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O. E. HEIE

The evolutionary history of aphids and a hypothesis on the coevolution of aphids and plants (*)

Abstract - Fossil aphids, including several specimens recently found in amber from the Cretaceous and the Lower Tertiary, not yet described, and comparison between the aphid fauna of the past and the recent fauna, indicate two major faunal changes, which are confirmed by the new findings. The first change happened at or close to the Cretaceous-Tertiary boundary, 50-70 million years ago. The composition of the faunas, respectively about 75-80 million years old and about 35-45 million years old, are described and compared. Most aphid families present in the Cretaceous became extinct before the Lower Tertiary, the period in which the Baltic amber was produced. In the Lower Tertiary most recent families were present, but the families Aphididae and Lachnidae were much less rich in species than they are today, so the second change happened after the Oligocene. These changes are described as consequences of changes of the dominant flora elements, 1) from gymnosperms to angiosperms at the K-T-boundary, and 2) from predominantly woody angiosperms to herbs in the middle of the Tertiary, especially herbs belonging to the plant families Poaceae and Asteraceae, which became rich in species during the Upper Tertiary and now contain the hosts of most aphids.
Among new species of Cretaceous age are representatives of the families Canadaphididae and Palaeoaphididae, previously only known from Canadian amber deposited in a secondary site and from the former USSR. Two additional specimens of *Canadaphis carpenteri* Essig, 1938, show a long rostrum, not visible in the holotype. The presence of siphuncular pores shows that Canadaphidoidea is a synonym of Aphidoidea. Also a representative of Tajmyraphididae, previously only known from Russia with a long rostrum and bilobed posterior end of the abdomen has been found in the Cretaceous Canadian amber. Instead of siphuncular pores it carries small cuticular fields with very small pale spots.

Riassunto - *Ipotesi evolutiva degli afidi in correlazione alle loro piante ospiti.*
Lo studio degli afidi fossili, sviluppatosi essenzialmente negli ultimi 30 anni,

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ha consentito di tracciare la storia evolutiva di tale gruppo di insetti. Il confronto tra l'afidofauna del passato e quella attuale evidenzia due cambiamenti fondamentali avvenuti nel corso della sua evoluzione; ciò anche alla luce di ulteriori recenti ritrovamenti, nell'ambra del Cretaceo e del Terziario inferiore, di vari esemplari ancora in corso di descrizione.
Il primo cambiamento si è verificato 50-70 milioni di anni fa, al limite tra il Cretaceo e il Terziario, come emerge comparando la composizione dell'afidofauna di 70-80 milioni di anni addietro (Cretaceo superiore) con quella di 35-45 milioni di anni fa (Terziario inferiore). Molte famiglie di afidi presenti nel Cretaceo si estinsero prima del Terziario inferiore, periodo nel quale si costituì l'ambra del Baltico. Molte famiglie attuali erano già presenti in quest'ultimo periodo, ma le famiglie degli Aphididae e dei Lachnidae apparivano molto meno ricche di specie di quanto non siano oggi. Ciò in quanto una seconda modificazione dell'afidofauna è avvenuta dopo l'Oligocene.
Tali cambiamenti sono stati consequenziali a quelli della flora predominante dei rispettivi periodi, quali: 1) il passaggio della dominanza dalle Gimnosperme verso le Angiosperme, tra il Cretaceo e il Terziario; 2) il passaggio della dominanza delle Angiosperme legnose a quelle erbacee nel Terziario medio e in particolare con lo sviluppo delle Poaceae e delle Asteraceae, le quali diventano molto ricche di specie durante il Terziario superiore, rappresentando oggi le piante ospiti di molti afidi attuali.
Tra le nuove specie del Cretaceo vi sono rappresentanti delle famiglie Canadaphididae e Palaeoaphididae, in precedenza conosciute soltanto nell'ambra canadese depositata in un sito secondario (Cedar Lake, Manitoba) e nei sedimenti cretacei dell'ex URSS. Due ulteriori esemplari di *Canadaphis carpenteri* Essig, 1918, evidenziano un lungo rostro (non visibile nell'olotipo) e la presenza di sifoni poriformi, dimostrando così che Canadaphidoidea è sinonimo di Aphidoidea (unica superfamiglia dotata di sifoni). Inoltre, un rappresentante dei Tajmyraphididae (fam. estinta, dotata come i Palaeoaphididae di sette articoli antennali e in precedenza conosciuta solo dalla Russia) con rostro lungo e parte posteriore dell'addome bilobato, è stato rinvenuto nell'ambra canadese del Cretaceo; esso non ha sifoni, ma al loro posto evidenzia piccoli campi cuticolari dotati di macchioline chiare.

Key words: Aphidina, coevolution, host plants, fossil aphids.

Introduction: The evolutionary history

Until about 30 years ago fossil aphids and their evolutionary history was only little known. Since that the number of finds and our knowledge about their systematic positions have increased considerably. Unfortunately many fossil specimens kept in museums in several countries are still undescribed, but it may be hoped that they will be described in the near future and give additional information about the aphid faunas of the past.

The history began in the Triassic, but from that period only two specimens have been found, one in Australia and one in North Asia. From the Jurassic 6 species are known, represented by 19 specimens, from the Cretaceous 63 species represented by 261 specimens, from Lower Tertiary (Paleocene, Eocene and Oligocene) 102 species with nearly 500 specimens and from Upper Tertiary 18 species with 182 specimens.

We do not know, of course, the host plants of fossil aphids with certainty. What has been the basis of supposition of host affiliations is partly the contemporary composition of the vegetation in the surroundings of the fossil sites, partly knowledge of host associations of recent relatives.

The oldest fossil angiosperms are from Lower Cretaceous, so the only available hosts of the aphids living in the Triassic and the Jurassic were spore plants and gymnosperms. All recent aphids living on spore plants (only a few not interrelated species) are closely related to various aphids feeding on angiosperms and obviously aquired spore plants as hosts rather recently. Therefore, it seems highly probable that the first aphids lived on gymnosperms. Angiosperms *could* be aquired as hosts in the Cretaceous, but the fossil record indicates that several or even most aphids in the Cretaceous and in the beginning of the Tertiary were still associated with gymnosperms, Coniferae. A bias may be that many fossils, both from the Cretaceous and from the Lower Tertiary, have been found in amber produced by coniferous trees. The fossils found in clay or other sediments show, however, the same picture.

Among the Cretaceous aphid families known to be conifer feeders are Mesozoicaphididae (7 species, 40 specimens), Elektraphididae (4 species, 56 specimens) and primitive Drepanosiphidae related to *Neophyllaphis* (at least one species, *Aniferella*, perhaps a total of 6). It seems possible that some aphids used the opportunities for conquering angiosperms as soon as they were available from the beginning of the Cretaceous, but the fossil record indicates that angiosperms became the dominant host plants only after the Eocene. It is interesting to compare the composition of aphid faunas of different geological periods with regard to representation of families. The Cretaceous fossils belong to at least 10 families (4 species are of unknown family), viz. 8 extinct families with 52 species and 246 specimens and 2 recent families with 7 species and 9 specimens. Seven of the ten families were probably oviparous as the recent families Adelgidae and Phylloxeridae. Seven of the eight extinct families disappeared before the Eocene, so something must have happened at the Cretaceous-Tertiary boundary, perhaps extinction of host plants. At the same time or somewhat earlier most recent families appeared, including a family associated with conifers, the Mindaridae.

The aphids from the Lower Tertiary (Palaeocene, Eocene and Oligocene) belong to 9 families (10 species are of unknown family), viz. 1 extinct family (Elektraphididae) with 9 species and 17 specimens and 8 still existing families with 83

species and more than 450 specimens. All recent families except Adelgidae, Phylloxeridae, Phloeomyzidae (with only one recent representative) and Lachnidae were present at that time, at least in the Oligocene.

It is a pity that only very few fossil aphids of Miocene or Pliocene age have been discovered. Only a few outcrops with aphids from these periods have been discovered, among them one in Spain (Penalver & Seilacher, 1995), the aphids from which have not yet been described. In the beginning of that period the world climate and vegetation changed. It became colder, and large areas previously covered by forests became steppes and savannas. Especially the grasses spread. The earliest unequivocal grasses have been recorded from the Palaeocene-Eocene boundary by Crepet and Feldman in 1991 (Collinson et al., 1993), and modern grass genera have been found from the Lower Miocene onwards. Fossil composites are known since the Eocene (Collinson et al., 1993), but only at the end of the Tertiary the composites became the angiosperm family richest in species. Most recent aphid species have host plants belonging to these two plant families (Poaceae and Asteraceae) and most of them have evolved during that period, viz. several species of Pemphigidae, Anoeciidae and Drepanosiphidae and most species of Aphididae, and the latter became the aphid family richest in species, which it had not been before. The Aphididae were represented by one species (*Aphidocallis caudatus*) among the 63 Cretaceous species and by only four species among the 102 species known from the Lower Tertiary. Today more than 55% of all aphid species in the world belong to the Aphididae.

Three families appeared in the Upper Tertiary for the first time, the Greenideidae with three fossil specimens from Balkan described as three species of *Aphis* (Heer, 1853) and at least one undescribed species from Spain (Penalver & Seilacher, 1995) in the Miocene, the Lachnidae with four species (of the still existing genera *Longistigma, Stomaphis* and *Cinara*) in the Miocene, and Adelgidae with one species (of the genus *Adelges*) in the Pliocene.

Today most Lachnidae live on coniferous trees, but the recent Lachnidae wih most plesiomorphous characters live on broadleaved trees as two of the Miocene genera, *Longistigma* and *Stomaphis*. The genus *Cinara,* of which three species recently have been described from China (Zhang, 1989), must have become associated with conifers in the Miocene and gone through an adaptive radiation rather close to our time, because the similarities between the many recent *Cinara* species, indicate a late speciation event, an adaptive radiation.

The Alberta site, 75-80 mio. years old

The Canadian amber was produced near the coast of a ocean. The vegetation consisted mainly of coniferous trees and – on the bottom of the forest – ferns. The fossil aphids previously described from Alberta (Heie & Pike, 1992) probably lived on coniferous trees, a species of the family Cretamyzidae and four species

of Mesozoicaphididae, a family closely related to the extant Adelgidae, but with a much longer rostrum and more than three antennal segments in apterae.

Later findings – not yet described (two will be described in Heie & Pike, in press, and two in Heie, in prep.) – belong to the same two families, most of them to Mesozoicaphididae, some of them to Canadaphididae and Palaeoaphididae, previously known from Canadian amber on a secondary site at Cedar Lake, Manitoba (Richards, 1966) and Cretaceous sediments in Russia, and one to Tajmyraphididae, previously only known from North Russia (Kononova, 1975). A few may belong to a sixth extinct family, Oviparosiphidae and the extant Drepanosiphidae.

The number of specimens until now found in Canadian amber, age about 75-79 mio. years, is 51: Oviparosiphidae (doubful determination): 1, Cretamyzidae: 3, Canadaphididae: 4, Palaeoaphididae: 5, Tajmyraphididae: 1, Drepanosiphidae: 1 (doubtful determination), Mesozoicaphididae: 33, unknown families: 4. All these families except Drepanosiphidae became extinct before the Baltic amber was produced, age about 40 mio. years, viz. before or during the Lower Tertiary.

Two specimens of *Canadaphis carpenteri* Essig decribed in Heie & Pike (in press) show that the species has a rather long rostrum, as also found in another species of *Canadaphis* from North Asia by Wegierek (1993), and siphuncular pores. Both characters were invisible in the holotype described by Essig (1938), so Canadaphidoidea becomes a synonym of Aphidoidea, the only superfamily with siphunculi or siphuncular pores.

Another species belonging to Tajmyraphididae has like members of Palaeoaphididae seven antennal segments (while all recent aphids have six or less) and a bilobed posterior end of abdomen (probably abdominal tergite VIII) as in some previously described representatives of the same family. Siphuncular pores are not present, but each margin of abdominal segment V or VI carries 7-8 very small pale spots instead of a siphuncular pore.

The Baltic amber forest, 35-45 mio. years old

The forest in which the Baltic amber was produced in the Lower Tertiary consisted also primarily of coniferous trees, but at least part of it grew on higher altitudes. Its climate was colder, and it contained several genera of broadleaved trees. The herbs are little known.

The aphids belonged to one extinct family, Elektraphididae, related to the recent Adelgidae, which is associated with coniferous trees, and several extant families, primarily Pemphigidae, tribe Prociphilini, whose recent relatives use coniferous trees as their secondary hosts, Mindaridae, also associated with coniferous trees, and Drepanosiphidae. Woody angiosperms, broadleaved trees, had probably been aquired as hosts at that time, e.g. Aceraceae and Fagaceae (both re-

ported from the Cretaceous (Collinson et al., 1993)), and most Drepanosiphidae today feed on broadleaved trees. Among the few species belonging to Aphididae are some with three ommatidia in apterae like the recent East Asian aphid *Parachaitophorus* (on *Spiraea*), and some with long siphunculi and similarity to the extant genera *Macrosiphum* and *Illinoia*. A species of the latter feeds on conifers today, but the host spectrum of the subtribes Rhopalosiphina and Macrosiphina indicates an old association with host plants of the order Rosales (Hille Ris Lambers, 1939). A leaf of Cretaceous age have been described as *Crataegites borealis*, but more reliable evidence consisting of fossil flowers and fruits of Rosales (related to *Spiraea* and *Prunus*) are from the Lower Tertiary (Collinson et al., 1993).

Many recent additions to the collection at the Zoological Museum of Copenhagen confirm the previous assumption: Pemphigidae (species of *Germaraphis*, related to the recent genus *Prociphilus*), Mindaridae and Drepanosiphidae (e.g. of the genus *Palaeosiphon*) were common in this forest, while species of Aphididae were rare and Lachnidae absent.

The recent aphid fauna

It is my hypothesis that an adaptive radiation of aphids took place after the Oligocene, in Miocene or later, when the herbaceous angiosperms became the dominating plants on large areas, especially steppes and savannas, as the world climate became colder. In such areas grasses and composites were common at that time and aquired as host plants of aphid groups able to survive on them. Adelgidae could not, but Hormaphididae, Anoeciidae, some Pemphigidae, some Drepanosiphidae and most Aphididae succeeded. The family richest in species today, Aphididae, had developed a new kind of host alternation, which made it easy for them to conquer herbs, at first as secondary hosts, in several cases later as the only hosts. Aphids similar to *Macrosiphum* or *Rhopalosiphum*, originally monoecious on Rosales, conquered grasses as secondary hosts like *Sitobion fragariae*, *Metopolophium dirhodum* and *Rhopalosiphum padi* today, and several others survived on grass as their only host as *Sitobion avenae* and *Metopolophium festucae* today. Other herbs were acquired by other macrosiphines, and a major part lives on composites today. Also most Tramini within the Lachnidae acquired composites as their hosts, and it can be concluded that this tribe is a relatively young one.

Conclusions

Recently discovered fossil aphids confirm the assumption that the Mesozoic fauna persisted until the Upper Cretaceous, and that the recent families were poorly represented until the Lower Tertiary. The two changes of the aphid fauna coincides with 1) the changes from gymnosperms as the dominant flora element to wider and wider distribution of woody angiosperms during the Cretaceous and

2) from dominating forest areas to open areas with herbs in the middle of the Tertiary or later, especially grasses and composites.

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PROF. OLE E. HEIE - Department of Biology, DLH, Emdrupvej 101, DK-2400 Copenhagen NV, Denmark.

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