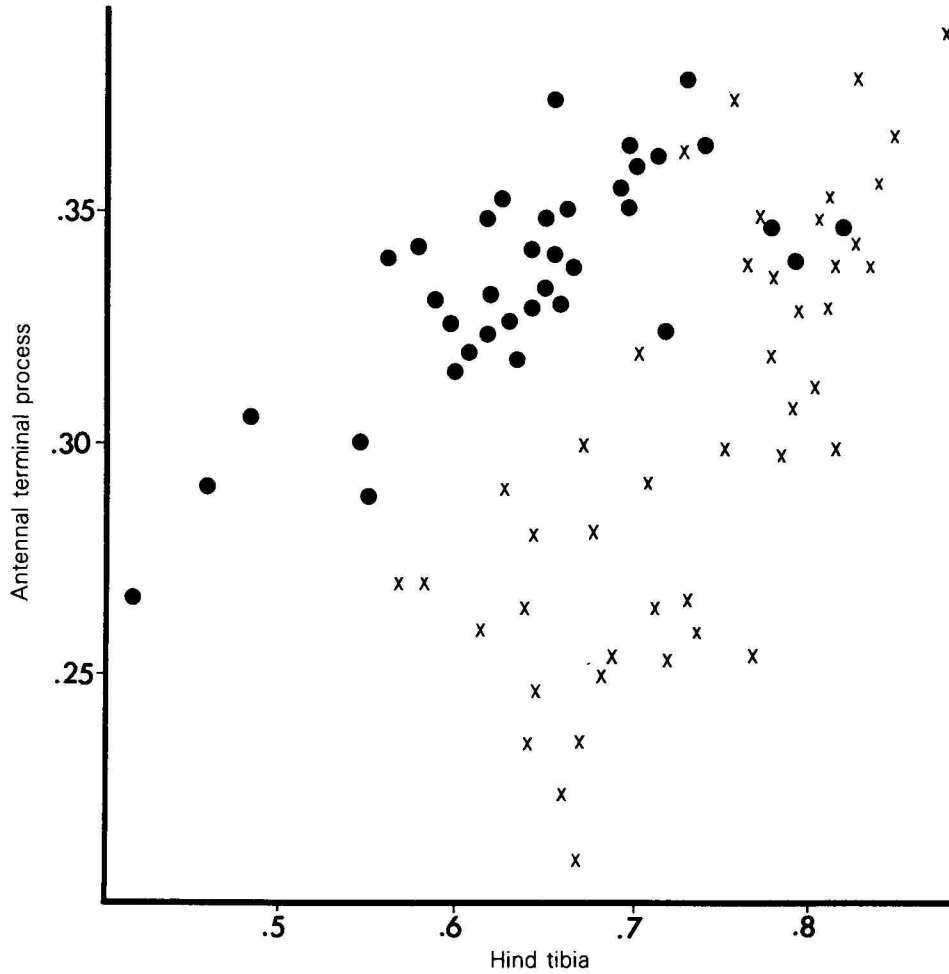


Figure 2. Plot of the measurements (in mm) of the length of the antennal terminal process against the length of the hind tibia for apterae of *Melanaphis* from sorghum (crosses) and sugar cane (circles) from many parts of the world, indicating the probable existence of two species.



*M. dirhodum* overwinters as eggs on wild or cultivated *Rosa* spp in cold temperate climates, but anholocyclic—overwintering of parthenogenetic morphs—is now widespread wherever winter temperatures permit. Numerous species of Gramineae, and some other monocots such as *Iris*, are colonized, so alatae of *M. dirhodum* can usually find hosts at a suitable growth stage at all seasons. In northwest Europe, where holocyclic predominates, the migration to cereals is normally too late to have a significant effect on yield. However, like *Sitobion avenae* (Fabricius), *M. dirhodum* is a rather active aphid, generally forming small colonies that readily produce more alatae (Cannon 1985), so that it may be important in spreading virus both through and between crops. Alatae leaving crops may also spread virus to late-maturing wild Gramineae, maize, and volunteer cereals.

Cannon (1986) studied populations of *M. dirhodum* over three summers in England, including an exceptionally large outbreak in 1979, and Dewar and Carter (1984) developed a decision tree for assessment of the risk of outbreaks. Development of spring populations on *Rosa* has recently been studied in Germany (Gruppe 1985) and the Netherlands (Hand and Hand 1986). Weber (1985b) set up 120 clones of *M. dirhodum*, all holocyclic, from cereal crops in Germany and found a wide variation in their ability to colonize barley, wheat, and oats (*Avena sativa* L.). The presence or absence of a sexual generation presumably has a major effect on population genetics and a parallel study in an area where *M. dirhodum* overwinters anholocyclically could be informative.

*M. dirhodum* recently reached Australia and New Zealand. In New South Wales it has been shown to be an efficient vector of a PAV-like isolate (Waterhouse and Helms 1985). In New Zealand it occurs on a succession of cereals and grasses throughout the year (Stufkens and Farrell 1985).

On cereals, living *M. dirhodum* are rather easy to distinguish from *M. festucae cerealium* by the broad bright green

longitudinal dorsal stripe present in both immature and adult apterae and by the dusky apices to antennal segments III, IV and V. *M. fasciatum* Stroyen, the only other *Metopolophium* with these features, migrates between *Rosa canina* L. and *Arrhenatherum elatius* and has not been recorded from cereals.

*Metopolophium festucae cerealium* Stroyan is the name applied to the large, long-legged form of *M. festucae* (Theobald) that colonizes cereals in Europe and sometimes builds up damaging populations on pasture grasses. Work with laboratory cultures and detailed morphometric studies have established that the differences from the exclusively grass-feeding form are not merely due to better nutrition (Stroyan 1982), but the genetic relationships between the two forms and their respective host plant ranges are not yet clearly established. Both are predominantly anholocyclic, but both are also known to produce sexual morphs occasionally on grasses, so hybridization may occur.

Plumb's (1974) record of transmission of three isolates of BYDV by *M. festucae* should presumably be applied to *M. festucae cerealium*. This aphid is regarded as of generally low pest status on cereal crops in Europe. There is even some evidence that the early presence of *M. festucae cerealium* in the crop may be beneficial, allowing the buildup of populations of parasitoids that later attack *Sitobion avenae*. However, in laboratory experiments wheat was more susceptible to it than any grasses (Dent and Wratten 1986). The paradox is unexplained and it seems possible that in other circumstances (for example, if introduced outside Europe, or on other cereal cultivars) its attacks on cereals could become more serious.

Apterae of *M. festucae cerealium* tend to be larger, paler, and yellower than those of *M. festucae s. str.*, and pink populations are unknown. Alatae typically have dark and well-developed transverse dorsal abdominal bands. The best single morphometric character for distinguishing the two forms of *festucae*

is the length of the hind tibia, but a discriminant function involving six characters is needed to provide a reliable separation (Stroyan 1982).

### **Rhopalosiphum**

*Rhopalosiphum* have strong taxonomic affinities with *Melanaphis* and *Schizaphis*, and the species share a similar biology with these two genera, typically having a sexual phase on *Prunus* or Pyroidea and migrating for the summer to monocotyledenous plants, mainly Gramineae. It is a difficult genus to define morphologically; a characteristic feature is the embossed polygonal pattern of small, bead-like or irregularly shaped nodules on the dorsal abdominal cuticle (Figure 3f), but this is difficult to see in unprepared specimens. The cereal-feeding species have rather characteristically shaped siphunculi: cylindrical, vasiform, or slightly swollen distally, but with a constriction just proximal to a well-developed apical flange (Figure 3g-j). The siphunculi and cauda of *Rhopalosiphum* species are dark and the cauda is rather short, always shorter than the siphunculi.

Of about 13 recognized species of *Rhopalosiphum*, 4 are proven vectors of BYDV (*R. insertum* (Walker), *R. maidis* (Fitch), *R. padi* (L.), and *R. rufiabdominalis* (Sasaki)). The biology of some of the other species is little known and they may include potential vectors. *R. padiiformis* Richards, described from British Columbia and distinguishable from *R. padi* by the long, pointed hairs on the posterior abdominal tergites (Richards 1962), has been collected on wheat in Montana, USA. Its life cycle is unknown.

*Rhopalosiphum insertum* (Walker) overwinters as eggs on Pyroidea (*Malus*, *Pyrus*, *Crataegus*, *Sorbus*, *Cotoneaster*) and migrates to various Gramineae (especially *Poa* and *Festuca*), where it normally feeds at the base of the stem or below ground and is probably frequently overlooked. It will colonize wheat, barley, and oats in the laboratory, but the only field record from cereals that we know of is from Victoria, Australia, in 1983 — its first appearance in Australia (M. Carver, personal communication). Anholocyclic overwintering does not normally occur.

The synonymy of this aphid is very confused; the names *R. crataegellum* Theobald and *R. oxyacanthae* Schrank have been applied to it by European workers, and North American taxonomists have been reluctant to accept that their *R. fitchii* Sanderson is the same species. The uncertainty has arisen partly because the subterranean populations are virtually unknown in North America, and alatae transferred from primary hosts to Gramineae in the laboratory have tended to form colonies above ground. The apterae from such aerial colonies are shorter-haired than those from subterranean populations of *R. insertum* in Europe, and also in life show some color differences (Smith and Richards 1963). Both hair length and color may be affected by environmental conditions during development, and especially by the differences in light and humidity above and below ground. Sun and Robinson (1965) showed that the range of Pyroidea used as primary hosts was as wide in Canada as in Europe, and Robinson and Chen (1969) obtained subterranean laboratory colonies on barley roots in Canada. The only record from a secondary host plant in the field in North America is from the "basal shoots" of *Alopecurus pratensis* L. (Smith and Richards 1963). This is strange considering the very large numbers that leave primary hosts such as *Crataegus*. Further work on this problem would clearly be desirable.

The first tests on BYDV transmission by *R. insertum* were conducted with aphids from primary host populations on *Crataegus* and *Malus* (Orlob and Arny 1960), of which only oviparae (in autumn) and immature progeny of the fundatrix (in spring) could transmit. Failure of gynoparae, males, and fundatrices to act as BYDV vectors may be explained by their non-acceptance of barley as a host plant. However, in the single test conducted with alate fundatrigeniae (= spring migrants) from *Malus*, these also failed to transmit. In comparative tests with *R. padi* (Smith and Richards 1963), *R. insertum* was less efficient at transmitting all but 1 of 15 isolates, but the fact that most of these isolates had previously passed through *R. padi* needs to be taken into account. In Britain, large numbers of infective gynoparae of *R. insertum* are flying in

the autumn of some years (A'Brook and Dewar 1980), but these are migrating to primary hosts and it seems unlikely that they would spread virus in autumn-sown cereal crops.

*Rhopalosiphum maidis* (Fitch) is apparently permanently parthenogenetic on Gramineae throughout the world. Males occur sporadically in various parts

of the world, but sexual females and overwintering in the egg stage have never been observed. Although readily recognizable by its narrow shape, short siphunculi (Figure 3j) and short terminal process to the antenna (Figure 3e), *R. maidis* is nevertheless a problem for the taxonomist, as there is increasing evidence that the name is being applied

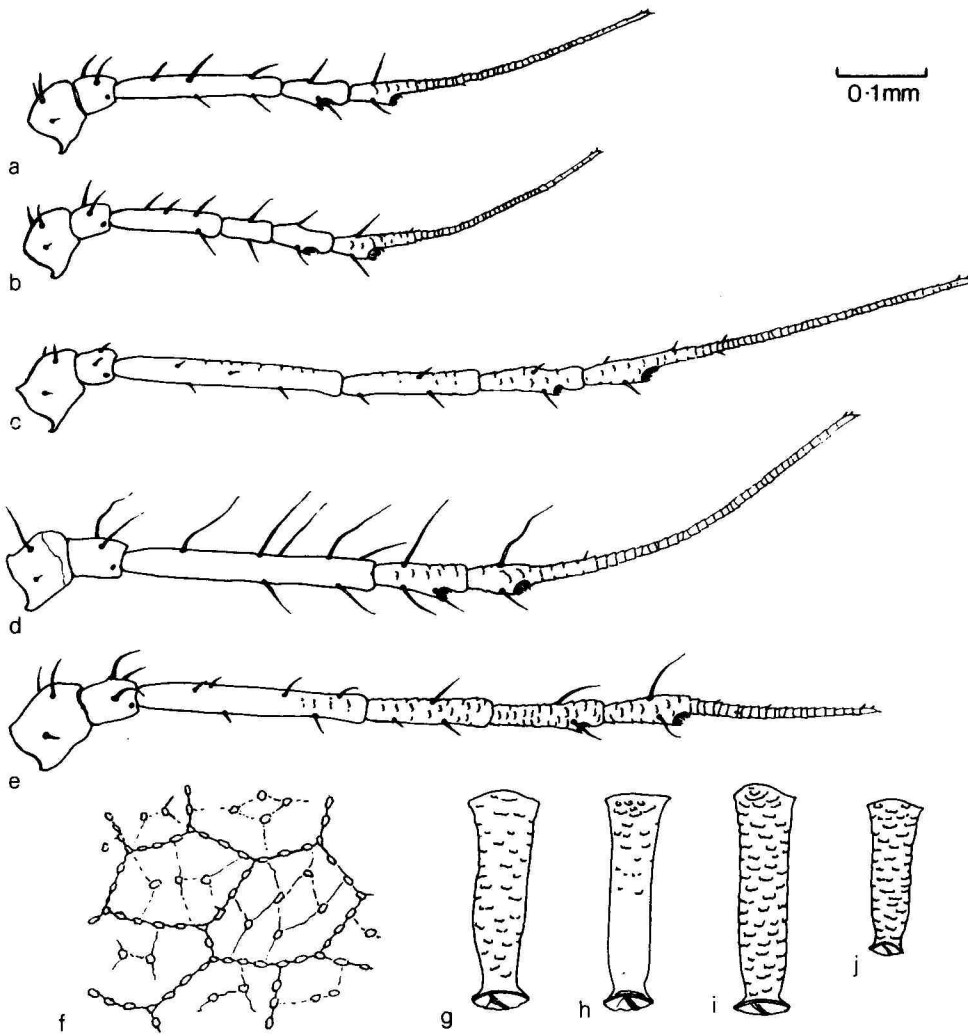


Figure 3. Some morphological characteristics of *Rhopalosiphum* spp. apterae. (a-e) Antennae of apterae of (a) *insertum*, 5-segmented form; (b) *insertum*, 6-segmented form; (c) *padi*; (d) *rufiabdominalis*; (e) *maidis*; (f) Dorsal abdominal sculpturing characteristic of *Rhopalosiphum* spp. (g-j) Left siphunculus of apterae of grass-feeding generations of (g) *insertum*; (h) *padi*; (i) *rufiabdominalis*; (j) *maidis*.

to a number of separate taxonomic entities isolated by their permanent parthenogenesis. But as the number of separate lineages (= clones) that may exist throughout the world is virtually unlimited, how necessary or useful is it to recognize these that occur, for example, in any one year in Kansas, USA?

A partial answer seems to be that, while it is clearly impractical to define the properties of every clone of *R. maidis* from every part of the world, populations can be grouped into certain major

divisions, recognizable particularly according to their karyotype and their association with certain host plants. A form with 10 chromosomes is found predominantly on barley and panicoid grasses in the northern hemisphere. It has a slightly longer terminal process to the antenna (Figure 4), and can be distinguished by multivariate analysis from populations with 8 or 9 chromosomes that occur throughout the world on maize and sorghum (Blackman et al. 1987; Brown and Blackman 1988). As in the case of *Melanaphis sorghi/sacchari* discussed previously, the

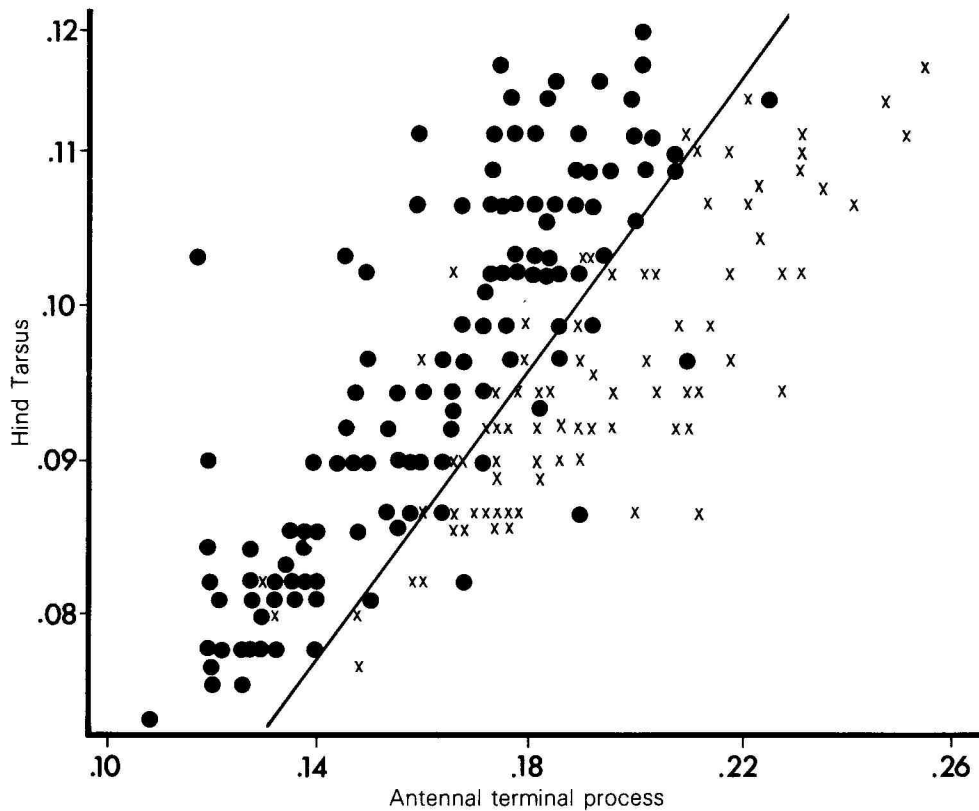


Figure 4. Plot of the measurements (in mm) of the length of the second segment of the hind tarsus against the length of the antennal terminal process for apterae of *Rhopalosiphum maidis* from all parts of the world, showing how those with 10 chromosomes (crosses) tend to have a longer antennal terminal process than those with 8 or 9 chromosomes (circles).

host plant association is not absolute and seems to depend to some extent on which hosts are available. Nevertheless anyone working with *R. maidis* needs to take into account the possibility, and in some cases the probability, that populations on different hosts would be better regarded as separate taxonomic entities. More karyotypic and morphometric studies need to be conducted on a world-wide scale in order to clarify this rather complex situation. At the same time, studies at a more local level can use enzyme electrophoresis to investigate clonal structure of *maidis* populations, and the extent of their migration (see, for example, Steiner et al. 1985).

*Rhopalosiphum padi* (L.) is rather specific in its choice of primary hosts, migrating mainly to *Prunus padus* L. in Europe and to *P. virginiana* L. in North America. Its secondary hosts are numerous species of Gramineae as well as many other monocotyledonous plants, and some dicotyledonous weeds such as *Capsella bursapastoris* (L.) Medic. *Lolium perenne* L. is a particularly favored host. The sexual phase on *Prunus* is dispensed with wherever winter conditions permit.

Numerous studies on the ecology and population dynamics of *R. padi* in recent years have addressed such topics as the timing of sexuales production (Ward et al. 1984); selection of primary hosts by gynoparae (Leather 1986); overwintering survival of eggs on *P. padus* (Hand and Hand 1986); overwintering survival of parthenogenetic generations on grasses and weeds (Dedryver and Gellé 1982), and on cereals (Wikteliu and Ekbon 1985); development of populations on autumn-sown cereals (Pike and Schaffner 1985); development of spring populations on the primary host (Dedryver 1983); fecundity of spring migrants (Wikteliu and Chiverton 1985); and the finding (Ahman et al. 1985) and selection (Leather and Dixon 1982) of secondary host plants. Spring migrants from *Prunus* are reported to have a greater readiness to colonize cereals than alatae from grasses (Leather and Dixon 1982); and if this is generally true it could help to explain why *R. padi* in Europe is most important as a pest of spring-sown cereals. However, the significance of

Leather and Dixon's results is difficult to assess without more information about the origin of the test aphids and the number of clones involved.

Another consideration seems to have been left out of all these studies. When a pest aphid has a variable life cycle, maintaining the "options" from year to year of either sexual reproduction followed by overwintering as eggs, or anholocyclic overwintering by continuous parthenogenesis, it is important to try to determine how the system works genetically, in order to understand how the integrity of the species as a whole is maintained. Is there any gene flow between the clones that overwinter parthenogenetically and those that produce sexual forms in autumn? Without some means of "dipping into the gene pool," anholocyclic populations would consist of isolated lineages that might be expected to show some divergence of genetic structure and properties from those that continue to have an annual sexual phase. In *Myzus persicae* (Sulzer), the production of males in autumn by otherwise anholocyclic clones (androcycly) provides the means for maintaining some gene flow, as well as a possible mechanism for maintaining the alternative methods of overwintering from year to year (Blackman 1974). In *R. padi* and other important cereal pests that frequently overwinter anholocyclically (*Metopolophium dirhodum*, *Schizaphis graminum* (Rondani), *Sitobion avenae*) we still cannot answer this basic question about their population genetics.

Apterae of *R. padi* are distinguishable from those of *R. insertum* and *R. rufiabdominalis* by their short antennal hairs (although, as discussed for *R. insertum*, hair length is very dependent on rearing conditions) and always 6-segmented antennae (Figure 3a-d). Methods of discriminating the various alate morphs from those of *R. insertum* are provided by Stroyan (1984).

*Rhopalosiphum rufiabdominalis* (Sasaki) has a sexual phase on various *Prunus* spp. in Japan, but it is permanently parthenogenetic on roots of rice and many other Gramineae in most parts of

the world, especially warmer regions. It also colonizes the roots of some Solanaceae. In North America it appears to have recently extended its range northward into Canada, where it has been shown to transmit RPV-like, RMV-like and nonspecific isolates of BYDV to cereals (Paliwal 1980). It has been confused in the past with *R. padi*, but is readily distinguished from this species and from *R. insertum* by its much longer antennal and dorsal body hairs. The terminal process of the antenna is also rather noticeably curved (Figure 3d). The ecology of *R. rufiabdominalis* as a pest of rice is reviewed by Yano et al. 1983, but little is known of its biology and importance as a BYDV vector.

### **Schizaphis**

The 40-or-so species of *Schizaphis* have affinities with *Melanaphis* and *Rhopalosiphum*, but the alatae differ by invariably having forewings with once-branched media (always twice-branched in *Melanaphis*, and usually so in *Rhopalosiphum*). In cereal-feeding *Schizaphis*, both cauda and siphunculi are mainly pale in color, and the siphunculi are longer than the cauda and taper from base to apex with only a small apical flange (Figure 1). Like the other two genera, *Schizaphis* undoubtedly have a primitive association with Pyroidea as primary hosts, but most species have lost this association and are monoecious on Gramineae or Cyperaceae.

*Schizaphis graminum* (Rondani) provides a very good example of the limitations of the biotype concept. The available evidence suggests that *S. graminum* is a Palearctic species that has been introduced into North America on (at least) two separate occasions, the first in about 1882 and the second in about 1968. In both cases there were severe economic consequences for cereal growers in the Great Plains area of the USA, probably because strong, adaptable genotypes were being presented with large acreages of susceptible host plants free of natural enemies. There were obvious founder effects; the second introduction ("biotype C") differed morphologically from the first in certain respects, rapidly established itself as a major pest of sorghum, and later acquired insecticidal resistance.

In about 1980, populations of *S. graminum* in the Great Plains area were found to have the ability to colonize varieties of wheat and sorghum that were previously resistant to other known biotypes, and were designated as "biotype E" (Porter et al. 1982). Recently, the host plant responses of samples of *S. graminum* from Oklahoma, Ohio, and Maryland were compared with the three extant Great Plains biotypes (B, C, and E), and found not to conform with any of them, the Ohio culture being regarded as sufficiently distinct to be designated a new biotype, "F" (Kindler and Spomer 1986).

*S. graminum* is regularly holocyclic in the northern USA (Webster and Phillips 1912), overwintering particularly on *Poa pratensis* L. (a host plant of palearctic origin, like the aphid). Further south, biotypes C and E both readily produce sexuales and eggs in the laboratory under appropriate conditions, but completion of egg diapause requires over 3 weeks at temperatures at or below 1.7°C (Puterka and Slosser 1986). In the Great Plains area, with conditions mainly favoring anholocyclic overwintering rather than egg development, large crop monocultures will favor single, well-adapted aphid genotypes and thus promote the observed "biotype phenomenon." A much-needed genetic approach has recently been adopted by Eisenbach and Mittler (1987a, b), who have obtained some evidence that a) males of biotype E prefer to mate with their own oviparae rather than the oviparae of biotype C, and b) the ability of biotype E to colonize sorghum IS 809 may be maternally inherited (although the numbers of clones studied were too small to rule out Mendelian inheritance). These findings indicate other factors that may be contributing to the maintenance of the independent status of the Great Plains biotypes.

Multivariate morphometrics has also recently been used to separate samples identified by their host plant responses as biotypes B, C, and E (Fargo et al. 1986; Inayatullah et al. 1987). However, the method of canonical variates analysis is a very powerful tool that can separate individual genotypes, so there is no guarantee that the morphological characters correlated with host plant



responses in the three samples studied would be the same if samples from other sources were analyzed. What is needed is a more extensive analysis of clones established from numerous sources, including comparison between regions where anholocyclic overwintering predominates and areas with cold winters where a holocycle is the general rule, to see whether clones grouped according to the recognized biotypes. Electrophoretic studies could also contribute information about the number of "meaningful taxonomic units" involved.

Apart from the North American biotype problem, there are a number of close relatives of *S. graminum* that are very similar in morphology but more specific in their host plant relationships. *S. hypersiphonata* Basu has a longer antennal terminal process, longer siphunculi, and longer hairs on the 8th abdominal tergite than *S. graminum* and occurs in the Indian subcontinent, Southeast Asia, and Australia. Although most frequently found on *Digitaria*, it has been collected on cereals in Australia and the Philippines, but it is not recorded as a BYDV vector and is not a damaging pest. Orlob (1961) found an aphid similar to *S. graminum* feeding specifically on *Phleum pratense* L. in New Brunswick, Canada, and this aphid transmitted BYDV with rather low efficiency in laboratory tests. Other close relatives of *S. graminum* currently regarded as subspecies occur respectively on *Agrostis* spp. and *Holcus* spp. in Europe (Stroyan 1984).

### *Sipha*

*Sipha* are small aphids with thick, spine-like hairs and short stump-shaped siphunculi. They live all the year on Gramineae. *Sipha glyceriae* (Kaltenbach), which can be injurious to rice crops, and *S. agropyronensis* (Gillette) have been tested as BYDV vectors and found not to transmit, but the three other species found commonly on cereals have not, to our knowledge, been tested. They are: *S. maydis* Passerini (in Europe and Asia eastward to India and Pakistan, and introduced into South Africa); *S. flava* Forbes (in North and South America); and *S. elegans* del Guercio (= *agropyrella*) (in Europe, Central Asia and introduced into North America). *Sipha* tend to infest cereal crops mainly in warm, dry climates. In central Europe *S. elegans* is more abundant in dry summers and on sparse stands of cereals (Honek 1985).

### *Sitobion*

About 75 species are currently placed in the genus *Sitobion*. About 20 species are associated with Gramineae, and several of these overwinter on Rosaceae (*Rosa* or *Rubus*) or other plants (*Akebia*). The known cereal virus vectors may be recognized by their tapering black siphunculi bearing an apical band of polygonal reticulation. They are generally distinguishable as three species (*S. avenae*, *S. miscanthi* (Takahashi) and *S. fragariae* (Walker)) by the shapes and relative lengths of the cauda and siphunculi (Figure 5). In Europe *S. avenae* and *S. fragariae* are distinct, but *S. miscanthi* in the Far East and

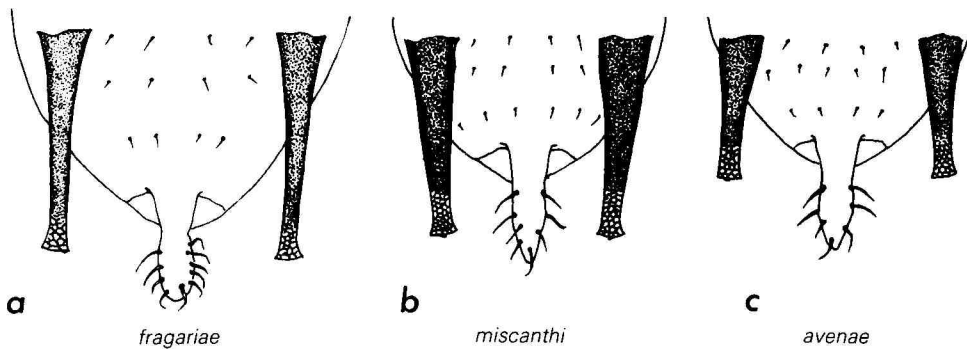


Figure 5. Rear of abdomen in dorsal view of typical apterae of cereal-feeding *Sitobion* spp.



Australia is somewhat intermediate between these two in its morphology (e.g., Figure 6), and has been confused with both of them.

*Sitobion avenae* (F.) occurs on many Gramineae including barley, wheat, and oats as well as some Cyperceae and Juncaceae, and it is occasionally found on the leaves of cultivated *Gladiolus* and

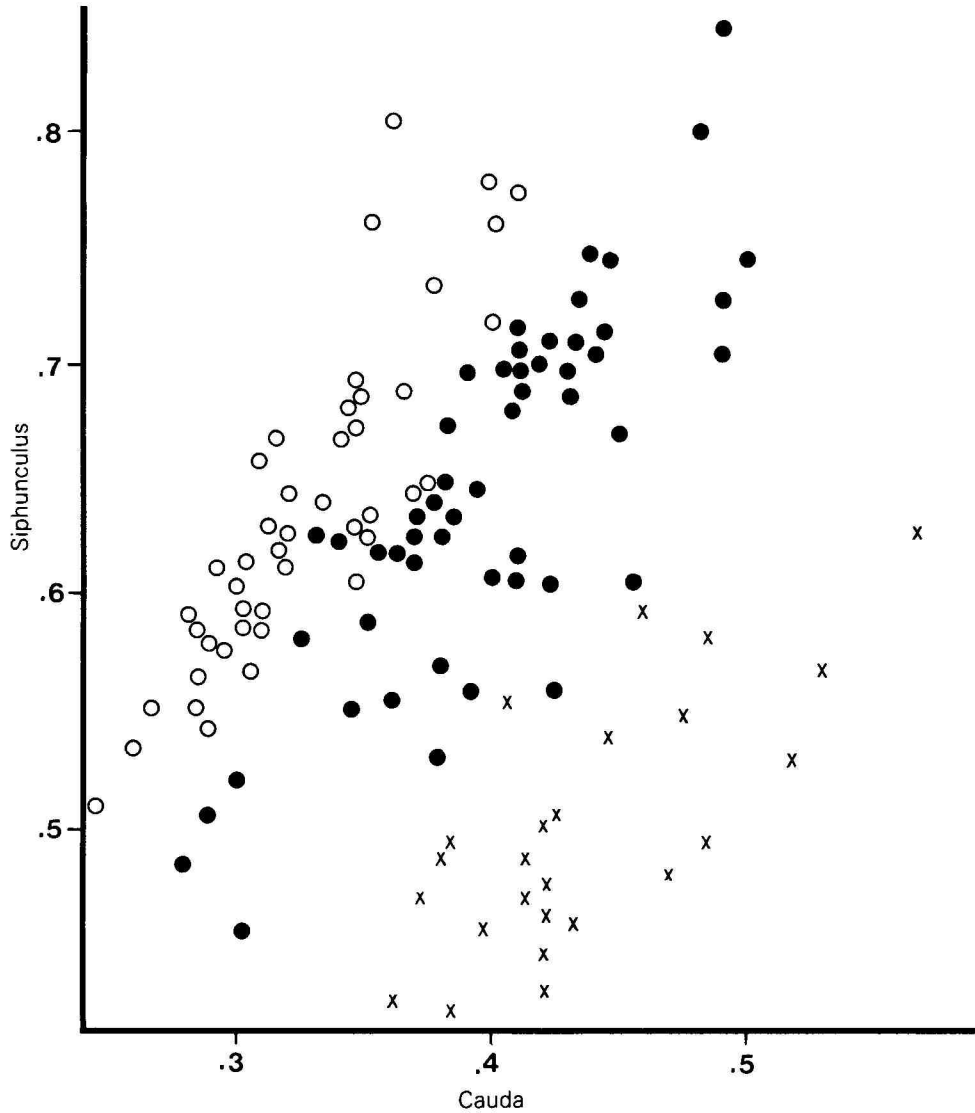


Figure 6. Plot of the measurement (in mm) of length of siphunculus against length of cauda for alatae of *Sitobion* spp. from various parts of the world, showing differences between *fragariae* (open circles), *miscanthi* (black circles) and *avenae* (crosses).

*Iris* (Iridaceae). It is widespread in Europe and the Mediterranean region, and eastward to Iran. It has spread through North and South America and was more recently introduced into Africa south of the Sahara (first records from Kenya 1964, South Africa 1971, and Zimbabwe 1976).

A form with rather paler bases to the siphunculi occurs in the Mediterranean region and eastward to Pakistan, Kashmir, Punjab, and Uttar Pradesh. The taxonomic status of these populations is uncertain, as British *S. avenae* reared at high temperatures retain the dark bases to the siphunculi. Possibly it is a single anholocyclic clone.

Far Eastern and Australasian records of *S. avenae* mostly or entirely apply to other species, principally *S. miscanthi*.

Although sexuales of *S. avenae* occur, many populations overwinter parthenogenetically in temperate climates, even through quite cold winters (Hand and Hand 1986). Weber (1985a) found that populations in a river valley contained anholocyclic clones, destined to overwinter parthenogenetically, whereas genotypes from more exposed areas all produced sexuales. He also found genetic adaptation to food plants. Other recent studies of variation within *S. avenae* were by Walters and Dixon (1982), on ovariole number and behavior, and by Loxdale and Tarr et al. (1985a, b) on enzyme systems.

The enormous literature on *S. avenae* includes recent studies of fecundity (Watt 1984), temperature requirements (Lykouressis 1985), production of sexual morphs (Hand and Wratten 1985), feeding behavior relevant to virus transmission (Scheller and Shukle 1986), and simulation models of the effect of natural enemies (Vorley and Wratten 1985). Population forecasting has received much attention; e.g., Watt et al. (1984), Dewar and Carter (1984), Vorley and Wratten (1985) and Entwistle and Dixon (1986). Watt et al. (1984) discuss the economics of control practice. Every year the Review of Applied Entomology summarizes numerous articles concerning *S. avenae*.

*Sitobion fragariae* (Walker) overwinters in the egg stage on *Rubus* and probably sometimes on *Rosa*, and occurs in the summer on many Gramineae including wheat, barley, and oats. It may also be found on Juncaceae, on the flower stalks of Cyperaceae, and on the leaves of some Liliaceae (e.g., *Fritillaria*). It is widespread in Europe and the Mediterranean region, eastward to Iran. Since at least 1941 it has occurred in the USA west of the Rockies (California, Oregon, Washington), where it overwinters on *Rubus* and is common on *Bromus* in early summer. More recently it was introduced to South Africa (first record 1969), Tasmania (1965), mainland Australia (1972), the Antipodes (1969), and New Zealand (1971).

Some large alatae from Australian populations (and one specimen from New Zealand) bear secondary rhinaria on the 4th antennal segment, a character unknown for *S. fragariae* from anywhere else in the world (108 specimens from 48 samples from 11 countries from 1847 onward were examined). The genotype introduced to Australasia is therefore unusual and there must be some doubt about its identity.

*Sitobion miscanthi* (Takahashi) occurs on many Gramineae including barley, wheat, and oats, and also on some herbaceous dicotyledons, including *Capsella* and *Polygonum hydropiper* L. It occurs in Japan, China, India, Bangladesh, Malaya, Indonesia, Philippines, Australia, New Zealand, Fiji, Hawaii, and Tonga. *S. akebiae* (Shinji), which overwinters in the egg stage on *Akebia* and other plants in Japan (Miyazaki 1971), is closely related to and possibly identical with *S. miscanthi*.

*S. miscanthi* was common in Australia and New Zealand in 1959 and 1960, and all samples received from this area by the British Museum (Natural History) between 1928 and 1964 were *S. miscanthi*. Between 1965 and 1971, however, it seems to have been largely replaced by *S. fragariae*. Since 1965 two of the three samples of *Sitobion* received from Australia and all of the many samples from New Zealand have been *S. fragariae*.

### Possible Virus Sources and their Vectors outside the Crop

Certain aphid species have been recorded as experimental vectors of members of the BYD group of viruses, but are unlikely to be of any importance in the field because their normal hosts are not Gramineae. They include: *Aphis glycines* Matsumura, which feed on *Glycine soya* Max. and other legumes in eastern Asia and some Pacific islands; *Aulacorthum (Neomyzus) circumflexum* Buckton, which colonizes many monocotyledons, particularly Araceae and their relatives, as well as some dicotyledons, but rarely Gramineae; *Cavariella salicicola* Matsumura, which migrates between *Salix* and a few genera of Umbelliferae in the Far East; *Ceruraphis eriophori* (Walker), which migrates between *Viburnum* and mainly Cyperaceae in Europe and North America; *Myzus persicae* (Sulzer), very polyphagous and sometimes found on grasses such as *Lolium perenne*, but unlikely to remain on cereals long enough to be an effective vector; and *Tuberocephalus momonis* (Matsumura), which migrates between *Prunus* and an unknown host in the Far East.

*Rhopalomyzus poae* (Gill) is a Gramineae-feeder and a recorded vector of BYDV (Orlob et al. 1961), but unlikely to be of any significance in crop habitats. It is a small, shiny brown-black aphid living on the basal parts of grasses close to soil level and often on etiolated stems under stones.

Perhaps more worthy of consideration are the numerous Gramineae-feeding aphids that have not been tested for BYDV transmission. About 250 species in more than 50 genera feed on Gramineae. Two of the main groups of genera, in the subfamilies Hormaphidinae (*Astegopteryx*, *Ceratovacuna*, *Pseudoregma*, etc.) and Drepanosiphinae (*Takecallis*, *Phyllaphidoides*, etc.) only occur on bamboos. The role of bamboos as reservoirs of BYDV in areas where they are used as windbreaks for horticultural crops has not been investigated. Such bamboo windbreaks are often also colonized by *Rhopalosiphum padi* and *R. maidis* living under the old leaf bases.

Members of the small family Israelaphidinae feed entirely on Gramineae. There are three species known only from the Mediterranean region and their alatae seem to be rare, so they are unlikely to be significant as virus vectors. In addition there are about 16 other small genera of Aphidinae, each with a few species living on Gramineae. Some of these aphids live on the leaves or flower stems but others feed inconspicuously on the leaf bases in turf. Any of these are potential introducers of BYD-type viruses from permanent pastures and wild grasses to cereals.

### Concluding Remarks

Traditional taxonomic methods erect a classification framework and provide check-lists of species based on perceived morphological differences. However, some groups of organisms are studied more intensively on account of their economic or medical importance, and in these groups it is almost invariably the case that taxonomic relationships at the species level need further revision, because the conventionally recognized species are not in reality the lowest "meaningful taxonomic units."

The well-developed polymorphism of aphids has meant that experimental methods, especially rearing and host plant transfers, have for many years played a major part in addition to morphology for species recognition. Nevertheless, most of the more important crop pests aphids are highly adaptable, relatively polyphagous and widely distributed, and therefore subject to diverse selection pressures. Genotypes best fitted to the time and place will always tend to be favored, and in warm climates permanent parthenogenesis may cause populations to consist of one or a few selected genotypes (the "biotype phenomenon").

It is axiomatic in biology that the taxonomic status of a particular clone or population needs to be defined as rigorously as possible. We have tried to show in this paper how we believe that the necessary rigor is lacking in the case of most cereal aphids. More work needs to be done. In particular, more knowledge is required of the genetic structure of cereal aphid populations, the

nature and consequences of life cycle variation, and the extent of specialization to particular host plants. Experimental studies in which comparisons are made between clonal laboratory populations, multivariate morphometrics, electrophoresis, DNA comparisons, and karyological studies all have a part to play in acquiring the necessary information.

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