Aphids, Plants and Other Organisms

V. F. Eastop

ABSTRACT The relationships between aphids, plants, other organisms and some physical components of the environment are reviewed. Aspects considered include year cycles, polymorphism, fecundity, relationship of different groups of aphids with particular groups of plants, honeydew, alarm pheromones, aposematic colouring, camouflage, colour variation within species, morphological variation within species, multivariate analysis and problems of its interpretation, parasitism, stridulating mechanisms, predators, coevolution of plants and aphids, plant galls, trapping aphids and the interpretation of trap catches, and curation of aphid collections References are given to sources of information about aphids, with special reference to the Korean fauna.

KEY WORDS Aphids, plants, environment

Aphids (Superfamily Aphidoidea) feed on plant sap by tapping the phloem with their mouthparts, which as in other Hemiptera are modified into twin tubes. Saliva goes down the narrower tube and sap comes up the wider. When they do this they damage the plant, at least by the removal of sap, but the saliva may also be toxic, and they may transmit virus diseases. Feeding on sap entails consuming more water and sugar than is required, and when it is excreted (honeydew) it may fall on the leaves and act as a substrate for fungi which may interfere with photosynthesis.

Aphids may have many generations a year, commonly 15~20 and up to 40 in the tropics. All but one of these generations consist of parthenogenetic females. Males and the sexually reproducing females that produce the overwintering eggs occur at most once a year. In a few groups the sexual generations do not have mouthparts, although they moult several times, presumably living on the reserves provided by their sap-feeding mothers.

In most species of aphids the adult parthenogenetic females may be either apterous or winged. Commonly there are several wingless generations and when the plant becomes overcrowded, a winged generation is produced. In some species the production of apterae and alatae seems to be under more direct genetical control, with the first generation

being apterous and the second alate, or the first two generations apterous and the third is winged.

Two groups, Adelgidae and Phylloxeridae, are oviparous in all generations, but in true aphids (Aphididae) only the sexually reproducing females are oviparous, the parthenogenetic generations being viviparous. In most Aphididae the oviparae are apterous, but in a few subfamilies alate oviparae are produced.

In *Phloeomyzus* only the sexuales are alate, all the parthenogenetic generations being apterous. The individual developing from the overwintering egg is known as a fundatrix and in most subfamilies is apterous, but is alate in some Drepanosiphinae. Males may be either alate or apterous, sometimes even in the same species.

Aphid life cycles are geared to benefit from flushes of plant growth and the generations are compressed. An adult parthenogenetic female has embryos which have embryos developing within them. Immature aphids thus contain large embryos and can start reproducing almost as soon as they are adult. At medium temperatures most of the aphid pest species take about 10 days from birth to maturity and then produce from 60-120 young at a rate of from 3 to 10 a day for 15 to 30 days, depending on species, the nutritative status of the food plant and other environmental conditions such as tempe-

Entomology Department, Natural History Museum, Cromwell Road, London, SW7 5BD, UK

rature.

More than 4,400 species of aphids are known
and all are polymorphic. The great majority have
at least five distinct forms, a fundatrix, usually with
short appendages, apterous and alate parthenogene-
tic viviparae (parthenogenetic oviparae in Adelgidae
and Phylloxeridae) and sexually reproducing ovipa-
rae and males Nearly half the known aphids live
for at least part of their life on trees. Each major
group has its own characteristic biology, and these
are summarised in table 1, together with a summary
of the biologies of the major groups of the related
superfamilies Coccoidea and Psylloidea. Host plant
alternation has apparently evolved separately on a
number of occasions as it is achieved by different
methods in different groups. In the Aphidinae host
alternating species have alate males which fly back
from the secondary to the primary host to mate
with apterous oviparae, which are the progeny of
alate gynoparae produced a generation earlier on
the secondary host. In host-alternating aphids be-
longing to other subfamilies both males and females-
are apterous and are produced on the primary host
by alate sexuparae which have flown from the se-
condary host.

Phytophagous insects are not distributed evenly
over their plant hosts (Table 1). Some families of
plants have many aphids and coccids feeding on
them but few psyllids and aleyrodids. Table 2 gives
the most favoured host plant families of aphids, psy-
llids, aleyrodids and diaspid coccids. There are pro-
bably a variety of reasons for these different host-
plant preferences. History probably plays a large
role, the similarity between aphids and coccids on
one hand and psyllids and aleyrodids on the other
probably results both from their phylogenetic rela-
tionships and the development of aphids and coc-
cids in the old northern continents and psyllids and
aleyrodids in the South Thus coccids and aphids
are more abundant on Coniferae, Fagaceae and Ro-
saceae while psyllids and aleyrodids are more fre-
quent on Leguminosae and Myrtaceae. Host alter-
nation never developed in the southern hemisphere
aphids. An economically important consequence of
the absence of host alternation is that aphids coloni-
sing a member of the Leguminosae are likely to

have flown from other legumes and are thus more
likely to transmit a virus to their new host than
aphids colonising Rosaceae which are more likely
to have flown from a member of a different plant
family. The known alternate host plants of aphids
were tabulated in Harris & Maramorosch (1977).

Aphid species not only have a number of mor-
phologically different forms, but the appearance of
an individual can be greatly affected by the condi-
tions under which it develops, such as temperature
or the nutritive status of the host plant (Blackman
& Spence 1994). Intermediates between morphs
can also be produced under critical conditions. Alati-
form apterae with at least some of the sense organs
characteristic of alatae, such as ocell and sclerotised
thorax may occur, as may alatae with poorly develo-
ped wing muscles and lacking some of the sense
organs characteristic of alatae. This variation within
morphs and intermediates between morphs has
been responsible for much taxonomic confusion.
The variation not only leads to the erroneous desc-
ription as distinct species of individuals of the same
species, but also the extensive variation obscures the
distinction between real but closely related biologica-
lly distinct species.

Another taxonomic difficulty exacerbated by the
existence of parthenogenetic generations is caused
by founder effects A single female introduced to
another continent can give rise to a large population
of aphids of identical genotype (apart from muta-
tion) until or unless sexual reproduction occurs. The
introduced population will have only part of the ge-
nome of the parent population. Many species have
been described from single, probably clonal samples,
and taxonomists have looked in detail at comparati-
vely few specimens of most species. It takes time
to make good preparations and to observe and re-
cord the data from each specimen. At 12 minutes
a specimen, five hours per day at the microscope
and 220 working days per year, there is a limit of
5,500 specimens per year. Thus studying say, 55
specimens of each species gives a limit of 100 spe-
cies per year, and this assumes that the specimens
are already well prepared in a well curated collec-
tion. Of course in practice less than 55 specimens
of the rarer species are known, but enquiring for

Table 1. Host plant preferences of the major groups of Sternorrhyncha
(Number of described species of insects in parentheses)

PSYLLOIDEA.
Psyllidae
 Aphalarinae (310) – trees, shrubs particularly Moraceae and herbs
 Liviinae (25) – Cyperaceae and Juncaceae
 Spondyliaspinae (200) – Leguminosae and Myrtaceae
 Homotominae (27) – Ulmaceae and Moraceae
 Psyllinae
    Arytainini (205) – Leguminosae, sensu latiore
       Arytainina (175) – Papilionaceae
       Ciriacremina (30) – Caesalpiniaceae
    Psyllini (275) – deciduous trees
    Diaphorinini (58) – Anacardiaceae and mostly 'higher' dicotyledons, e g. Apocynaceae, Oleaceae,
                        Solanaaceae and Compositae
    Calophyinae (33) – Anacardiaceae and Burseraceae
    Phacopterinae (24) – mostly sapindales
Triozidae
    Carsiddarinae (37) – mostly Sterculiaceae and Bombacaceae
    Triozinae (500) – many and various, including some herbs
ALEYRODOIDEA:
 Aleyrodidae (1127) – mostly on woody Angiiosperms
APHIDOIDEA:
 Adelgidae (49) – alternation from galls on Picea to other Pinaceae, holarctic
    Pineini (21) – *Picea* to *pinus*
    Adelgini (28) – *Picea* to *Larix, Pseudotsuga*, etc
 Phylloxeridae (8/75 : 7/64) – Dicotyledons, holarctic
    Phylloxerinini (7) – Salicaceae
    Phylloxerini (68) – mostly Juglandaceae and Fagaceae, a few spp on Ulmaceae, Rosaceae and Vitaceae
Aphididae
 Pemphiginae (319) – dwarf arostrate sexuales, oviparae produce only one egg
    Eriosomatini (96) – galls or pseudogalls on Ulmaceae to various angiosperms, often on roots, with ants;
                        holarctic
 Pemphigini (168) – holarctic
    Pemphigina (78) – galls on *Populus* to roots of various herbs, more rarely trees or aerial parts of herbs
    Prociphilina (90) – pseudogalls on various dicot trees to roots of Coniferae, more rarely other plants
 Fordini (55) – alternation from galls on Anacardiaceae
    Fordina (41) – *Pistacia*, mostly to grass roots with ants, mostly Mediterranean and East Asia,
                   1 American genus
    Melaphidina (14) – *Rhus*, mostly to mosses, mostly oriental, 1 American genus
 Hormaphidinae (183) – host alternating, with small rostrte sexuales
    Cerataphidini (91) – galls on *Styrax* to Gramineae (esp. Bambuseae), Palmaceae, Zingiberaceae, where often
                         with ants; oriental
    Hormaphidini (11) – galls on Hamamelis to *Betula*, holarctic
    Nipponaphidini (81) – galls on *Distylium* to Lauraceae, Fagaceae, etc., where often with ants; oriental
 Phloeomyzinae (1 ?+) – *Populus*, alate sexuales; all viviparae apterous; holarctic
 Thelaxinae (12) – Betulaceae. Fagaceae, Juglandaceae, often with ants. small apterous sexuales; holarctic
 Anoeciinae (34)
    Aiceonini (14) – Lauraceae; alate males; Asia
    Anoeciini (20) – alternation, *Cornus* to roots of Gramineae, sexuparae producing small apterous males
 Mindarinae (5) – Pinaceae; *Picea* and *Abies*, few generations per year, holarctic

Continued

Drepanosiphinae (530) – free-living on leaves, mostly on trees, fundatrices often alate, oviparae apterous, many without ants

Drepanosiphini (45) – Aceraceae; all viviparae alate; holarctic

Phyllaphidini (410) – many on Fagaceae and Betulaceae, some on Lauraceae, Annonaceae, Magnoliaceae, Ulmaceae, Juglandaceae, Combretaceae, Burseraceae, Rosaceae, Leguminosae, bamboo, often all viviparae alate

Saltusaphidini (75) – Cyperaceae and Juncaceae; apterous viviparae common; holarctic

Chaitophorinae (159) – free-living on leaves and shoots, apterous viviparae common, often with ants

Chaitophorini (138) – holarctic

Chaitophorina (91) – Salicaceae

Periphyllina (47) – Aceraceae

Siphini (21) – Gramineae; holarctic

Greenideinae (154) – dicot trees, esp. Fagaceae, mostly East Asia

Greenideini (132) – oviparae often alate

Cervaphidini (22) – mostly southern hemisphere: 4 genera in Australia, 1 in South America

Aphidinae (2517) – fundatrices and oviparae large, males apterous or alate; worldwide but mostly holarctic

Pterocommatini (49) – Salicaceae, without host alternation; holarctic

Aphidini (665) – alternation in many genera but many species are monoecious; often with ants

Aphidina (585) – mostly Rosidae and Asteridae

Rhopalosiphina (80) – alternation, Rosaceae to Gramineae and Cyperaceae

Macrosiphini (1803) – alternation in many genera but many species are monoecious on herbs, often without ants

Lachninae (361) – fundatrices and oviparae large, males alate or apterous (sometimes small), often with ants

Lachnini (57) – mostly Fagaceae and Rosaceae; holarctic, esp. central and eastern palaearctic

Cinarini (269) – Coniferae; holarctic, most numerous in nearctic

Tramini (35) – roots, mostly Compositae; palaearctic, esp. central and eastern

COCCOIDEA·

Margarodidae (250) – many on Coniferae and Fagaceae, some on Aceraceae, Leguminosae and Gramineae

Ortheziidae (90) – mostly American species living on 'recent' plants such as Compositae and Gramineae

Eriococcidae (450) – many hosts, particularly Myrtaceae and Gramineae

Dactylopiidae (9) – cochineal insects and close relatives on *Opuntia* in Central America

Kermesidae (70) – twigs and bark of Fagaceae

Pseudococcidae (1947) – many angiosperms including roots and under the leaf sheaths of Gramineae

Aclerdidae (53) – mostly on Gramineae, possibly common ancestry with African Combretum-feeders

Asterolecaniidae (200) – in the temperate region most live on Fagaceae, while many of the tropical species are on bamboo

Lecanodiaspididae (71) – on trees belonging to many families, but particularly Moraceae and Leguminosae

Coccidae (1100) – many on deciduous trees in the north temperate region

Stictococcidae (18) – on African trees of many families including Annonaceae, Sapindaceae, Leguminosae, Malvaceae, Myrtaceae and Sterculiaceae

Kerridae (Lacciferidae) (65) – living within the lac they secrete and found on plants belonging to many families

Beesoniidae (3) – one forming galls on *Dipterocarpus* and the other on *Quercus*

Conchaspididae (18) – many plants but particularly palms and orchids

Diaspididae (1800) – on many woody plants including Coniferae, Gnetales, Fagaceae, Lauraceae, Leguminosae, Myrtaceae and Gramineae

Halimococcidae (20) – on Palmae and Pandanaceae

Phoenicococcidae (1) – date palms

Table 2. Most favoured hosts of aphids, psyllids, aleyrodids, and diaspid scales

Aphids		Psyllids		Aleyrodids		Diaspid scales	
Compositae	605	Myrtaceae	212	Leguminosae	58	Leguminosae	74
Coniferae	363	Leguminosae	125	Myrtaceae	43	Myrtaceae	46
Rosaceae	293	Compositae	84	Lauraceae	42	Coniferae	45
Gramineae	242	Saliceae	71	Moraceae	42	Fagaceae	37
Saliceae	216	Anacardiaceae	32	Gramineae	38	Euphorbiaceae	32
Fagaceae	211	Moraceae	29	Euphorbiaceae	25	Lauraceae	22

further specimens takes time. Also it is not only the number of specimens but even more the number of samples of each species that is important. Practical taxonomy is a compromise between examining enough specimens to appreciate the morphological variation, and the time it would take to acquire, examine and analyse the data. Detailed studies of major pests often reveal previously undetected related species.

The holocentric chromosomes of Hemiptera may allow the broken parts of chromosomes to divide normally at mitosis. Thus karyological variations that would be eliminated from species in which the chromosomes have centromeres, may survive in Hemiptera, and possibly lead to fixed differences between species.

Some characters that are very variable in some species may be almost constant in another, and vice versa. *Sitobion avenae* is a major pest of cereals in many parts of the world and *Myzus persicae* is well known as a virus vector in many crops. The ultimate rostral segment of *S. avenae* has almost constantly six accessory setae on the ultimate rostral segment and this is the normal condition in most other members of the genus. The subgenital plate of *S. avenae* however has a very variable chaetotaxy. The progeny of one parthenogenetic female may have from 2 to 7 hairs on the anterior half of the plate. In *M. persicae* the ultimate rostral segment may have 2~7 accessory hairs in the progeny of one parthenogenetic female but the subgenital plate has almost constantly only 2 hairs. In both cases the variation within the progeny of one parthenogenetic female is the same as the variation known from each species world wide. The existence of species complexes of very similar species and the

large amount of variation within these species has led to the use of multivariate analysis for taxonomic purposes The method of canonical variates is a very powerful tool for discriminating populations, but like other powerful tools should be used with care. The progeny of the same parthenogenetic population reared at different temperatures may be well discriminated, often on the second canonical variate (Blackman & Paterson 1986)

Plants may defend themselves from pests by physical or chemical defences and by seasonal times of appearance or rates of growth. The population of pests that can colonise plants may also be limited by environmental factors such as temperature and precipitation and by other organisms, predators, parasites and fungal and bacterial diseases. The ants collecting honeydew from aphid colonies may protect the colonies from predators. Some aphids can dab fast drying siphuncular wax on to the mouthparts of predators, and can escape as the predator cleans them. This siphuncular wax was probably originally just a convenient substrate for a volatile alarm pheromone which evaporated from the wax on exposure to air Some aphid colonies move synchronously when disturbed and in *Toxoptera aurantii* this rhythmic movement produces a sound audible to humans. Other aphids are greatly flattened and may not be detected by predators which walk over them Some apterous aphids bear long spines or projections resembling the hairs of their host plants. This seems likely to be a tactile camouflage against predators hunting by touch which are looking for a spherical object

Plants also protect themselves from pests by a variety of chemical and physical defences. The hairs mimicked by the aphids may originally have been

a defence against other phytophagous insects. There is evidence that some hairy varieties of cultivated plants suffer less from some pests than glabrous varietes. Aphids feeding on plants protected by dense long sticky hairs may have an elongate ultimate rostral segment and short tarsi, while aphids feeding on smooth leaved plants tend to have a short ultimate rostral segment and long and sometimes very hairy tarsi.

Several groups of aphids distort plants in various ways. Characteristic galls are formed on a number of plant families, particularly *Picea* (Coniferae), *Ulmus* and *Zelkova* (Ulmacae). *Carya* (Juglandaceae), *Hamamelis* and *Distylium* (Hamamelidaceae), *Populus* (Saliceae), *Pistacia* and *Rhus* (Anacardiaceae) and *Styrax* (Styracaceae). As gall formation involves the reaction of the plant to the saliva and the feeding pattern of the aphids, and as related species of aphids form similar galls on related species of plants in different continents, gall formation is regarded as evidence of an evolutionarily old association.

The ability of an aphid to overcome a plant defence has considerable evolutionary potential. For instance the European lettuce aphid, *Nasonovia ribinigri* lives during the summer in flower heads of wild lettuce and other Compositae protected by sticky hairs. This aphid also colonises introduced plants protected by sticky hairs such as *Nicotiana. Petunia* (Solanaceae) and *Martynia* (Martyniaceae). The Solanaceae may have come to rely on physical defences against sucking insects and secondary plant substances of low water solubility against chewing pests. The explosive radiation of *Solanum* on the relatively aphid-free Andes allowed most species to survive without sticky hairs. This may have made them susceptible to virus diseases, perhaps originating from Leguminosae and transmitted by insects not living on Solanaceae. At all events most of the major virus diseases of potato are now transmitted by aphids which had not encountered potatoes until a few hundred years ago.

Plant defences and the strategies adopted by aphids to overcome or avoid them raises the question of co-evolution. Can any antagonistic relationship really be called co-evolution? It is reasonable to think that sticky hairs developed through time

to protect the plants, and that the aphids' tarsi got shorter and the aphids learned to walk more carefully as a result. But the hairs may originally have protected the plant against a different enemy, and the aphids may have modified their behaviour on a quite different sticky plant. Also of course there is little evidence that such relationships have much long term effect on the course of evolution, compared for instance with pollination. The problem is that the effects of past antagonistic relationships are likely to be difficult to detect or interpret, whereas mutually beneficial relationships such as pollination can give clearly linked modifications such as, tongue length and corolla tube length.

The abundance of aphids makes them the food of many other animals, birds, spiders, mites and many groups of insects. Some genera of Coleoptera, Diptera and Neuroptera have specialised in feeding on aphids. Coccinellidae, Syrphidae and Chrysopidae consume large quantities of aphids, but being large and somewhat specialised, the females may only lay their eggs in the presence of enough aphids for their larvae to develop to maturity. Some of the smaller predators (Cecidomyidae, Chamaemyidae and scymnine Coccinelidae) and less specialised predators such as Staphylinidae and Carabidae which are active early in the year, may be of greater agricultural importance. These insects can be effective when aphid populations are low and we need to know, what keeps aphid populations low and prevents pest outbreaks rather than what eats large number of aphids after an outbreak.

The economic importance of aphids has led to a study of their movement. Virologists are interested in their landing behaviour Growers generally are interested in the sources of the winged aphids that colonise crops and there is also an academic interest in this aspect of population dynamics. Aphids are easy to trap, but it can be difficult to interpret the results. A trap catch is the product of a number of variables including the absolute number (density) of the insects, the activity of the insects, the way in which the trap samples the population (attraction, disorientation etc) and the way in which the changing environment affects the sampling ability of the trap. The nature of the problem to be solved deter-

mines the appropriate trap There are also practical questions of cost, whether it is best to have a lot of simple traps or a few that are more sophisticated, the availablity of power (really a matter of cost), etc. It must always be remembered that the aim is to get the smallest statistically reliable sample Sorting trap catches is time consuming and thus expensive, usually much more expensive than the traps themselves.

Virologists are likely to be interested in the aphids landing on plants and the number of aphids passing a one mile front per hour For this purpose traps coloured like plants, or plants themselves give an estimate for the first and nets can be used for the second Ecologists needing aerial density must sample known volumes of air at different altitudes. Nets can work at high wind speeds but may loose their catch in a lull. Suction traps are the preferred choice.

The choice of sites for traps is also dependent on the reason for trapping Traps to investigate landing need to be at crop level With a rapidly growing crop this causes problems. Should the trap be moved as the plant grows? If not it either starts far above the crop or will be shaded by the crop later. In either case another variable is introduced Many ecologists accept that a trap on a tower 40 feet above the ground gives a measure of the flying population that is not overtly influenced by purely local conditions. There is a large literature on trapping techniques and the use of coloured traps. This has led in turn to the use of repellants to deter aphids from landing, aluminium foil for high value crops, rice husks have been used in other cases.

The identification of trap catches or any identification service involves the maintenance of a reference collection. Aphids are usually cleared and mounted on slides. Canada balsam is of proved (ca. 150 years) permanance Collections can be kept in systematic order, or in alphabetical order of either genera and species or of species. For the regular user a systematic order is of most use as similar looking aphids are likely to be near each other in the same drawer or box For the occasional user an alphabetical order will make it quicker to find a particular species, but may involve visits to many different dra-

wers to name an unknown species In general it is best to keep the easily recognised major groups in systematic order and to divide large genera into subgenera, kept in alphabetical order with species within the subgenera also in alphabetical order This compromise keeps similar genera and species together and also facilitates finding a particular species. A collection purely for reference can be kept on flat trays or in slotted slide boxes, but a research collection needs to be readily expandable and a 'file-card' system with the slides on edge with incorporated labelled name cards makes for speedy curation and incorporation of any biological data of interest at the time (Eastop 1985).

There are still many remaining taxonomic problems concerning aphids There is a general agreement about the major groups, but not always about their status or their precise relationships to one another. The generic classification is generally satisfactory although there are problems in a number of areas. The great problems are at species level Partly it is a matter of discovering the alternate hosts of host alternating species. Obviously a satisfactory generic classification is unlikely until this is done. Many species are described from a single sample of a few specimens and there is little idea of the amount of variation within the species. More samples of many species should be studied and also successive samples from the same population are needed to study seasonal variation

If seventy years of pest control has reduced the number of all insects except for the pests, two hundred and fifty years of taxonomy has revealed a previously undreamed of number of unsolved taxonomic problems !

Sources of Information Concerning Apids

References to regionally classified, faunal works, general biology, morphology, anatomy and physiology, genetics and development, migration and dispersal, relationship with other insects, host plant relationships and bibliographies were gives on pages 379-384 of 'Aphids on the World's Crops' by Blackman, R.L. & Eastop, V F. 1984 (reprinted 1985, 1989). Subsequent publications and others of particular relevance to the Korean aphid fauna include

roptera, 'Nauka', Leningrad (aphids pp 546-686)

ACKNOWLEDGMENTS

General Biology

Minks, A.K. & Harewijn, P.(Eds) 1987-9. Aphids, their Biology, Natural Enemies and Control. World Crop Pests, A 450pp (1987), 2B 364pp (1988), 2C 444pp (1994).

Blackman, R.L. & Paterson, A.J.C. 1986 Separation of *Myzus* (*Nectarosiphm*) *antirrhinii* (Macchiati) from *Myzus* (*N.*) persicae (Sutzer). Systematic Entomology 11: 267-276

Blackman, R.L. & Spence, J M 1994. The effects of temperature on aphid morphology, using a multivariate approach. *Eur. J. Entomol.* 91: 7-22

Dixon, AFG. 1985. Aphid Ecology, Blackie, Glasgow, 157pp.

Moran, N.A. 1989. A 48-million-year-old aphidhost plant association and complex life cycle: biogeographic evidence. science 245: 173-175.

Virus transmission:

Harris, K.F. & Maramorosch, K 1977. Aphids as Virus Vectors. Academic Press, New York, 559pp.

Identification and Taxonomy

Paik, W H. 1972. Aphidoidea Illustrated Encylopedia of Fauna and Flora of Korea. Volume 13, Insecta 5: 751pp. remains the standard reference work on the Korean Fauna. The following recent publications may also assist identification:

Akimoto, S. 1983 Eriosomatini. *Insecta Matsum.* 27: 37-106, 31: 1-79, 97-98

Blackman, R.L. & Eastop, V F. 1994. Aphids on the World's Trees. CAB International, Wallingford. 986pp+16 plates (ISBN 0851988776).

Chin, H.T. & Tao, C.C. 1989 Pictorial guide to Common Aphids of Taiwan. Taohsiane Wenhua Shihyeh Ltd, 117pp (ISBN 4-88137-017-0)

Eastop, V.F. 1985 The acquisition and processing of taxonomic data. *Proc. Symp. Evolution and Biosystematics of Aphids, Jablonna,* pp.245-270

Moritsu, M. 1983. Aphids of Japan in Colours. Zenkoku Nosan, Tokyo, 545pp

Pashchenko, N F. 1988. 'Aphidinea-aphids' in Ler, P.A. (ed) Keys to the Identification of Insects of the Soviet Far East, vol 2. Hemiptera and Hete-