

Why are there so few aphid species in the temperate areas of the southern hemisphere?

OLE E. HEIE

Department of Biology, DLH, Emdrupvej 101, DK-2400 Copenhagen NV, Denmark

Aphids, zoogeography, southern hemisphere, evolution

Abstract. An answer to this question is proposed on the basis of the assumed evolutionary history of aphids based on palaeontological studies, zoogeographical data and estimated origin of each aphid genus in the world. An adaptive radiation of Aphididae and Lachnidae occurred rather late in the Tertiary on the northern hemisphere, and the tropics acted as a barrier. Most aphid genera endemic to the temperate regions of the southern hemisphere belong to other groups. The life cycles of aphids are discussed, and it is concluded, that the life cycles characteristic to most aphids in the temperate regions of the northern hemisphere are developed as an adaptation to the climatic conditions there.

INTRODUCTION

Contrary to most other taxa of high range, the species richness of aphids is greater in the temperate regions than anywhere else. Two explanations have been given.

According to the first one (Bodenheimer & Swirski, 1957; Heie, 1980) aphids are adapted to climates with cold winters. They lay diapause eggs in autumn. Among the arguments contradicting this hypothesis are the occurrence of two-years cycles and the occurrence of aphids with diapause eggs in the tropics. According to the second one (Dixon, 1985; Dixon et al., 1987) the low species richness in the tropics is due to a high plant diversity, making the chance of migration between conspecific hosts very small. Among the arguments contradicting this hypothesis is the occurrence of monophagous species in the tropics. These hypotheses do not explain why there are so few aphid species in the temperate regions of the southern hemisphere.

THE ZOOGEOGRAPHY OF APHIDS

The species richness of a certain area (A) can be compared with that of other areas when the number of species (S) is divided by A^z , where z is given the value 0.25 (Dixon et al., 1987). It is important that the areas compared have been intensively studied with regard to aphid faunas. A bias may be that the areas best studied occur in the temperate regions of the northern hemisphere. So the number of species in Argentina may be too small, while the number in New Zealand is more reliable. Another bias is the occurrence of deserts in some regions, so that the species richness of Australia may be underestimated.

All areas in Table 1 with S/A^z larger than 100 are found in the temperate and some subtropical regions of the northern hemisphere. The reason for the high species richness in India is the rich fauna of the Himalayas at high altitudes.

TABLE 1. Species richness of various areas.

| | A | S | S/A ^z |
|--------------------|------|------|------------------|
| Alaska (1) | 1478 | 29 | 5 |
| Greenland (2) | 341 | 20 | 5 |
| Canada (1) | 9215 | 632 | 65 |
| Manitoba (1) | 548 | 247 | 51 |
| USA (1) | 9167 | 1008 | 103 |
| California (1) | 405 | 497 | 107 |
| Utah (3) | 213 | 450 | 118 |
| Pennsylvania (1) | 116 | 347 | 106 |
| Florida (1) | 140 | 175 | 51 |
| Mexico (4) | 1973 | 220 | 33 |
| Cuba (4, 5) | 111 | 83 | 26 |
| Venezuela (6,7) | 912 | 51 | 13 |
| Chile (6) | 973 | 82 | 16 |
| Argentina (6) | 1780 | 110 | 15 |
| Denmark (12) | 43 | 458 | 178 |
| Netherlands (4) | 34 | 550 | 228 |
| UK (4) | 245 | 528 | 133 |
| Poland (4) | 313 | 591 | 141 |
| Lithuania (8) | 65 | 300 | 106 |
| Eur. Russia (4) | 3000 | 750 | 101 |
| France (4) | 551 | 700 | 144 |
| Portugal (4) | 92 | 340 | 110 |
| Sicily (9) | 26 | 311 | 138 |
| Zamora, Spain (10) | 11 | 225 | 124 |
| Korea (11) | 130 | 345 | 102 |
| Turkey (4) | 780 | 252 | 48 |
| India (4) | 3268 | 640 | 85 |
| E. Africa (4) | 1759 | 125 | 19 |
| S. Africa (4) | 1221 | 101 | 17 |
| Australia (4) | 7687 | 130 | 14 |
| New Zealand (4) | 269 | 91 | 22 |

A = area in 1000 km², S = number of species, z = 0.25. (1) = Smith & Parron, 1978; (2) = Hille Ris Lambers, 1952, 1960 (icefree areas only); (3) = Knowlton, 1983; (4) = Dixon et al., 1987; (5) = Holman, 1974; (6) = Smith & Cermeli, 1979; (7) = Cermeli, 1965, 1970, 1973; (8) = Rakauskas, Rupais & Juronis, 1992; (9) = Barbagallo & Stroyan, 1980; (10) = Mier, 1978; (11) = Paik, 1965; (12) = Heie, unpubl.

GENERA ENDEMIC TO THE SOUTHERN HEMISPHERE

The difference between the faunas north and south of the subtropics on the northern hemisphere becomes more obvious when a distinction between endemic and introduced aphids is made. Most species in tropical and southern temperate countries are recently introduced. Many of them are cosmopolites and anholocyclic and/or polyphagous. Only 10 species of aphids in Cuba (Holman, 1974) can be regarded as endemic to the islands in the Caribbean sea. Among the aphids of New Zealand (Cottier, 1953) only 6 are probably not introduced by man. The inequality is even more obvious with regard to genera.

The total number of genera in the world is 500 (with 4425 species). Fig. 1 and Table 2 show their probable origin. Only 14% of the genera of Aphididae and 9% of Pemphigidae are not of Holarctic origin, while the percentages are greater for Anoeciidae (50%, viz. *Aiceona* Takahashi), Hormaphididae (52%), Drepanosiphidae (24%) and Greenideidae

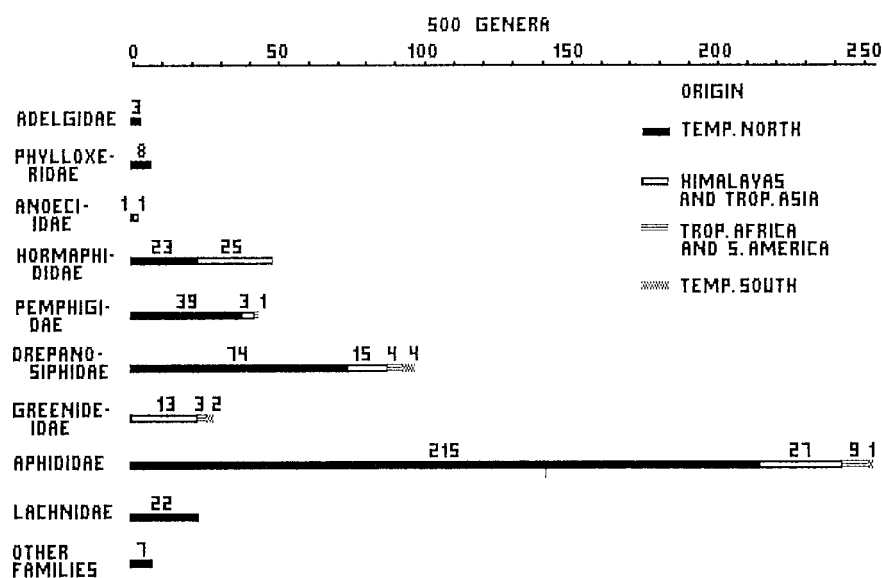


Fig. 1. Origins of 500 aphid genera.

(100%). A total of 392 or 78% are of Holarctic origin, among them all genera of Adelgidae, Phylloxeridae, Mindaridae, Thelaxidae and Lachnidae, and 55% of these 392 genera belong to Aphididae, only 25% to Drepanosiphidae + Hormaphididae + Greenideidae; 84 or 17% of all genera are from the Himalayas and tropical Asia and 17 or 3% from tropical South America and Africa; only 36% of these 101 (84 + 17) genera belong to Aphididae, while 60% belong to Drepanosiphidae + Hormaphididae + Greenideidae. Seven genera or 1% of the genera of the world are from the subtropical and temperate regions on the southern hemisphere: Drepanosiphidae: *Neuquenaphis* Blanchard, *Neosensoriaphis* Quednau, *Taiwanaphis* Takahashi (syn. *Sensoriaphis* Cottier) and *Ceriferella* Carver & Martyn; Greenideidae: *Anomalaphis* Baker and *Meringosiphon* Carver; Aphididae: *Casimira* Eastop (closely related to *Aphis* L.). So there is a gradient towards the south from a low to a high representation of Greenideidae and primitive Drepanosiphidae (Neophyllaphidini on gymnosperms and Neuquenaphidini mainly on *Nothofagus*) (see also Table 3).

TABLE 2. Origin of genera (total 500).

| | 1 A = 67,500 | | 2 A = 48,000 | | 3 A = 12,000 | |
|-----------------|-----------------|------------------|-----------------|------------------|-----------------|------------------|
| | G | G/A ^z | G | G/A ^z | G | G/A ^z |
| Hormaphididae | 23 | 1.4 | 25 | 1.7 | 0 | 0.0 |
| Pemphigidae | 39 | 2.4 | 4 | 0.3 | 0 | 0.0 |
| Drepanosiphidae | 74 | 4.6 | 19 | 1.3 | 4 | 0.4 |
| Greenideidae | 0 | 0.0 | 16 | 1.1 | 2 | 0.1 |
| Aphididae | 215 | 13.3 | 36 | 2.4 | 1 | 0.1 |
| Other families | 41 | 2.5 | 1 | 0.1 | 0 | 0.0 |
| Total | 392 | 24.3 | 101 | 6.8 | 7 | 0.7 |

G = number of genera, A = area of region in 1000 km², z = 0.25, 1 = Holarctic region except arctic parts, 2 = tropical regions, including the Himalayas, 3 = subtropical and temperate parts of the southern hemisphere.

TABLE 3. Origin of species.

| | 1 | | 2 | | 3 | |
|-----------------|------------|------------------|------------|------------------|------------|------------------|
| | A = 67,500 | | A = 48,000 | | A = 12,000 | |
| | S | S/A ^z | S | S/A ^z | S | S/A ^z |
| Hormaphididae | 75 | 4.7 | 122 | 8.2 | 0 | 0.0 |
| Pemphigidae | 277 | 17.2 | 28 | 1.9 | 0 | 0.0 |
| Drepanosiphidae | 550 | 34.1 | 94 | 6.4 | 26 | 2.5 |
| Greenideidae | 0 | 0.0 | 139 | 9.4 | 3 | 0.3 |
| Aphididae | 2293 | 142.3 | 263 | 17.8 | 9 | 0.9 |
| Other families | 517 | 32.1 | 29 | 2.0 | 0 | 0.0 |
| Total | 3 712 | 230.3 | 675 | 45.6 | 38 | 3.6 |

S = number of endemic species (estimated, rather uncertain; some genera have species belonging to different regions), A = area of region in 1000 km², z = 0.25; 1–3: three regions: 1 = Holarctic region except arctic parts, 2 = tropical regions, including the Himalayas, 3 = subtropical and temperate parts of the southern hemisphere.

THE COMPOSITION OF THE APHID FAUNA IN THE PAST

The species richness on the family level in the past was remarkably different. While most species belong to Aphididae today, viz. more than 58%, only few fossils of this family have been found (Heie, 1990, in press). The first appeared in Upper Cretaceous, and only 4 species are known from Lower Tertiary, 4% of the total number. Most species from Lower Tertiary have been placed in Drepanosiphidae and Pemphigidae.

Most recent genera of tropical or southern origin belong to groups, which occurred on the northern hemisphere in the Tertiary. Fossils of Hormaphididae (*Electrocornia antiqua* Heie from Baltic amber), Greenideidae ("*Aphis*" *macrostyla* Heer, *morloti* Heer and *pallescens* Heer from Miocene, Yugoslavia) and the drepanosiphid tribes with recent occurrence in tropical or southern regions Lizerini (*Mindazerius* Heie & Poinar from Dominican amber and some genera from Baltic amber, e.g. *Oligocallis* Heie) and Neophyllaphidini (*Aniferella* Richards from Cretaceous Canadian amber) were all found on the northern hemisphere, and *Palaeosiphon* Heie from Baltic amber seems to be related to the tropical/southern genus *Taiwanaphis* Takahashi (Neuquenaphidini).

All families alternate between parthenogenetic generations and a generation of sexuales, so this must be an old phenomenon, developed during a warm period in the Mesozoic. It was not originally an adaptation to climates with cold winters. Some developed two-years cycles. *Neophyllaphis*, which is an old genus (Eastop, 1966), produces sexuales from May to November in Japan and in November (spring) in New Zealand (Cottier, 1953), and sexuales are also known from regions without seasonal variation. *Mindarus*, which was richer in species in Lower Tertiary than now, develops sexuales in early summer.

DISCUSSION AND CONCLUSIONS

The Aphididae became rich in species during the last part of the Tertiary. An adaptive radiation took place, and the reasons were partly environmental changes and partly the fact that Aphididae was a little specialized group able to exploit the new environment. It consisted of species with only small differences between morphs, few reduced or specialized

characters and ability to feed on more than one or two plants. This family covers today a wider range of host plants than any other aphid family.

During the Tertiary the global climate became colder, especially at high latitudes, and finally ice caps covered the polar regions. The vegetation changed. Herbaceous angiosperms originated in the end of the Cretaceous, but they did not form large plant societies like grassland until after the Lower Tertiary.

It became advantageous to produce diapause eggs before the cold season and to acquire herbaceous hosts in summer, as the phloem sap here was richer in nutrients than that of woody plants (Dixon, 1985).

The hosts of most or all recent representatives of Adelgidae, Phylloxeridae, Mindaridae, Drepanosiphidae, Thelaxidae, Pemphigidae, Hormaphididae, Greenideidae and Lachnidae are woody plants. Host alternation between two woody plants developed early in Adelgidae, Pemphigidae and Hormaphididae. Also *Anoecia* Koch acquired host alternation, but the secondary hosts were grasses as in the case of some Pemphigidae. All these taxa have apterous males, born by sexuparous alatae, and strongly specialized fundatrices. Some of them (Adelgidae, Hormaphididae and the tribe Fordini) have two-years cycles.

The formation of grassland seems to have resulted in association with grasses during the Tertiary, not only as secondary hosts as in Anoeciidae and Pemphigidae, but also as the only hosts of some Drepanosiphidae (e.g. Siphini in the subfamily Chaitophorinae).

Aphididae became grass-feeding too. The reason for their rapid evolution and speciation rate was that they were little specialized and capable to adapt contemporarily with the environmental changes. They developed a new kind of host alternation remarkably different from all others. Not only one, but two morphs return to the primary host, the gynopara and the alate male, and the sexuales are morphologically similar to the parthenogenetic morphs. Two-years cycles are unknown in this family, so their ecology fits climates with cold winters. Host alternation between a woody host and a herb made it possible to utilize the phloem sap of leaves and stems of herbs, in the beginning probably grasses, during summer, when woody plants pay sap poor in nitrogen. Hille Ris Lambers (1939) pointed out that many genera of Aphididae are associated with Rosales, and that their ancestor probably lived on plants of this group. Obviously the ancestor of Aphidinae (not Pterocommatinae) acquired the above-mentioned new kind of host alternation between a woody plant and a herb, and the ancestor of *Rhopalosiphum* Koch, *Metopolophium* Mordvilko and *Macrosiphum* Passerini became host alternating between a woody plant within the Rosales and one or several grass species.

It would be more advantageous to leave the primary host totally, so apparently some constraints existed. Moran (1988) pointed out that the specialization of the fundatrix impeded this evolutionary step. To overcome this constraint a new fundatrix had to be developed. It has happened in several cases, where the morphology of the fundatrices of species monoecious on herbs are more similar to later generations of apterae than the fundatrices of related host alternating species. Not only fundatrices, but also sexuales are little specialized in Aphididae, so the constraint is weaker than in other heteroecious families. At present a very large number of rhopalosiphines and macrosiphines are monoecious on grasses and other herbs. The evolutionary plasticity of most genera of Aphidinae is so large that change from heteroecy to monoecy on herbs and also acquisition of new hosts have occurred several times and still occur.

Drepanosiphidae, also with little specialized fundatrices and sexuales, acquired herbaceous hosts too, but they did not host-alternate, and so had to get a new host totally in one step.

At the same time species of Lachnidae, which originally were monoecious on woody angiosperms (Lampel & Burgener, 1987), became associated with coniferous trees, among them the ancestor of *Cinara* Curtis. When large areas on the northern hemisphere became covered with conifers, another adaptive radiation took place, so that we today have more than 200 species of *Cinara*.

According to both explanations of the low species richness in the tropics, spreading of the numerous new species, especially Aphididae, towards the south was so difficult that only few could penetrate the tropical region and get to the temperate regions on the southern hemisphere. Tertiary representatives of Drepanosiphidae, Hormaphididae and Greenideidae were adapted to climatic conditions similar to that of the tropics and the subtropics of today. They could survive in the tropics during the end of the Tertiary, but in many cases not in the colder climates in the north. Some descendants can now be found in temperate regions on both hemispheres, but the fauna in the south is more like the Tertiary fauna that in the north, because the great evolutionary events took place on the northern hemisphere separated by the tropical barrier.

It might be argued that the tropics could be penetrated by polyphagous aphids from the northern hemisphere, if they were able to develop anholocyclic strains, and then – when arrived at temperate regions on the southern hemisphere – switch to production of sexuales in response to cues that indicate the approach of winter. This has apparently not happened before the modern introduction of appropriate plants by man. Even the polyphagous species that remained anholocyclic on the southern hemisphere, e.g. *Myzus ascalonicus* Doncaster and *Jacksonia papillata* Theobald, seem to have arrived in historic time.

REFERENCES

- BARBAGALLO S. & STROYAN H.L.G. 1980: Osservazioni biologiche, ecologiche e tassonomiche sull'afidofauna della Sicilia. *Frustula Entomol. (N.S.)* **3**: 1–182.
- BODENHEIMER F.S. & SWIRSKI E. 1957: *The Aphidoidea of the Middle East*. Weizmann Science Press, Jerusalem, 378 pp.
- CERMELI M. 1965: Lista preliminar de los afidos de Venezuela y sus plantas hospederas. *Agron. Trop.* **14**: 253–260.
- CERMELI M. 1970: Los afidos (Homoptera, Aphididae) de Venezuela y sus plantas hospederas. Suplemento I. *Ibid.* **20**: 249–256.
- CERMELI M. 1973: Los afidos (Homoptera, Aphididae) de Venezuela y sus plantas hospederas. Suplemento II. *Ibid.* **23**: 163–173.
- COTTIER W. 1953: Aphids of New Zealand. *Bull. N.Z. Dep. Scient. Ind. Res.* **106**.
- DIXON A.F.G. 1985: *Aphid Ecology*. Blackie & Son, Glasgow, 157 pp.
- DIXON A.F.G., KINDLMANN P., LEPS J. & HOLMAN J. 1987: Why there are so few species of aphids, especially in the tropics. *Am. Nat.* **129**: 580–592.
- EASTOP V.F. 1966: A taxonomic study of Australian Aphidoidea (Homoptera). *Aust. J. Zool.* **14**: 399–592.
- HEIE O.E. 1968: Pliocene aphids from Willershausen (Homoptera: Aphidoidea). *Beih. Ber. Naturhist. Ges. (Hannover)* **6**: 25–39.
- HEIE O.E. 1980: *The Aphidoidea (Hemiptera) of Fennoscandia and Denmark. I. General part. The families Mindaridae, Hormaphididae, Thelaxidae, Anoeciidae and Pemphigidae*. Fauna Entomologica Scandinavica 9. Scandinavian Science Press, Klampenborg, 236 pp.
- HEIE O.E. 1990: Recent advances in palaeoaphidology. *Acta Phytopathol. Entomol. Hung.* **25**: 253–260.

- HEIE O.E. (in press): Aphid ecology in the past and a new view on the evolution of Macrosiphini. *Proc. Symp. Norwich 1992*.
- HEIE O.E. & POINAR G.O. 1988: *Mindazerius dominicanus* nov. gen., nov. sp., a fossil aphid (Homoptera, Aphidoidea, Drepanosiphidae) from Dominican amber. *Psyche* **95**: 153–165.
- HILLE RIS LAMBERS D. 1939: Contributions to a monograph of the Aphididae of Europe. II. *Temminckia (Leiden)* **4**: 1–134.
- HILLE RIS LAMBERS D. 1952: The aphid fauna of Greenland. *Meddr Grønland* **136**(1): 1–33.
- HILLE RIS LAMBERS D. 1960: Additions to the aphid fauna of Greenland. *Ibid.* **159**(5): 1–18.
- HOLMAN J. 1974: *Los Afidos de Cuba*. Inst. Cubano del Libro, Habana, 304 pp.
- KNOWLTON G.F. 1983: Aphids of Utah. *Res. Bull.* **509**. Utah State Univ., 155 pp.
- LAMPEL G. & BURGNER R. 1987: The genetic relationships between Lachnid taxa as established by enzyme-gel-electrophoresis. In Holman J., Pelikán J., Dixon A.F.G. & Weissmann L. (eds): *Population Structure, Genetics and Taxonomy of Aphids and Thysanoptera*. *Proc. Int. Symp. Smolenice*. Publishing House of the Slovak Academy of Sciences, Bratislava, pp. 71–95.
- MIER DURANTE M.P. 1978: *Estudio de la Afidofauna de la Provincia de Zamora*. Caja de Ahorros Provincial, Zamora, 226 pp.
- MORAN N. 1988: The evolution of host-plant alternations in aphids: Evidence for specialization as a dead end. *Am. Nat.* **132**: 681–706.
- PAIK W.H. 1965: *Aphids of Korea*. Seoul National University, Seoul, 160 pp.
- RAKAUSKAS R., RUPAIS A. & JURONIS V. 1992: *The Check-list of Lithuanian Aphidodea. New and Rare for Lithuania Insect Species, Records and Descriptions of 1992*. Inst. of Ecology, Lithuanian Entomol. Soc., Vilnius, pp. 83–100.
- SMITH C.F. & CERMELI M.M. 1979: An annotated list of Aphididae of the Caribbean Islands and South and Central America. *Tech. Bull. N. Carol. Agric. Res. Service, No. 259*.
- SMITH C.F. & PARRON C.S. 1978: An annotated list of Aphididae (Homoptera) of North America. *Tech. Bull. N. Carol. Agric. Exp. Stn., No. 255*.