Identification guide to Nordic aphids associated with mosses, horsetails and ferns (Bryophyta, Equisetophyta, Polypodiophyta) (Insecta, Hemiptera, Aphidoidea)

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Abstract. Keys and diagnoses of North European aphids (Hemiptera, Aphidoidea) associated with mosses, horsetails and ferns are given, based on fresh and freeze-dried material. Numerous externally visible and thus informative characters, that are absent in cleared, slide-mounted specimens, such as body shape colours, wax coating and pattern etc., are utilized. Most of the species are illustrated by photographs of live specimens and drawings. Root-feeding species living in the moss layer or otherwise often present in moss samples are also included, even if their hosts were spermatophytes. The combination of colour images and diagnoses, utilizing easily observed characters, allows the identification of a large number of species already in the field, and many more at home with the aid of a stereo microscope. Host plant relationships and association with ants are summarised, including new records. Brief accounts on aphid life cycles, freeze-drying preparation techniques, etc. are also given to support the use of the keys.

Keywords. Aphids, Bryophyta, Pteridophyta, identification, photographs.

Introduction
Aphids are notorious for being difficult to identify and traditionally demanding clearing and mounting procedures before they can be studied, procedures that many beginning students experience as tedious and time-consuming. The preparations include preservation in ethanol, maceration by heating in alcohol and potassium hydroxide (KOH), neutralizing in acetic acid (CH₃COOH), rinsing in distilled water, embedding in a suitable medium (e.g., Polyviol, Canada balsam or Euparal) on a microscopic slide, covered by a cover slip and finally drying, preferably in a heated cabinet. Recipes and instructions for the procedures are given in, e.g., Danielsson (1985), Heie (1980, 1986) and Blackman & Eastop (1994, 2014). The clearing and mounting procedures, however, destroy many obvious and useful diagnostic characters, such as shape, colour, wax pattern and grades of sheen and lustre. Disabling these characters forces the identification to rely on counts, measurements and indices based on them.
This guide is, as far as possible, based on fresh and freeze-dried material, which maximizes the number of characters that can be used, including colouration and wax pattern. The measurements and indices available on slides are naturally also available on freeze-dried specimens, so slide-based keys can very well be used. Just as for slide-mounted material, knowledge of the host plant is of great help for the identification. Most aphids are monophagous or oligophagous, and closely related species usually feed on different plants, which makes plant-based keys fast and easy to use. A clear majority of the species are readily identifiable based on host plant data, diagnoses, colour images of live specimens, fresh or freeze-dried material and the aid of a good stereo microscope. Often just a glance at a photograph will appear to give the correct identification, but sibling species may be involved, so it should always be kept in mind that host plant association alone is not enough. Descriptions and figures should always be consulted before the decision is made. In some cases fine details need to be studied, and measurements may have to be taken. In most cases the necessary measurements can be taken on fresh and freeze-dried material, without any further processing. Sometimes, however, a water preparation on a slide, e.g., of a leg, is helpful, and in critical cases cleared and mounted specimens are needed. It should be borne in mind that all characters visible in slides are present also in freeze-dried material, and if not directly visible, always can be made so by clearing and mounting the specimen.

The present article is focused on the aphids associated with cryptogams of Finland and Scandinavia, including Iceland, Greenland, The Faroes and Svalbard. Included are also most of the species occurring in adjacent parts of north-eastern Europe, the Baltic region and northern central Europe, including the British Isles. Some species feeding on spermatophytes, but often occurring in moss samples, are also included. Accounts on aphid life cycles, preservation and terminology are also given here, but they are kept short, and more or less limited to subjects needed for using the keys and diagnoses. This article is intended to be followed by papers dealing with aphids feeding on other plants, and the ultimate goal is to cover all aphids occurring in North Europe.

The keys, instead of being dichotomous, consist of multi-character diagnoses and synopses grouping the diagnoses into sections sharing one or a few easily observed characters. Accompanied by photographs and drawings the data given in the diagnoses should in most cases be enough to allow correct identifications, or when that is not the case, to give sufficient reason to doubt the results and seek additional information elsewhere in the literature. As a contrast to keys based on slide material, this article also aims at enabling the student to learn species in advance and to recognise them as they are encountered in the field.

Material and methods

The host records and distribution data are according to Blackman & Eastop (1994, 2006, 2014), Heie (1980, 1986, 1992, 1994, 1995, 2004), Holman (2009) and the database of the Finnish Expert Group on Hemiptera (http://biolcoll.utu.fi/hemi/tyoryhma/tyoryhma_eng.htm), comprising most of the aphid data recorded from Finland (predominantly by O. Heikinheimo and myself), with additional records from adjacent countries. The photographs and drawings are original, unless otherwise stated. My own records of hosts are marked with asterisks (*) in the host lists of the diagnoses and in the host tables (Appendices 1 and 2), as are records by Osmo Heikinheimo and other Finnish collectors whenever I have been able to confirm the relationships (e.g., from Heikinheimo’s field notes).

The identifications underlying the figures, keys and diagnoses have all been confirmed by checking against keys and descriptions based on cleared specimens. The diagnoses are kept short, particularly when photographs are available, and the emphasis is on the parthenogenetic morphs, particularly aptera. In many cases, characteristics of juveniles are also included. More elaborate descriptions of all morphs are given in, e.g., Heie (1980, 1986, 1992, 1994, 1995, 2004) and references therein. The diagnoses are, whenever possible, based on my own observations on fresh and freeze-dried material supplemented by data from Heie (1980, 1986, 1992, 1994, 1995, 2004), Blackman 2010 and Blackman & Eastop (1994,
Preservation and labelling

For students who wish to preserve aphid material or build a reference collection without spending excessive time with the slide mounting process, here is an easy recipe for freeze-dried specimens:

1. Collect the aphids in small test tubes or other suitable vials, with or without part of the host plant. A slip of tissue paper may be inserted to absorb excess moisture. Label the vial and close it, e.g., with a cotton wool stopper. Keep the vial out of direct sunshine.

2. At home, put the vials into a container with a layer of desiccant (Silica gel, Rubin gel) on bottom in the freezer (-18°C is suitable) and close the container (Fig. 1A). Petri Ahlroth (pers. comm.) uses silica gel cat litter as desiccant, and his aphid specimens are excellent. More material can be added when needed. Some specimens can be pinned on micro-pins and the wings set at this stage. It may be useful to pin the specimens from below, in which case the blunt end of the micro pins may be sharpened (Fig. 1B). Pinned specimens should preferably be mounted on a piece of, e.g., foam polystyrene to support the legs during the drying process. The wings of alatae can also be set (Fig. 1C).

3. After a few months the aphids are dry and ready for the collection, as such in tubes or other vials (Fig. 1D), pinned, or glued to cardboard. Galls usually take at least six months to dry properly. For examples of dry, pinned specimens, see Fig. 1E–G.

To speed up the drying process, vacuum equipment can be used (e.g., Albrecht 1994), but that is by no means necessary.

Please note that in addition to the basic information on the labels (place, date and collector) it is of utmost importance to add information on the aphid’s position and occurrence on the plant. Just the name of the host plant is not enough to ascertain a true aphid-host relationship. “Cirsium arvense. Dense colony on upper part of stalk.” is a correct host plant statement, whereas “Cirsium arvense” alone denotes a substrate or (the worst scenario) a subsequently added inferred “host” name, and its role as host is not determined. Sadly enough, museum collections consist too often of many inadequately labelled aphid samples, and many temporary substrates may have entered published host lists. An addition of attendant ants is also welcome: “Attended by Lasius niger”, preferably accompanied by a couple of preserved ants. If the attending ant species cannot be identified with certainty, as is often the case with, e.g., wood ants (Formica), it is better to leave the species name out instead of implying a certain identification.

Aphid life cycles

This chapter is intentionally kept very brief. I will just try to give the information needed for using my keys. Most of the information is embedded in the figures. The accounts of life cycles given here are just examples of frequently occurring patterns, and are by no means intended to be complete. For more thorough accounts, see, e.g., Blackman (2014) or Heie (2004). Characteristically, the life cycle comprises one sexual generation consisting of oviparous females and males (sexuales), alternating with one or more parthenogenetic generations. The parthenogenetic females are viviparous (Aphididae) or oviparous (Adelgidae, Phylloxeridae). Except in the Adelgidae, hibernation takes place in the egg stage. Life cycles including both sexual and parthenogenetic generations (complete life cycle) are called a holocycle, whereas cycles lacking the sexual generations are called anholocyclic. Some life cycles involve host alternation where the sexual reproduction and hibernation takes place on one host, the primary host, usually a woody plant, with migration to secondary host(s) in spring, and back in autumn. The secondary hosts are usually herbaceous plants, but migration to roots of trees and shrubs is common.
Fig. 2. Monoecious one-year life cycles. In the outer zone an ordinary monoecious holocycle in Aphididae. The fertilized egg overwinters and in spring the first viviparous parthenogenetic generation, the fundatrix (stem-mother) hatches. Upon the fundatrix follows a variable number of viviparous females (viviparae), apterous and/or alate. In autumn (sometimes earlier) sexuparae are born and in turn give birth to oviparous (sexual) females (ovipara) and males, which mate, and the oviparae lay eggs. The inner zone shows an anholocycle, with only parthenogenetic females (viviparous in Aphididae, oviparous in Adelgidae).

Fig. 3. Dioecious one-year holocycle (*Rhopalosiphum padi*). The inner zone represents the primary host (bird cherry, *Prunus padus* and allies), the outer zone the secondary (usually graminoids). The fundatrix gives birth to apterae, which in turn give birth to alatae, most of which migrate to the secondary hosts. In autumn males and gynoparae (viviparae giving birth to oviparae) migrate to the primary host, where mating and egg-laying take place. A small fraction of the viviparae may remain on the primary host throughout the summer.
Fig. 4. Dioecious one-year holocycle accompanied by a continuous anholocycle on the secondary host, e.g., *Pachypappella lactea* (leaf galls on aspen, *Populus tremula*; roots of spruce, *Picea abies*) or *Tetraneura ulmi* (leaf galls on elm, *Ulmus*; subterranean parts of grasses, *Poaceae*). Zones as in Fig. 3. In some years the Finnish populations on the primary hosts (for *P. lactea* in South Finland) may be more or less absent, and their existence is dependent on the populations on the secondary hosts.

Fig. 5. Dioecious two-year holocycle in Adelgidae, e.g., *Adelges laricis* (shoot galls on spruce, *Picea*; needles of larch, *Larix*). All females oviparous. The fundatrix (hatched from a fertilized egg) overwinters as a larva, and induces the formation of a pineapple-like gall on the primary host. All her offspring are alate (gallicolae) and migrate to the secondary host, where they lay eggs on the needles. The aphids hatching move to the twigs where they hibernate as young larvae (the ‘neosistens’ stage). In spring they move back to the needles and become adults (sistentes). Their offspring are either alate sexuparae and migrate to spruce, or apterous ‘progredientes’. In autumn the sexuparae fly to spruce and lay eggs which become sexual females and males, which mate. The females then lay eggs out of which new fundatrices hatch.
in Eriosomatinac. Species that complete their life cycle on one host are called monoecious (Fig. 2), whereas species with host alternation are called dioecious (or heteroecious) (Fig. 3). In many species holocycles are accompanied or supported by anholocyclic populations (Fig. 4). Most aphids have one-year cycles, but also two-year cycles do occur, e.g., in Eriosomatinac (Fordini) and Adelgidae (Fig. 5).

Often used morphological terms are shown in Fig. 6.

![Fig. 6. Often used morphological terms (Uroleucon cirsii (Linnaeus, 1758), freeze-dried specimen.).]
Abbreviations used in this paper

ad. = adult
al. = alata, alate, winged
ant. = antenna
apt. = aptera, apterous
HT2 = second segment of hind tarsus
juv. = juvenile, nymph
ov., ovp. = oviparous, ovipara (=oviparous female)
PT = Processus Terminalis (apical part of ultimate antennal segment)
B = Basal part of ultimate antennal segment
R = Rostrum
siph. = siphunculus
viv. = viviparous

The presence of the species in the Nordic countries is based on Heie (1980, 1982, 1986, 1992, 1994, 1995, 2004) and my own databases. The countries are denoted by letters as follows:
D = Denmark
F = Finland
Fa = Faroes
Gr = Greenland
I = Iceland
N = Norway
S = Sweden
Sv = Svalbard

Results

Phylum Arthropoda von Siebold, 1848
Class Insecta Linnaeus, 1758
Order Hemiptera Linnaeus, 1758
Superfamily Aphidoidea Latreille, 1802
Family Aphididae Latreille, 1802

Synoptic key and diagnoses for aphids on mosses, horsetails and ferns

For a summary of the host-plant relationships of aphids feeding on mosses, horsetails and ferns, see Appendix 1 and 2. In the diagnoses my own host records and relevant others from the database are denoted by an asterisk (*) after the host name. For geographical and phenological records from Finland, see Albrecht (2010).

Aphids on mosses (Bryophyta). Key A………………………………………………………… p. 8
Aphids on horsetails (Equisetophyta). Key B…………………………………………………… p. 30
Aphids on ferns (Polypodiophyta). Key C……………………………………………………… p. 39

Key A. Aphids on mosses (Bryophyta)

Synopsis
AA. Siphunculi elongate, more or less cylindrical…………………………………………… p. 9
AAA. Siphunculus with distinct apical flange………………………………………… p. 9
AAB. Siphunculus without flange……………………………………………………… p. 14
AABA. Siphuncular aperture terminal………………………………………………  p. 14
AABB. Siphuncular aperture subterminal…………………………………………… p. 16
AB. Siphunculi absent or present as pores, at most raised on low cones................. p. 19
ABA. Body extremely flattened, circular or broadly oval........................................ p. 19
ABB. Colour pink to orange; siphuncular pores on low cones.............................. p. 20
ABC. Colour cream to light brown; dorsum with brown spatulate hairs................... p. 21
ABD. Colour whitish, cream pale green or pale yellow; dorsal hairs pointed.......... p. 22
ABDA. Body robustly built, global or ovoid, 0.5–1.5 mm. Tarsi with segments fused (prac-
tically 1-segmented); antennae 4–5-segmented. Legs, antennae and rostrum short
and stout................................................................................................................... p. 22
ABDB. Body elongate, 1–2.5 mm. Legs, antennae and rostrum more slender; tarsi 1–2-
segmented; antennae 5–6-segmented............................................................... p. 25
ABDBA. RIV+V with a broad, distinct, pale subapical zone. Head without wax gland plates
............................................................................................................................... p. 25
ABDBB. Pale subapical zone on RIV+V narrow, indistinct or absent. Wax glands may be
present on head......................................................................................................... p. 27

AA. Siphunculi elongate, more or less cylindrical
AAA. Siphunculus with distinct apical flange

Subfamily Aphidinae Latreille, 1802
Tribe Macrosiphini Wilson, 1910
Genus Decorosiphon Börner, 1939

*Decorosiphon corynothrix* Börner, 1939
Fig. 7

Diagnosis

Apterae 1.2–1.7 mm, shiny olive, brownish yellow or reddish brown, juveniles green–olive brown, with
whitish wax dusting, the rupture lines (which break at moulting) exceptionally distinct, due to denser
wax coating. Antennae longer than body. Siphunculi strongly swollen distally, with well-developed
apical flange. Hairs on body and appendages very long, with spatulate distal part. Ad. and juv. can
be found all the year. Peat bogs, damp places in coniferous forests, also deciduous forests. Often on
*Polytrichum* interspersed in *Sphagnum* tussocks. Monoecious, seems to prefer Polytrichaceae. Not ant-
attended.

Recorded hosts

Hylocomiaceae: *Rhytidadelphus squarrosus*; Polytrichaceae: *Atrichum undulatum* *, Polytrichastraum
formosum, Polytrichum commune, juniperinum, strictum*.

Distribution

D F N S.

Genus *Myzodium* Börner, 1949

*Myzodium modestum* (Hottes, 1926)
Fig. 8

Diagnosis

Apterae 1.3–1.7 mm, shape *Myzus*-like, bronze to bronzy black; dorsal cuticle heavily sclerotized, rugose;
thinly wax-covered below. Juveniles paler, with shorter body, smoother dorsum and more extensive
wax dusting, also dorsally. Frontal tubercles well developed, rounded, nodulose. Siphunculi slightly
s-curved, with distinct apical constriction and flange. Aduls and juveniles can be found all year. Peat

Recorded hosts
Bryaceae: *Pohlia*; Grimmiaceae: *Racomitrium*; Polytrichaceae: *Atrichum undulatum*, *Polytrichum commune*; Sphagnaceae: *Sphagnum* (perhaps only interspersed on other mosses).

Distribution
F Gr S.

Fig. 7. *Decorosiphon corynothrix* Börner, 1939. A. Apt. and juv. in *Polytrichum commune* sample. B. Apt. on *Sphagnum magellanicum* (with interspersed *Polytrichum strictum*). C. Apt. juv. on *Polytrichum commune*. D. Apt. juv. on *S. magellanicum*, showing rupture line.
Fig. 8. Myzodium modestum (Hottes, 1926). A–B. Apt. and juv. from Polytrichum commune sample.
Genus *Pseudacaudella* Börner, 1950

*Pseudacaudella rubida* (Börner, 1939)

**Fig. 9**

**Diagnosis**

Apterae 0.7–1.2 mm, shiny green, grey-green, olive or brown, sometimes with rusty patches. Half-grown juveniles often brownish yellow. Adult apterae with transverse, partly fused, segmental sclerites on thorax and abdomen. Wax-dusted between sclerites and ventrally. Hibernating juveniles dark olive or purple, covered in a thick, easily cracking wax coating. Frontal tubercles undeveloped. Siphunculi with distinct apical constriction and flange. Can be found all year, during the cold season as hibernating nymphs. A ubiquitous species, occurring on a wide range of mosses on dry rock and stones, on the

**Fig. 9.** *Pseudacaudella rubida* (Börner, 1939). **A.** Apt. and juv. from *Hylocomium splendens* sample (grid 1 mm). **B.** Apt. and **C.** hibernating juv. on *Pleurozium schreberi*. **D–E.** Hibernating juv on *Calliergon cordifolium*. 
forest floor and in damp depressions of spruce and pine forests, fallow fields, deciduous forests, even submerged in forests swamps. Monoecious. Not ant-attended.

**Recorded hosts**

**Distribution**
D F S.

**Genus Cryptaphis** Hille Ris Lambers, 1947

*Cryptaphis poae* (Hardy, 1850)

**Fig. 10**

**Diagnosis**
Apterae 1.3–2.0 mm, shiny, greyish, olive, green or yellowish with brownish markings, to brownish black. Body hairs long, stiff, capitate. Siphunculi straight, with apical flange. Monoecious. Feeds on grasses at or below soil level or in moss tufts, and is sometimes found in moss samples.

**Distribution**
D F N S.

**Fig. 10. Cryptaphis poae** (Hardy, 1850). Apt. from *Rhytidiadelphus squarrosus* sample. Grid 1 mm.
AAB. Siphunculus without flange
AABA. Siphuncular aperture terminal

Genus *Jacksonia* Theobald, 1923

*Jacksonia papillata* Theobald, 1923

Fig. 11

**Diagnosis**
Diagnosis based on Heie (1994, 2004). Apterae 1.3–1.9 mm, green-olive-brown-reddish. Cuticle rough, squamous or nodulose, particularly on head and antennae. Antennal tubercles well developed, their inner sides converging. Siphunculi squamose, from a thick base narrowing to a slender apical half; aperture small, terminal. Monoecious. Lives on basal parts of grasses and may, in addition to grasses, also feed on mosses.

**Recorded hosts**

**Distribution**
D Fa I N S.
Genus *Muscaphis* Börner, 1933  
Subgenus *Muscaphis* Börner, 1933

*Muscaphis musci* Börner, 1933  
Fig. 12

**Diagnosis**
Diagnosis based on Blackman & Eastop (2014) and Heie (2004). Apterae 0.5–1.0 mm, shiny, greyish yellow, pale brown or dark olive. Siphunculi reddish brown, cylindrical; apex truncate without constriction or flange; aperture terminal. Monoecious?

**Recorded hosts**

**Distribution**
D.

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*Fig. 12. Muscaphis musci* Börner, 1933. Aptera with siphunculus. (photo Roger Blackman, from Blackman 2010, with license from The Royal Entomological Society).
AABB. Siphuncular aperture subterminal

Subgenus *Aspidaphium* Börner, 1933

*Muscaphis escherichi* (Börner, 1939)

Fig. 13

**Diagnosis**

Apterae 0.7–1 mm, shiny red-brown, ochreous or olive brown. Legs and antennae slightly paler. Dorsum reticulate, abdominal mid-dorsum fairly smooth, siphunculi squamose. Siphunculi narrowly conical, slightly dorsoventrally flattened, tapering towards a rounded apex; aperture small, subapical. PT/B = 0.6–1.16; RIV+V/HT2 = 1.2–1.5. Shady broad-leaved, mixed and coniferous forests, mesotrophic meadows. Can be found all year. Monoecious. Not ant-attended.

**Recorded hosts**


**Distribution**

D F N S.

**Note**

The question of whether the moss-feeding *M. escherichi* represents the secondary host generations of the *Sorbus*-feeding *M. drepanosiphoides* (Börner, 1939), which would make the two taxa synonymous (Blackman & Eastop 2014), has not yet been definitely resolved, and is awaiting results from molecular analyses. Until then, I prefer to continue regarding the two taxa as separate species, because they are morphologically distinctive. Among other characteristics are the siphunculi, which are generally quite constant throughout the parthenogenetic morphs. In the *Sorbus*-feeding fundatrix and alatae they are long, black and truncate, with a large terminal aperture. The transfer experiments of *M. drepanosiphoides* from *Sorbus* to *Plagiothecium laetum* performed by Stekolshchikov & Shaposhnikov (1993) would, however, give support for the synonymy.

*Muscaphis cuspidata* (Stroyan, 1955)

Fig. 14

**Diagnosis**

Apterae 0.7–1 mm, dark greenish brown to black, abdominal dorsum and siphunculi black, legs brown. Dorsum reticulate, siphunculi conical, distinctly dorsoventrally flattened, squamose–papillose, aperture small, subapical. PT/B = 1.2–1.5, RIV+V/HT2 = 0.9–1.15. Can be found all the year round. Pond and stream margins, often submerged. Monoecious. Not ant-attended.

**Recorded hosts**

Amblystegiaceae: *Drepanocladus aduncus*; Brachytheciaceae: *Brachythecium rivulare*; Hypnaceae: *Calliergonella cuspidata*.
Distribution

Fig. 14. Muscaphis cuspidata (Stroyan, 1955). A–B. Apt. on Brachythecium rivulare. C. Ovip on Brachythecium rivulare.
AB. Siphunculi absent or present as pores, at most raised on low cones
ABA. Body extremely flattened, circular or broadly oval

Subfamily Hormaphidinae
Tribe Hormaphidini
Genus *Hormaphis* Osten-Sacken, 1861

*Hormaphis betulae* (Mordvilko, 1901)
Fig. 15

**Diagnosis**
Apterae 1–2 mm, pale yellow, circular, flat; older juveniles and adults on secondary host with marginal wax rim. Dioecious. Alternates between witch-hazel *Hamamelis* (Hamamelidaceae) and birch *Betula*

Fig. 15. *Hormaphis betulae* (Mordvilko, 1901). Apt. (ad. and juv.) on *Betula pubescens*. 
(Betulaceae). Anholocyclic in Northern Europe, living on birch. Overwintering in the moss layer of mixed coniferous forests and bogs, and during the cold season seen in moss samples.

**Distribution**

F.

**ABB. Colour pink to orange; siphuncular pores on low cones**

Subfamily Eriosomatinae

Tribe Eriosomatini

Genus *Tetraneura* Hartig, 1841

*Tetraneura ulmi* (Linnaeus, 1758)

Fig. 16

**Diagnosis**

Apterae 1.5–3 mm, pink, orange or purple, with a thin iridescent wax layer that is easily worn off. Siphuncular pores elevated on low cones. Dioecious. Alternating between elm *Ulmus* (Ulmaceae) and

![Image of Tetraneura ulmi](image-url)
grass roots (Poaceae). Anholocyclic populations on secondary hosts common all year, and particularly juveniles are often seen in moss samples. Often in association with ants.

**Distribution**
D F N S.

**ABC. Colour cream to light brown; dorsum with brown spatulate hairs**

Tribe Fordini
Genus *Geoica* Hart, 1894

*Geoica utricularia* (Passerini, 1856)
Fig. 17

**Diagnosis**
Apterae 1.2–2.2 mm, cream to light brown, dusted with white wax. Legs and antennae short and stout, tarsi two-segmented. Body with numerous brown spatulate hairs. Dioecious, alternating between leaf

![Image of Geoica utricularia](image.png)

**Fig. 17.** *Geoica utricularia* (Passerini, 1856). Apt. on grass root.
galls on pistachio *Pistacia* (Anacardiaceae) and grasses (Poaceae). In Northern Europe anholocyclic on grass roots (Poaceae). I have observed a few individuals feeding on *Polytrichum commune* (Polytrichaceae) in a *Lasius flavus* nest mound during extreme drought when the grasses had dried out. Always accompanied by *Lasius* ants.

**Distribution**

DFS.

**Recorded moss host**

Polytrichaceae *Polytrichum commune* (occasionally).

**ABD. Colour whitish, cream, pale green or pale yellow; dorsal hairs pointed**

**ABDA. Body robustly built, global or ovoid, 0.5–1.5 mm. Tarsi with segments fused (in practice 1-segmented); antennae 4–5-segmented. Legs, antennae and rostrum short and stout**

Genus *Melaphis* Walsh, 1867

*Melaphis rhois* (Fitch, 1866)

**Diagnosis**

Diagnosis based on Pike *et al.* (2012). Resembling *Pachypappella lactea* but marginal wax gland plates on segments 1–6 in six longitudinal rows (in *P. lactea* in four rows on segments 3–6). Legs, antennae and rostrum short and stout; tarsi 1-segmented, ant. normally 4-segmented. RIV+V without pale subapical zone. Dioecious, alternating between leaf galls on *Rhus glabra* and *R. hirta* (syn. *typhina*, Anacardiaceae) and mosses (Bryophyta). In northern Europe anholocyclic on mosses. For detailed descriptions, see Pike *et al.* (2012).

**Recorded secondary hosts**


**Distribution**

S (if correctly identified: Heie’s (1980) fig. 243 based on material from Sweden is probably *Pachypappella lactea*).

Tribe Pemphigini

Genus *Pachypappella* Baker, 1920

*Pachypappella lactea* (Tullgren, 1909)

Fig. 18, 19D

**Diagnosis**

Apterae ovoid, robustly built, 0.6–1 mm, whitish, with a thin wax-dusting and exuding wax tufts from spinal and pleural wax gland plates on abdominal segments 3–6 (4 longitudinal rows of plates); marginal wax gland plates absent. Legs, antennae and rostrum short and stout. Antennae 4–5-segmented. Hind femur not distinctly thickened. RIV+V with a rather narrow and indistinct pale subapical zone. Tarsal segments fused (the segment border depicted in fig. 66b by Blackman & Eastop (1994, 2014) looks anomalous, and may be an artefact).

Dioecious, alternating between leaf galls on aspen *Populus tremula* (Salicaceae) and Norway spruce *Picea abies* (Pinaceae), where the aphids live on thin roots within and above the mor layer (a compacted
humus layer beneath the moss layer), among moss or litter. The apterae reside in nests of dense wax wool, 1.5–2 mm across, usually one aphid in each. The nests often occur in small groups, often within the looser, wider and less distinctly delimited wax exudate of *Prociphilus xylostei* (deGeer, 1773) and *Pachypappa* species. *P. lactea* has a continuous anholocyclic population on spruce roots. Not associated with ants. Danielsson (1990a, 1990b) gives keys and descriptions of the root-feeding generations of *Pachypappella, Gootiella* and *Pachypappa*. See also Carter & Danielsson (1991).

**Distribution**

F N S.

**Genus Gootiella** Tullgren, 1925

**Gootiella tremulae** Tullgren, 1925

Fig. 19C

**Diagnosis**

Diagnosis based on Danielsson (1990b). Apterae globular to ovoid, 0.9–1.5 mm, grey, covered in white wax. In many respects resembling *Pachypappella lactea*, but readily distinguished by the remarkably thickened hind femora. Antennae 5-segmented. Dioecious, alternating between *Populus tremula* (Salicaceae) and juniper *Juniperus communis* (Cupressaceae), where the aphids live in wax nests similar to those of *P. lactea*, and commonly overwinter there (Danielsson 1990b).

**Distribution**

D F N S.

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**Fig. 19.** *Gootiella, Pachypappa* and *Pachypappella*. Apt. alienicolae (born on secondary host). A–B. Spinal wax gland on abd. terg. 6 of *Pachypappa populi* (Linnaeus, 1758) (A) and *P. vesicalis* Koch, 1856 (B). C. Hind leg of *Gootiella tremulae* Tullgren, 1925. D–G. Hind tibia and tarsus of *Pachypappella lactea* (Tullgren, 1909) (D), *Pachypappa tremulae* Tullgren, 1925 (E), *P. populi* (Linnaeus, 1758) (F) and *P. vesicalis* Koch, 1856 (G). A–B and D–G after Carter & Danielsson 1991, C after Danielsson 1990b. All modified.
ABDB. Body elongate, 1–2.5 mm. Legs, antennae and rostrum more slender; tarsi 1–2-segmented; antennae 5–6-segmented

ABDBA. RIV+V with a broad, distinct, pale subapical zone. Head without wax gland plates

Genus *Pachypappa* Koch, 1856

*Pachypappa populi* (Linnaeus, 1758)

Fig. 19 A, F; 20

**Diagnosis**

Apterae 1–2 mm, pale yellowish with wax tufts posteriorly. Cells in abdominal wax gland plates with a small central spot (Fig. 19A). Segments 1 and 2 of tarsi less distinctly separated than in *P. tremulae* (Linnaeus, 1761) and *P. vesicalis* Koch, 1856. Legs longer, hind femur more than 4 × its maximum width. Antennae usually 6-segmented, PT finger-like. Spines at apices of tibiae weak, not much stronger than the hairs on first tarsal segment. Hind tibia on dorsal side bearing 2–5 spine-like hairs with short, blunt apices. Dioecious. Alternating between *Populus tremula* (Salicaceae) and *Picea abies* roots (Pinaceae), where wax-covered colonies are formed. Anholocyclic hibernation occurs.

**Distribution**

F N S. See also Carter & Danielsson (1991).

Fig. 20. *Pachypappa populi* (Linnaeus, 1758). Apt. from mycorrhizal *Picea abies* root in the moor layer of a shady spruce forest.
Fig. 21. *Prociphilus xylostei* (deGeer, 1773). A–B. Apt. on mycorrhizal *Picea abies* roots under *Pleurozium schreberi*.
**Pachypappa tremulae** (Linnaeus, 1761)
Fig. 19E

**Diagnosis**
Apterae 1–2 mm. Resembling *P. populi*. Cells in abdominal wax gland plates with a larger central spot (as in Fig. 19B). Segments 1 and 2 of all tarsi distinctly separated from each other. Spines at apices of tibiae very robust, much stronger than hairs on first tarsal segment. Dorsal hairs on hind tibia with fairly short and blunt apices. Life cycle as in the previous species. Anholocyclic hibernation on roots of spruce *Picea* is common.

**Distribution**
D F N S. See also Carter & Danielsson (1991).

**Pachypappa vesicalis** Koch, 1856
Fig. 19B, G

**Diagnosis**
Diagnosis based on Carter & Danielsson (1991). Resembling *P. populi*. Antenna usually 5-segmented, PT extremely short. Cells in abdominal wax gland plates with a larger central spot (Fig. 19B). Spines at apices of tibiae very robust, much stronger than the hairs on first tarsal segment. Dorsal hairs on hind tibia with long, pointed apices. Dioecious. Alternates between white poplar *Populus alba* (Salicaceae) and *Picea* roots (Pinaceae) where the aphids live in wax nests similar to those of *Pachypapella lactea* (Carter & Danielsson 1991).

**Distribution**
F S.

**Prociphilus xylostei** (deGeer, 1773)
Fig. 21

**Diagnosis**
Apterae 1.2–2 mm, pale green with large wax gland plates (and wax tufts unless worn off) on head and abdomen. RIV+V = 0.2 × HT2, without pale subapical zone. Legs and antennae slender. Dioecious. Alternating between honeysuckle *Lonicera* (Caprifoliaceae) and thin, mycorrhizal *Picea abies* roots (Pinaceae), where the colonies are coated with wax wool and where the aphids may hibernate. *P. xylostei* apparently has a continuous anholocyclic population on spruce roots. Common in moss samples from spruce forests.

**Distribution**
D F N S.
**Prociphilus pini** (Burmeister, 1835)

Fig. 22

**Diagnosis**

Apterae 1.2–2 mm. As *P. xylostei* but cream or pale pinkish rather than greenish or yellowish. RIV+V as long as HT2, with narrow and indistinct subapical zone. Dioecious. Alternating between *Crataegus*

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**Fig. 22.** *Prociphilus pini* (Burmeister, 1835). **A.** Colony on thin *Pinus sylvestris* root in the moor layer of a pine forest on rock. **B–C.** Apt. from *Polytrichum commune* sample.
(Rosaceae) and thin roots of *Pinus* (Pinaceae). May be found all the year in moss samples in pine forests, especially on rock.

**Distribution**

D F N S.

*Prociphilus bumeliae* (Schrank, 1801)

**Diagnosis**

Diagnosis based on Heie (2004). Apterae about 2.9 mm, wax-covered. Two pairs of wax gland plates on head. Posterior plates on head better developed than anterior ones. A narrow pale subapical zone on RIV+V distinct. Dioecious, alternating between ash *Fraxinus excelsior* (sometimes other Oleaceae) and fir *Abies* (Pinaceae), where it feeds in wax-covered colonies on the roots.

**Distribution**

D F S.

*Prociphilus fraxini* (Fabricius, 1777)

**Diagnosis**

Diagnosis based on Heie (2004). Apterae 1.8–2.7 mm, pale, wax-covered. Very similar to *P. bumeliae*, but the posterior wax gland plates on head weakly developed, sometimes absent. Dioecious, alternating between *Fraxinus excelsior* (Oleaceae) and roots of *Abies* (Pinaceae), where wax-covered colonies are formed.

**Fig. 23.** *Aphis equisetica* Ossiannilsson, 1964. Aptera (redrawn after Heie 1986).
Key B. Aphids on horsetails (Equisetophyta)

Synopsis

BA. Siphunculi present, half as long as cauda or longer…………………………………… p. 30
BAA. Lateral frontal tubercles hardly developed; antennae shorter than body……… p. 30
BAB. Lateral frontal tubercles well developed; antennae usually longer than body

BABA. Lateral frontal tubercles with diverging inner margins………………………… p. 33
BABBB. Lateral frontal tubercles with parallel or converging inner margins…………… p. 35
BB. Siphunculi absent……………………………………………………………………..……  p.  37

BA. Siphunculi present, half as long as cauda or longer

BAA. Lateral frontal tubercles hardly developed; antennae shorter than body

Subfamily Aphidinae Latreille, 1802
Tribe Aphidini Latreille, 1802
Genus Aphis Linnaeus, 1758

Aphis equisetica Ossiannilsson, 1964
Fig. 23

Diagnosis

Diagnosis based on Heie (1986). Aptera 1.4–2.0 mm, light or dark green without markings. Head, antennae, tarsi and tips of tibiae rather dark. Antennae about half as long as body. Siphunculi shorter than cauda, dusky or pale, with dark apices. Monoecious.

Recorded hosts

Equisetum pratense, E. sylvaticum.

Distribution

S.

Aphis gossypii Glover, 1877

Diagnosis

Aptera 0.8–1.7 mm. Pale green to blackish green; siphunculi black. Small, pale yellow specimens occur in in crowded colonies or hot conditions. In cold temperate regions mostly in glasshouses. Dioecious with several unrelated plants as primary hosts, in Europe, however, mostly anholocyclic. Very similar to A. beccabungae Koch, 1855 (Fig. 24) and other species of the A. frangulae group. See Blackman & Eastop (2014) and Heie (1986) for differences and a more complete account. Dioecious but usually anholocyclic, polyphagous.

Recorded Equisetum host

E. sylvaticum.
Genus *Rhopalosiphum* Koch, 1854

*Rhopalosiphum padi* (Linnaeus, 1758)

**Fig. 25**

**Diagnosis**

Aptera 1–2.4 mm, olive mottled with darker green. Siphuncular area and often also tip of abdomen rust-red. Juveniles paler, matt, with thin wax dusting. Siphunculus almost straight, longer than cauda, with subapical constriction and apical flange. Dioecious, alternating between *Prunus* and graminoids (Poaceae, Cyperaceae, Juncaceae), rarely on other hosts, exceptionally on *Equisetum*. Recorded from *E. sylvaticum*.

**Distribution**

D N F Fa I S.

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**Fig. 24.** *Aphis beccabungae* Koch, 1855. Apt. and juv. on *Galeopsis speciosa*. *A. beccabungae* is very similar to *A. gossypii* Glover, 1877.
Fig. 25. *Rhopalosiphum padi* (Linnaeus, 1758), apt. and juv. on *Poa pratensis*.
BAB. Lateral frontal tubercles well developed; antennae usually longer than body
BABA. Lateral frontal tubercles with diverging inner margins

Tribe Macrosiphini Wilson, 1910
Genus *Macrosiphum* Passerini, 1860

*Macrosiphum equiseti* (Holman, 1961)

Fig. 26

**Diagnosis**
Aptera 1.6–3 mm, bright green without markings, body with thin whitish wax dusting on venter (adults) or all over (juveniles). Siphunculi length rarely over 1.35 × cauda length. Holocyclic, monoecious. Damp, shady broad-leaved and spruce forests.

**Recorded hosts**
*Equisetum arvense, E. pratense, E. sylvaticum*, *E. telmateia*.

**Distribution**
F S.

Genus *Sitobion* Mordvilko, 1914

*Sitobion avenae* (Fabricius, 1775)

Fig. 27

**Diagnosis**
Aptera 1.2–3.5 mm, green with black muscle sclerites. Legs and antennae partly black. Siphunculi black. Cauda pale. Abdominal dorsum sclerotised, shiny, all green, all black, or green with grey or black transverse bars. Juveniles matt, apt. juv. green, al. juv. brown. Holocyclic, monoecious on grasses (Poaceae), exceptionally on *Equisetum sylvaticum*. Not ant-attended.

**Distribution**
D F N S.

*Sitobion fragariae* (Walker, 1848)

**Diagnosis**
Similar to *S. avenae*, but generally paler, usually without blackened patches on dorsum. Siphunculi longer, more than 1.7 × cauda. Holocyclic, dioecious, alternating between *Rubus* subgenus *Rubus* and grasses (Poaceae). Exceptionally on *Equisetum*, recorded from *E. sylvaticum*.

**Distribution**
D F Fa N S.
Fig. 26. Macrosiphum equiseti (Holman, 1961) on Equisetum sylvaticum. A–C. Apterae. D–E. Juveniles.
BABB. Lateral frontal tubercles with parallel or converging inner margins

Genus *Aulacorthum* Mordvilko, 1914

*Aulacorthum solani* (Kaltenbach, 1843)

Fig. 28

**Diagnosis**

Aptera 1.2-2.6 mm, green with dark green spots in front of siphunculi. At most with very slight wax dusting ventrally. Occupying a wide range of habitats, also a common indoor pest. Holocyclic or anholocyclic, monoecious, polyphagous. Not ant-attended.

**Recorded Pteridophyta hosts**


**Distribution**

D F I N S.

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Fig. 27. *Sitobion avenae* (Fabricius, 1775). Apterae and juveniles on A. *Dactylis glomerata* and B. *Elytrigia repens*.
Fig. 28. *Aulacorthum solani* (Kaltenbach, 1843). Apterae and juveniles on *Abutilon* sp.

Fig. 29. *Neomyzus circumflexus* (Buckton, 1876). Aptera. (from Dransfield & Brightwell 2015, licensed under Creative Commons Attribution 3.0, downloaded 30 Jun. 2015).
Genus *Neomyzus* van der Goot, 1915

*Neomyzus circumflexus* (Buckton, 1876)

**Fig. 29**

**Diagnosis**
Diagnosis based on Heie (2004). Rather similar to *Aulacorthum solani*. Whitish, yellow or green; abdomen with brown or black markings, usually including a horseshoe-shaped patch. Monoecious, polyphagous, apparently anholocyclic (sexuales not recorded).

**Recorded Pteridophyta hosts**

**Distribution**
D F N S, in Northern Europe mainly indoors.

Genus *Myzus* Passerini, 1860

*Myzus cerasi* (Fabricius, 1775)

**Fig. 30**

**Diagnosis**
Aptera 1–1.5 mm, shining black, almond-shaped. Legs and antennae partly pale. Juveniles brown. Holocyclic, dioecious, alternating between *Prunus* and herbs of several families, rarely on *Equisetum*.

**Recorded Pteridophyta host**
*Equisetum* sp.

**Distribution**
D F N S.

**BB. Siphunculi absent**

Subfamily Eriosomatinae

Tribe Fordini

Genus *Paracletus* von Heyden, 1837

*Paracletus cimiciformis* von Heyden, 1837

**Fig. 31**

**Diagnosis**
Aptera 2.2–3.4 mm, broadly oval, flattened, rather shining cream with brown legs and antennae. Dioecious, alternating between leaf galls on *Pistacia* and roots of grasses and herbs. In N. Europe anholocyclic, normally feeding on grass (Poaceae). In xerothermic habitats. Lives in association with ants, usually *Tetramorium caespitum* (Linnaeus, 1758).

**Distribution**
F S.
Fig. 30. *Myzus cerasi* (Fabricius, 1775). Apt. and juv. on *Prunus cerasus*.

Fig. 31. *Paracletus cimiciformis* von Heyden, 1837. Apera in nest of *Tetramorium caespitum* (Linnaeus, 1758).
Recorded Pteridophyta host
Equisetaceae: Equisetum arvense.

Key C. Aphids on ferns (Polypodiophyta)

Synopsis

CA. Black with pale legs and siphunculi, and pale-ringed antennae………………………… p. 39
CB. Green, brown, yellowish or reddish aphids……………………………………………… p. 40
CBA. Lateral frontal tubercles hardly developed; mainly on aquatic plants……… p. 40
CBB. Lateral frontal tubercles with diverging inner margins………………………… p. 41
CBBA. Siphunculi distinctly swollen distally…………………………………………… p. 41
CBBB. Siphunculi at most slightly swollen……………………………………………… p. 41
CBC. Lateral frontal tubercles with parallel or converging inner margins……………… p. 43

CA. Black with pale legs and siphunculi, and pale-ringed antennae

Subfamily Aphidinae Latreille, 1802
Tribe Macrosiphini Wilson, 1910
Genus Idiopterus Davis, 1909

Idiopterus nephrelepidis Davis, 1909
(Fig. 32)

Diagnosis

Diagnosis based on Heie (1994). Aptera 1.2–1.6 mm. Apparently anholocyclic, monoecious, in N Europe in greenhouses.

Fig. 32. Idiopterus nephrelepidis Davis, 1909. Aptera (photo Roger Blackman, from Blackman 2010, with license from The Royal Entomological Society).
Recorded hosts

Distribution
D S.

CB. Green, brown, yellowish or reddish aphids
CBA. Lateral frontal tubercles hardly developed; mainly on aquatic plants

Tribe Aphidini Latreille, 1802
Genus *Rhopalosiphum* Koch, 1854

*Rhopalosiphum nymphaeae* (Linnaeus, 1761)

Fig. 33

Diagnosis
Aptera 1.5–2.5 mm, brown to olive, dusted with greyish wax, particularly on venter and margins, including legs and antennae. Siph. swollen, with a distinct constriction before the apical flange. Holocyclic, dioecious, alternating between *Prunus* and many unrelated, mostly aquatic or semiaquatic plants. Not ant-attended.

Fig. 33. *Rhopalosiphum nymphaeae* (Linnaeus, 1761). Aptera on *Myriophyllum spicatum*. 
Recorded Pteridophyta hosts
Marsileaceae: *Marsilea quadrifolia*, *M. strigosa*; Salviniaceae: *Azolla caroliniana*, *A. filiculoides*, *Salvinia auriculatia*, *S. natans*.

Distribution
D F N S.

CBB. Lateral frontal tubercles with diverging inner margins
CBBA. Siphunculi strongly swollen distally

Tribe Macrosiphini Wilson, 1910
Genus *Amphorophora* Buckton, 1876

*Amphorophora ampullata* Buckton, 1876
Fig. 34

Diagnosis
Aptera 3–5 mm, bright green without markings. Eyes red. Holocyclic, monoecious. Shady places, parks, gardens, mixed and deciduous forests. Not ant-attended.

Recorded hosts

Distribution
D F N S.

CBBB. Siphunculi at most slightly swollen

Genus *Macrosiphum* Passerini, 1860

*Macrosiphum lapponicum* Shaposhnikov, 1964

Diagnosis

Recorded host
Athyriaceae: *Athyrium distentifolium*.

Distribution
Known from NW Russia only.
Fig. 34. Amphorophora ampullata Buckton, 1876. A. Aptera on Dryopteris carthusiana. B–C. Apterae and juveniles on Athyrium filix-femina (B) and Matteuccia struthiopteris (C), aptera in C parasitized.
Macrosiphum dryopteridis (Holman, 1959)
Fig. 35

Diagnosis
Aptera 2.5–4.2 mm, yellowish green (rarely bright green). Eyes black. Abd. dorsum sclerotised (but neither darkened nor distinctly glossy), segmental borders obliterated. Siphunculi slightly swollen distally. Ant. segment 3 with 0–10 rhinaria. rIV+V less than 0.14 mm. Holocyclic, monoecious. Shady places, parks, gardens, mixed and deciduous forests. Not ant-attended.

Recorded hosts

Distribution
F N S.

Macrosiphum ptericolens Patch, 1919

Diagnosis
Diagnosis based on Blackman & Eastop (2006). Rostrum IV+V more than 0.14 mm long. Aptera 2.3–3.3 mm, yellowish green to dark green. Siphunculi slender, tapering distally. Holocyclic, monoecious.

Recorded host
Dennstaedtiaceae: Pteridium aquilinum.

CBC. Lateral frontal tubercles with parallel or converging inner margins
Genus Aulacorthum Mordvilko, 1914

Aulacorthum solani (Kaltenbach, 1843)
Fig. 28

Diagnosis
Green with dark green patches in front of siphunculi. See p. 35, under BABB.

Genus Neomyzus van der Goot, 1915

Neomyzus circumflexus (Buckton, 1876)
Fig. 29

Diagnosis
Whitish, yellow or green with brown or black horse-shoe shaped marking. See p. 37, under BABB.
Fig. 35. Macrosiphum dryopteridis (Holman, 1959). Apterae on Athyrium filix-femina.
Genus *Myzus* Passerini, 1860

*Myzus persicae* (Sulzer, 1776)

Fig. 36

**Diagnosis**

Aptera 1.2–2.2 mm, almond-shaped, pale yellow to dirty yellow, olive, green, brownish, purple or reddish. Siphunculi twice as long as cauda or more, slightly swollen beyond middle. Dioecious.

Fig. 36. *Myzus persicae* (Sulzer, 1776). Apterae and juveniles on *Capsella bursa-pastoris*.
alternating between peach (Prunus persica) and plants of more than 40 families. Anholocyclic in the north and in the tropics. Usually in urban environments, also a common indoor pest.

**Recorded Pteridophyta host**

Pteridaceae: Adiantum sp.

**Distribution**

D F N S.

**Discussion**

Up to now, identification keys for aphids have been based on macerated specimens on microscopic slides, much of the emphasis being laid on measurements and indices based on them; in most cases only the ranges are given, without statistical parameters. Attempting to identify fresh or freeze-dried aphids using these keys may at first thought feel troublesome, but for the present that is the way we have to go. And it works, provided you have a good stereo microscope. Almost all of the characters described in the keys are well visible in unmacerated material, so slides need only exceptionally be made. And often a leg or antenna immersed in water on a slide is enough. One goal of this guide is to enhance the use of characters lost in the maceration process, many of which participate in the distinctiveness of the species and make it possible to identify as many of them as possible even in the field, although it is always advisable to look up the species in the literature and check the identification.

Most aphids are easily found by simply inspecting the plants, keeping the eyes open for abnormal growth, the presence of ants and other phenomena that may indicate the presence of aphids. Aphids associated with mosses are, however, generally considered rare and difficult to find. Aphids feeding on mycorrhizal conifer roots are readily revealed by the white wax wool they produce, but the genuine moss-feeders are almost impossible to spot in the field. Besides being small, they live hidden in the moss tussocks and are often cryptically coloured. In funnel samples they usually die before reaching the collection jar, which perhaps explains the seeming rarity of moss aphids. The best way of finding them is to dry all excess water from the moss, sieve it through a 1–2 mm mesh and study the sample alive under a stereo loupe. It seems quite safe to anticipate that, with the right methodology applied, moss aphids will prove to be surprisingly common throughout Northern Europe.

**Acknowledgements**

Among the numerous persons and institutions that have contributed to this guide, I wish to thank the Ministry of the Environment and the Finnish Museum of Natural History for allowing me to participate in the Putte Programme, which enabled me to study aphids full-time for five years, getting me started on the project, and for further support. Special thanks are due to my friend Jouni Issakainen for fruitful discussions and excursions leading to the discovery of numerous new interesting records of aphids. Above all, I want to thank my wife Margareta for fully accepting my work with these minute animals, for letting me set up a laboratory at home, and for time after time offering me a helping hand. My colleague Lauri Kaila kindly commented on the manuscript and suggested many valuable improvements. Thanks are also due to Dr Bill Blakemore of The Royal Entomological Society for allowing me to use copyrighted photographs.

**References**


*Manuscript received: 17 April 2015*

*Manuscript accepted: 11 August 2015*

*Published on: 21 October 2015*

*Topic editor: Koen Martens*

*Desk editor: Kristiaan Hoedemakers*

Printed versions of all papers are also deposited in the libraries of the institutes that are members of the EJT consortium: Muséum National d’Histoire Naturelle, Paris, France; Botanic Garden Meise, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Natural History Museum, London, United Kingdom; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark.
Appendix 1

Summary of the host relationships of moss-feeding aphids of northern Europe. (Colours: Green = monoecious. Blue = dioecious, on primary host (none in this table). Red = dioecious, on secondary host. * = my own records).

**BRYOPHYTA**

*Sphagnaceae* Dumort.

*Sphagnum* L.

- *Melaphis rhois*
- *Myzodium modestum magellanicum* Brid.
- *Pseudacaudella rubida* recurvum H.H.Blom
- *Pseudacaudella rubida*

**Polytrichaceae** Schwägr.

*Attrichum* P.Beauv.

- undulatum (Hedw.) P.Beauv.
  - *Decorosiphon corynothrix*
  - *Muscaphis musci*
  - *Myzodium modestum*

*Polytrichastrum* G.L.Sm.

-formosum (Hedw.) G.L.Sm.
  - *Decorosiphon corynothrix*

*Polytrichum* Hedw.

-commune Hedw.
  - *Decorosiphon corynothrix*
  - *Geoica utricularia* (occasionally on mosses)
  - *Melaphis rhois*
  - *Muscaphis musci*
  - *Myzodium modestum*
  - *Pseudacaudella rubida*
  - *juniperinum Hedw.*
  - *Decorosiphon corynothrix*
  - strictum Sull.
  - *Decorosiphon corynothrix*

**Grimmiaceae** Arn.

*Racomitrium* Brid.

- *Myzodium modestum lanuginosum* (Hedw.) Brid.
  - *Pseudacaudella rubida*

**Dicranaceae** Schimp.

*Dicranum* Hedw.

- *Muscaphis escherichi*
- *Pseudacaudella rubida*

**Pottiaceae** Schimp.

*Barbula* Hedw.

- *Muscaphis musci*

*Tortula* Hedw.

*muralis* Hedw.
Muscaphis musci

Bryaceae Schwägr.
Bryum Hedw.
  Muscaphis musci
pallens Sw. ex anon.
    Jacksonia papillata (see text)
Pohlia Hedw.
  Muscaphis escherichi
Myzodium modestum
Rhodobryum (Schimp.) Limpr.
roseum (Hedw.) Limpr.
  Muscaphis escherichi*

Mniaceae Schwägr.
Mniaceae s.lat.
  Pseudacaudella rubida
Mnium Hedw.
hornum Hedw.
  Muscaphis escherichi

Plagiommniaceae T.J.Kop.
Plagiomnium T.J.Kop.
affine (Blandow ex Funck) T.J.Kop.
  Muscaphis escherichi*
rostratum (Schrad.) T.J.Kop.
  Muscaphis escherichi
undulatum (Hedw.) P.Beauv.
  Muscaphis escherichi
Muscaphis musci

Climaciaceae Kindb.
Climacium F.Weber & D.Mohr
dendroides (Hedw.) F.Weber & D.Mohr
  Pseudacaudella rubida

Amblystegiaceae Kindb.
Amblystegium Schimp.
  Muscaphis musci
Drepanocladus (Müll.Hal.) G.Roth
aduncus (Hedw.) Warnst.
  Muscaphis cuspidata
Sanionia Loeske
uncinata (Schwägr.) Brid.
  Pseudacaudella rubida*

Calliergonaceae (Kanda) Vanderp., Hedenäs, C.J.Cox & A.J.Shaw
Calliergon (Sull.) Kindb.
  Muscaphis musci
cordifolium (Hedw.) Kindb.
  Pseudacaudella rubida*

Thuidiaceae Schimp.
Thuidium Schimp.
tamariscinum (Hedw.) Schimp.
  Pseudacaudella rubida

Brachytheciaceae Schimp.
Pseudoscleropodium (Limpr.) M.Fleisch.

purum (Hedw.) M.Fleisch.

Muscaphis escherichi
Muscaphis musci

Eurhynchium Schimp.

Eurhynchium s.lat.

Muscaphis musci

striatum (Hedw.) Schimp.

Melaphis rhois

Cirriphyllum Grout

piliferum (Hedw.) Grout

Muscaphis escherichi*

Kindbergia Ochyra

praelonga (Hedw.) Ochyra

Muscaphis escherichi

Sciuro-hypnum Hampe

oedipodium (Mitt.) Ignatov & Huttunen

(syn. Brachythecium curtum)

Pseudacaudella rubida*

Muscaphis escherichi*

Brachythecium Schimp.

albicans (Hedw.) Schimp.

Pseudacaudella rubida*

rivulare Schimp.

Muscaphis cuspidata*

rutabulum (Hedw.) Schimp.

Muscaphis musci

Brachytheciastrum Ignatov & Huttunen

velutinum (Hedw.) Ignatov & Huttunen

Muscaphis musci

Pseudacaudella rubida

Hynpaeae Schimp.

Calliergonella Loeske

cuspidata (Hedw.) Loeske

Muscaphis cuspidata
Muscaphis escherichi
Muscaphis musci
Pseudacaudella rubida

Hyocomium Bruch & Schimp.

armoricum (Brid.) Wijk & Margad.

Jacksonia papillata (see text)

Melaphis rhois

Hypnum Hedw.

Melaphis rhois
cupressiforme Hedw.

Muscaphis escherichi

Jacksonia papillata (see text)

Ptilium De Not.
crista-castrensis (Hedw.) De Not.

Muscaphis escherichi
Hylocomiaceae (Broth.) M.Fleisch.  
*Hylocomium* Schimp.  
  *splendens* (Hedw.) Schimp.  
    *Muscaphis musci*  
    *Pseudacaudella rubida*  
*Pleuroziun* Mitt  
  *schreberi* (Willd. ex Brid.) Mitt.  
    *Muscaphis escherichi*  
    *Pseudacaudella rubida*  
*Rhytidiadelphus* (Limpr.) Warnst.  
  *loreus* (Hedw.) Warnst.  
    *Muscaphis escherichi*  
  *squarrosus* (Hedw.) Warnst.  
    *Muscaphis escherichi*  
    *Decorosiphon corynothrix*  
    *Pseudacaudella rubida*  
Plagiotheciaceae  
*Plagiothecium* Schimp.  
*laetum* Schimp.  
    *Muscaphis escherichi*
Appendix 2

Summary of the host relationships of the Northern European aphids feeding on horsetails and ferns.
(Colours: Green = monoecious. Blue = dioecious, on primary host (none in this table). Red = dioecious, on secondary host. * = my own records)

PTERIDOPHYTA
EQUISETALES DC. ex Bercht. & J. Presl
Equisetaceae Michx. ex DC.
Equisetum L.
    Myzus cerasi
arvense L.
    Aulacorthum circumflexum*
    Macrosiphum equiseti
    Paracletus cimiciformis (exceptionally?)
fluviatile L.
    Aulacorthum solani*
pratense Ehrh.
    Aphis equisetica
    Macrosiphum equiseti
sylvaticum L.
    Aphis equisetica
    Aphis gossypii
    Macrosiphum equiseti*
    Rhopalosiphum padi (exceptionally)
    Sitobion avenae (exceptionally)
    Sitobion fragariae (exceptionally)
telmateia Ehrh.
    Macrosiphum equiseti

SALVINIALES Bartl.
Marsileaceae Mirb.
Marsilea L.
quadrifolia L.
    Rhopalosiphum nymphaeae
strigosa Willd.
    Rhopalosiphum nymphaeae
Salviniaceae Martinov
Azolla Lam.
caroliniana Willd.
    Rhopalosiphum nymphaeae
filiculoides Lam.
    Rhopalosiphum nymphaeae
Salvinia Ség.
auriculata Aubl.
    Neomyzus circumflexus
    Rhopalosiphum nymphaeae
natans (L.) All.
    Rhopalosiphum nymphaeae

POLYPODIALES Link
Dennstaedtiaceae Lotsy
Dennstaedtia Bernh.
   Amphorophora ampullata
   Idiopterus nephrelepidis
Pteridium Gled. ex Scop.
aquilinum (L.) Kuhn
   Amphorophora ampullata
   Macrosiphum dryopteridis
   Macrosiphum ptericolens
Pteridaceae E. D. M. Kirchn.
Adiantum L.
   Neomyzus circumflexus*
   Idiopterus nephrelepidis
   Myzus persicae
capillus-veneris L.
   Aulacorthum solani
Pteris L.
   Idiopterus nephrelepidis
Cystopteridaceae Shmakov
Cystopteris Bernh.
montana (Lam.) Desv.
   Amphorophora ampullata
Gymnocarpium Newman
dryopteris (L.) Newman
   Amphorophora ampullata
   Macrosiphum dryopteridis
   robertianum (Hoffm.) Newman
   Macrosiphum dryopteridis
Aspleniaceae Newman
Asplenium L.
   Amphorophora ampullata
   Neomyzus circumflexus
   adiantum-nigrum L.
   Idiopterus nephrelepidis
ruta-muraria L.
   Idiopterus nephrelepidis
scolopendrium L.
   Idiopterus nephrelepidis
   trichomanes L.
   Aulacorthum solani
Thelypteridaceae Pic. Serm.
Phegopteris (C. Presl) Fée
   connectilis (Michx.) Watt
   Amphorophora ampullata
   Macrosiphum dryopteridis
Thelypteris Schmdel
   palustris Schott
   Amphorophora ampullata
   Macrosiphum dryopteridis
Onocleaceae Pic. Serm.
Matteuccia Tod.
struthiopteris (L.) Tod.
  Amphorophora ampullata*
  Neomyzus circumflexus

Onoclea L.
  Amphorophora ampullata

Blechnaceae Newman
Blechnum L.
  Idiopterus nephrelepidis

Athyriaceae Aston
Athyrium Roth
distentifolium Tausch ex Opiz
  Macrosiphum dryopteridis
  Macrosiphum lapponicum

filix-femina (L.) Roth
  Amphorophora ampullata*
  Aulacorthum solani*
  Macrosiphum dryopteridis*

Dryopteridaceae Herter
Cyrtomium C. Presl
  filicatum (L.f.) C. Presl
    Neomyzus circumflexus
    Idiopterus nephrelepidis

Dryopteris Adans.
  carthusiana (Vill.) H. P. Fuchs
    Amphorophora ampullata*
    Macrosiphum dryopteridis*

  cristata (L.) A. Gray
    Macrosiphum dryopteridis*

dilatata (Hoffm.) A. Gray
  Amphorophora ampullata
  Macrosiphum dryopteridis

filix-mas (L.) Schott
  Amphorophora ampullata
  Macrosiphum dryopteridis

Polystichum Roth
  Amphorophora ampullata

lonchitis (L.) Roth
  Neomyzus circumflexus

Nephrolepidaceae Pic. Serm.
Nephrolepis Schott
  Neomyzus circumflexus

  exaltata (L.) Schott
    Idiopterus nephrelepidis

Polypodiaceae J. Presl & C. Presl
Polypodium L.
  vulgare L.
    Neomyzus circumflexus
    Aulacorthum solani
    Macrosiphum dryopteridis