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Morphological and cytological separation of *Amphorophora* Buckton (Homoptera: Aphididae) feeding on European raspberry and blackberry (*Rubus* spp.)

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Abstract

Aphids of the genus *Amphorophora* collected from European raspberry, *Rubus idaeus*, have a chromosome complement of 2n(♀)=18, whereas *Amphorophora* from *R. fruticosus* agg. (blackberry, brambles) have a basic chromosome complement of 2n(♀)=20. Canonical variates analysis based on eight characters measured on numerous samples of apterous virginoparae showed that *Amphorophora* on European *Rubus* can be separated morphologically into two groups consistent with the differences in host plant and karyotype, and these two groups are concluded to be separate species. The correct name for the aphid on raspberry that is a vector of European raspberry viruses is *Amphorophora idaei* (Börn.), and the species on blackberry is *A. rubi* (Kalt.). Simple biometric methods of discriminating between *A. idaei* and *A. rubi* based on pairs of variables are suggested, and their reliability is discussed. Taxonomic problems in the European and North American *Rubus*-feeding species of *Amphorophora* are considered with particular reference to their importance in applied entomology.

Introduction

The presence of a distinct, large, green species of aphid on raspberries was first noted by Joshua Major (1829), who stated that it was 'considerably larger than any yet described. It is very active and appears alarmed when anything approaches it. It reigns principally in July when the first fruit is ripe, a time that would be improper to apply anything for its destruction.' Kaltenbach (1843) provided a valid name (*Aphis rubi*) and a formal description distinguishing the large greenfly occurring from June to September on *Rubus* species (*caesius*, *corylifolius*, *fruticosus*, *discolor*, *idaeus*, etc.) from greenfly on other plants. Schouteden (1906) transferred *Aphis rubi* Kaltenbach to *Amphorophora* and since then all large green aphids with clavate siphunculi on *Rubus* in western Europe have generally been regarded as the one species, *Amphorophora rubi* (Kaltenbach).

Börner (1939), however, decided on the basis of host-plant transfers and morphological studies that there were two distinct *Rubus*-feeding species of *Amphorophora* (although he used the generic name *Nectarosiphon*); one feeding on *R. idaeus* (European raspberry), which he called *idaei*, and the other on *R. caesius*, *R. fruticosus* agg., etc., which he regarded as the true *rubi* (Kaltenbach). The characters he gave for distin-

guishing the two species were colour, numbers of rhinaria on the third antennal segments of alatae and apterae, and number of caudal hairs. Börner's separation has not been widely accepted. Hille Ris Lambers (1949) in his account of western European *Amphorophora* said of *rubi* and *idaei* (p. 241): 'It appears from my material that none of the characters (given by Börner) holds, although this does not prove that the two forms are identical.' Hill (1953) examined numerous *Amphorophora* from wild *R. fruticosus* (bramble) in Scotland and apparently compared them morphologically with aphids from raspberry (although this is not clear from his paper), but found no evidence to convince him that two species were present.

Briggs (1959) regarded Börner's aphid from *R. caesius* as a 'strain' of *A. rubi*, treating it as equivalent to other strains of *Amphorophora*, which are important as vectors of raspberry viruses. In a later paper, Briggs (1965) postulated single gene differences between 'strains' colonising different raspberry varieties, but did not refer again to the possible genetic relationship between raspberry- and blackberry-feeding *Amphorophora*.

Thus the taxonomy of *Amphorophora* on *Rubus* in Europe has remained confused and the raspberry- and blackberry-feeding forms are generally regarded as host-plant races, or at most, subspecies, of the one species, *A. rubi*. This leaves unanswered the important question of whether wild brambles can provide a natural reservoir for aphids carrying raspberry viruses.

Preliminary morphological comparison of *Amphorophora* from raspberries and blackberries in the British Museum (Natural History) collection indicated slight but consistent differences in the ranges of certain characters, particularly those used by Börner to separate *rubi* and *idaei*. For example, alate specimens from *R. fruticosus* have 41–83 rhinaria on the third antennal segment at a density of 44–69 per mm in May, 36–65 per mm in June, and 30–56 per mm in July-August. Alate specimens from *R. idaeus* have 23–60 rhinaria on the third antennal segment at a density of 34–49 per mm in June and 22–47 per mm in July. A more detailed biometric and cytological study was therefore undertaken to clarify the taxonomic relationship between the two forms and to find reliable characters by which to distinguish them.

Materials and methods

For cytological studies, embryos were dissected out of immature apterous virginoparae in 0·75% potassium chloride solution and fixed immediately in 3:1 methanol/acetic acid. The smallest embryos were transferred to a drop of 45% propionic acid on a clean microslide and squashed under a cover-slip. After preliminary examination by phase contrast the preparations were made permanent by freezing off the cover-slip, air-drying and staining in Giemsa (10% in phosphate buffer at pH 6·8).

The biometric study was based solely on the most commonly found morph, the apterous virginopara. Eight characters were used, which were chosen from preliminary studies as the most likely to show differences between the raspberry and blackberry forms of *Amphorophora*. These were:

1. Body length (from tip of antennal tubercle to tip of sub-anal plate).
2. Length of siphunculus.
3. Length of cauda.
4. Length of third antennal segment.
5. Length of processus terminalis of sixth antennal segment.
6. Length of ultimate rostral segment (Fig. 1).
7. Length of second segment of hind tarsus.
8. Number of hairs on cauda.

The study material comprised 34 clones and 11 non-clonal field-collected samples. Twenty-six clones were started from single virginoparae collected on *R. fruticosus*, and eight from single aphids collected on *R. idaeus*, all from different localities in

southern England. All clones were reared on excised leaves of their respective host-plants at 15°C. Effects of temperature and host-plant on morphology were examined by rearing sub-cultures of five of the clones on blackberry at a lower temperature (6°C), and one of them on an excised leaf of *R. idaeus* (at 15°C). Field-collected samples came from England, Czechoslovakia, Germany, France and Finland. In all, 58 separate samples were measured with 4–12 individuals in each sample, yielding data on 487 separate specimens.

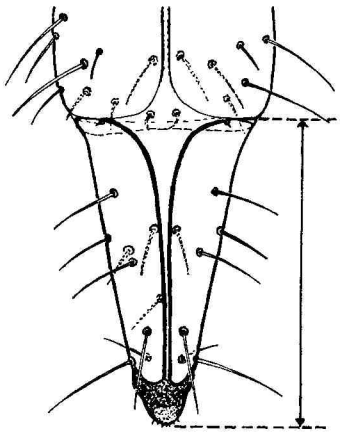

Fig. 1.—Ultimate rostral segment of an apterous virginopara of *Amphorophora rubi*, indicating the measurement of its length.

The data were analysed by the method of canonical variates (often called discriminant analysis). Details of the procedure followed are given in the section on biometrics.

Results

Cytology

Twenty-one samples of *Amphorophora* from European raspberry all had a chromosome complement of 2n(♀) = 18 (Plate V *a*). One pair of chromosomes is much longer than the others. The cells of male embryos were examined and found to have only one of these long elements, which must therefore be the X-chromosomes.

Of the 36 samples of *Amphorophora* from *R. fruticosus* that were examined cytologically, 28 had the karyotype shown in Plate V *b*. In comparison with the aphids from raspberry there is an additional short chromosome pair, so that 2n(♀)=20. The remaining eight samples from *R. fruticosus* all had 21 chromosomes, which appears to be a variant of the 2n=20 karyotype derived from it by dissociation into two parts of one of the autosomes (Plate V *c*). In addition, 17 samples of *Amphorophora* were taken from different plants in the *Rubus* collection at the Royal Botanic Gardens, Kew, on 12.vi.75, and found to be all of 2n=20 karyotype. According to the labels, most of these plants were members of the *fruticosus* group (*diversifolius*, *insularis*, *koehleri*, *leightonii*, *micans*, *myricae*, *polyanthemus*, *radula* and *vedrariensis*), with two of *fruticosus*×*idaeus* hybrid origin (*frondosus*, *nessensis*), one of *caesius*×*fruticosus* hybrid origin (*dumetorum*), and five other species (*adenotrichopodus*, *caesius*, *ellipticus*, *occi-*

dentalis and *saxatilis*). The aphids on plants labelled *koehleri*, *occidentalis* and *radula* were collected as single specimens not forming colonies.

No aphids with 2n=18 have been found on *R. fruticosus*. On only one occasion were aphids with 2n=20 collected from *R. idaeus*, and these were single individuals found wandering on raspberry growing entangled with brambles that had a massive infestation of 2n=20 aphids.

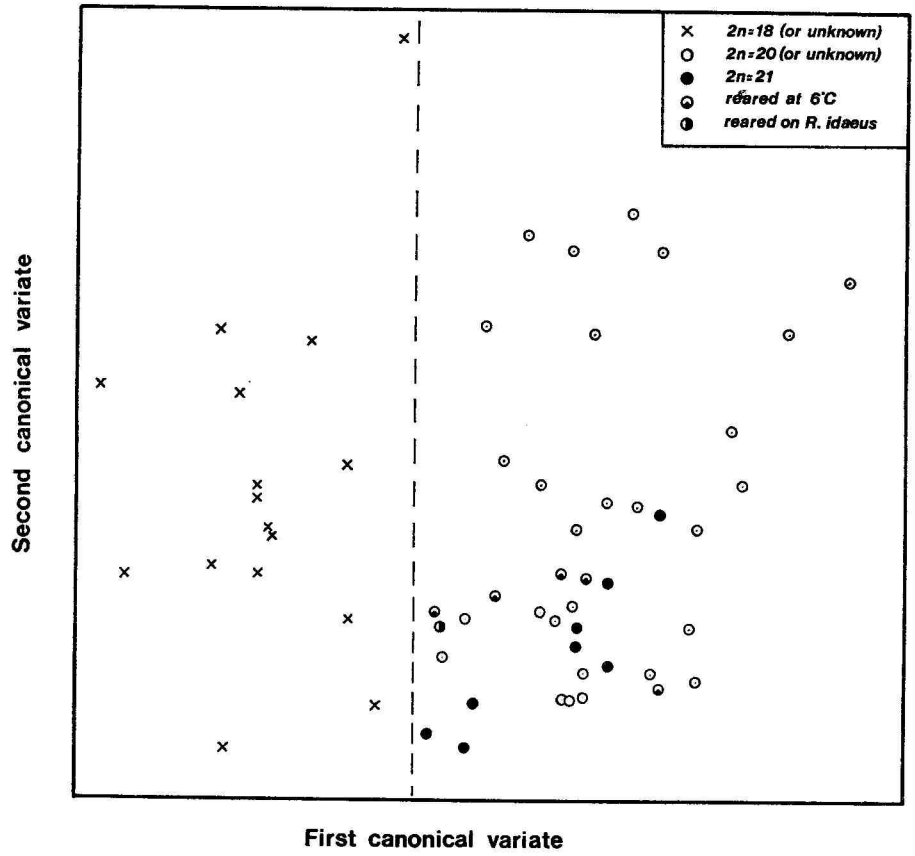

Fig. 2.—Plot of the scores on the first and second canonical variates, based on eight characters, for reared and field-collected samples of *Amphorophora* originating from *Rubus idaeus* (crosses) and *R. fruticosus* (circles).

Biometrics

Fig. 2 shows a plot of the scores on the first two canonical variates for each of the 58 samples, using all eight variables. Scores on the first canonical variate are evaluated as a linear combination of the original variables, chosen so as to maximise the differences between samples relative to the differences between individuals within samples. The second canonical variate is also evaluated as a linear combination of the original variables, which discriminates well between groups and satisfies the additional requirement that values of the first and second canonical variates are uncorrelated within groups (see Ashton *et al.*, 1957, for an account of this method). It is clear from Fig. 2

TABLE I. *Mean value and range for each character in each of seven groups (see text)*

	1	2	3	4	5	6	7
Host plant:	Blackberry	Blackberry	Blackberry	Blackberry	Blackberry	Raspberry	Raspberry
Rearing condition:	15°C	6°C	6°C	15°C	field	field	15°C
Chromosome number:	20	20	21	21	—	—	18
Number of specimens:	203	27	11	66	39	43	98
1. Body length (mm)	2·81 (2·2–3·4)	2·55 (2·3–2·9)	2·74 (2·6–2·8)	2·66 (1·9–3·2)	3·23 (2·6–4·0)	2·83 (1·7–3·9)	2·92 (1·9–3·7)
2. Siphunculus length (mm)	0·78 (0·59–1·00)	0·71 (0·60–0·80)	0·73 (0·69–0·78)	0·73 (0·57–0·89)	0·88 (0·74–1·03)	0·78 (0·55–1·13)	0·80 (0·61–1·00)
3. Cauda length (mm)	0·33 (0·24–0·40)	0·31 (0·25–0·36)	0·33 (0·31–0·36)	0·32 (0·20–0·40)	0·41 (0·33–0·49)	0·34 (0·22–0·55)	0·34 (0·24–0·43)
4. Antennal segment III (mm)	0·94 (0·69–1·17)	0·93 (0·78–1·06)	0·91 (0·86–0·96)	0·89 (0·71–1·07)	1·10 (0·94–1·30)	1·02 (0·72–1·27)	1·01 (0·71–1·17)
5. Processus terminalis (mm)	0·98 (0·78–1·19)	1·09 (1·02–1·15)	0·85 (0·81–0·88)	0·92 (0·68–1·14)	1·13 (0·95–1·31)	1·08 (0·89–1·23)	1·12 (0·87–1·32)
6. Ultimate rostral segment (μm)	161·4 (142–176)	163·2 (150–175)	158·1 (150–162)	156·2 (141–171)	171·3 (160–185)	146·7 (125–169)	150·9 (132–163)
7. Hind tarsal segment II (μm)	132·2 (112–150)	131·5 (125–137)	125·3 (122–126)	128·2 (121–140)	148·5 (137–162)	128·5 (112–152)	132·1 (119–145)
8. Number of caudal hairs	12·5 (8–19)	11·8 (8–15)	10·8 (9–13)	11·8 (8–15)	12·6 (9–17)	13·5 (9–20)	14·4 (8–21)

that, using all eight variables, the first canonical variate alone is discriminating between 2n=18 and 2n=20/21 samples, or, where the karyotype is unknown, between aphids collected on *R. idaeus* and *R. fruticosus*. The discrimination holds for clones reared at both 6 and 15°C, and for the 2n=20 clone reared in the laboratory on an excised leaf of *R. idaeus* for three generations. No distinction was found between 20- and 21-chromosome samples. The second canonical variate seems to be related to the general size of the specimens. Field-collected aphids were often larger than laboratory-reared specimens; the seven highest values of the second canonical variate were all from field-collected samples (one from *R. idaeus* and six from *R. fruticosus*).

The next step was to determine whether a smaller number of variables would do as well, or nearly as well. The 58 samples were formed into seven groups, corresponding to chromosome number (where known) and temperature at which the clones were reared. Table I gives mean values, together with ranges, for each character and for each group. It is clear that group 5 is composed of rather larger specimens than the other groups. Group 5 apart, comparison of the mean values for each variable show that for all characters except 5 and 7 there are slight but consistent differences between the raspberry- and blackberry-inhabiting forms of *Amphorophora*. Mean caudal hair number (character 8) is greater in *Amphorophora* from raspberry, where high numbers of caudal hairs (16–21) occurred much more frequently, but the values for individual samples differed widely and this character could not be used reliably for discrimination. The best discriminating character appears to be 6, the length of the ultimate rostral segment.

TABLE II. *Correlations between characters, within the 58 samples*

	1	2	3	4	5	6	7	8
1. Body length	1·00							
2. Siphunculus length	0·70	1·00						
3. Cauda length	0·70	0·74	1·00					
4. Antennal segment III length	0·67	0·77	0·70	1·00				
5. Processus terminalis length	0·40	0·56	0·43	0·56	1·00			
6. Ult. rostral segment length	0·52	0·54	0·50	0·52	0·45	1·00		
7. Hind tarsus II length	0·50	0·60	0·50	0·57	0·42	0·52	1·00	
8. No. of caudal hairs	0·13	0·10	0·15	0·13	0·14	0·07	0·04	1·00

TABLE III. *Correlations between characters within the eight groups*

	1	2	3	4	5	6	7	8
1. Body Length	1·00							
2. Siphunculus length	0·76	1·00						
3. Cauda length	0·76	0·83	1·00					
4. Antennal segment III length	0·76	0·84	0·79	1·00				
5. Processus terminalis length	0·43	0·53	0·46	0·49	1·00			
6. Ult. rostral segment length	0·57	0·67	0·66	0·64	0·48	1·00		
7. Hind tarsus length	0·64	0·79	0·66	0·68	0·48	0·64	1·00	
8. No. of caudal hairs	0·01	0·01	0·08	−0·02	0·20	0·16	−0·06	1·00

Tables II and III show the correlations between characters, pooled over all 58 samples and pooled over the seven groups. It appears that the first four variables are all highly correlated with each other, and that variable 6, the ultimate rostral segment length, is also positively correlated with this group but to a lesser degree. The fact that the correlations are similar within the 58 samples and within the seven groups indicates that it is reasonable to replace the 58 samples by the seven groups for the purpose of selecting the best characters. Information from Tables I, II & III suggests that a combination of character 6 and *one* of the first four characters might give good discrimination. Only one of the first four is required because of the high degree of correlation between them. Fig. 3 shows a plot of the mean values of the variables 1 and 6 in the 58 samples.

In order to obtain a discriminant function between the two forms of *Amphorophora*, the canonical variates analysis was repeated, but this time based on variables 1 and 6 only, and using log data. The use of logs concentrates attention on the relative

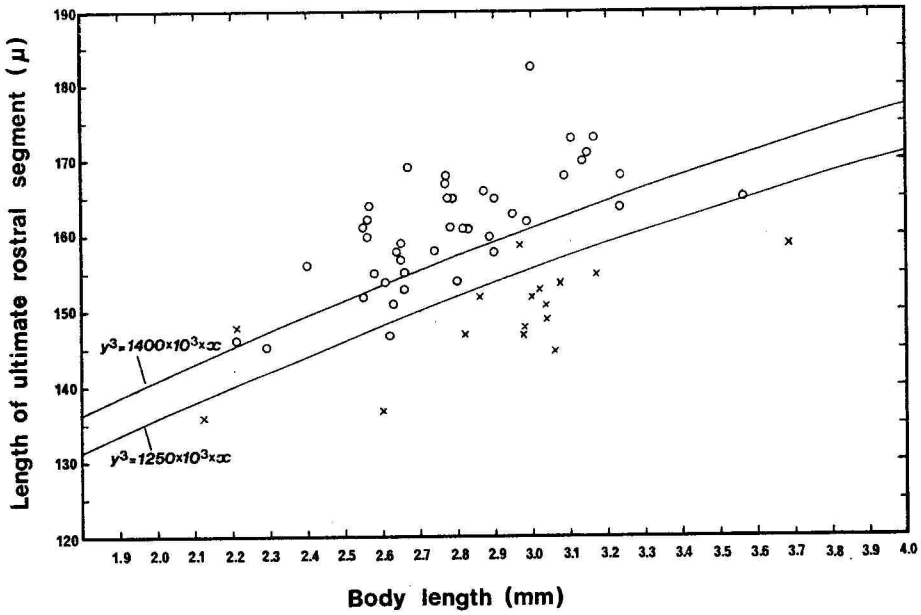

Fig. 3.—Plot of variable 1 (body length) against variable 6 (ultimate rostral segment length) for the 58 samples of *Amphorophora* originating from *R. idaeus* (crosses) and *R. fruticosus* (circles). The curves correspond to different values of 'k' in the equation $y^3=k\times10^3\times x$, chosen to define a region of uncertainty in the discrimination of the two forms of *Amphorophora* (see Discussion). The region between the two curves is the region of uncertainty.

size of characters, which usually provides a more satisfactory discrimination than absolute size. The discriminating lines produced by this analysis had (approximately) the general equation

$$y^3=k\times10^3\times x,$$

where y is the length of the ultimate rostral segment and x is the body length. The selection of values of k for discriminating between the two forms of *Amphorophora* is discussed in the next section.

In spite of the high degree of correlation between characters 1 to 4, it seemed worthwhile to test another of these variables against character 6 to see whether a better discrimination could be obtained, and also to provide a discriminant which could be used in cases where body length was not measurable. Accordingly, the above procedure was repeated using variable 4, the length of the third antennal segment, instead of body length. Fig. 4 is a plot of the mean values for the 58 samples using variables 4 and 6. Discriminating lines in this case also had (approximately) the general equation

$$y^3=k\times10^3\times x,$$

where y is the length of the ultimate rostral segment and x is the length of the third antennal segment.

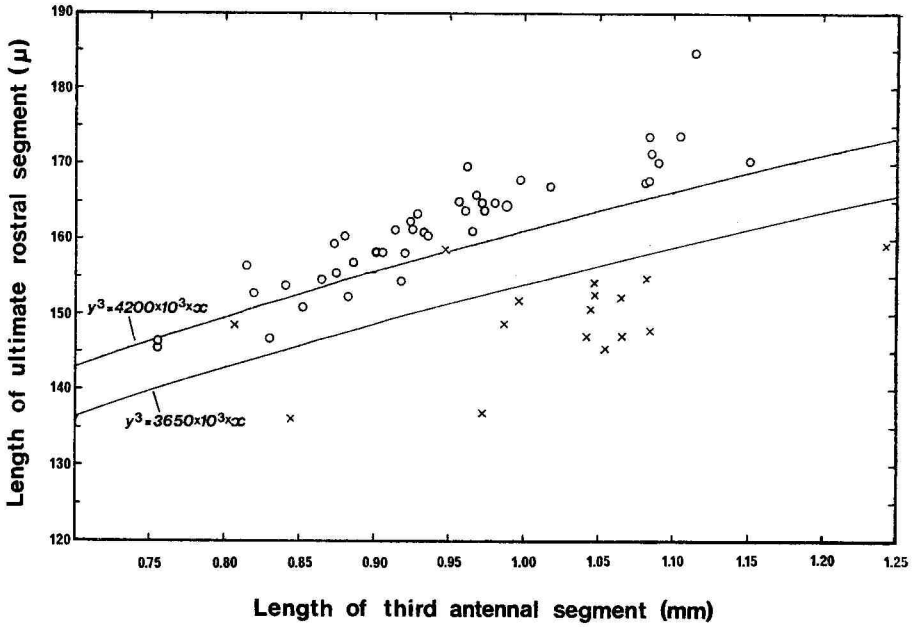

Fig. 4.—Plot of variable 4 (third antennal segment) against variable 6 (ultimate rostral segment length) for the 58 samples of *Amphorophora*, with curves and symbols corresponding to those in Fig. 3.

Discussion

Taxonomy and nomenclature

A combination of cytological and biometric methods clearly demonstrated the existence of two distinct taxa in the material studied, which must now be classified as separate species. The results fully support Börner's separation of *rubi* and *idaei*, and *Amphorophora idaei* (Börner) must now be regarded as the correct name for the species on European raspberry, the name *A. rubi* (Kaltenbach) being reserved for aphids colonising *R. fruticosus* agg. and probably *R. caesius* and other *Rubus* species of the blackberry group.

The difference in karyotype between the two species makes hybridisation unlikely, but not impossible. No evidence of hybridisation, in the form of individuals with 19 chromosomes, was found. The isolating mechanism is unknown. Both species seem to be specific in their choice of host plants between *R. idaeus* and *R. fruticosus* under field conditions, although this specificity may break down in senescing plants in late summer. It is possible to maintain *A. rubi* on excised leaves or shoots of certain raspberry varieties in the laboratory. To what extent this specificity extends to other *Rubus* species is still uncertain. A sample of *Amphorophora* collected from *R. caesius* near Rostock, German Democratic Republic, on 8.viii.74 and kindly sent to us by F. P. Müller, was found to be *A. idaei*, with 2n=18. However, all other material from *R. caesius* in the British Museum collection appears to be *A. rubi*, so this may have been an exceptional occurrence, and Börner's (1939) conclusion is probably essentially correct.

Müller in fact noted (pers. comm.) that the colour of the aphids he collected from *R. caesius* was yellowish, like those normally found on *R. idaeus*. There can be a rather obvious difference in colour between the two species, especially when they are observed

in the field at the same time on adjacent raspberries and blackberries, *A. rubi* being distinctly green or yellowish-green and *A. idaei* greenish-white or pale yellow. Colour is, however, affected by season of the year and host plant species and condition, as well as by the age and condition of the aphids, and can hardly be regarded as a reliable taxonomic character.

Morphological separation based on pairs of characters

When only two variables are used, there is clearly a region of uncertainty between the two species into which certain specimens of both species will fall, leaving their true identity in doubt. In discriminating between *rubi* and *idaei* it has therefore been our aim to provide some kind of definition of this region of uncertainty in terms of the proportion of individuals of each species which are likely to fall within it.

Two discriminant functions, D_1 and D_2, were derived from the general equation, $y^3 = k \times 10^3 \times x$, which was obtained by canonical variates analysis:

$$D_1 = \frac{(\text{ultimate rostral segment length})^3}{\text{body length}}$$

$$\text{and } D_2 = \frac{(\text{ultimate rostral segment length})^3}{\text{third antennal segment length}}$$

where all measurements are in μm. Values of D_1 and D_2 were calculated for all 487 specimens measured. Figs. 5 and 6 show the cumulative relative frequency distributions of D_1 and D_2 for both species. From these two figures it is possible to decide on a region of uncertainty for each discriminant. For D_1, if limits of the region of uncertainty are drawn at 1250 and 1400, then 17% of *idaei* and 20% of *rubi* fall within these limits, while 8% of *idaei* and 7% of *rubi* will be on the 'wrong side', and therefore

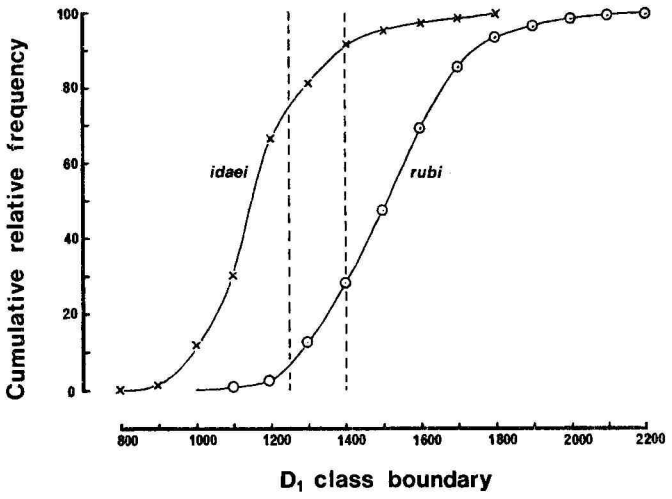

Fig. 5.—Cumulative relative frequency distributions of discriminant D_1 (based on ultimate rostral segment length and body length) for 346 specimens of *Amphorophora rubi*, and 141 specimens of *Amphorophora idaei*. Vertical dashed lines indicate limits of the region of uncertainty (see text), at $D_1 = 1250$ and 1400.

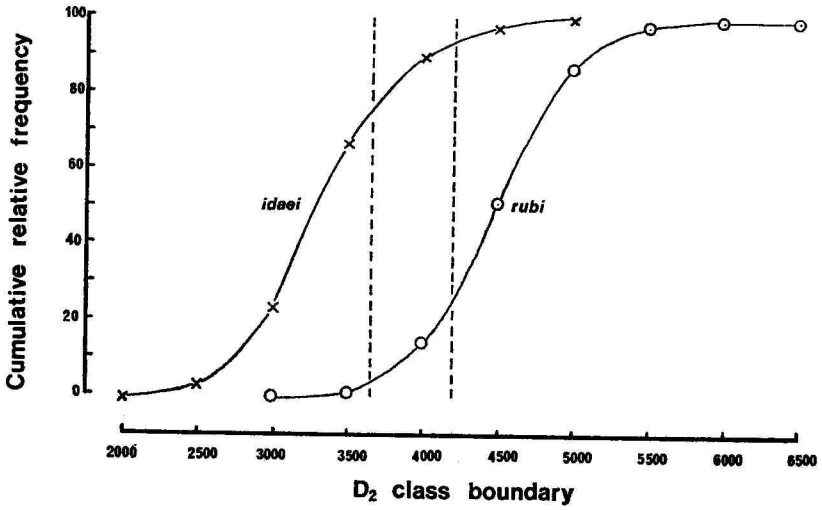

Fig. 6.—Cumulative relative frequency distributions of discriminant D_2 (based on ultimate rostral segment length and third antennal segment length) for 346 specimens of *A. rubi* and 141 specimens of *A. idaei*. Vertical dashed lines indicate the limits of the region of uncertainty (see text), at $D_2=3650$ and 4200.

misclassified. For D_2, if the limits of the region of uncertainty are drawn at 3650 and 4200, then 18% of *idaei* and 18% of *rubi* fall within these limits, while 7% of *idaei* and 3% of *rubi* will be misclassified. These limits are, of course, chosen empirically, and give some indication of the probability of assigning single specimens and samples to the correct species. Curves corresponding to both limits for D_1 and D_2 are drawn in on Figs. 3 and 4.

In order to establish the identity of a specimen or sample it is therefore necessary to measure body length and/or third antennal segment length, plus the length of the ultimate rostral segment (see Fig. 1), all in μm. The resulting values can then either be plotted on Fig. 3 or Fig. 4 and identification made visually, or each specimen can be assigned to one or other species according to the calculated values of D_1 and D_2. It is essential to have an accurately calibrated micrometer, as a 5% error in measurement can lead to large differences in the values of D_1 and D_2. Note that in Fig. 3 and 4 some samples are on the wrong side of the limits and therefore misclassified. This serves to emphasise that there is an inevitable degree of doubt about any identification based on a small number of variables, even if several specimens are measured. In fact, the simplest and most reliable single indicator of taxonomic identity (apart from karyotype) is the species of host plant colonised.

To check whether the discriminants D_1 and D_2 could successfully distinguish aphids of unknown identity, a test was conducted with ten coded samples (A–J) of *Amphorophora* kindly provided by Dr M. Lyth of East Malling Research Station. Five of these samples originated from raspberry and five from blackberry. Morphometric studies (by V.F.E.) were conducted independently from karyotype determinations (by R.L.B.), and the results were then compared. Table IV shows the results of the test and the identity concluded for each sample. Values of both D_1 and D_2 clearly discriminated between the two species, although the values of D_2 for *A. idaei* were rather higher than expected. In the case of sample F, a positive determination was not possible using the discriminants D_1 and D_2 alone, but the high caudal hair number (column 5 in Table IV) provided the additional morphological evidence necessary to identify this sample as *idaei*.

TABLE IV. *Determination of ten coded samples of* Amphorophora *using morphological discriminants D_1 and D_2, caudal hair number and karyotype*

Sample	No. of specimens	D_1	D_2	Mean no. of caudal hairs	2n(♀)	Determination
A	7	1280	3740	12·57	18	*Amphorophora idaei*
C	4	1180	3676	14·00	18	,, ,,
F	10	1275	4195	15·20	18	,, ,,
G	9	1068	3592	16·89	18	,, ,,
I	6	1143	3780	19·33	18	,, ,,
B	8	1660	4861	11·35	20	*Amphorophora rubi*
D	5	1533	4672	12·80	20	,, ,,
E	9	1611	4961	12·78	20	,, ,,
H	8	1587	4714	11·38	20	,, ,,
J	10	1496	4525	10·80	20	,, ,,

Economic aspects

Confusion over the taxonomic identity of *Amphorophora* species of economic importance has arisen, not because of any real 'blurring' of species boundaries by hybridisation or incipient speciation, but because several perfectly good biological species are very similar in their gross morphology. In North America, the name *rubi* has been erroneously applied to several native species, as well as to *idaei* recently introduced from Europe. In the 1930s, this caused the puzzling problem that the raspberry variety Lloyd George, which in Britain is highly susceptible to virus diseases transmitted by *A. idaei*, was not colonised at all by *Amphorophora* when exported to North America and therefore did not contract virus diseases there (Huber & Schwartze 1938, Dicker, 1940). The simple explanation to this problem was only discovered in the 1960's when the resistance of Lloyd George in America suddenly broke down, because the real *idaei* was introduced from Europe. It was found (Kennedy *et al.*, 1962; Eastop, unpublished work) that the common North American raspberry aphid was a different species, *A. agathonica* Hottes, associated with the native raspberry subspecies, *R. idaeus strigosus*. The earlier raspberry breeding work in North America was therefore against *A. agathonica*, and not against *A. idaei* (called *rubi*), as had been supposed.

Specimens of *A. agathonica* collected in Oregon by R. Converse were examined cytologically and found to have 2n(♀) = 14 (Plate V *d*), in agreement with the karyotype reported by Robinson & Chen (1969). Two other North American species, *A. rubitoxica* Knowlton and *A. stolonis* Robinson, have much higher chromosome numbers (Blackman, unpublished). It appears that *Rubus*-feeding *Amphorophora* are unusual among aphids in having considerable variation in karyotype between species, and cytological studies will probably be of further use in the taxonomy of this genus.

Experiences with *Amphorophora* demonstrate forcibly the need for 'correct' taxonomy in applied entomology. Misidentification of the North American raspberry aphid for many years hid the fact that *R. i. strigosus* has genes for resistance to most populations of *A. idaei*, while *R. i. idaeus* is, as far as is known, resistant to *A. agathonica*. Raspberry breeders are now able to make use of this information in their breeding programmes. In Europe, failure to recognise that a common aphid on wild brambles and an important vector of raspberry viruses were distinct species led to a confused situation in which it was impossible to assess the importance of brambles as a source of aphids carrying the viruses. It is still possible that alatae of *A. rubi* may alight and probe on raspberry and sometimes transmit non-persistent viruses, but this can be regarded as a minor and entirely separate problem from that caused by *Amphorophora idaei*.

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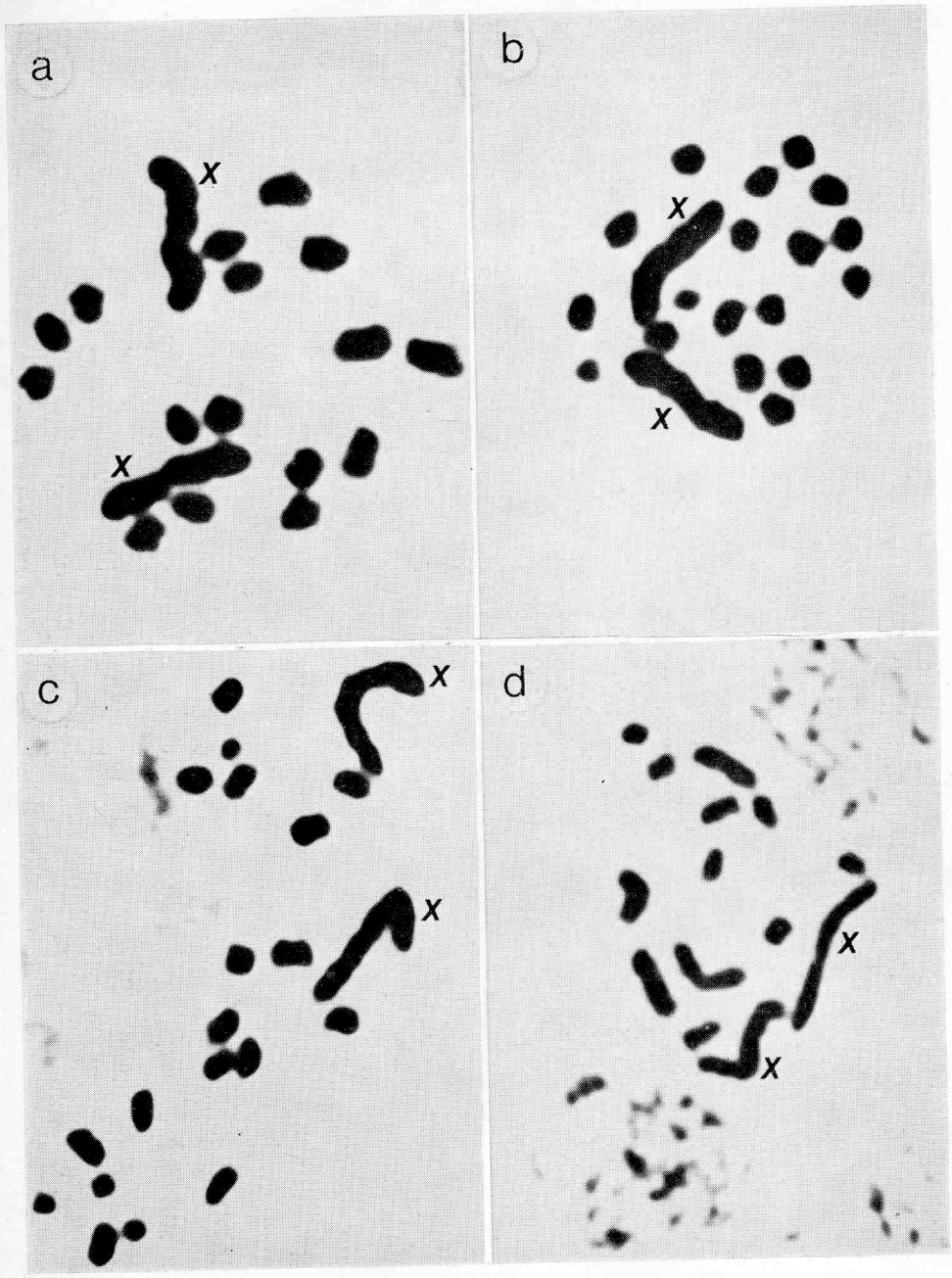

FIG. a. Somatic metaphase of *Amphorophora* from *Rubus idaeus* (*A. idaei*), 2n = 18. FIG. b. Somatic metaphase of *Amphorophora* from *Rubus fruticosus* (*A. rubi*), 2n = 20. FIG. c. Somatic metaphase of *Amphorophora* from *Rubus fruticosus* (*A. rubi*), 2n = 21. FIG. d. Somatic metaphase of *Amphorophora* from *Rubus strigosus* (*A. agathonica*), 2n = 14.