

The existence of two species of *Euceraphis* (Homoptera: Aphididae) on birch in Western Europe, and a key to European and North American species of the genus

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ABSTRACT. Aphids formerly regarded as *Euceraphis punctipennis* (Zetterstedt) are distinguished as two species, *E.punctipennis* and *E.betulae* (Koch), on the basis of cytological and morphological differences. *E.punctipennis* is primarily associated with *Betula pubescens* Ehrh., and *E.betulae* with *B.pendula* Roth. Seasonal variations in morphometrics, pigmentation and development of wax glands in the two species are described and compared. A key to European and North American species of *Euceraphis* is provided.

Introduction

The commonest aphids on birch (*Betula* spp.) in Western Europe belong to the genus *Euceraphis* Walker. In this genus, the adults of all morphs, except the ovipara, are alate. There is considerable variation in the colour and general appearance of these aphids, especially in the extent of sclerotic pigmentation of the abdomen and the development of wax, but this variation is thought to be mainly seasonal, and hitherto only one species has been recognized, for which the earliest name is *Aphis punctipennis* Zetterstedt 1828.

Cytogenetic studies (Blackman, 1976) have revealed that there are two distinct species of *Euceraphis* in southern England. Nuclei of somatic cells of one species have two pairs of autosomes, whereas those of the other have only a single autosome pair. The two species also show differences in their mode of spermatogenesis. The present paper examines the morphological differences between the two species, paying particular attention to the problem of seasonal variation.

Nomenclature

The name *Euceraphis punctipennis* (Zetter-

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stedt) has been applied to the common birch aphid in Europe since the discovery of Zetterstedt's types by Wahlgren (1939). Previously, *nigritarsis* (Heyden) was most widely used. Linnaeus' name *betulae* was misapplied to *punctipennis* by Walker (1870) and subsequent workers, and the plenary powers had to be invoked to validate *punctipennis* as the type species of *Euceraphis* (Hille Ris Lambers & Stroyan, 1960). It has not been possible to compare aphids of known karyotype with the type specimens, but on the basis of Wahlgren's description the species with a single autosome pair appears to be Zetterstedt's *punctipennis*. Heyden's (1837) description of *nigritarsis* is sufficiently detailed about the pigmentation of the antennae and legs, and the relative proportions of the antennal segments, to make it fairly certain that his aphid also is the species with a single autosome pair.

Koch (1855) described and illustrated *Callipterus betulae*, which has been synonymized with *E.punctipennis*. Koch's description and figure agree well with the species with two pairs of autosomes. The name *Euceraphis betulae* (Koch) is therefore allocated to this species.

Shinji (1927) studied the cytogenetics of an aphid which he variously called *E.betuli-cola* Kalt., *E.betulaecolens* Kalt. and *E.betulae* Kalt. in different places in the same work, but which was evidently *E.betulae* (Koch), as

listed in his table of contents. In Baker's (1917) revision of North American *Euceraphis*, the name *betulae* seems to have been assigned correctly, although he described what was apparently a fundatrix of *E. betulae* as a new species (*brevis*). Glendenning (1926) described two species of *Euceraphis* from British Columbia, *E. sitchensis* collected from *Alnus sitchensis*, and *E. variabilis* collected from *Sambucus racemosa*. Eastop & Hille Ris Lambers (1976) have synonymized *variabilis* with *sitchensis*. Judging from paratypes in the British Museum collection, neither *sitchensis* nor *variabilis* seem to be distinguishable from *betulae* (Koch), and both are therefore placed as synonyms of this species. The principal synonymies of the two species are therefore as follows:

Euceraphis punctipennis (Zetterstedt)

Aphis punctipennis Zetterstedt 1828

Aphis nigritarsis Heyden 1837

Euceraphis betulae (Koch)

Callipterus betulae Koch 1855

Euceraphis brevis Baker 1917

Euceraphis sitchensis Glendenning 1926

Euceraphis variabilis Glendenning 1926

Vagrants of a *Euceraphis* described as *Aphis cerasicolens* by Fitch (1851) could also be *betulae* (Koch), according to Baker (1917).

Cytology

Shinji's published observations on the cytogenetics of *Euceraphis betulae* relate only to the germ cells. He noted that spermatogonia apparently had two pairs of autosomes and four (unpaired) X-chromosomes, so that the sex determination system was $X_1X_2X_3X_4O$. Kuznetsova & Shaposhnikov (1973) deduced a diploid female chromosome number of $2n = 12$ on the basis of Shinji's results. However, two of Shinji's supposed X-chromosomes behave as accessory ('B') chromosomes, and are present in unreduced condition in male cells (Blackman, 1976). There are thus only ten chromosomes in the normal diploid set of *E. betulae*, comprising two pairs of autosomes, two pairs of X-chromosomes and (usually) two B-chromosomes (Fig. 1).

Females of *E. punctipennis*, however, have only one pair of very long autosomes (Fig. 2). The X-chromosomes and B-chromosomes of

E. punctipennis are similar to those of *E. betulae*. Comparison of the relative lengths of the autosomes of *E. betulae* and *E. punctipennis* (Blackman, 1976) supports the idea that one karyotype has arisen from the other by a simple fusion (or fragmentation) process involving only the autosomes.

Differences between the two species in the mode of spermatogenesis have also been described (Blackman, 1976). The first meiotic division of *E. betulae* is of typical aphid form, except that both X-chromosomes and B-chromosomes (four elements in all) become stretched on the spindle during anaphase-I, and all eventually pass into one daughter cell. *E. punctipennis* has a highly anomalous form of spermatogenesis in which the autosome number is reduced from two to one by elimination of one homologue during prophase of a single maturation division.

Morphology

A detailed generic description of *Euceraphis* is provided by Stroyan (1976). The present account will concentrate on a comparison of morphs and seasonal variants of adults of the two species.

Morphometrics

E. punctipennis is a larger species than *E. betulae*. The size ranges of adults of the two species overlap considerably (Table 1), but comparing populations of the same morph collected at the same time of year the mean body length is 8–9% greater for *E. punctipennis* than for *E. betulae*. The legs and antennae are proportionately longer in *E. punctipennis*. For comparable populations of virginoparae, the length of antennal segment III is 10–14% more, and the length of the hind femur 16–17% more, in *E. punctipennis* than in *E. betulae*. The comparative elongation of the appendages of *E. punctipennis* reaches its extreme in the base of antennal segment VI, which is on average 20–25% longer than that of *E. betulae*. The length of the base of antennal segment VI is therefore a good character for separating the two species (Fig. 3), although small specimens of *E. punctipennis* still overlap somewhat with large specimens of *E. betulae*.

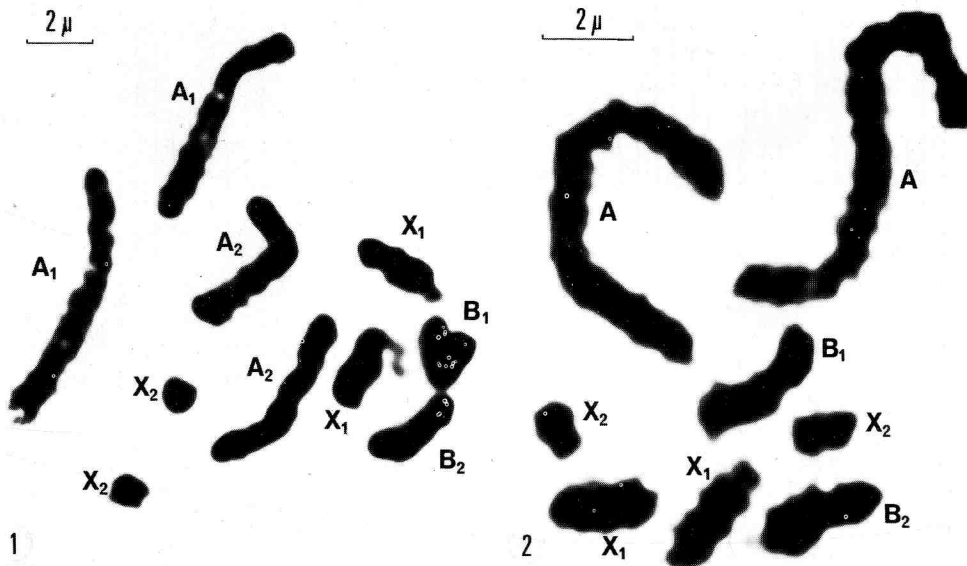


FIG. 1. Prometaphase chromosome set of *E. betulae*, comprising two pairs of autosomes (A_1 , A_2), two pairs of X-chromosomes (X_1 , X_2) and two B-chromosomes (B_1 , B_2). Squash preparation, stained with Giemsa.

FIG. 2. Prometaphase chromosome set of *E. punctipennis*, comprising one pair of autosomes (A), two pairs of X-chromosomes (X_1 , X_2) and two B-chromosomes (B_1 , B_2). Squash preparation, stained with Giemsa.

TABLE 1. Comparative morphometric data for different morphs and seasonal variants of *Euceraphis punctipennis* and *Euceraphis betulae*

Morph	Species	Ranges (mm)						
		Length of body	Antennal seg. III	Hind femur	(a) Base of ant. seg. VI	(b) Hind tarsal seg. II	Ratio a/b	No. measured
Fundatrix (April)	<i>punctipennis</i>	3.8–4.7	1.59–1.86	1.34–1.52	0.29–0.35	0.22–0.25	>1.25	19
	<i>betulae</i>	3.1–4.0	1.32–1.70	1.20–1.34	0.17–0.28	0.22–0.24	<1.23	28
Virginopara (June)	<i>punctipennis</i>	3.1–4.0	1.60–1.88	1.33–1.70	0.30–0.41	0.20–0.24	>1.34	26
	<i>betulae</i>	3.0–3.6	1.46–1.68	1.25–1.41	0.23–0.33	0.22–0.25	<1.32	54
Sexupara (Sept.–Oct.)	<i>punctipennis</i>	3.0–4.8	1.43–1.90	1.48–1.81	0.29–0.41	0.22–0.24	>1.32	16
	<i>betulae</i>	3.0–4.2	1.36–1.82	1.32–1.68	0.23–0.33	0.22–0.25	<1.32	19
Ovipara (Oct.–Nov.)	<i>punctipennis</i>	3.5–4.2	0.96–1.29	1.12–1.40	0.25–0.36	0.20–0.24	>1.15	23
	<i>betulae</i>	3.1–3.9	0.63–0.99	1.08–1.23	0.19–0.27	0.22–0.24	<1.12	28
Males (Oct.–Nov.)	<i>punctipennis</i>	3.0–3.8	1.32–1.53	1.27–1.58	0.30–0.41	0.21–0.25	>1.35	15
	<i>betulae</i>	2.8–3.8	1.22–1.45	1.16–1.33	0.24–0.32	0.20–0.24	<1.36	21

In contrast to all the other characters measured, the second segment of the hind tarsus is proportionately, and often actually, shorter in *E. punctipennis* than in *E. betulae*.

Thus, the ratio

$$\frac{\text{Length of base of antennal segment VI}}{\text{Length of hind tarsal segment II}}$$

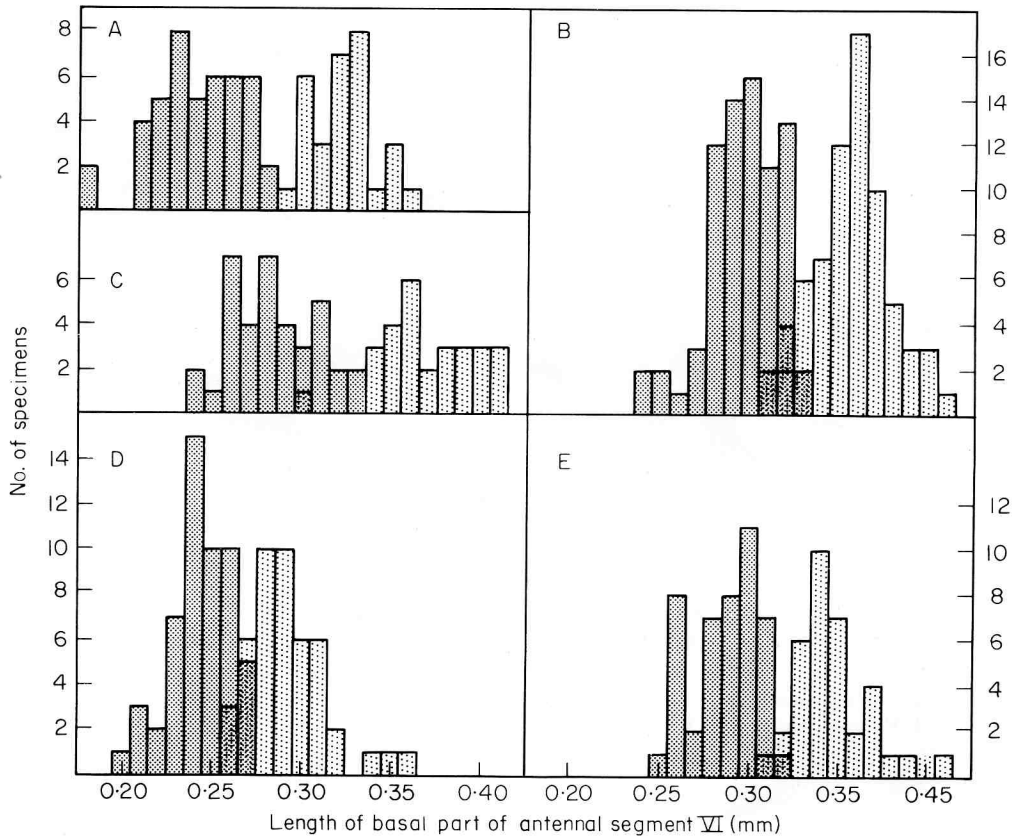


FIG. 3. Frequency histogram for measurements of the length of the basal part of antennal segment VI in *E. betulae* (heavier stippling) and *E. punctipennis*. A: fundatrices; B: alate virginoparae collected in June; C: sexuparae; D: oviparae; E: males.

provides an absolute separation of the two species in all morphs, except possibly the males (Fig. 4). In the last column of Table 1, discriminating values for this ratio are given for the various morphs of the two species collected at different times of year.

Pigmentation

Both *E. betulae* and *E. punctipennis* vary greatly in the extent and distribution of pigmentation of both immature stages and adults. In both species the greatest variation is found in the first parthenogenetic generation, the fundatrix, which generally becomes adult in mid-April in south-east England. Fundatrices of *E. betulae* usually have a conspicuous segmental pattern of dark sclerotic transverse bars on the abdominal dorsum. The sclerotization is most extensive on the third,

fourth and fifth tergites but is also usually present on segments 1, 2, 6, 7 and 8 (Fig. 5). The dorsal abdominal wax glands are often totally encompassed by these sclerotic areas and thus rendered very conspicuous. However, fundatrices of *E. betulae* also occur in which the dorsal abdominal pigmentation is very weakly developed, and occasionally it is completely absent. All variations between the two extremes may occur within one population, although individuals with at least some sclerotization of abdominal tergites 1-7, or 1-8, predominate. The extent of abdominal pigmentation seems to be correlated with pigmentation of the antennae, legs and siphunculi; in the most pigmented specimens the basal parts of the third and fourth antennal segments, the bases of the femora and the siphunculi are quite black, whereas in individuals with little or no abdominal pigmen-

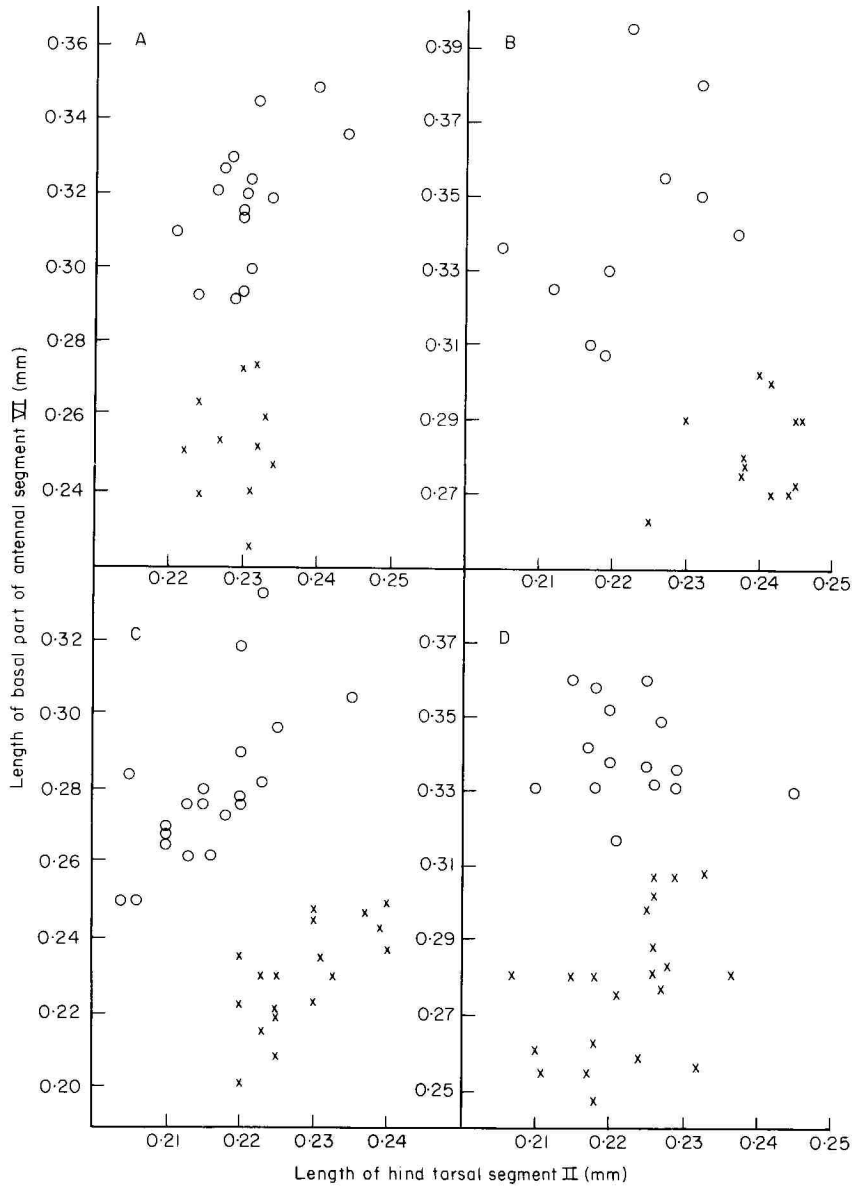


FIG. 4. Plots of measurements of the length of the basal part of antennal segment VI against measurements of the length of the second segment of the hind tarsus, for *E. betulae* (X) and *E. punctipennis* (O). A: fundatrices; B: alate virginoparae, all collected at one locality on one day in June (15.vi.75); C: oviparae; D: males.

tation the bases of the appendages and the siphunculi are also relatively unpigmented. Pigmentation of the immature stages of the fundatrix is also related to that of the adult. Fourth instar larvae of a dirty yellow to brown coloration, which is due mainly to yellow-brown sub-epidermal pigment, moult

into adults with well-developed dorsal abdominal pigmentation, whereas fourth instar larvae of predominantly yellow-green coloration, due to yellow-green pigment both in the cuticle and beneath the epidermis, moult into adults with little or no dorsal abdominal pigmentation.

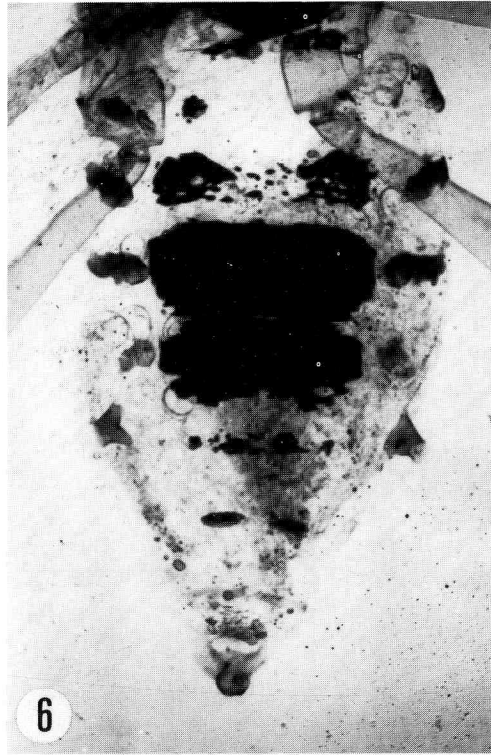


FIG. 5. Photograph of a mounted specimen of *E. betulae* (a fundatrix), showing the maximum extent of sclerotization of the abdominal tergites.

FIG. 6. Photograph of a mounted specimen of *E. punctipennis* (a sexupara), showing the maximum extent of sclerotization of the abdominal tergites.

Fundatrices of *E. punctipennis* are most often either completely without dorsal abdominal pigmentation, or with central sclerotic areas only on abdominal tergites 3 and 4. They never have the segmental pattern of transverse bars commonly present in fundatrices of *E. betulae*. In its most extreme form, the sclerotization extends across the whole of the fourth abdominal tergite and most of the fifth, any sclerotization of other tergites not extending across the mid-line (Fig. 6). Pigmentation of the base of the femur, the sensoriated part of the third antennal segment, the basal half of the fourth antennal segment, and the siphunculi varies in *E. punctipennis*, but these parts are usually rather pale and never black. Immature stages of the fundatrix vary less in colour than those of *E. betulae* and always have green sub-epidermal pigment.

The generation after the fundatrix (funda-

trigenia), adults of which are present in south-east England in mid-May to June, is markedly different in pigmentation in both species. The immature stages are invariably pale-coloured; in *E. punctipennis* pale green and in *E. betulae* pale yellow-green. The adults of both species have a pale green abdomen with either no dorsal sclerotization at all or a small, central sclerite of irregular shape on the fourth tergite, and rarely also on the fifth. Where present these sclerites tend to be larger in *E. punctipennis* than in *E. betulae*, but the two species are now indistinguishable in this respect. Pigmentation of the legs and antennae, however, now shows less intraspecific variation than in the fundatrix and more consistent differences between the species. In *E. betulae*, for example, the basal parts of antennal segments III and IV are pigmented, whereas in *E. punctipennis* they are pale. In *E. betulae* the fore tibia is distally pigmented

and scabrous for at least a third of its total length, whereas only the distal extremity of the fore tibia of *E.punctipennis* is pigmented and scabrous, the pigmentation never extending for more than one quarter of the total length.

Most adults collected in July and August in south-east England are probably of the second generation after the fundatrix. These individuals are even paler than the fundatrigeniae and very rarely have any dorsal abdominal pigmentation. The legs and antennae of *E.betulae* are much paler than in May–June collected specimens, and in the extent of their pigmentation cannot be distinguished from those of *E.punctipennis*.

Sexuparae are found in September and October in England. Sexuparae of both species almost invariably have some sclerotization of the abdominal tergites, although in *E.punctipennis* this is practically confined, as in the fundatrix, to the fourth and fifth segments. Sexuparae of *E.betulae* also often have abdominal pigmentation restricted to the fourth and fifth tergites, but in other individuals there may be a complete segmental pattern of transverse sclerotic bars.

It has not been possible to distinguish the sexual morphs of the two species on the basis of pigmentation. Oviparae of both species vary greatly both in the extent and pattern of dorsal abdominal sclerotization and in general pigmentation. Males are heavily sclerotized with a strong pattern of transverse bars on the abdomen in both species.

Wax glands

Wax glands occur on the antennae, legs, head, thorax and abdomen of all morphs except the oviparae in both species. In mounted specimens the dorsal abdominal wax glands are most conspicuous in dark individuals as they occupy relatively pale areas in heavily sclerotized cuticle. The abdominal wax glands of individuals without dorsal abdominal sclerotization can sometimes only be seen by use of phase contrast or dark field illumination. However, in the living aphids the covering of fine, bluish-white wax, especially on the legs and antennae, is more conspicuous in pale individuals than in those with dark pigmentation. Variation in the amount of wax

may be due more to the age and physiological condition of the individual rather than to any differences in the size or number of wax glands.

Distribution and host plants

In the British Museum collection there are over 300 specimens of *E.betulae*, from Austria, Czechoslovakia, Germany, England, Scotland, Sweden, Japan, Australia, New Zealand, Canada and U.S.A. The host plant is usually recorded as birch or *Betula* sp. In the Royal Botanic Gardens, Kew, Surrey, where numerous *Betula* species grow within a relatively small area, alate females of *E.betulae* have been collected (mainly by V. F. Eastop) from *papyrifera*, *pendula*, *platyphylla*, *populifolia* and *pubescens*. However, *E.betulae* adults have also been collected from *Crataegus*, *Bambusa*, *Luzula*, *Pinus*, *Rubus* and many other plants. For a better indication of the true host plant relationships of the species it is necessary to consider only the wingless forms, that is, the immature stages and the oviparae. Where the host plant has been identified to species, immature stages (identified cytologically) and oviparae of *E.betulae* have so far been recorded exclusively from *B.pendula*.

Specimens of *E.punctipennis* in the British Museum collection are from Austria, Germany, England, Scotland, Wales, Finland, Sweden and Iceland. Additionally, there are some specimens from *Betula* sp. in Utah, U.S.A., collected by G. F. Knowlton, which seem to be morphologically intermediate between *punctipennis* and *gillettei*. Further work on North American species of *Euceraphis* will be necessary to establish the identity of these aphids. With regard to the host plants of *E.punctipennis*, the same considerations apply as with *E.betulae*. Alate individuals have been collected from *Betula albosinensis*, *grossa*, *jaquemontii*, *nana*, *papyrifera*, *pendula*, *populifolia* and *pubescens*, but also from such plants as *Picea*, *Populus*, *Fraxinus* and *Achillea millefolium*. Immature stages and oviparae have been collected only from *B.pubescens*.

Thus both species may be much more specific in their host plant relationships than is readily apparent. *E.betulae* has spread with

B. pendula to many parts of the temperate world. *E. punctipennis* may be restricted by the distribution of *B. pubescens*, which has not been planted widely outside its natural range. In Europe, *B. pubescens* has a more boreal distribution than *B. pendula* and is the commoner species in Scotland and most of Scandinavia, occurring also in Iceland which is outside the range of *B. pendula*.

Key to alate virginoparous females of European and North American species of *Euceraphis*

This key is based on specimens in the British Museum collection, except for *pilosa*, which has not been seen by the author.

- 1 Longest hairs on antennal segment III more than twice as long as basal diameter of segment. (On *Betula* sp.; central Asia, ?eastern Europe)
 - pilosa* Nevskii
 - Hairs on antennal segment III short, shorter than basal diameter of segment 2
- 2 Basal part of antennal segment VI much elongated, more than three times length of processus terminalis. (On *Betula* sp., North America)
 - deducta* Baker
 - Basal part of antennal segment VI often similar in length to processus terminalis, often longer, but never more than 2.5 times as long. 3
- 3 All tibiae uniformly and deeply pigmented, except for small pale region at base. No dorsal abdominal pigmentation. Base of antennal segment VI more than twice as long as hind tarsal segment II. (On *Betula nigra*, North America)
 - mucida* (Fitch)
 - Pigmentation of tibiae not uniform; if mainly dark, the palest part is in the middle and the distal part is scabrous and completely black. With or without dorsal abdominal pigmentation. Base of antennal segment VI one to three times as long as hind tarsal segment II. 4
- 4 Length of basal part of antennal segment VI 0.17–0.33 mm, but only more than 0.29 mm in large specimens (body length more than 3.4 mm), and then it is less than 1.32 times the length of hind tarsal segment II. (On *Betula pendula*; Europe, Asia, Australasia, North America)
 - betulae* (Koch)
 - Length of basal part of antennal segment VI more than 0.29 mm, and (except in some fundatrices of *E. punctipennis* – see Table 1) more than 1.32 times the length of hind tarsal segment II. . 5
- 5 Hind tibia with a longitudinal dorsal stripe. Base of antennal segment VI more than 0.45 mm long, 2.1–3.0 times as long as hind tarsal segment II. (On *Betula populifolia*, North America)
 - lineata* Baker
 - Hind tibia often with some pigmentation but not

- in the form of a longitudinal stripe. Base of antennal segment VI 0.29–0.52 mm long, 1.3–2.5 times the length of hind tarsal segment II. . 6
- 6 Basal part of antennal segment VI 0.33–0.52 mm long, 1.6–2.5 times length of hind tarsal segment II (but only less than 1.8 times in spring generations). Abdomen without dorsal sclerotic markings. (On *Alnus* spp. and *Betula occidentalis*, North America) *gillettei* Davidson
- Basal part of antennal segment VI 0.29–0.43 mm long, 1.3–1.8 times length of hind tarsal segment II. Abdomen with or without pigmented sclerites on tergites 4 and 5. (On *Betula pubescens*, Europe and ?North America)
 - punctipennis* (Zetterstedt)

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