

Aphid mysteries not yet solved /Hemiptera: Aphidomorpha/

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Abstract

After having studied aphids during half a century I have met riddles difficult to solve and questions difficult to answer. These questions are concerning the following fields: The choice of host plants, host alternation, variation in sizes of populations, morphology, geographical distribution, paleontology and evolution. It is asked if the composition of the aphid fauna is changing in these years, at least in northern Europe.

Introduction

When a person like me has been studying aphids in more than 50 years, it is nearly impossible not to ask some questions, which seem impossible or nearly impossible to answer. Maybe some other persons can try to answer some of these questions in the future. Now I unfortunately am so old, that I probably cannot do it myself.

Questions concerning the choice of host plants

The first question must be: How are alate aphids able to land on exactly that plant, on which they can feed and reproduce? In many cases it is only one single plant genus or even species. Why are so many aphids monophagous?

This specialisation is found in 82% of all aphid species known from Denmark. The particular plant species may even be rather rare and grow in a place far away from the place where the alate aphid started its flight. Perhaps they use their vision, perhaps their sense of smell, or perhaps they only can use their sense of taste. Vision may be involved, at least in some species, which react on borders between two kinds of vegetation, e.g. borders between different agricultural crops or between low vegetation and forests. If aphids of the same species are present on the plant where the arrival takes place, then the sense of smell is likely. Then they smell aphids of their own kind. This seems at least to be the case for sexuparae of *Anoecia corni*, which in autumn leave grass roots to migrate to *Cornus*, because one can observe a few leaves with several specimens, often 5-7 or even more, while the majority of leaves carry no aphids. The sense of smell must at least in this case be important and probably also in other cases. Alate females have namely more rhinaria (olfactorial organs) on their antennae than apterous females, and alate males have even more, corresponding to the fact that the oviparous females have scent plaques on their hind tibiae. If taste is the only involved sense, then alate aphids have to land on several plants before arriving to the right one, and that will only be possible in few cases.

Some questions naturally concern the choice of host plant. As alate aphids often accidentally land on non-hosts, one may wonder why aphids do not acquire new host plants, but stick to the old one, and why some very common plants never have been conquered as new hosts by any aphid species. Common plants as *Syringa*, *Platanus* and *Ampeloxis* (wild vine) never have aphids.

Even much more common plants are rarely attacked by aphids, though some aphids use them as hosts. One example is *Taraxacum*, which can be attacked by at least three species, but two of them, *Uroleucon taraxaci* and *Aulacorthum palustre*, curiously enough must be described as extremely rare. Another example is the common nettle *Urtica dioica*, whose two aphid species rather rarely are found.

Most aphids have – as mentioned above – only one genus or even one species of plant as host. This must mean, that each aphid species has developed a very specific preference, that means taste to a specific kind of sap. The advance could well be that competition between aphid species could be avoided or narrowed. It is of course natural to mean that the sap of many plants contain substances, which are not acceptable to parasites, but even the poisonous *Delphinium* and *Aconitum* are rather often attacked by *Delphiniobium junackianum*, and the insect-eating *Drosera* can serve as a host for some aphids. Consequently an explanation for specific taste for a single plant is the fact that many plants develop measures to deter parasites, and that an aphid only feeds on a plant, whose deterring measures it has become immune against.

Competition is difficult to imagine as most plants in the nature are without the aphids that are able to live on them, and we have many examples that several species attack the same host, apparently not narrowing each other in any way, and they all can form large colonies at the same time without bothering each other. Even on plants attacked by aphids most leaves are free of aphids.

Only on some cultivated plants in monocultures like sugar beets, cereals and potatoes enormous numbers of aphids can occur so that no space for additional numbers seems present, and furthermore the plants become sick or perhaps even die if not aphid enemies as ladybirds, parasitic wasps, syrphid larvae or fungi kill the aphids before that. Also as a consequence of overcrowding winged specimens normally evolve, so that spreading to new plants can take place before the colonies become too big. This probably happens as a result of touching neighbours.

Anyway it is a considerable riddle why the taste should be so specific. It must be a disadvantage to be particular concerning choice of host, because the chance for landing on the right plant must be extremely small.

However, not all aphids have special tastes. Some of them are polyphagous as e.g. *Myzus persicae* (the green peach aphid). I once thought that it was the most common aphid in Denmark, as I have found it at more localities than any other species, but the reason was that I in the 1950'ies concentrated on studies of aphids on beets and potatoes. This species is as mentioned above polyphagous, so it might be thought to be found on any plant, but the reality is, that I almost only have found it on beets, potatoes, peaches and some other cultivated plants, mainly indoors, but curiously enough only very rarely on wild plants in the nature. This is also the case with regard to the polyphagous *Macrosiphum euphorbiae*, while *Aphis fabae* is very common on many herbaceous plants, also early in summer even though its primary hosts *Euonymus*, *Viburnum* and *Philadelphus* not are among the most common bushes in agricultural areas.

Hille Ris Lambers once told me that the preference for a certain host plant changed when the aphid went far away towards the north. That is a strange riddle. After a visit to Iceland I have been able to confirm this statement, as I discovered species on plants there, which they normally do not prefer (HEIE, 1964). *Acyrtosiphon auctus*, which normally feeds on *Honckenya peploides*, occurred here on *Stellaria* and *Capsella*, *Macrosiphum euphorbiae* was observed on *Achillea millefolium*, which is not a normal host for it, and a colony of *Macrosiphum cholodkovskyi*, normally living on *Filipendula ulmaria*, was found on *Chamaenerium angustifolium*. I will call this phenomenon "host disturbance on northern latitudes".

So preference for certain plants can be different in different parts of the world. While the very common *Macrosiphum rosae* (the rose aphid) in Den-

mark and most of Europe is host-alternating between rose and members of the family Dipsacaceae, I have found it on *Chamaenerium angustifolium* in Sweden. That has never happened in Denmark. Perhaps it is another example of "host disturbance on northern latitudes".

Another example of a species with variation in choice of hosts is *Lipaphis erysimi*. In Europe it goes on Brassicaceae except *Brassica*, while this species in the rest of the world is a pest to *Brassica* under the name *Lipaphis pseudo-brassiccae* (which is a synonym). The only country in Europe, where it has been found on a species of *Brassica*, is Denmark, where I once found it on *B. napus rapifera*.

Questions concerning host alternation

We do not know how often host alternation evolved in the past. It happened at least more than once, between three and seven times, perhaps even more often, as more than one kind of host alternation exist. In Aphididae two morphs fly from the primary host to the secondary host in autumn, at first, alate gynoparae, viz. the parthenogenetic females giving birth to apterous oviparous females, and then alate males. In all other cases it is performed by alate sexuparae, alate parthenogenetic females giving birth to apterous oviparous females and apterous males. Some of the latter kind of aphids have life cycles of two years, viz. Fordinae within Eriosomatidae and the families Hormaphididae and Adelgidae. This seems to show that seasons of the year do not always decide the time for migration from one host to another. Neither temperature nor daylength seem to be important as in many other aphids, at least not in the first year of their life cycles.

It is a question how often host alternation has evolved. Did it happen in the ancestor of several families as Hormaphididae, Eriosomatidae and Anoeciidae together, in the ancestor of a whole family group like Eriosomatidae, in the ancestors of various subgroups as Eriosomatinae, Pemphginae and Fordinae or several times in individual genera and species? If the latter is true, then the tendency of development into host alternation must have been present in the ancestors. Is it possible to believe that such a tendency existed in a group of aphids long before the evolution of host alternation in the same group as a result of mutations resulting in dormant genes? In Aphididae such hidden tendency could be opened and be a reality in single genera or species as long as the males were alate. We know of course of species being dioecious in genera, where other species are monoecious, so this solution may well be true.

The way of host alternation among the adelgids is especially extremely difficult to understand. Both hosts are trees. While the primary host always is *Picea*, the secondary host is another conifer, and as mentioned above two years go between migration from *Picea* to the other tree and the same migra-

tion next time. Here it is very difficult to see the advantage of host alternation, especially because several species have changed from being host-alternating into being not host-alternating on *Picea* or on the original secondary host. Maybe the latter is hazardous in the long run because inbreeding and reproduction by parthenogenetic females alone results in a shorter existence than the outbreeding of the host-alternating species.

Among host-alternating aphids several conditions seem difficult to understand, e.g. that an aphid species often can be found either only on its primary host or only on its secondary host. *Myzus lythri* is an example. It is rather often seen on its secondary host, *Lythrum salicaria*, but never on its primary host, *Prunus mahaleb*, which furthermore is very rare. It might be supposed that overwintering could take place on *Lythrum*, but if so, it should happen as eggs, but rarely aphids lay eggs on a secondary host. This is only known for *Macrosiphum euphorbiae*, which lives both on rose and a large number of herbaceous plants. *Hyperomyzus rhinanthi* has often in Denmark been observed on its secondary host *Rhinanthus*, but only in Iceland I have seen it on its primary host *Ribes* (HEIE, 1964). Zooecidia of *Cryptomyzus korschelti* are very common on the primary host *Ribes alpinum*, while the aphid is rare on its secondary host *Stachys*. To the contrary the primary host *Prunus padus* of *Rhopalosiphum padi*, which is not extremely common in Denmark, nearly always is heavily attacked by its aphid, so that it is easy to understand that its aphid is a common pest to its secondary hosts, various grasses, including cereals.

Several more riddles are connected with host alternation. Some host-alternating aphids may stay on their primary hosts from spring to autumn, but a few of them are peculiar by having the alate males developed on secondary hosts only, while the alate females, gynoparae, which bear the apterous oviparous females, with which the males shall mate, develop both on primary and secondary hosts. This is the case for *Aphis sambuci*, host-alternating between *Sambucus* and various herbs as e.g. *Rumex* and *Melandrium*, where it feeds on the roots, and also for *Dysaphis sorbi*, host-alternating between *Sorbus* and members of the family Campanulaceae, and for *Hyalopterus pruni*, host-alternating between *Prunus* and *Phragmites*. This means that the host alternation of these species is necessary for fertilization of the overwintering eggs. Maybe the explanation is that the advantage of outbreeding is secured in that way.

The host alternation has been explained as a consequence of differences in quality of plant sap in the sieve tubes in the leaves. In woody plants it contains more amino acids in spring, when new leaves and branches need protein for growth, and in autumn, when amino acids shall be transported away from the leaves before they fall off, than it does during the summer. In summer woody plants are bad hosts, because the sap then is almost only sugar water with little nutritional value. The advance caused by richness in the sap of trees in autumn has however no importance for the sexuparae and sexuales of Eriosomatidae,

which do not feed at all. The sap in herbaceous plants is nearly always rich in amino acids, because they grow also in summer and therefore constantly need proteins. This fact does however not explain host alternation in Adelgidae, as their secondary hosts are woody plants.

Many non-host-alternating aphids which stay on woody plants throughout the summer do not grow or reproduce during this period, e.g. *Drepanosiphum* spp. on *Acer* and *Euceraphis* spp. on *Betula*, or they have some special strategies.

In the genus *Periphyllus* on *Acer* some species survive summer as summer nymphs (dimorphs), which do not feed and avoid water loss by being flat and having their back covered with skin-thickenings like a turtle and flat, leaf-shaped hairs along the body sides (*P. testudinaceus*, *P. hirticornis* and *P. californiensis*), while other species have dimorphs sitting very close to each other in rather big colonies covered with long hairs (*P. acericola* and *P. aceris*). Some other species solve the problem by laying the overwintering eggs early in summer as *Aphis farinosa* on *Salix*, *Glyphina betulae* on *Betula* and *Mindarus abietinus* on *Abies*. The last mentioned species has only three generations per year.

In this connection two questions arise: 1) Why do host-alternating aphids not become non-alternating on the herbaceous secondary host, where amino acids always are present? and 2) Why do aphids without host alternation on woody plants not become host-alternating?

The answer to the first question has been guessed to be a consequence of specialisation of the first spring generation, the stem mother or fundatrix, so that it cannot feed on other plants (MORAN, 1988). But it is known that many species have succeeded in changing from being dioecious to being monoecious, e.g. species of *Cryptomyzus*, which from being host-alternating between *Ribes* and Labiatae have changed to being non-host-alternating on Labiatae (but the opposite has also happened, from being host-alternating to being non-alternating on *Ribes*). The fundatrix of these species is curiously enough not as specialised as the fundatrices of the host-alternating species and more similar to the following generations. How can their morphological changes be explained?

The second question is not a riddle, however. In the past some non-host-alternating species have evolved into host-alternating species. It must have happened many times, because the Cretaceous aphids must have lived on woody plants exclusively without host alternation.

Viteus vitifoliae (previously called *Phylloxera*) has a special kind of host alternation, viz. alternation between the upper parts of wine to the roots of wine. Feeding on roots during summer is not a riddle, because roots also of woody plants grow in summer and therefore contain amino acids in the sap. Roots of woody plants are used by many eriosomatids too as secondary hosts, e.g. by *Prociphilus* spp.

Representants of the family Eriosomatidae is primarily a family of host-alternating members, stronger associated with this kind of life cycle than the Aphididae. Rarely species of this family have aquired new hosts through millions of years.

The common rose aphid, *Macrosiphum rosae*, has a relative with paler siphunculi, *M. euphorbiae*, which probably arrived to Europe from North America as late as in the beginning of the 20th century. In its homeland it was common on rose, while it in Europe, including Denmark, for a long time never was seen on rose, being very common on potato and many other herbs. It is polyphagous as *Myzus persicae*. In the last part of the 20th century it suddenly could be found on rose also in Europe, including Denmark. So it seems as though the sense of taste can change during a rather short time, and that host alternation can be lost, and then later develop again. Perhaps the necessary genes have been present all the time but been "sleeping" until a certain time, or a new invasion from America has taken place.

Within the family Lachnidae most genera are living on trees as their only hosts. The only exception is the group, which contains the genera *Trama*, *Protrama* and *Neotrama*. They are anholocyclic, which means that they reproduce by parthenogenesis all year and do not have males and overwintering eggs, and during the whole year feed on roots of herbs. It is a riddle what their original primary host has been, because it must be supposed that their ancestor was host-alternating, though no lachnids today have host alternation. It is however possible that their ancestor conquered herbs as its only hosts, in one step (CZYLOK, 1990). If the former is correct, then it is a question when host alternation evolved, in the few surviving genera of Traminae, in the ancestor of Traminae, in the ancestor of Lachnidae or earlier, in the ancestor of the two sister groups Aphididae and Lachnidae.

Questions concerning variation in size of populations.

Most people probably believe that all aphids are very common, only because they observe many of them on roses or sugar beets, but the truth is that they normally are rather difficult to find. During an excursion of 2-3 hours in summer I can be lucky to find 12-15 species, but more often I only see 2-3, in 2006, 2007 and 2008 normally zero.

The chance for finding aphids varies from year to year, but it cannot be called a riddle that for instance the year 2007 has been a year poor of aphids, because for some time the weather was very hot and dry and for a long time to the contrary very wet. Both high temperatures and strong rain are bad for the life of aphids. In 2007 I consequently observed only 36 species, most of them in the beginning of the summer. Furthermore 2006 was a still poorer year, when only 22 species were seen, so only a small number of overwintering eggs can

have been laid. It should, however, be considered that I no longer easily can bent down, so roots and low herbs have not been observed as much as earlier. Some normally very common aphid species have been impossible to find since 2006, e.g. *Macrosiphoniella artemisiae* on *Artemisia vulgaris*, *M. millefolii* on *Achillea millefolium* and *Myzocallis coryli* on *Corylus* (hazel), which is surprising. Especially the years 1957 and 1958 were rich in aphids, with 155 and 154 observed species, respectively (HEIE, 1960-1970). In 2000 78 species were seen, which may be close to the normal number. In 2005 the number was 44, in 2008 again rather normal, viz. 62. I have begun to fear that many of our aphid species are close to extinction, a fear which probably is not shared by others. It will be interesting to see, how the climatic changes may influence our aphid fauna in the future. It is a question how much the composition of the aphid fauna changes from century to century, and it may be asked if such big changes are developing just in these years.

It ought to be added that a large part of the species known from Denmark have only been found once, namely 93 out of 481, which is about 20%, e.g. *Microlophium primulae* on *Primula*, *Anthracosiphon hertae* on *Comarum palustre*, *Tinocallis platani* on *Ulmus* and *Aulacorthum palustre* on composites. *Pleotrichophorus persimilis* has also only been found once on its host *Artemisia campestris*, and it is a riddle why this species and four others, which are able to feed on this plant species, are very rare, while those feeding on *A. vulgaris* are common (HEIE, 1980-95).

Aphids can live together on the same plant without competition, because they prefer different parts of their host or use the resources in different times of the year or in different ways. This has been explained by DIXON (2009). Rarely two species are found in mixed colonies, though it may happen on birch and sugar beets. It must however wonder why some plants, as e.g. *Betula*, *Salix* and *Artemisia*, can be attacked by many aphid species, while only a single aphid or two species are attached to most plant species.

Usually aphids on trees and bushes are observed earlier in the year than species feeding on herbs. It is easy to understand when talking about species with host alternation, but difficult concerning those living only on herbs during their whole life cycle. Maybe their overwintering eggs hatch later?

In some cases it is very difficult to understand how overwintering is possible at all. Species on herbs must of course lay their eggs on these herbs, but what do aphids on annual plants do? This is for instance the case for *Impatiens* spp. on *Impatiens* spp. Their hosts hibernate only as seed in or on the ground.

Questions concerning morphology

Aphids have only few defence weapons against their many enemies. Most aphids are camouflaged, as those living on leaves are green or yellowish green

like the leaves or stems on which they sit. As mentioned below *Monaphis antennata* on birch is a good example, also *Macrosiphoniella millefolii*, as it is whitish and green like the flowers of its host *Achillea millefolium*, and the bluish green *Delphiniobium aconiti*, which lives on the bluish green stems and flowers of *Aconitum*, and also *Corylobium avellanae* and *Symydobius oblongus*, which look like the bark of young twigs of their host plants, hazel and birch respectively. Most enemies of aphids have a fine sense of vision, except the blind syrphid larvae, which however have mothers with a good sense of vision.

However, why are some other aphids richly coloured and very easy to see? This is for example the case for *Callipterinella tuberculata* on leaves of birch. It is yellow with a brown head, a red anterior part of the body and a black spot on the posterior part of the back. *Eucallipterus tiliae* lives on leaves of *Tilia*, but it is not green as the leaves. It is a very beautiful, yellow and black aphid with black spots on the wings and therefore easy to discover. It is difficult to understand, unless these aphids are poisonous to their enemies, killing them or prevent them from reproduction. Many aphids are black and for that reason easy to detect on green or yellow background, especially because they often form large colonies, but – of course – they are often attended and defended by ants. *Aphis nerii*, which does not occur in Denmark, forms easily visible large colonies on *Nerium* in the subtropics. *Uroleucon tanacetii* is bright red, but lives hidden on undersides of lower, yellowish leaves of *Tanacetum*. When many aphids occur on undersides of leaves, the reason is however not that they shall be hidden and unseen by enemies, but probably rather because they shall be protected against rain or strong sunshine and perhaps also because it then is easier to get their honeydew removed.

A very peculiar colour for aphids not living on roots is white. This colour has *Macrosiphum lisae*, which feeds on yellow leaves of *Chamaenerium*, but only on plants growing in shadow without flowering. Its males are however pink!

So the colour may be different in different generations. An example is *Rhopalosiphum padi*. Its fundatrix on *Prunus padus* is light green with red spots at the bases of the siphunculi, the following generations of virgins on *P. padus* are dark brown or black with whitish wax powder, while the generations on the secondary hosts, grasses, are dirty greenish or brownish with reddish spots at the bases of the siphunculi. It is a riddle how many morphologically different morphs can evolve within the same aphid species, when the genes are the same.

The colour of *Hyalopterus pruni* is exclusively green on plum, the primary host, but – curious enough – on *Phragmites*, the secondary host, some individuals are red and some others are green. It is a question if these colours are caused by the genes or the environment, probably by both.

Many other aphids, e.g. *Macrosiphum rosae*, can have both green and red individuals born by the same mother. A single time I have observed a colony consisting of yellow individuals only. Other species can also suddenly appear with a new colour.

Most aphids have black eyes, but some, e.g. species of the genus *Macrosiphoniella*, have red eyes. That is astonishing.

It cannot wonder that aphids visited by ants have shorter siphunculi than aphids not visited by ants. Long siphunculi may be a disadvantage, if the aphids are visited by ants tapping the honeydew from their anus. The liquid coming from the siphunculi gives off vapour alarming other aphids of the same clone has no essential importance for aphids defended by ants. But why then do species of the genus *Euceraphis* on birch have very short siphunculi, while the related species of the genus *Drepanosiphum* on *Acer* have very long siphunculi? None of them are visited by ants. Another peculiar character of many aphids is swelling of the siphunculi. Enormous swellings of siphunculi are found in e.g. *Pseudorhopalosiphoninus calthae* on *Caltha*, in *Rhopalosiphoninus lathyris*, which is polyphagous, where they are nearly globular, and in *Decorosiphon corynothrix* on moss. They are not closely interrelated. Nobody knows the function of swollen siphunculi! Not either the function of reticulation on the siphunculi found in some members of Chaitophorinae and Macrosiphinae.

The importance of some other morphological characters is also a riddle. Many aphids, e.g. *Phorodon humuli*, migrating between *Prunus* and *Humulus*, and to a lesser degree species of the genera *Myzus* and *Ovatus*, have prominent frontal tubercles, the function of which is totally unknown. Perhaps they support the antennae? *Ctenocallis setosus* on *Sarothamnus* and species of the genera *Israelaphis* and *Matsumuraja* wear very curious processi on their bodies. Also the function – if any – of the rose-thorn-like tubercle on the back of *Tuberolachnus salignus* on *Salix* is unknown. The same is the case concerning the supracaudal process found in species of *Cavariella*, which migrate between *Salix* and umbellifers, and especially the big one found in *Aspidaphis adjuvans* on *Polygonum aviculare*. These species are not at all interrelated. Maybe these characters have no function, but are only secondary products of genes with some other function, which is useful? It is much easier to understand, why *Staticobium staticis* has lids over its stigmal pores because it lives on *Statice* that grows in marshes with tides where water may drown the aphids at times with high level. It is also easy to understand why some Drepanosiphidae as e.g. *Drepanosiphum* and *Saltusaphis* have enlarged femora giving them ability to jump when disturbed, but it is difficult to understand why some of their relatives as e.g. *Chaitophorus* and *Thripsaphis* have lost this character.

The ultimate segment of rostrum is blunt and broad in aphids feeding on grasses, while it is pointed and prolonged in aphids living on the composite group Anthemideae. It may have something to do with the character of the

surface of the leaves, but until now no explanation has been given. Both kinds of aphids consist of species, which are not interrelated at all.

Many members of Drepanosiphidae have a sclerotic stiffening at the base of the rostrum. Its function is probably strengthening of the rostrum when the aphid starts to feed, but why have some drepanosiphids, which have originated from ancestors with this stiffening, lost it again as e.g. the Chaitophorinae?

The cauda has a function, as it can throw away the sticky drops of honeydew, so that the aphids avoid being stick. It is easy to understand that the cauda has become nearly absent or very short and rounded in aphids attended by ants, but this is also the case with nymphs of all aphids. They throw the honeydew away by their hind legs, so why is it necessary for adults to have a cauda at all?

Questions concerning geographical distribution

There are many riddles combined with distributional patterns of aphids. It is for instance peculiar that *Tinocallis nevskyi* is very common on *Ulmus* in southern Denmark in most years, but rare north of the middle of Jutland, when it occurs far to the north in Sweden, where I found it in Dalsland in Middle Sweden. It arrived in Denmark from Central Asia as late as in the end of the 1970'ies or the beginning of the 1980'ies, It may be so because it still had not reached the northern Jutland, when I looked for aphids there the last time.

Corylobium avellanae on twigs of hazel is another example of a distribution up to the middle of Jutland, though it occurs in Middle Sweden and Finland.

It is not a riddle that *Uroleucon cichorii* until now has only been found in eastern Denmark, because its host, *Cichorium* is extremely rare in western Jutland. Not either that *Myzocallis myricae* only has been found in western Jutland, because its host *Myrica gale* has the same distribution. To the contrary it is a riddle that some other species has lopsided distribution in Denmark. Though *Leontodon autumnalis* and *Hypochoeris* spp. are very common plants all over the country, it is rare to find *Uroleucon hypochoeridis* on these plants on Zealand, and until now it has not been seen on Funen, though it is very common in Jutland on these two plants. Several other aphid species can feed on them, but are rarely observed on them. It is also very peculiar that *Callipterinella tuberculata* has been found several times on birch in the Copenhagen area, but never outside this city. I have looked for aphids in Jutland in about 30 years, but never observed it there, though the species is rather common and widespread in our neighbouring countries.

Compared with the small size of the country it is surprising that as much as 10% of all aphid species in the world have been found in Denmark, viz. 481 out of about 4700. This is however not a riddle, because most aphids do not tolerate strong sunshine or intensive rain well, so they are underrepresented in the

tropics contrary to most other groups of insects, but prefer temperate climates. Exceptions from this rule are two families, viz. Hormaphididae and Greenideidae, which mostly are tropical. Why? Nobody knows! And why were many families common in the warm Cretaceous period?

Most aphid species occur in the temperate zone on the northern hemisphere, and some are found on both sides of the Atlantic ocean. Some of them may have crossed it long time ago, when the continents lied closer to each other, while others have crossed the sea in our time by ship together with their host plants or by aeroplane. I have once observed an alate aphid inside an aeroplane, however only between two cities in Denmark.

A few aphids have immigrated into Europe from North America in the latest decades, from about 1970 or later, as e.g. *Illinoia lambersi* (on *Rhododendron*), *I. azaleae* (on azalea), *Uroleucon erigeronensis* (on *Erigeron canadensis*), *Macrosiphum albifrons* (on *Lupinus*) and also the pest to *Trifolium* named *Nearctaphis bakeri*, which not yet has been found in Denmark, but in other European countries.

Also species from Central Asia, as *Impatientinum asiaticum* and *Tinocallis nevskyi*, have immigrated to Denmark and other European countries. It has been guessed that they arrived by ship or by flight on introduced plants, while others have arrived on their own wings. Winged aphids may be brought through the air several thousands of kilometers. It is interesting to see if further immigrants may arrive in the future.

It is a riddle, how the North American *Illinoia lambersi* immigrated into Denmark and other countries in western Europe. It seems to be rather common here now, but mostly in the last part of the summer. According to American aphidologists it overwinters as virgins, not eggs (this is called anholocyclic overwintering), so probably it does not overwinter here, but arrives every or nearly every year from other countries in Europe if not from America crossing the Atlantic. There may be another explanation, namely that it can hibernate in glass houses on rhododendrons.

In this connection it is interesting that *Tuberolachnus salignus* on *Salix*, has only been found three times in Denmark, viz. in 1872, 1918 and 1931. It must be supposed that it arrives from other European countries crossing the Baltic Sea with long intervals, and then disappears before winter. It is anholocyclic like *Illinoia lambersi*, but in this case overwintering in glass houses seems completely improbable.

It is a riddle why *Myzus ascalonicus* have been found all over the world since 1940, but never before. Did it live isolated on an island far away from the rest of the world before 1940 or did it evolve at that time? As it is rather similar to *Myzus persicae*, it might have been identified as this species, but this is apparently not true. It has not been found in any aphid collection older than 1940. Is it a hybrid, the parents belonging to two interrelated species? Is that

the reason for its exclusive anholocycly, because its chromosomes cannot cooperate?

The previously mentioned aphid on birches, *Monaphis antennata*, is common in Middle Europe and has once been found in southern Sweden, but hitherto not in Denmark (HEIE, 1980-95). It is difficult to believe that climatic conditions should prevent it from living north of the Baltic Sea. As said above I have studied aphids on birches trough several years without finding it, and I still look for it. It is of course very well camouflaged, looking like a green bud, and its nymphs sit on uppersides of leaves with their thick and black antennae lying parallel to the side ribs of the leaf. However, I had no difficulty in finding this species in the Netherlands, Central Germany, Austria, Slovakia and Hungary. It is not only rare in Scandinavia, but also in England. So it probably has reached its northern border, or its migration northwards is hampered because it has a heavy body and small wings and furthermore bears all its offspring at once, and consequently has difficulties in being spread.

Questions concerning paleontology and evolution

It is well known that the aphids existed as early as in the Triassic and consequently originated in the Triassic or in the end of the Permian (HEIE, 1967). For a long time its has been supposed that their origin took place on the northern hemisphere, because the great majority of species live there today, but EASTOP (2001) doubts this, at least for the large family Aphididae, on the basis of some very interesting findings in New Zealand. The question is now: Did the first aphids live on the southern hemisphere and not on the northern? In this connection it is interesting that the fossil species *Triassoaphis cubitus* from the Triassic was found in Australia, while other Triassic aphids have been found in East Asia.

Twelve families of aphids exist in the present time, but from the Cretaceous we know 22 families, among these four or five of the recent ones. More of the recent families must also have been present at that time because each of them is the sister group to some other recent family among those found. This means that the biodiversity was much larger in the Cretaceous than today, though the supply of host plants must have been limited. Mainly spore plants and conifers and other gymnosperms were available, because angiosperms appeared rather late during the Cretaceous and must have consisted of rather few genera, only. This large biodiversity is surprising, not least because only less than 80 Cretaceous species are described, while the number of recent species is about 4700.

At the transition between the Cretaceous and the Tertiary all Cretaceous families except the recent families and two more (Elektraphididae and Naibiiidae) became extinct. Some of these disappeared earlier, namely in the middle of the Cretaceous, but a mass extinction seems to have happened at the end of

that period at the same time as disappearance of many other animals, among these the dinosaurs. The explanation may be that a large meteoric fall or large volcanic eruptions or changes of the oceanic streams happened at that time, all of these catastrophies being followed by climatic changes. Any of these cases caused changes of the flora, which must have resulted in mass extinctions of herbivores like aphids. Then the angiosperms began to dominate. The gymnosperms, which in the Cretaceous must have been the dominating hosts, gradually played a smaller roll and after some time became poorer in species. If some of the old aphids lived on spore plants, they obviously have become extinct. The very few recent aphid species feeding on ferns, horsetails or mosses are not interrelated, but related to different species within the family Aphididae, the ancestors of which conquered angiosperms during the Tertiary, so they got spore plants as hosts rather late in that period, changing from life on angiosperms.

Also most aphids on gymnosperms conquered them as hosts rather late, during the Tertiary, apart from the Adelgidae and perhaps also the eriosomatids related to *Prociphilus*.

It is a question why the evolution of aphids during about 200 million of years did not result in great morphological changes. Compared with other animals their evolution seems to have been very slow (HEIE & WEGIEREK, 2009). During the Tertiary no new families except Lachnidae evolved, while in mammals many new orders developed. The explanation may be that their adaptations could only influence choice of host plants, development of certain defence strategies and life cycles, not involving large morphological changes but only development of sense organs and ability to survive on a host plant. Their evolution was probably mainly directed towards magnification of reproduction. That happened in the three still existing superfamilies, Phylloxeroidea, Adelgoidea and Aphidoidea, when apterous individuals evolved with a larger fecundity than alate sisters. Therefore it seems peculiar that all parthenogenetic females of some Drepanosiphidae are alate. They must long time ago have had apterous morphs as most of their relatives.

It is interesting that the genus *Mindarus*, which feeds on conifers, contained about the same number of species in the beginning of the Tertiary than it does today, while the Aphididae, which today contains more than half of all recent species and whose members mainly are associated with angiosperms as hosts, was represented by only four described species in the beginning of the Tertiary. It is a pity that very few fossil aphids have been found from the middle and the end of that period, what is rather surprising.

Association with distinct host plants seems to have been very strong during long periods, as the species within many genera have interrelated hosts. In the family Eriosomatidae it seems to be the rule with regard both to primary and secondary hosts, but it is also the case in other families. Among Aphididae most

species of *Uroleucon* feed on composites, all species of *Cryptomyzus* feed on *Ribes* spp. and/or Labiatae, all species of *Metopolophium* feed on grasses, and all species of *Cinara* feed on conifers. There may be three explanations: 1) The ancestor became split into several subspecies, which later became good species at the same time as the original host plant became split into species. This means that the evolution of aphids and plants took place in parallel. 2) The ancestor conquered more hosts among relatives of the original host, and on the new hosts specialisation took place among its descendants. 3) The ancestor originally lived on many plants, but its descendants specialized on each of them. It is a riddle what explanation is the right one, or perhaps there are more explanations. Perhaps different explanations should be given for various genera.

The association with the host plants is stronger among adelgids and erio-somatids than among aphidids and must have required a longer adaptation time. This can also be understood from the fact that the zooecidia of the former two are closed galls on *Picea* and deciduous trees like *Populus* and *Ulmus*, respectively, while zooecidia in Aphididae usually are only curled leaves with a few exceptions as for instance the galls of *Cryptosiphum artemisiae* on *Artemisia vulgaris* and *Dysaphis* spp. on Pomaceae.

The first aphids must have been oviparous in all generations. Parthenogenesis must have developed rather early in their history before the development of viviparous reproduction. Siphunculi and siphuncular pores are as mentioned above organs producing alarm pheromones that warn members of the same species against enemies. The aphid producing the pheromone is already attacked and probably condemned itself, so the pheromone is only useful to other aphids. Therefore siphunculi must have evolved when the members of the same colony were genetically identical, so that even if the single individual died its genotype would survive. This will be the case if reproduction takes place by diploid parthenogenesis. As the fundatrix does not have genetically identical sisters because it has hatched from a fertilized egg, it is a kind of a mystery that it also has siphunculi. Only *Longicaudus trirhodus*, which is host-alternating between rose and *Aquilegia*, has a fundatrix without siphunculi.

The extinct genus *Oviparosiphum*, which as said by its name is oviparous, with three described species from the Lower Cretaceous, is the oldest known genus with siphuncular pores (SHAPOSHNIKOV, 1989). It is exciting to see if more fossils with siphuncular pores should appear from older periods in the future.

It is a riddle when viviparous reproduction of parthenogenetic females evolved. As four of the recent families with vivipary are known from the Upper Cretaceous it seems probable that it happened earlier, which will mean in the middle of the Cretaceous or perhaps even as early as in the Jurassic.

Aphids with all generations being oviparous and without siphuncular pores still exist today, viz. the Adelgidae on conifers and the Phylloxeridae on oak, wine and other woody angiosperms. It is logical to suppose that they in the

Lower Cretaceous or earlier must have separated from the branch of the phylogenetic tree, which contains all other families of aphids. This of course means that their ancestors went their own way before the origin of *Oviparosiphum*.

This part of the tree, containing all viviparous families and the majority of all known species, has hitherto not been finally drawn, probably because its branches split from each other nearly simultaneously as a „Big Bang”, namely in the Upper Cretaceous and close to the beginning of the Tertiary. Since the end of the Cretaceous no new families developed, except the Lachnidae, as mentioned above. I am looking forward to seeing further attempts for solving this riddle.

It would be interesting to get it clear, where the Lachnidae belongs on the phylogenetic tree. I think it is the sister group of the Aphididae.

It is still an unanswered question when host alternation evolved. It is a specialisation that with certainty – as mentioned above – must have developed several times. Most times this specialisation went into the direction of developing alate virgins (sexuparae) which in autumn migrate to another host to bear apterous sexuales, oviparous females and males, there. It is possible to guess that it happened for the Eriosomatidae as early as before the Lower Tertiary, because nymphs of the genus *Germaraphis*, which look like recent eriosomatids, viz. *Prociphilus* spp., have been found in Baltic amber from the Lower Tertiary (about 40 million years old) (HEIE, 1967; HEIE & WEGIEREK, 1998). *Prociphilus* spp. are today host-alternating between deciduous trees and roots of conifers. It can reasonably be guessed that these old *Germaraphis* spp. also had host alternation, maybe between two species of conifers between upper parts of one and roots of the other one or of the same?

In Aphididae the migration from the secondary host to the primary one in autumn is – as said above – different from the kind of host alternation found in other families. Here two kinds of individuals carry out the migration, partly alate virgins (gynoparae), which bear the apterous sexual females, partly alate males. In my opinion this kind of migration is so special, that it must have evolved only once, but VON DOHLEN *et al.* (2006) give arguments for three times. This discrepancy will be described more precisely below.

Constantly new discoveries give birth to new theories concerning relation, and some of them are very surprising, e.g. the demonstration of a close relationship between *Pterocomma* and *Cavariella* in spite of rather large morphological differences (VON DOHLEN *et al.*, 2006). This statement has been achieved by means of DNA-analyses, and it certainly is by this kind of studies that we can reach to a correct reconstruction of the phylogenetic tree. Morphological studies are more uncertain because many groups of aphids have characters impossible to interpret, because the evolution very often has resulted in reduction of morphological characters so that it is difficult to distinguish between new characters (apomorphies) and old ones (plesiomorphies). There are also many

examples of development of convergent characters so that it becomes impossible to believe that similarity means close relationship. The genus *Pterocomma* is a good example. It ought to be mentioned, that this genus previously has been thought to belong to a special subfamily within the family Aphididae, Pterocommatinae, and regarded as a sister group to all other aphidids. The reason is that it looks very different from them. Now there is basis for looking on the differences in a new way. For example the strong hairyiness, the short cauda and the lack of frontal tubercles are not as previously thought plesiomorphies, but to the contrary apomorphies. Development of a short cauda is a consequence of adaptation to association with ants, because these easier can get the honeydew when the anus is not covered by the cauda. *Cavariella* is not attended by ants, and therefore its cauda is not reduced. However, it is true that there are not many similarities between these two genera. If *Pterocomma* does not descend from host-alternating aphids, then host alternation must have developed three times within the family Aphididae, viz. in the ancestor of Aphidinae, the ancestor of *Cavariella* and the ancestor of the majority of the Macrosiphinae. In my opinion it seems unlikely that the very special way of migrating in autumn by two kinds of individuals should have evolved more than once. I think that it is much more probable that *Pterocomma* descends from an ancestor migrating from *Salix* to some unknown secondary hosts and later became monophagous on *Salix* or *Populus*. VON DOHLEN *et al.* (2006) give several arguments for the opposite opinion. Even though I was a coauthor, I cannot totally agree, but it is of course possible that the presence of alate gynoparae and alate males in monoecious species perhaps makes development of host alternation easy several times (VON DOHLEN, oral comm.), more often than previously believed. It should however be taken into consideration that such monoecious species may have evolved from host-alternating ancestors with the aphidid kind of host alternation and still have the genes for being host-alternating again.

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Nierozwiązane tajemnice mszyc /Hemiptera: Aphidomorpha/

Streszczenie

Przez pół wieku badań nad mszycami spotkałem zagadki trudne do rozwiązania i pytania na które nie znam odpowiedzi. Pytania te dotyczą następujących obszarów: wybór roślin żywicielskich, zmiana żywiciela, zmienność wielkości populacji, morfologii, rozmieszczenia geograficznego oraz paleontologii i ewolucji mszyc. Pojawia się więc pytanie: czy fauna mszyc zmienia się w naszych czasach, zwłaszcza w Północnej Europie?