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MORPHOMETRIC VARIATION WITHIN AND BETWEEN POPULATIONS OF THE BALSAM WOOLLY APHID, ADELGES PICEAE (RATZEBURG 1844) (HOMOPTERA: ADELGIDAE), IN NORTH AMERICA

by

Robert George Foottit

B.Sc., Simon Fraser University, 1973

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

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Morphometric variation within and between populations of the balsam woolly aphid, Adelges piceae (Ratzeburg 1844) (Homoptera: Adelgidae), in North America

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ABSTRACT

Morphological variation within and between North American populations of the balsam woolly aphid, Adelges piceae (Ratzeburg 1844) (Homoptera: Adelgidae) was studied using univariate and multivariate statistical techniques.

Morphological characters of the first instar and adult were studied. Multiple discriminant analysis and cluster analysis of Mahalanobis Generalized Distances were computed from 18 population samples collected on several species of true fir (Abies). Characters chosen from the adult stage gave the most interpretable classification of the samples. Three distinct groups were determined: a "Maritimes" group consisting of samples from Newfoundland and Nova Scotia; an "Intermediate" cluster consisting of samples from North Carolina, Oregon, and Washington; and a "British Columbia" group consisting of samples from that province.

The multivariate analyses showed that most of the observed variation was the result of differences in the size and shape of individuals in the samples. Allocation of individual specimens to the three groups, using identification functions calculated from measurements of specimens from the three groups, showed that the morphological characters measured in the adult stage correctly allocated 85.6% of the specimens to the three groups.

Within-population morphological variation was studied using samples taken from Abies amabilis at a site near Duncan on Vancouver Island, British Columbia. No consistent differences between trees or between different sample times on the same tree were found. Inclusion of these samples with the other 18 population samples did not have an effect on the discrimination of the three systematic groups.

Comparative multivariate morphology is a useful approach to the study of adelgid systematics. Based on the morphometric analyses and on certain qualitative attributes, three subspecies of A. piceae are proposed: A. piceae piceae, A. piceae canadensis, and A. piceae occidentalis, which correspond to the "Maritime", the

"Intermediate", and the "British Columbia" groups respectively. A taxonomic key to these subspecies is presented.

The balsam woolly aphid is believed to have been introduced into North America on nursery stock from Europe. It is suggested that observed systematic differences are the result of A. piceae being introduced from the same or different source areas in Europe. Future investigations into the control of this pest insect should take into account these systematic differences as they may reflect other important biological characteristics.

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1. INTRODUCTION

The balsam woolly aphid (BWA)[1], Adelges piceae (Ratzeburg 1844) (Homoptera:Adelgidae), is a minute sucking insect. It is indigenous to Europe, where it occurs throughout most of the range of its principal host plant, Abies alba Miller (Pschorn-Walcher 1964). It feeds on the bark cortex of the stem and crown of the tree. Feeding can result in structural damage to the bark and wood and, as a consequence, in reduced growth; a heavy stem attack can seriously disturb the metabolic functions of the tree which may die as a result (Balch 1952; Bryant 1974; Varty 1956). Whereas the aphid causes little obvious damage to A. alba in Europe, it is capable of attacking and seriously damaging other, more susceptible, true firs (Abies spp.) (Steffan 1972). Since its introduction into North America, BWA has been reported as a serious pest of several economically important fir species (Bryant 1974; Johnson & Wright 1957; Mitchell 1966).

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1 "Balsam woolly aphid" is henceforth abbreviated as "BWA".

1.1 Distribution in North America

There is evidence that BWA was introduced from Europe into eastern North America, presumably with imported nursery stock, on several occasions before 1900 (Balch 1952). It was first reported from Maine in 1908 and from New Hampshire in 1916 (Kotinsky 1916); and it probably invaded Nova Scotia before 1910 (Balch 1952). The BWA subsequently spread from the original infestation sites and was found on balsam fir, Abies balsamea (L.) Mill., in some parts of eastern Canada (Quebec, New Brunswick, Nova Scotia, Prince Edward Island, and Newfoundland) and of the northeastern United States (New York, Maine, Massachusetts, New Hampshire, and Vermont) (Balch 1952; Clark et al. 1971; McGugan & Coppel 1962). It was discovered on A. fraseri (Pursh.) Poir., in Virginia in 1956 (Amman 1962) and in North Carolina in 1957 (Speers 1958).

In western North America, BWA was found first on several different Abies species in Golden Gate Park, near San Francisco, California in 1928 (Annand 1928).

It was reported next from Oregon in 1930 (Keen 1952); and since 1954, severe infestations have been observed at numerous locations in Washington and Oregon (Johnson & Wright 1957). The first record of BWA in British Columbia was on ornamental trees at Vancouver by Silver (1959). The extent of damage to the trees led him to suggest that the aphid had been present for at least eight years before it was discovered in 1958. At present BWA is confined to the southwestern region of the mainland and to southeastern Vancouver Island in British Columbia (Morris & Wood 1977). The fact that BWA was first noticed in parks and gardens suggests that it was also introduced to the west coast of North America with nursery stock from infested areas.

The principal fir species that serve as hosts of BWA in the Pacific Northwest are Abies grandis (Dougl.) Lindl., A. amabilis (Dougl.) Forbes, and A. lasiocarpa (Hook.) Nutt. The aphid also attacks a number of exotic Abies species, such as A. cephalonica Loudon and A. sachalinensis Masters, as well as other native firs including A. procera Rehder, A. magnifica var. shastensis Lemm., and A. concolor (Gord. and Glend.) Lindl. (Mitchell 1966; Wood 1968).

1.2 Life History

The life history of BWA in eastern Canada was described by Balch (1952) and Bryant (1971), in North Carolina by Amman (1962), and in the Pacific Northwest by McMullen & Skovsgaard (1972), Mitchell et al. (1961), and Tunnock & Rudinsky (1959).

The Adelgidae have a pentamorphic holocycle involving a primary host, which is always a species of spruce (Picea spp.), and a secondary host, which is a conifer of another genus (Abies, Larix, Pinus, Pseudotsuga, Tsuga). Whereas host alternation occurs in most species of Adelgidae, the BWA is anholocyclic, that is, all developmental stages and morphs occur on the secondary host plant, Abies spp. Reproduction is entirely parthenogenetic. The life cycle consists of two oviparous morphs i.e., the progrediens and the more numerous sistens morph. These morphs differ in the number of nymphal instars; there are three instars in the sistens and four instars in the progrediens. The first instar of both morphs, which is either a neosistens or a neoprogrediens, includes a motile crawler stage and a settled stage. These

stages were described by Balch (1952) and Varty (1956).

Two types of sistens generation occur on the stem and the branches of the host tree: the hiemosistens which overwinters usually in the neosistens stage; and the aestivosistens which undergoes an obligatory summer diapause in the neosistens stage. Depending upon local climatic conditions, there may be from one to three aestivosistens generations a year (Mitchell, Johnson & Rudinsky 1961).

The first eggs laid by females of the hiemosistens generation can give rise to the non-diapause progrediens generation, which may be either apterous or alate (Annand 1928; Balch 1952). The alate progrediens morph is sterile; it flies to or is blown by the wind to other fir trees or to other branches on the same tree. The apterous progrediens generation produces a sistens (aestivosistens) generation which is morphologically indistinguishable from other sistens generations (Balch 1952; Bryant 1972). The progrediens stage is found commonly in Newfoundland but less commonly in New Brunswick; in Newfoundland that stage comprises less than 3% of the population (Bryant 1972). The

progrediens morph has not been reported in western North America except by Annand (1928), who described both apterous and alate progrediens from material collected in California.

1.3 Previous taxonomic studies

Previous taxonomic work on the family Adelgidae was reviewed by Annand (1928), Pschorn-Walcher and Zwölfer (1958), Steffan (1961, 1968), and Varty (1956), who also described the family, genus, and species level taxa. Reviews of previous taxonomic work on A. piceae were by Annand (1928), Balch (1952), and Varty (1956).

Several authors attempted to differentiate between the morphologically similar species and forms[2] of Adelges (= Dreyfusia Börner) attacking Abies species

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2 Pschorn-Walcher and Zwölfer (1956, 1958) suggested the term "form" for morphologically separable isolates of BWA. The term "form" is taxonomically neutral; it implies a provisional classification.

(Busby 1962; Eichhorn 1958, 1967; Pschorn-Walcher & Zwölfer 1958, 1960). Varty (1956) determined in detail the morphological and biological differences between A. piceae and A. nordmannianae (Eckstein 1890) (=nuesslini Borner 1908) as they occur on firs in Scotland. Differences in the morphology and chromatographic properties of various stages, modifications of the holocyclic life cycle, and hostplant reactions have proved to be the most useful criteria for differentiating between the various species and forms. Most taxonomists have relied largely on differences between the first instarr stages, in particular on differences in the shape, number, and arrangement of the wax pores on the dorsal sclerites of the first instar.

Morphological variation in North American populations of BWA has been little studied so far. Annand (1928) provided incomplete descriptions of some stages and morphs collected in California. Balch (1952) described all stages of BWA from material collected in eastern Canada, examined specimens from the northeastern United States and from Oregon, but did not consider morphological variation within and between geographically isolated populations.

Different forms of BWA were described from some areas of North America. For example, A. piceae forma canadensis was described from populations on A. balsamea in the Maritime provinces of Canada and in the northeastern United States (Eichhorn 1956, 1957; Merker & Eichhorn 1956; Pschorn-Walcher & Zwölfer 1958). The neosistens of forma canadensis can be distinguished from the European forma typica by being more heavily sclerotized and having a higher number of wax pores in the central wax glands of the dorsal sclerites of the first instar. However, specimens resembling forma typica have been found on infested firs in Oregon, Washington, and British Columbia (Pschorn-Walcher 1960, 1964) and forma canadensis has been identified from among Scottish material (Busby 1962, 1964). In addition, the European species A. prelli Grosmann 1935 has proven diffficult to separate from A. piceae forma canadensis on the basis of morphological features (Busby 1962; Pschorn-Walcher 1964).

It is evident that BWA shows considerable biological variability in Europe and in North America including variability in its effects on the different host firs (Atkins 1972; Bryant 1974; Greenbank 1970; Mitchell 1966).

Puritch (1971) noted that differences between the type of damage done to A. grandis in Scotland and in North America may be the result of systematic differences between the two BWA populations.

As already mentioned, other adelgid species that closely resemble A. piceae have been described and at least one of them, A. nordmannianae, has been recorded from North America (Annand 1928; Balch 1952; Harris 1966). There is also some evidence suggesting that geographical differences exist between European and North American populations of BWA (Bryant 1974). Because the parthenogenetic mode of reproduction limits genetic exchange between populations, it is possible that much of the observed biological diversity is a consequence of differences in the origin of local (and isolated) populations of BWA. Such differences could lead to further divergence and, eventually, to the evolution of measurable differences that should be taxonomically recognized.

Bryant (1974) emphasized the need to determine whether or not observed variation in North American populations of BWA is the result of more than one species

of adelgid being present and/or of infraspecific differences among one species. To devise suitable control measures it will be necessary to determine whether or not there is a systematic basis to the observed biological variability of BWA. Preventative and control measures, to be effective against BWA, will depend on the reliable identification of the species and the forms of Adelgidae occurring on Abies (Bryant 1974).

The objectives of this study are: to define intra- and inter-population morphological variation in BWA in North America; to determine means of discriminating between morphologically distinct populations; and to interpret observed morphometric variation within the context of the known colonization history of BWA in North America.

2. METHODS AND MATERIALS

In previous studies of the systematic relationships between different adelgid taxa, relatively few of the available morphological characters were examined quantitatively . As mentioned above, emphasis has been placed on differences in the shape, numbers, and arrangements of wax pores on the dorsal sclerites of the first instar; however, counts of wax pores exhibit much variability and their ranges overlap considerably between taxa (Busby 1962; Eichhorn 1967; Pschorn-Walcher & Zwölfer 1958).

It has been stated (Blackith & Reyment 1971; Sneath & Sokal 1973) that a classification should be based on a wide range of characters. When only a few characters are studied the resultant classification is often unstable and taxonomic boundaries may change easily with the inclusion of additional characters. For that reason I used a wide range of characters taken from samples from throughout the range of BWA in North America. To determine if the emphasis on attributes of the first instar stage was misplaced and if additional taxonomic information could be found

by the use of more than one life history stage, characters of both the first instar and the adult were measured.

The geographic variation of an organism is believed to be the result of a multidimensional process resulting from the adaptation of numerous features to many interdependent environmental and biological factors, the relationships of which change over space and time (Gould & Johnson 1972; Sokal & Rinkel 1963). For this reason, multivariate statistical techniques were used to analyze the observed variability of the morphological characters. These procedures enable the simultaneous analysis of the variation and covariation of a large number of characters from many individuals and populations. They provide a means to describe and to summarize patterns of variation and to delineate groups of samples that are similar in these recognized patterns of variation. General reviews of the application of multivariate statistics to studies of biological variability are available (Blackith & Reyment 1971; Clifford & Stephenson 1975; Sneath & Sokal 1973). Gould & Johnson (1972) and Thorpe (1976) reviewed procedures for studying geographic variation.

In studies of geographic variation it is often difficult to standardize the samples studied with respect to the ontogenetic variation of individuals and the time of collection (Heryford & Sokal 1971). As the demonstration of geographic variation relies on character variation that is greater among the samples than that which is found within samples, within-population variation of BWA was studied at one location, and on one host tree species through the approximate time period covered by the collection of the other samples.

2.1 Collection and preparation of material

Samples of the first instar and adult stages of the sistens morph of BWA were obtained from populations on five species of Abies from 18 sites within the known areas of infestation in Canada and the United States (Table I). The collections were made either by myself or were provided by the staff of the Canadian and the United States Forestry Services.

Table I. Collection data of population samples of the balsam woolly aphid, Adelges piceae, used in the study.

Sample No.	Locality, altitude, date, and name of collector.	Host Tree
	BRITISH COLUMBIA (CANADA)	
1.	Fellow's Creek, near Duncan, Vanc. Isl.; 550m ; 23 July, 30 August, 3 October, 16 November 1973; R. Foottit	Abies amabilis
2.	Glenora Road, Duncan, Vanc. Isl.; 90m ; 30 July 1974; R. Foottit	Abies grandis
3.	Land's End Road, Saanich, Vanc. Isl.; 60m ; 31 July 1974. R. Foottit	Abies grandis
4.	Diamond Head, near Squamish; 920m; 10 August 1975; R. Foottit	Abies amabilis
5.	Seymour Valley, North Vancouver; 240m ; 13 August 1975; R. Foottit	Abies amabilis
6.	Eagle Mountain, Coquitlam; 470m; 27 July 1974; R. Foottit	Abies amabilis
7.	Widgeon Valley, Coquitlam; 210m; 29 July 1974; R. Foottit	Abies amabilis
8.	UBC Research Forest, Maple Ridge; 350m ; 2 September 1975; R. Foottit	Abies amabilis
	WASHINGTON (U.S.A.)	
9.	Point Roberts; 60m ; 6 September 1975; R. Foottit	Abies grandis
10.	Baker Lake, Mt. Baker; 760m ; 29 September 1975; R. Mitchell	Abies lasiocarpa
11.	Olympic National Forest, near Mt. Washington; 760m ; 7 August 1975; R. Foottit	Abies lasiocarpa

Sample No.	Locality, altitude, date, and name of collector.	Host Tree
	OREGON (U.S.A.)	
12.	Corvallis; 370m ; 15 September 1975; R. Mitchell	Abies grandis
13.	Umatilla National Forest; 1520m; 1 August 1975; R. Foottit	Abies lasiocarpa
	NORTH CAROLINA (U.S.A.)	
14.	Mount Mitchell; 1780m ; 20 September 1974; C.F. Speers	Abies fraseri
15.	Waynesville; 1680m ; 20 June 1975; T.R. Gentry	Abies fraseri
	NOVA SCOTIA (CANADA)	
16.	McPherson's Mills, Pictou Co.; 120m ; 18 July 1974; Canadian Forestry Service	Abies balsamea
17.	Marinette, Halifax Co.; 70m; 15 August 1974; Canadian Forestry Service	Abies balsamea
	NEWFOUNDLAND (CANADA)	
18.	Bellevue Beach; 30m ; 9 August 1974; D.G. Bryant	Abies balsamea

Within-population variability was measured in a BWA population infesting A. amabilis at Fellow's Creek, near Duncan, British Columbia (Sample No. 1). The site was situated at an altitude of 550 m; there were only minor changes (1 to 5 m) in elevation throughout the sampling area. The population had been there for a number of years and had caused some mortality to the 15- to 20-year-old trees. Populations were sampled on four occasions between 23 July and 16 November 1973; the sampling schedule was arranged so as to coincide with expected changes in generations. All trees sampled were of approximately the same height and diameter-at-breast-height. Intensity of attack by BWA and the relative conditions of the trees sampled were noted.

The aphids, together with the section of bark on which they were feeding, were removed from the stem of each tree; normally this was done with a 2.5 cm-diameter hollow drill. The bark and aphids were preserved in 70% ethanol for subsequent examination and mounting on microscope slides.

Settled first instar and adult aphids were removed from the bark under a dissecting microscope; a pair of fine tweezers was used to lift each aphid carefully off

the bark so that the stylets remained intact. The aphids were cleared in 5% KOH and chloralphenol and were mounted in Hoyer's medium on microscope slides (Hille Ris Lambers 1950). First instar nymphs were mounted with their ventral side up to facilitate measurement. The dorsal surfaces of the adult aphids were separated from the ventral section with a razor blade and were mounted separately to enable accurate counting of the dorsal wax pores. The ventral section of each body together with the attached appendages was mounted with its ventral side up.

Following mounting, the specimens were examined to verify the life history stages sampled. The first instar was identified by its characteristic irregularly shaped pore fields, and the adult stage was identified by the presence of an ovipositor (Balch 1952; Varty 1956).

2.2 Selection and measurement of morphological variables

Among the characters that appeared suitable for a morphometric study of BWA, continuous variables were

selected that satisfied the following conditions: the characters could be measured precisely within a reasonable amount of time and with a reasonable amount of effort and they should not or only insignificantly be distorted by the mounting procedure. In addition, characters were selected so as to include a reasonably large proportion of the aphid body. Both length and width measurements of certain features were taken to ensure that both changes in size and shape differences would be included.

Preliminary data sets from a sample taken at Pellow's Creek, British Columbia, were analyzed statistically. All continuous characters that either did not meet the above criteria or that were invariate, or largely so, or that had a coefficient of variation greater than 15%, were not analyzed further.

Table II lists all continuous variables that were measured in the first instar and adult stages and that were used in subsequent morphometric analyses. Figures 1 and 2 show the ventral surfaces of the first instar and adult stages respectively and the morphological features measured in each. The operational dimensions

Table II. Continuous variables measured in the first instar stage and the adult stage of the balsam woolly aphid, Adelges piceae.

	Character	First Instar	Adult
1.	Body - length	+	-
2.	Body - width	+	-
3.	Antennal segment II - length	+	+
4.	Antennal segment II - width	+	+
5.	Antennal segment III - length	+	+
6.	Antennal segment III - width	+	+
7.	Apical seta - length	+	-
8.	Femur - length	+	+
9.	Femur - width	+	+
10.	Tibia - length	+	+
11.	Tibia - width	+	+
12.	Tarsus - length	+	+
13.	Tarsus - width	+	+
14.	Tarsal hair - length	+	-
15.	Labial segment I - length	+	+
16.	Labial segment I - width	+	+
17.	Labial segment II - length	+	+
18.	Labial segment II - width	+	+
19.	Labial clamp - width	+	+
20.	Ocellus - diameter	+	+
21.	Stylet - length	+	-
22.	Ovipositor - length	-	+
23.	Anal plate - length	-	+

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Figure 1. Ventral surface of first instar balsam woolly aphid, Adelges piceae.

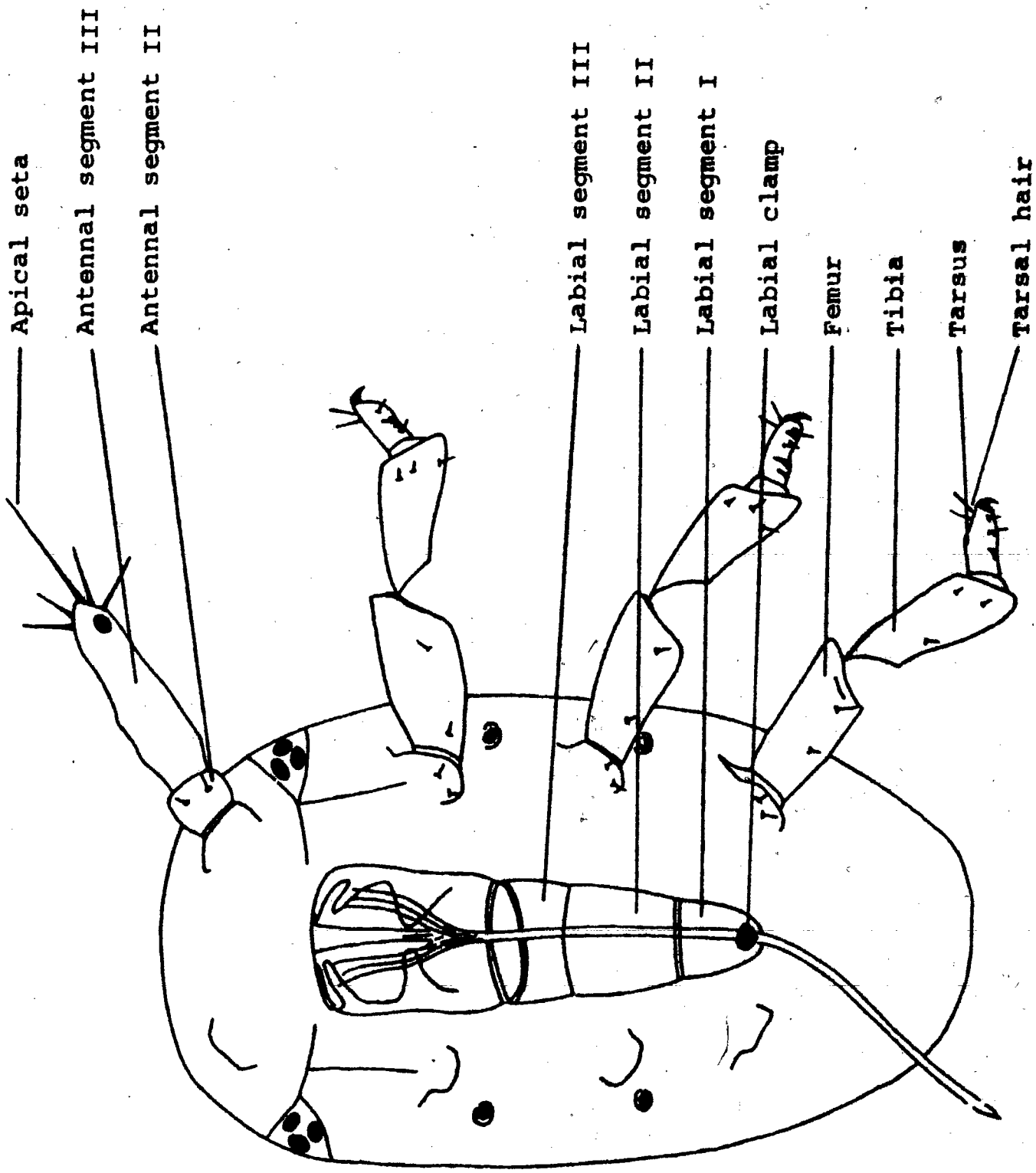
Apical seta
Antennal segment III
Antennal segment II
Labial segment III
Labial segment II
Labial segment I
Labial clamp
Femur
Tibia
Tarsus
Tarsal hair

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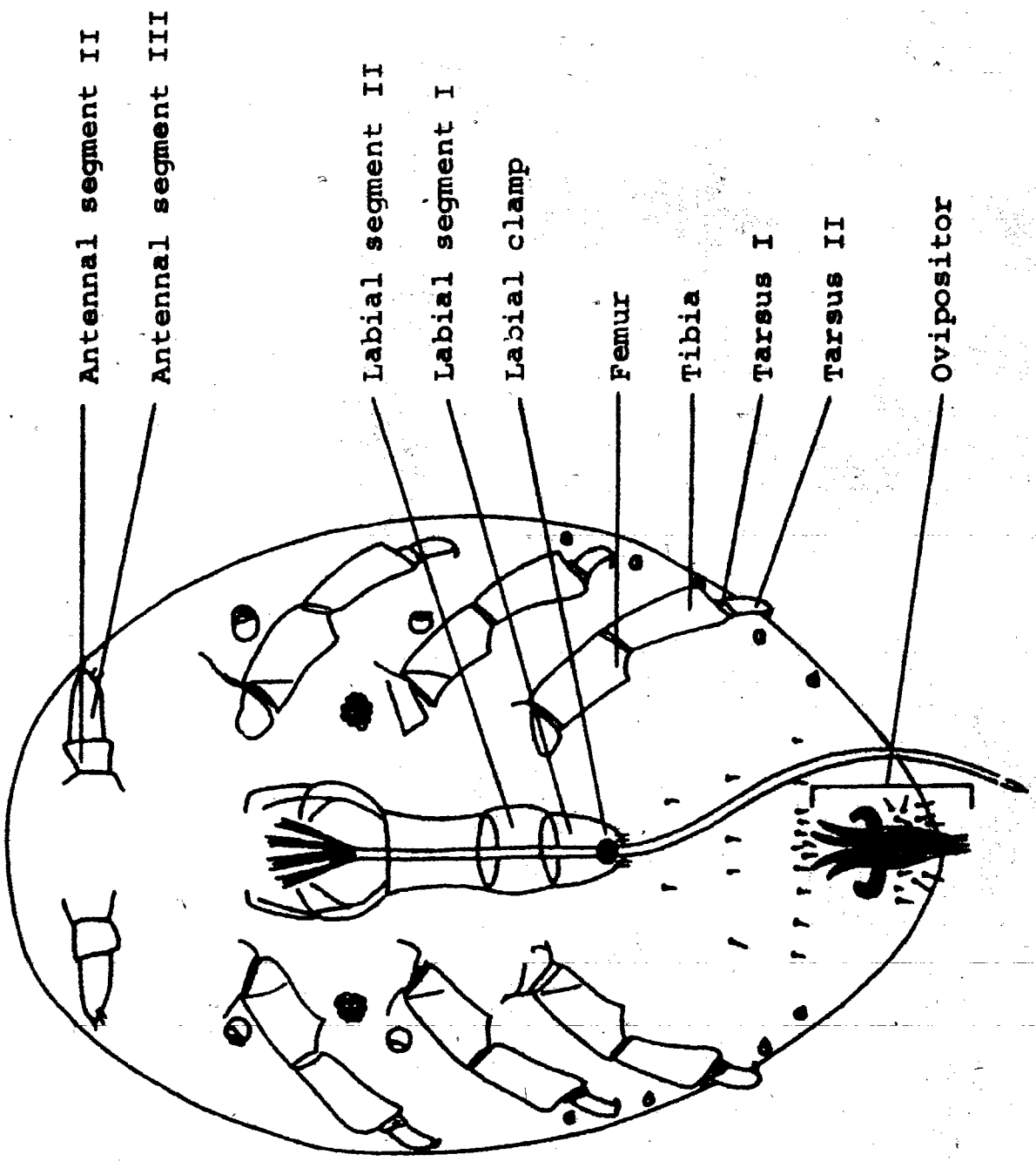
Figure 2. Ventral surface of adult balsam woolly aphid, Adelges piceae.


Antennal segment II
Antennal segment III
Labial segment II
Labial segment I
Labial clamp
Femur
Tibia
Tarsus I
Tarsus II
Ovipositor

of variables used in subsequent morphometric analyses are shown in Figure 3.

Because of ontogenetic differences between the two stages and because the mounting procedure varied in its effect on the variables, not all variables were measured in both stages. For example, the apical seta of the antennal segment was measured only in the first instar. It was not measured in the adult stage because it is very short and its distal end is imprecisely defined in the microscopic image.

All continuously variable characters with the exception of the stylet length were measured using a Leitz Oknor micrometer eyepiece[3]. The stylet length was estimated from its projected image using a camera lucida and a calibrated map measure.

Attempts to count the number of wax pores on the dorsal sclerites of the first instar stage were made. Counting was more difficult in some samples than in others; in samples from Vancouver Island, British Columbia, the first instar was weakly

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3 Ernst Leitz (Canada) Ltd., Midland, Ontario.

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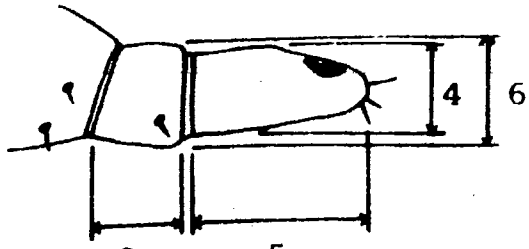
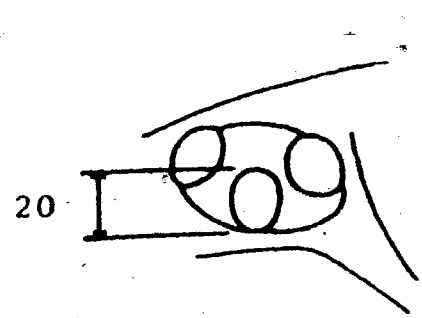
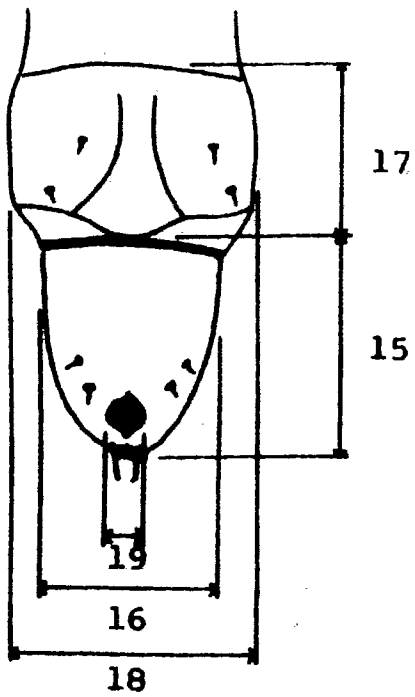
Figure 3. Operational dimensions of discriminating variables: (a) antenna; (b) rostrum; (c) hind leg; (d) ocellus; (e) anal plate. Numbers refer to variables as listed in Table II.



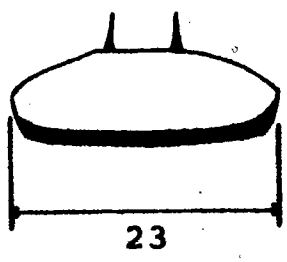
(a)



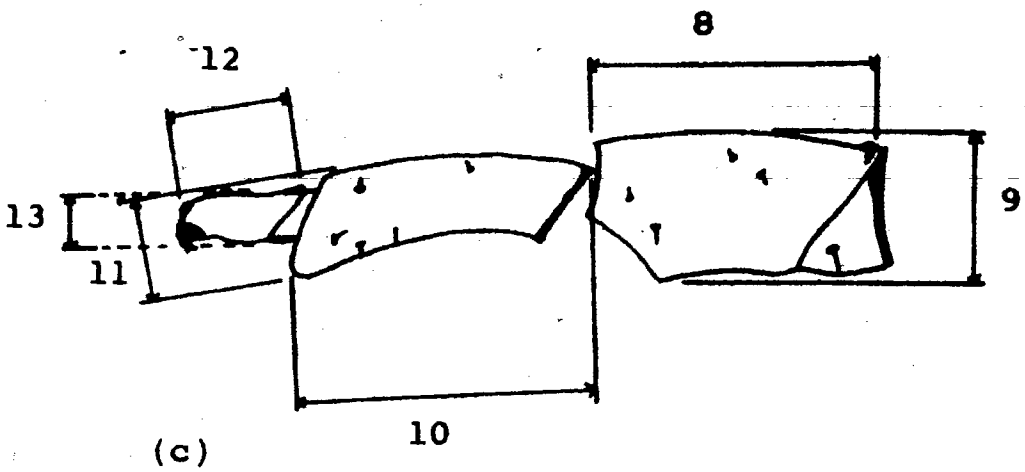
(d)



(b)



(e)



(c)

sclerotized, a fact that made it difficult to count the pores accurately.

Pore counts of the first instar stage have been used almost exclusively in systematic studies of species of Adelgidae (Bryant 1974). However, some authors (Bryant 1974; Busby 1962) considered the subjectivity of counting pores, of which some may be barely discernable or may be situated in a poorly defined central gland area. Therefore, I decided not to use these characters in any morphometric analysis as a complete and accurately counted data base would be required.

No such difficulty existed with counting the wax pores of the adult; these were always clearly defined and could be counted easily in cleared specimens. The distribution of the pore fields on the dorsal surface of the adult stage is shown in Figure 4.

Initially, the number of pores in all pore fields of 20 aphids each from two populations (Samples 1 and 18)

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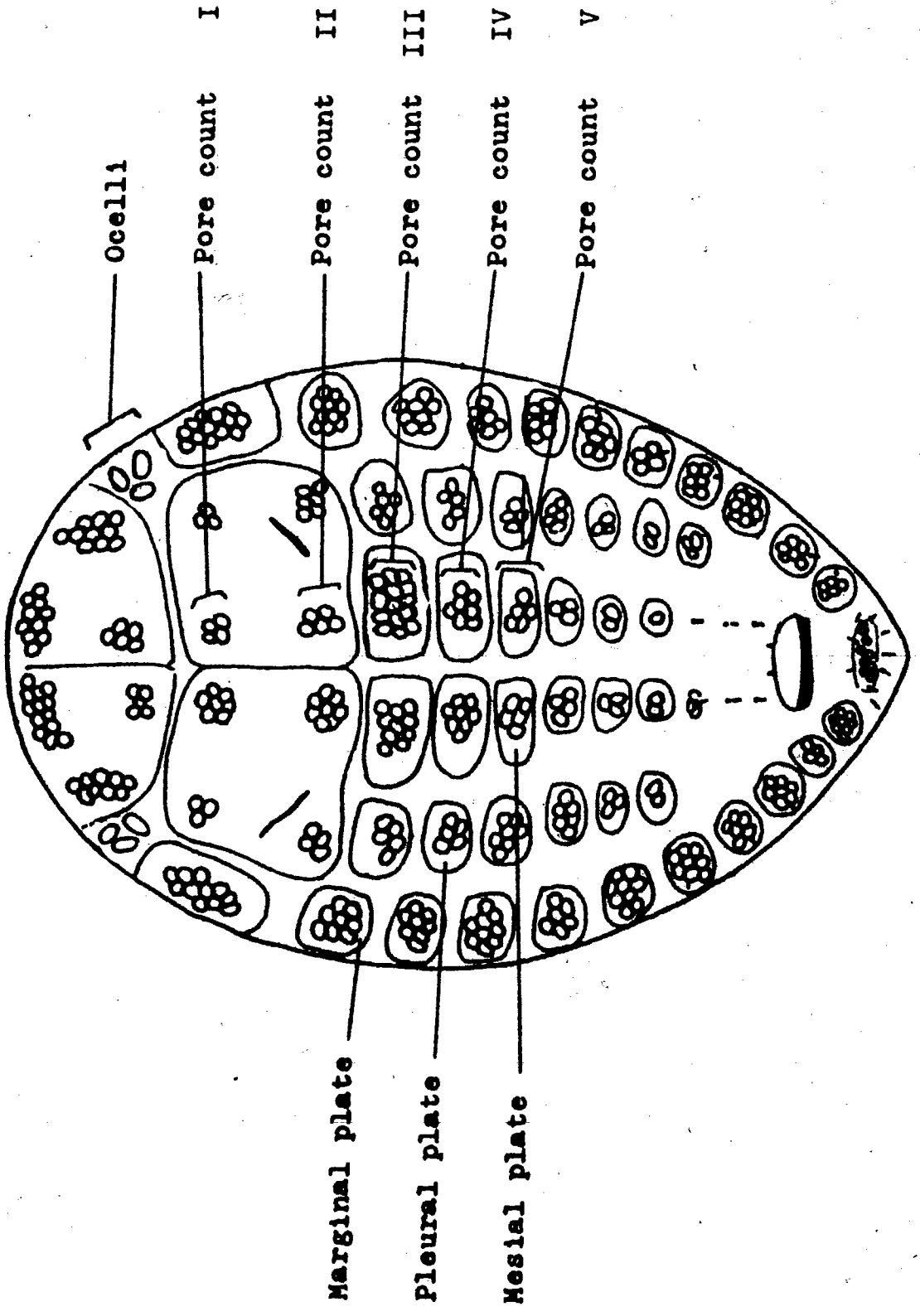
Figure 4. Distribution of pore fields on the dorsal surface of adult balsam woolly aphid, Adelges piceae.


Ocelli
I
Pore count
II
Pore count
III
Pore count
IV
Pore count
V
Pore count
Marginal plate
Pleural plate
Mesial plate

were counted. A comparison of the descriptive statistics of these counts showed that some pore fields were more variable than others; however, paired t-tests (Sokal & Rohlf 1969) showed that differences between the number of pores in corresponding fields on the left and right side of the body were non-significant. Therefore, subsequent counting was restricted to the pores in five fields of the mesial row (Figure 4). These fields were chosen because distortion caused by the mounting procedures was minimal.

Variations in other attributes were noted. These attributes included a qualitative assessment of the amount of sclerotization in the first instar and in the adult stages, the shape of the gland areas in the adult stage, and the form and the distribution of the pores within these areas.

2.3 Multivariate analysis

Taxonomic structure can be represented most usefully when both cluster analysis and an ordination technique are used (Sneath & Sokal 1973), a procedure that allows for one technique to compensate for some of the disadvantages of the other. I chose multiple-

discriminant analysis and cluster analysis of a dissimilarity measure for this study.

Cluster analysis is useful in that it may produce partitions of OTU's[4] that have a taxonomically meaningful order and, as a result, that supply useful summarizations of taxonomic groups. Ordination techniques do not impose a hierarchical structure on the data and, in cases where the variation is continuous, they may give a more meaningful taxonomic representation. Ordination techniques are particularly valuable for providing greater understanding of taxonomic relationships because trends in variability can be associated with the morphological attributes that cause them. The relative merits of the use of cluster analysis and of ordination techniques are discussed by Blackith & Reyment (1971) and Sneath & Sokal (1973).

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4 OTU = Operational Taxonomic Units. These are the lowest ranking taxa employed in a given study (Sneath & Sokal 1973). In this study they represent the population samples.

Multiple-discriminant analysis, which includes discriminant function analysis and generalized distance analysis, linearly combines discriminatory variables to maximize statistically the distinction between groups. The discriminant function was originally developed by Fisher (1936) for linear discrimination between two groups; it was later generalized tc many groups. The Mahalanobis Generalized Distance (D2 statistic) (Mahalanobis 1936), which can be derived from the discriminant function, is a measure of statistical distance between groups.

The linear combination of the discriminatory variables (i.e. the discriminant functions) emphasizes those variables with the least within-sample and the greatest among-sample variation. The result is the transformation of the original set of variables into a new, usually smaller, set of independent functions, of which the first discriminant function accounts for the largest possible proportion of the total variation, the second discriminant function accounts for the largest proportion of the remaining variation, etc., until all the variation among groups has been explained.

Calculation of discriminant functions involves the manipulation of two kinds of variation matrices which

contain measures of the absolute variation within and between variables. These are the within-group variance-covariance matrix, W, which is a measure of variation within a sample and the among-groups variance-covariance matrix, A, which is a measure of variation between the samples.

The variances and covariances between the variables in a group are calculated first. These are then averaged over all the groups to produce the pooled within-groups variance-covariance matrix, W. The sample means are then used to calculate the among-groups variance-covariance matrix, A. The equation,

$$\left| W^{-1} A - \lambda I \right| = 0 \qquad (1)$$

when solved, gives a set of roots (λ 's) which are the discriminant functions.

The discriminant functions can be expressed as

$$DF_i = d_i Z_i + d_{i2} Z_2 + \ldots + d_{ip} Z_p \qquad (2)$$

where DFi is the score on the discriminant function i,

the values di1, ..., dip are the discriminant function coefficients and the values Z1, ... , Zp are the standardized values of the p discriminating variables. The discriminant function coefficients are weighted, i.e., they are calculated so that they maximize differences between group means. The mathematical derivation of these coefficients was described by Cooley & Lohnes (1971) and Seal (1964).

The maximum number of possible discriminant functions is equal to the number of discriminatory variables provided that there are more groups than variables. If there are more variables than groups, then the maximum number of functions is one less than the number of groups. Often a large proportion of the potential discrimination can be obtained with less than the maximum number of discriminant functions.

Each discriminant function can be viewed as representing an axis in geometric space. All samples can be positioned along the set of n discriminant axes, i.e., all samples are situated in n-dimensional hyperspace. Each sample is situated along each discriminant axis on the basis of the equation

$$V_1 Y_1 + V_2 Y_2 + \cdots V_n Y_p = P_1 \quad (3)$$

where V1 ... Vn are eigenvectors representing the discriminant functions, Y1 ... Yp are the sample means for each variable, and P1 is the position of a sample on a particular axis. These mean discriminant scores for each group on the discriminant functions are the sample centroids. They can be plotted on pairs of axes representing the major components of variation and examined for systematic trends (ordination, Sneath & Sokal 1973).

Associated with each eigenvector is an eigenvalue, which is the variance of means on that discriminant axis. The sum of all the eigenvalues is a measure of the total variance in the p discriminatory variables. When expressed as a percentage of the sum of all eigenvalues, each eigenvalue is a measure of the relative discriminatory ability of each discriminant function. Standardized values of the discriminant function coefficients of each discrimiant function (Equation 1) can be used to measure the contribution of each variable to that function. Standardization is carried out by scaling each raw coefficient for a variable by multiplication with the pooled standard

deviation of that variable. Irrespective of sign, the magnitude of the standardized coefficient indicates the importance of a particular variable in discrimination along each independent axis.

Discriminant functions can be used as an objective basis for the assignment of single specimens into one of a number of a priori groups. This serves as a check of the discriminatory power of the variables. The identification procedure is carried out by calculating a set of separate identity functions (i.e. separate linear combinations of the variables) for each group. Probabilities of membership in each group are determined from the function scores, and an individual specimen is assigned to the group with which it shares the highest probability. Assignments of individual specimens can be compared with the actual group to which each belongs; the results of this can be summarized in the form of an identification table.

The Mahalanobis Generalized Distance (D2 statistic) may be used as a measure of phenetic similarity in that, as it is based on the discriminant function, it eliminates the effect of between-character correlation and allows the use of only that amount of discriminatory

information unique to a given character (Blackith & Reyment 1971; Goodman 1972). In discriminant function analysis, plots of the sample centroids onto the major discriminant axes, two or three at a time, will show systematic trends. However, ordination will not account for all the variability in any one projection. The D2 statistic provides another estimate of phenetic similarity which does take into account all the variability.

The D2 statistic is calculated by multiplying the vector of discriminant function coefficients that comprises the discriminant function calculated for any two groups by the vector of differences between the means of the discriminatory variables for the two groups. The D2 statistic can thus be calculated for all pairwise comparisons between groups. Samples sharing a D2 value of 0 would be identical while an increasingly larger value indicates that samples are phenetically more and more dissimilar with respect to the characters used. D2 can be converted to an F-statistic for tests of significance (Morrison 1967). The square root of D2, or D, can be used as a measure of taxonomic distance in Euclidean space; it can therefore be subjected to cluster analysis, the results

of which can be represented in the form of a phenogram[5].

Accounts of most aspects of multiple-discriminant analysis and the Mahalanobis Generalized Distance are given in Blackith & Reyment (1971), Cacoullos (1973), Cooley & Lohnes (1962), Morrison (1967), Lachenbruch (1975), and Sneath & Sokal (1973). Seal (1964), provides a detailed mathematical treatment under "Canonical Analysis".

Matrices of D values may be too large to be accurately inspected for taxonomic structure. Cluster analysis refers to a group of methods for searching for natural groups in data, i.e., for determining sets of similar entities from a previously unpartitioned set of entities. Cluster analysis can thus be used as a means of summarizing a set of D values between OTU's into a hierarchical form that can be interpreted taxonomically. The results of a cluster analysis of a matrix of measures of phenetic similarity can be summarized in the form of a phenogram.

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5 Diagrams of phenetic relationships, i.e. those based on similarity (Sneath & Sokal 1973).

An objective criterion is available that may be used to assess the effeciency of a particular clustering technique in summarizing the relationships inherent in a particular matrix of similarity values. This measure is the cophenetic correlation coefficient (rcs) of Sokal & Rohlf (1962) (Sneath & Sokal 1973), which is a measure of the distortion between the similarity values of the original otu x otu matrix and the similarity values between otu's as implied by the structural representation of the phenogram. Numerical examples of the calculation of rcs are given in Sokal & Rohlf (1962) and Sokal & Sneath (1963).

Sneath & Sokal (1973) recommended a value of rcs greater than 0.8 to indicate a satisfactory representation of taxonomic structure inherent in the original matrix. The method of cluster analysis chosen for this study was the UPGMA (= unweighted pair group method using arithmetic averages) method (Rohlf 1963; Sneath & Sokal 1973; Sokal & Rohlf 1962). Comparisons with other methods of cluster analysis (Farris 1969; Sokal & Rohlf 1962) have shown that this method produces a phenogram with the least distortion as indicated by rcs. A numerical example of the calculation of a UPGMA cluster

analysis is given in Sneath & Sokal (1973).

Reviews of the major aspects of cluster analysis and its application in systematic biology are provided by Blackith & Reyment (1971) and Sneath & Sokal (1973).

2.4 Morphometric Analysis of Population Samples

To determine within-population variation at the Fellow's Creek site 12 different population samples were analyzed. Each consisted of 40 first instar and 40 adult specimens, which had been collected on four trees at one sampling time. Additional samples of 40 first instar nymphs were taken from one of the same trees at three other sampling times. A sample of 40 adults was also taken from that tree on one other date. The dates of collection of the samples are given in Appendices 1 and 2.

Between-population variation was determined by comparing one sample from each of the 18 different locations representing the known areas of BWA infestations in North America. Each sample consisted of 40 first instar nymphs and 40 adults.

The sample size for each location, or for different sample times at the same location in the case of the within-population analysis, was uniformly set at 40. This was the level at which measures of sample variability were certain to have stabilized for all or most characters. It also enabled the subsequent splitting of samples for the purpose of validating certain of the statistical techniques without violating the assumptions of the techniques; and it permitted the effect of reduction in the number of variables needed for meaningful descrimination to be tested.

Descriptive statistics, including the mean, the range, the standard error, the standard deviation, and the coefficient of variation (Sokal & Rohlf 1969; Zar 1974), were calculated for each set of character measurements (n = 40) for each sample locality and/or sample time. Homogeneity and normality of the data were determined by calculating the measures of kurtosis and skewness $g1$ and $g2$ and D'Agostino's D (D'Agostino 1971; Zar 1974).

Multiple-discriminant analysis was carried out on all data sets. Discriminant functions and their associated eigenvalues were tabulated with the standardized discriminant function coefficients for each variable on

the major discriminant axes. The centroid of each sample was projected onto the major discriminant axes and the plots inspected for systematic trends. Where applicable, identification functions were computed and individual cases were allocated into the a priori groups. The results of this procedure were summarized in identification tables showing the number of correct and incorrect placements of individual specimens.

The Mahalanobis Generalized Distance (D2) statistic was computed for all pairwise combinations of samples of each data set and grouped in a sample x sample matrix. Square roots of these values were taken and the resulting matrix of D values clustered using the UPGMA method. The phenetic relationships between the groups, as indicated by the cluster analysis, were summarized in the form of a dendrogram. Cophenetic correlation coefficients were calculated in order to measure the amount of distortion between the original dissimilarity matrix and the structural representation of the dendrogram.

Other analyses were carried out on the data sets or on portions of them. Discussion of these statistical methods and their results are presented together to facilitate their interpretation.

All statistical analyses were carried out on Simon Fraser University's IBM System /370 155 computer. All phases of multiple-disriminant analysis were executed using the Statistical Package for the Social Sciences (SPSS; Nie et al. 1975). The Mahalanobis Generalized Distances were calculated using a program written by John A. Ludwig of New Mexico State University (Zimmerman & Ludwig 1974). Cluster analyses, development of phenograms and calculation of the cophenetic correlation coefficients were carried out using a system of multivariate statistical programs (NT-SYS) developed for numerical taxonomic studies (Rohlf, Kishpaugh & Kirk 1971).

3. RESULTS: ANALYSIS OF BETWEEN-POPULATION VARIATION

3.1 Univariate trends in the characters

The mean and standard error for each of the characters measured in all samples employed in the morphometric analyses are given in Appendix 1 for the first instar variables and in Appendix 2 for the adult variables. Some inter-locality patterns of morphological variation are evident in the means of both the first instar and the adult sets of measurements. Summary descriptions of the major trends in variation of these characters and comparisons between some of the samples are given below.

3.1.1 First instar characters

1. Body length, body width. The greatest mean body lengths are in samples from the Maritime provinces and from Mt. Mitchell, the lowest in BWA from the Olympic National Forest. There is considerable heterogeneity in the western samples and no obvious geographic trends. The pattern of body width variation is similar to that of body length.

2. Antennal measurements. In general, and especially in the Maritime samples, longer antennal length measurements are associated with larger body sizes. Comparisons between antennal lengths and widths show different trends. The Maritime samples tend to have smaller width measurements, particularly in antennal segment III, than do the other samples. However, Fellow's Creek has correspondingly larger length and width measurements and has longer antennal lengths and widths compared with other samples of similar general size.

3. Leg measurements. Trends similar to those in antennal measurements are shown in hind leg lengths and widths. The Maritime samples particularly show a tendency towards longer, but proportionately thinner leg dimensions, especially in the tibia. Again, the sample from Fellow's Creek shows long but also comparatively broad leg measurements.

4. Labial measurements. The largest labial measurements are in specimens from the Marinette, Nova Scotia, and Bellevue Beach, Newfoundland, samples. McPherson's Mills, Nova Scotia, with the largest overall size measurements, has proportionately shorter labial

width measurements. Fellow's Creek maintains relatively large length and width measurements.

Labial clamp width shows a marked increase in the Maritime samples. Stylet length is considerably larger in the Marinette and Bellevue Beach samples. These last two variables show considerable heterogeneity in other samples.

5. Ocellus diameter. With the exception of the lowest values, which occur in the two Nova Scotia samples, there are no noticeable trends.

3.1.2 Adult characters

1. Antennal measurements. There is considerable variability in all the measurements. McPherson's Mills shows higher values over most dimensions. As in the first instar, there is a trend towards proportionately smaller width measurements in the Maritime samples.

2. Leg measurements. The largest mean femur, tibia and tarsus lengths are in the Maritime samples. Femur length is approximately the same in samples 1 to 7 from British Columbia, then drops drastically

in the UBC Research Forest (No. 8) and Washington state samples (Nos. 9-11). A similar but less pronounced trend occurs with tibia length and tarsus length. This trend is also reflected in the width measurements of these variables.

3. Labial measurements. The Maritime samples have the largest mean lengths for labial segments I and II. This difference is less apparent in the width means of these variables. The most apparent trend in the width means is the smaller value in the UBC Research Forest, Pt. Roberts and Baker Lake samples. Samples 8 to 14 have a smaller mean labial clamp width.

4. Other continuous measurements. Ocellus diameter shows no definite trends between groups. Ovipositor length is smaller in samples 8 to 14. This trend is less definite in anal plate length.

5. Pore counts. The highest means for pore counts I and II are found in the McPherson's Mills and Bellevue Beach samples. For pore counts III, IV, and V, Umatilla National Forest also has relatively high means. The Glenora Road, Land's End Road, and Diamond Head samples from British Columbia consistently show

low means for all 5 pore counts.

Clearly, there are some trends in morphological variation that can be determined by inspection of the sample means for each character. There is a large component of size-related variation. For example, in both the first instar and the adult stage the larger specimens that make up the Maritime samples show the largest values for many of the variables considered. There is also a component of shape-related variation as evidenced in the changing relationships between length and width measurements of certain features when these are compared over the samples.

There are exceptions to the trends mentioned above. Inconsistencies exist in the sample means of some variables that cannot be correlated with geographic location. These circumstances emphasize the practical usefulness of multivariate analytical techniques in dealing with data of this type. They bring about a simplification of information and develop patterns based on the simultaneous covariation of the characters under study.

3.2 Variability and normality of the data

With few exceptions, the values of the coefficients of variation for all continuous variables over the between-site samples are consistent. Most had values of between 4% and 12%, a range that is considered optimal for good taxonomic characters because more reliable systematic comparisons can be made with variables that exhibit some but not unreasonably large variability within OTU's (Simpson, Roe & Lewontin 1960).

The coefficients of variation for the adult wax pore counts are high (range, 22.2% - 91.8%) compared to those for continuous measurements and show considerable variability between the samples. The higher values, particularly those in the Glenora Road, Land's End Road, and Diamond Head samples, are partly the result of a number of specimens having no pores in the pore fields counted while other specimens had relatively high numbers of pores in these fields. This situation results in an inflation of the value of the coefficient of variation. Similar observations were reported in studies of other meristic variables in aphids (Sokal 1952).

All the standard errors of the means are relatively small, with few exceptions. Thus the sample means are reliable estimates of the population means.

The multivariate statistical techniques used in this study assume that the populations are multivariate normal and that the a priori groups have equal variance-covariance matrices. In practice, these assumptions are difficult to achieve with biological material. However, these techniques are extremely robust and minimize irregularities caused by violations of the assumptions (Blackith & Reyment 1971, Lachenbruch 1975).

Normality of the data was determined with D'Agostino's D ($p \leq 0.01$); 4.58% of the adult continuous measurements, 6.8% of the adult pore counts and 6.9% of the first instar measurements were found to be non-normal by this statistic. This is not considered to be an inordinate amount of non-normality, and consequently the data were not transformed.

3.3 Multivariate analysis of first instar data

Table III gives the Mahalanobis D values calculated by multiple discriminant analysis of the inter-locality samples based on 21 first instar continuous characters. All comparisons were statistically significant at the 1% level except the Glenora Road - Seymour Valley (NS., $p > 0.05$) and the Fellow's Creek - Glenora Road (significant at $\alpha > 0.05$) comparisons. UPGMA cluster analysis (Figure 5) separated the Maritime samples from the other groups but did not provide any meaningful separations of the remaining groups. Some geographically adjacent samples are clustered together but no overall hierarchical order is apparent.

Discriminant function analysis of the same data set did not produce a better separation of the groups than did the cluster analysis. Projection of the sample centroids onto discriminant axis I (54.3% of total variation) and discriminant axis II (12.9% of total variation) (Figure 6) produced results similar to that of the cluster analysis.

3.4 Multivariate analysis of the adult data

The matrix of Mahalanobis D values calculated for all inter-locality samples of 18 continuous measurements of

Table III. Matrix of Mahalanobis D values for 18 population samples of the balsam woolly aphid, Adelges piceae, calculated from 21 continuous variables, first instar stage. D values in brackets are nonsignificant ($p \leq 0.05$); underlined values are significant at the 5% level but not at the 1% level; the remainder are significant at the 1% level.

Sample No.	1	2	3	4	5	6	7	8	9
1	0.000								
2	1.637	0.000							
3	3.240	1.982	0.000						
4	2.605	2.209	2.588	0.000					
5	2.429	(1.109)	2.029	2.084	0.000				
6	3.730	2.461	1.807	2.597	2.398	0.000			
7	3.202	1.933	1.778	2.806	2.086	2.401	0.000		
8	2.867	2.637	2.930	1.846	2.711	3.215	3.283	0.000	
9	1.930	2.255	2.926	1.875	2.241	3.045	3.071	2.054	0.000
10	2.168	2.165	2.748	2.528	2.021	3.321	2.450	2.524	2.147
11	2.758	2.233	2.806	2.101	3.014	2.669	2.104	2.307	2.527
12	2.234	1.834	2.321	2.835	2.005	3.105	3.010	3.308	2.793
13	3.363	3.612	3.406	3.239	3.602	3.738	4.008	3.287	3.413
14	3.556	2.796	4.428	3.933	2.765	3.984	4.354	5.258	4.240
15	3.143	2.394	2.606	2.023	2.214	2.371	3.021	3.004	2.454
16	4.803	4.561	5.715	5.229	4.305	5.144	5.209	5.081	5.877
17	4.880	5.092	6.194	5.139	4.659	7.465	6.536	4.901	4.838
18	4.728	4.787	6.225	5.455	4.664	6.607	5.683	5.512	5.163

Table III (Continued).

Sample No.

	10	11	12	13	14	15	16	17	18
10	0.000								
11	1.955	0.000							
12	2.572	3.545	0.000						
13	2.488	2.861	2.340	0.000					
14	3.092	5.398	3.141	4.913	0.000				
15	2.102	2.100	2.979	3.474	3.400	0.000			
16	4.053	6.051	4.940	6.738	4.213	5.870	0.000		
17	5.718	6.706	4.795	6.011	5.676	6.817	3.761	0.000	
18	4.381	6.098	5.075	6.776	5.213	5.259	3.214	2.898	0.000

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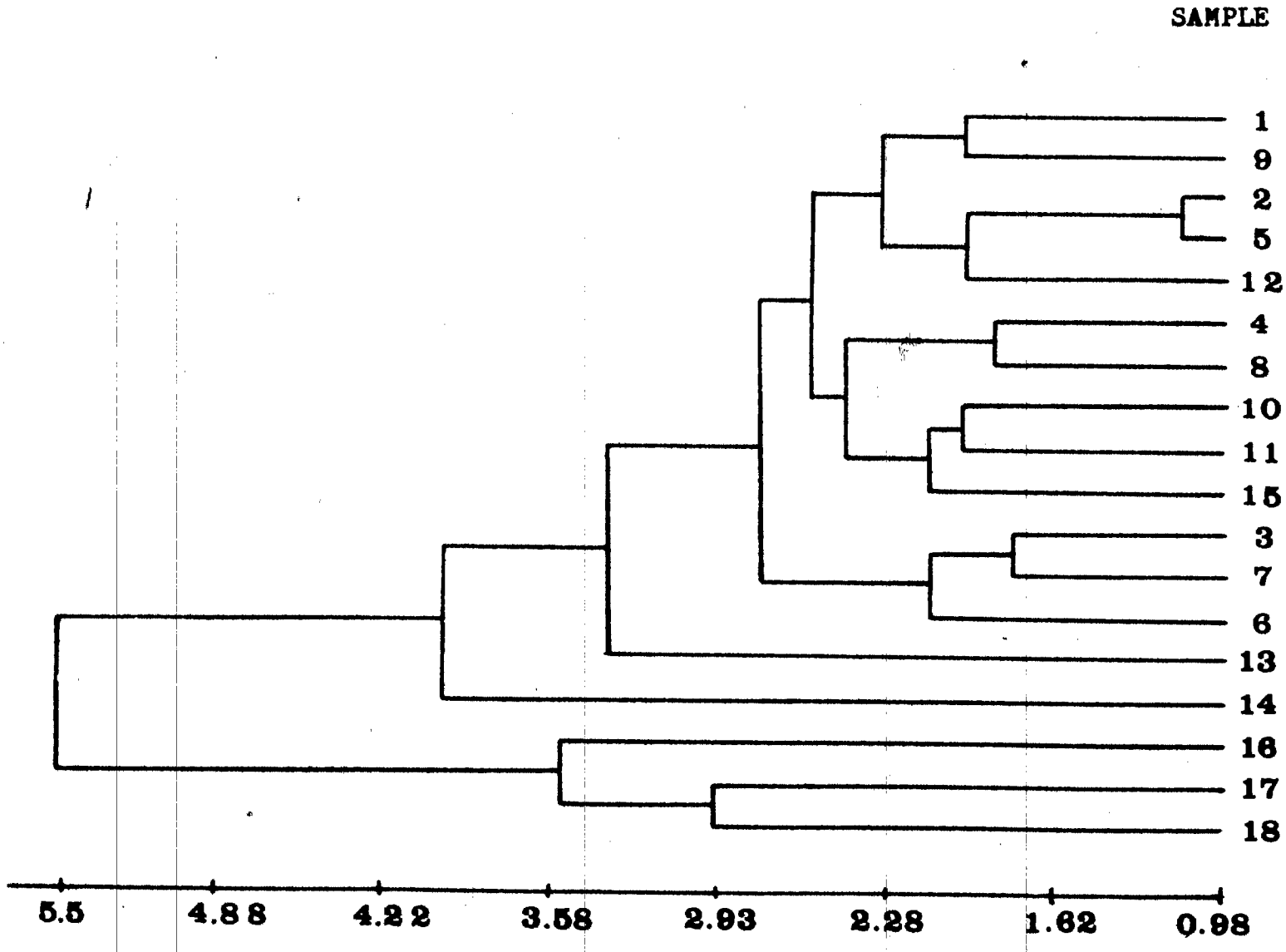
Figure 5. Phenogram for UPGMA cluster analysis of Mahalanobis Generalized Distance, D, (Table III) for 18 population samples of 21 continuous measurements of first instar balsam woolly aphid, Adelges piceae.


SAMPLE NO.
1
9
2
5
12
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8
10
11
15
3
7
6
13
14
16
17
18
5.5
4.88
4.22
3.58
2.93
2.28
1.62
0.98
MAHALANOBIS D VALUE

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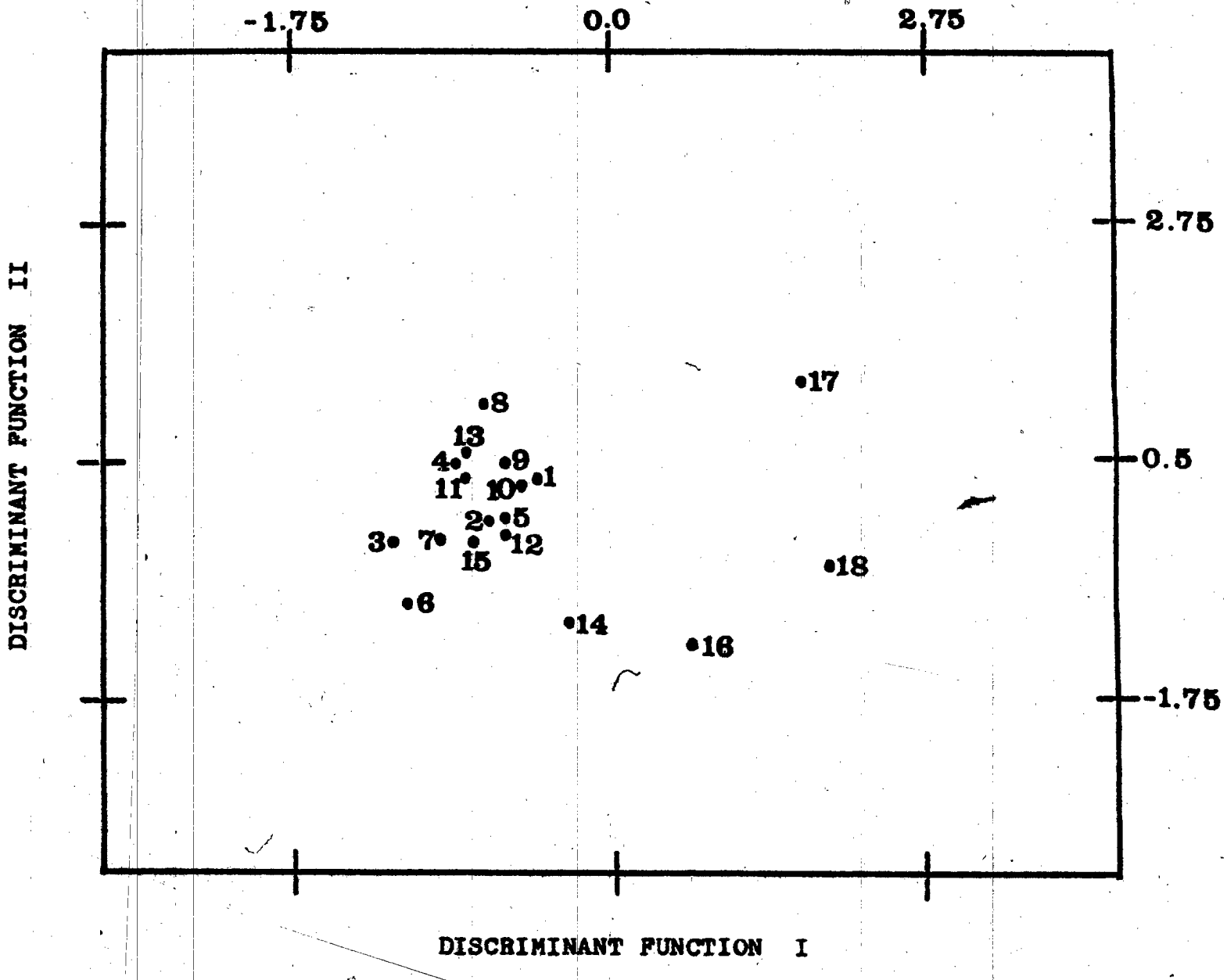
Figure 6. Centroids of 18 population samples of 21 first instar continuous measurements of balsam woolly aphid, Adelges piceae, projected onto the first and second discriminant axes.

Figure 6. Centroids of 18 population samples of 21 first instar continuous measurements of balsam woolly aphid, Adelges piceae, projected onto the first and second discriminant axes.


-1.75
0.0
2.75
2.75
0.5
-1.75
DISCRIMINANT FUNCTION II
DISCRIMINANT FUNCTION I
8
13
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16

adult BWA is given in Table IV. There is a wide range of D values, some being considerably higher than others (samples 17 - 4, 7.448; 17 - 5, 7.495; 17 - 13, 7.336). With the exception of the UBC Research Forest - Pt. Roberts comparison, all D values are statistically significant; the majority are significant at the 1% level.

Cluster analysis of this matrix of D values (Figure 7) produced three distinct clusters; a "British Columbia" cluster consisting of population samples 1 to 7, a "Maritime" cluster consisting of the Maritime samples (16, 17, and 18), with the Waynesville, North Carolina, sample (No. 15) joining it later, and an "Intermediate" cluster consisting of 8 samples (Nos. 8 to 14). This "Intermediate" cluster shows a number of subgroups that are consistent with the geographic locations of the samples.

The results of a discriminant function analysis of the adult continuous measurements shows that most of the variability between the 18 samples can be explained by the first two discriminant axes which account for nearly 75% of the total variation. Projection of the 18 group centroids onto discriminant axes I and II (Figure 8) gives results that reflect

Table IV. Matrix of Mahalanobis D values for 18 population samples of the balsam woolly aphid, Adelges piceae, calculated from 18 continuous variables, adult stage. Statistical significance as in Table III.

Sample No.	1	2	3	4	5	6	7	8	9
1	0.000								
2	3.099	0.000							
3	2.696	2.052	0.000						
4	2.475	1.631	1.930	0.000					
5	2.269	2.520	2.584	2.275	0.000				
6	2.151	2.326	1.550	1.664	2.531	0.000			
7	3.191	1.983	1.465	1.677	2.449	1.489	0.000		
8	3.295	4.589	3.710	4.371	3.099	3.529	3.964	0.000	
9	3.355	4.348	4.074	4.560	2.787	4.159	3.883	(1.224)	0.000
10	4.701	5.277	5.438	5.963	4.231	5.038	4.851	2.525	2.956
11	2.973	3.011	2.444	3.554	2.275	2.653	2.392	2.432	2.075
12	5.188	4.638	4.834	5.955	4.603	4.450	5.006	3.898	3.352
13	5.049	6.364	6.033	6.401	4.533	5.623	6.006	2.877	3.025
14	3.286	4.263	4.611	4.981	3.534	3.529	4.329	2.538	2.411
15	5.616	4.491	4.143	4.704	4.508	4.748	3.726	4.353	3.903
16	5.139	4.213	4.441	4.571	5.406	4.592	4.165	5.388	4.896
17	6.911	6.399	6.035	7.448	7.495	6.231	5.818	6.793	6.506
18	5.257	4.166	4.624	4.421	5.071	4.458	3.979	4.897	4.678

Table IV (Continued).

Sample No.

	10	11	12	13	14	15	16	17	18
10	0.000								
11	2.923	0.000							
12	2.870	2.989	0.000						
13	2.452	3.429	3.050	0.000					
14	2.408	2.215	2.717	2.791	0.000				
15	3.728	3.391	4.041	5.849	5.044	0.000			
16	5.673	5.000	4.504	5.993	5.150	4.275	0.000		
17	6.848	6.192	5.419	7.336	6.728	4.979	2.847	0.000	
18	4.412	3.849	4.160	5.409	4.897	3.157	1.882	2.463	0.000

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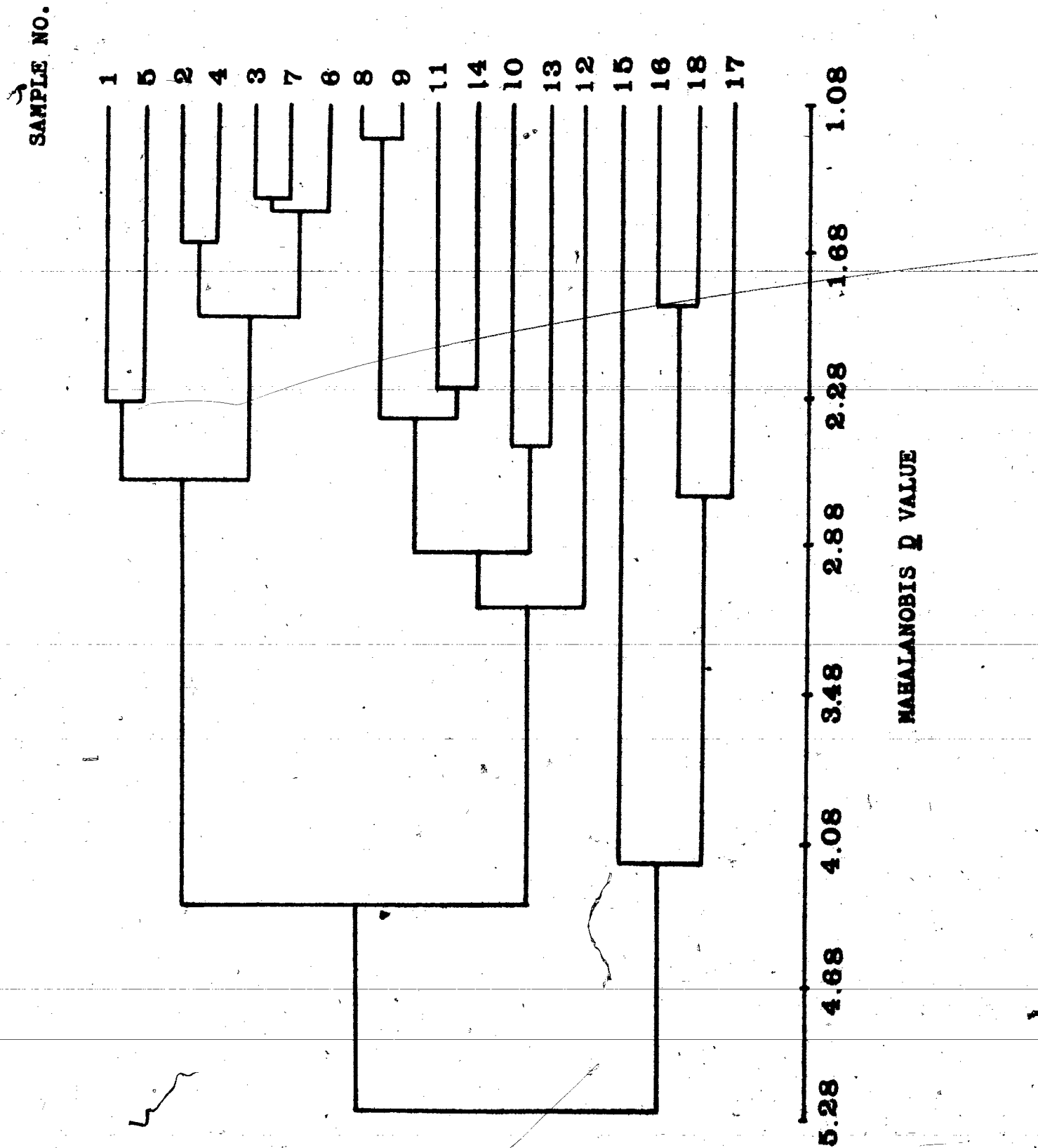
Figure 7. Phenogram for UPGMA cluster analysis of Mahalanobis Generalized Distance, D, (Table IV) for 18 population samples of 18 continuous measurements of adult balsam woolly aphid, Adelges piceae.


SAMPLE NO.
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12
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16
18
17
1.08
1.68
2.28
2.88
3.48
4.08
4.68
5.28
MAHALANOBIS D VALUE

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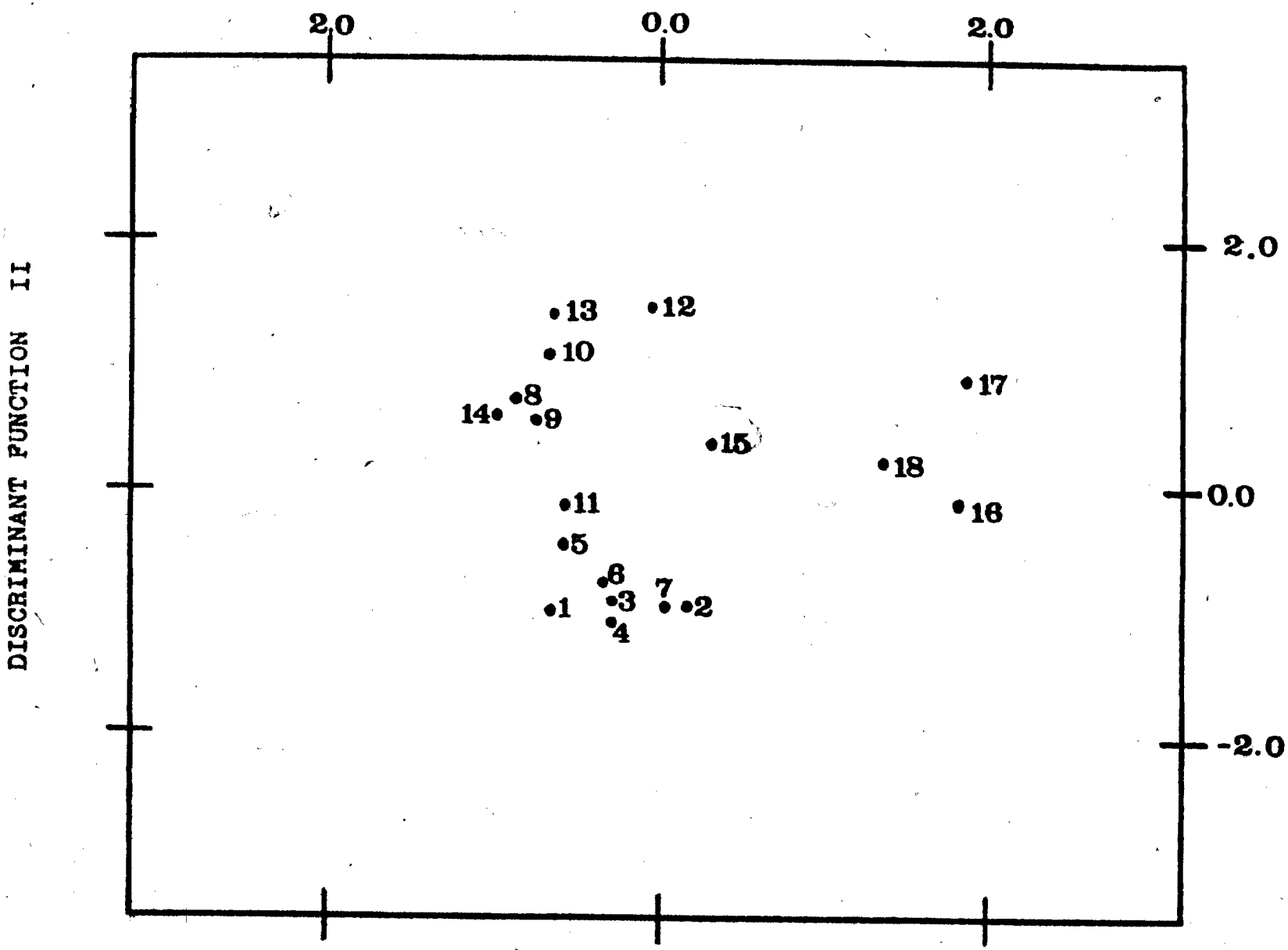
Figure 8. Centroids of 18 population samples of 18 continuous measurements of adult balsam woolly aphid, Adelges piceae, projected onto the first and second discriminant axes.


2.0
0.0
2.0
2.0
0.0
-2.0
DISCRIMINANT FUNCTION II
DISCRIMINANT FUNCTION I
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17
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3
2
1
4

the hierarchical structure determined by the cluster analysis. Though the cophenetic correlation coefficient for this phenogram is only 0.789, it represents adequately the associations of the corresponding Mahalanobis D matrix and gives results that are interpretable. Projections of the group centroids onto other combinations of the major discriminant axes did not provide a better separation of the samples.

Standardized discriminant function coefficients, which represent the absolute values of the contribution of each of the 18 continuous variables to discriminant functions I and II are shown in Table V. The largest contributions to discrimination among groups on the first discriminant axis (44.7% of variation) are provided by femur length, tibia length, labial segment I - length, and anal plate length. The largest contributions to the second discriminant axis are by antennal segment II - width, antennal segment III - length, femur length and width, tibia length and anal plate length. A number of variables (antennal segment II - width, ocellus diameter, tibia width, labial clamp width and ovipositor length) show low contributions to both discriminant functions. For reasons of economy of

Table V. Standardized discriminant function coefficients for the first two discriminant functions calculated from 18 population samples of 18 continuous variables of adult balsam woolly aphid, Adelges piceae.

	VARIABLE	DISCRIMINANT FUNCTION I	II
1.	Antennal segment II - length	-0.01921	0.16067
2.	Antennal segment II - width	-0.12975	-0.37537
3.	Antennal segment III - length	-0.11204	0.27004
4.	Antennal segment III - width	-0.01210	0.08844
5.	Femur - length	0.40501	-0.23735
6.	Femur - width	0.09349	-0.32220
7.	Tibia - length	0.33361	0.26200
8.	Tibia - width	0.05310	-0.01754
9.	Tarsus - length	0.07845	0.17623
10.	Tarsus - width	-0.01303	-0.25568
11.	Labial segment I - length	0.31514	0.05326
12.	Labial segment I - width	0.02843	-0.01953
13.	Labial segment II - length	0.07232	0.05453
14.	Labial segment II - width	0.05989	-0.03355
15.	Labial clamp - width	-0.00837	-0.01436
16.	Ocellus - diameter	0.02106	0.01898
17.	Ovipositor - length	0.03680	-0.07114
18.	Anal plate - length	-0.31663	-0.35475
	Relative Percentage of Variability	44.75%	29.91%

time and effort some of these variables could be eliminated without losing satisfactory discrimination of the samples.

The matrix of Mahalanobis D values for all inter-sample comparisons based on the adult pore counts is given in Table VI. Some nonsignificant differences are apparent. UPGMA cluster analysis of this matrix grouped some geographically adjacent samples but failed to provide any major hierarchical clusters (Figure 9). Discriminant function analysis and projection of the group centroids onto the first two discriminant axes (Figure 10) did not provide any meaningful separation of the groups, although these two axes accounted for 77.6% and 14.7%, respectively, of the total variability. The adult pore counts do not show any large groups and only serve to bring together a number of pairs of geographically adjacent samples. Discriminant function analysis and UPGMA cluster analysis using the 18 adult continuous variables combined with the 5 pore counts did not give a better discrimination between the groups than did the continuous variables alone.

Little information is available about the ecological significance of wax pores in the balsam woolly aphid or about the extent to which their number is influenced by

Table VI. Matrix of Mahalanobis D values for 18 population samples of the balsam woolly aphid, Adelges piceae, calculated from 5 pore counts, adult stage. Statistical significance as in Table III.

Sample No.	1	2	3	4	5	6	7	8	9
1	0.000								
2	1.140	0.000							
3	(0.887)	(0.813)	0.000						
4	1.050	0.945	1.135	0.000					
5	1.411	1.704	1.783	0.913	0.000				
6	1.043	1.579	1.553	1.359	1.011	0.000			
7	0.961	1.372	1.423	1.525	1.303	(0.423)	0.000		
8	1.481	1.970	1.900	1.429	0.811	0.790	1.148	0.000	
9	1.673	2.173	1.968	1.796	1.014	0.789	0.932	(0.452)	0.000
10	1.047	1.526	1.525	1.150	(0.528)	(0.523)	0.804	(0.632)	(0.698)
11	0.948	0.832	1.017	(0.217)	(0.671)	1.094	1.320	1.071	1.380
12	2.183	2.637	2.395	1.851	0.929	1.487	1.700	(0.688)	0.910
13	2.731	2.978	2.846	2.238	1.333	2.151	2.230	1.269	1.467
14	(0.389)	0.931	0.940	0.793	1.000	0.854	0.865	1.257	1.416
15	1.246	0.998	1.261	(0.714)	(0.738)	1.320	1.488	1.228	1.474
16	2.749	2.979	2.892	2.680	1.922	2.283	2.261	1.853	1.963
17	0.970	1.512	1.483	1.418	0.897	(0.424)	(0.730)	(0.464)	(0.457)
18	2.209	2.432	2.477	2.343	1.323	1.606	1.573	1.147	1.121

Table VI (Continued).

Sample No.

	10	11	12	13	14	15	16	17	18
10	0.000								
11	0.921	0.000							
12	0.889	1.306	0.000						
13	1.410	1.630	(0.736)	0.000					
14	(0.764)	(0.751)	1.731	2.279	0.000				
15	0.985	(0.615)	1.210	1.217	0.938	0.000			
16	1.883	2.209	1.543	1.363	2.481	1.890	0.000		
17	(0.532)	1.150	0.791	1.382	0.910	1.378	1.826	0.000	
18	1.332	1.868	0.954	0.929	2.107	1.761	0.846	1.241	0.000

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Figure 9. Phenogram for UPGMA cluster analysis of Mahalanobis Generalized Distance, D, (Table VI) for 18 population samples of 5 pore counts of adult balsam woolly aphid, Adelges piceae.

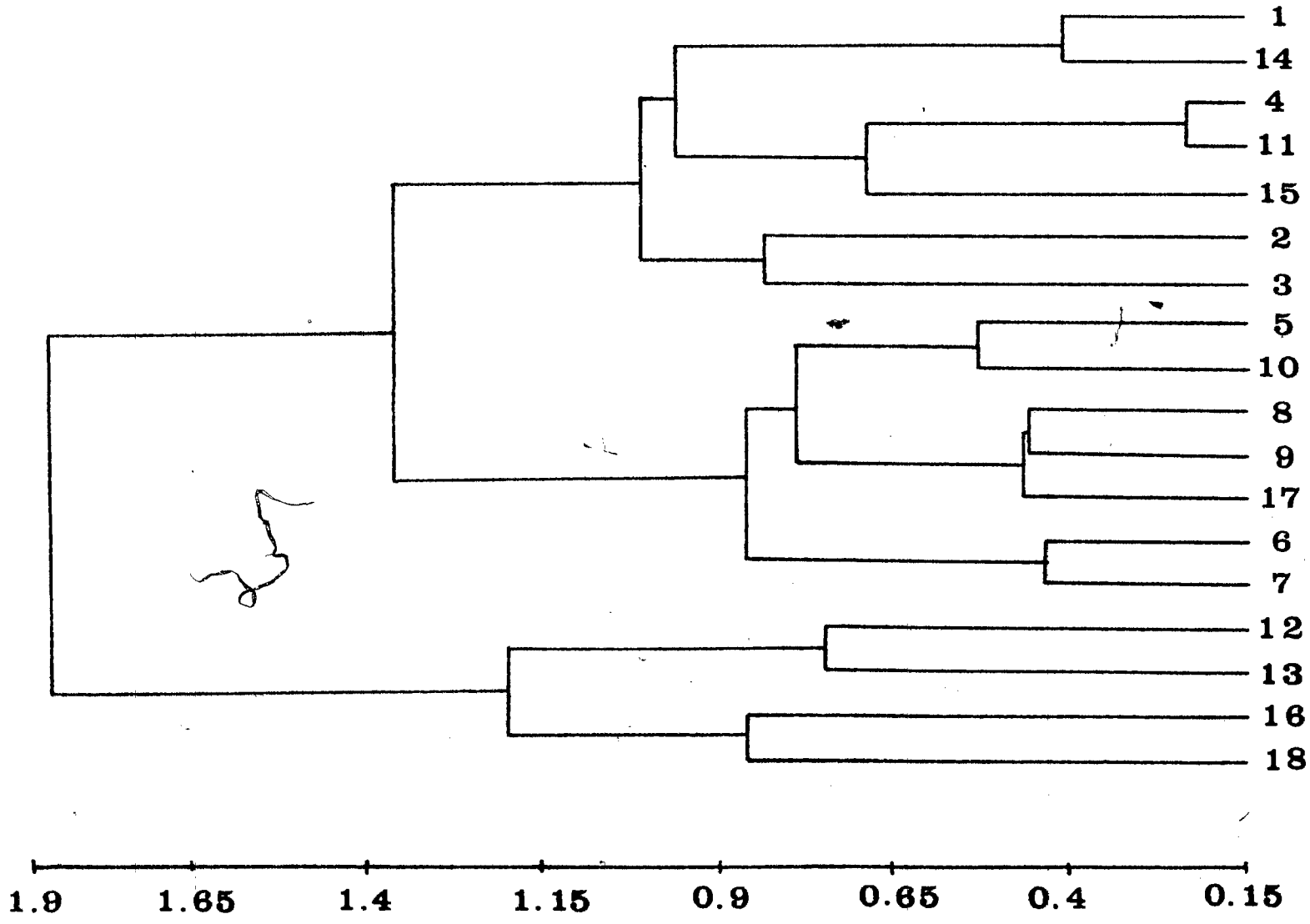
SAMPLE NO.
1
14
4
11
15
2
3
5
10
8
9
17
6
7
12
13
16
18
1.9
1.65
1.4
1.15
0.9
0.65
0.4
0.15
MAHALANOBIS D VALUE

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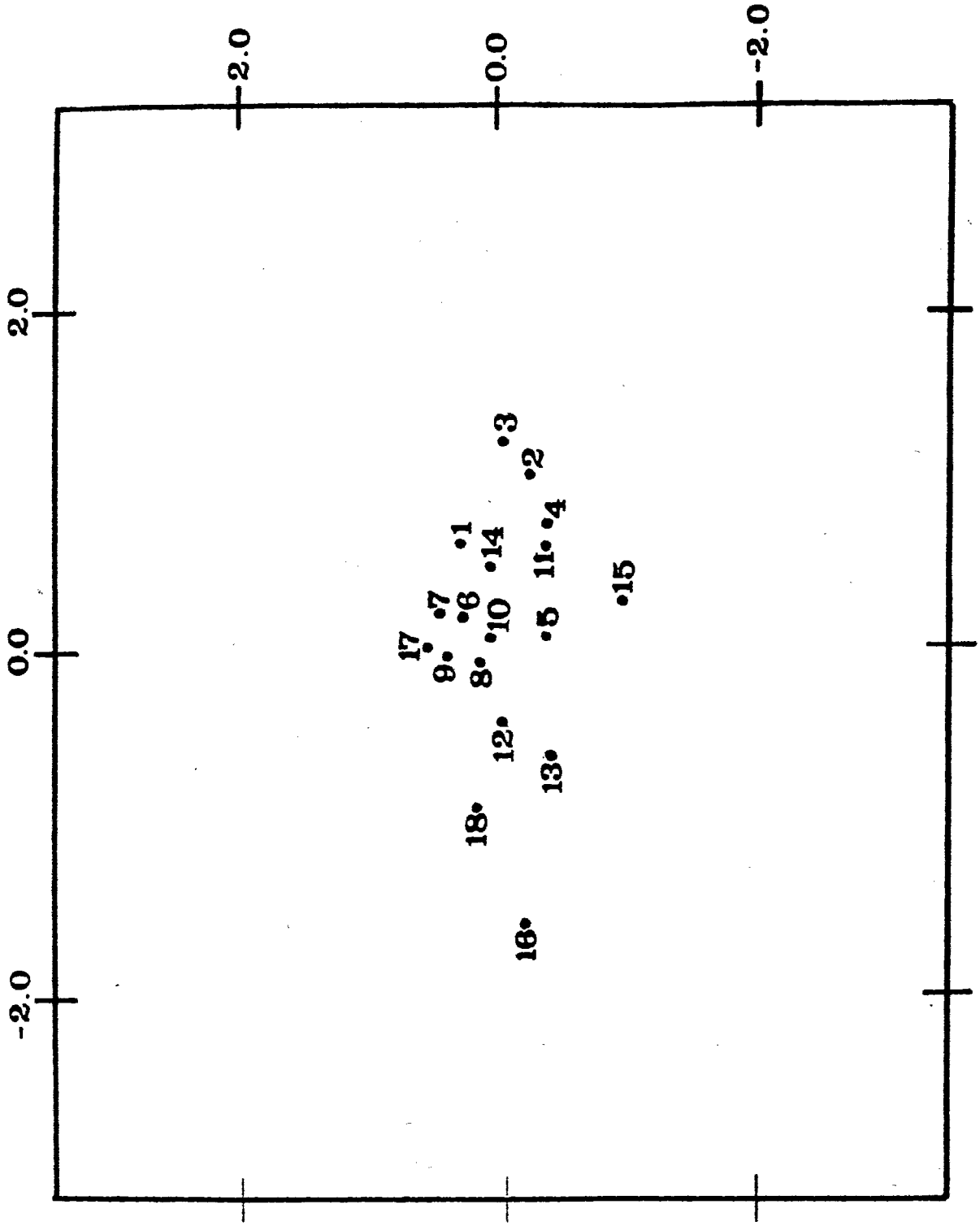
Figure 10. Centroids of 18 population samples of 5 pore counts of adult balsam woolly aphid, Adelges piceae, projected onto the first and second discriminant axes.

Figure 10. Centroids of 18 population samples of 5 pore counts of adult balsam woolly aphid, Adelges piceae, projected onto the first and second discriminant axes.


2.0
0.0
-2.0
2.0
0.0
-2.0
DISCRIMINANT FUNCTION I
DISCRIMINANT FUNCTION II
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environmental and/or genetic factors. It is possible that these pore counts may be more useful in discriminating between geographically restricted groups. UPGMA cluster analysis of the Mahalanobis D values of samples 1 to 9, based on the 5 pore counts alone, gave results (Figure 11) that are consistent with the geographic locations of the samples.

3.5 Allocation of individual specimens into a priori groups

Identification functions and identification matrices, where individual specimens are allocated into the group with the closest sample centroid in multivariate space, were computed using the full sets of first instar and adult continuous variables. There is an upward bias in the allocation procedure when it is based on the specimens that were also used in the original calculation of the identification functions. The extent of this bias is determined by the number of groups, the sample size and the number of discriminatory variables (Frank, Massy & Morrison 1965; Morrison 1969). However, this procedure enables comparisons to be made between the first instar and adult sets of discriminating variables and shows the extent of phenetic overlap of the samples

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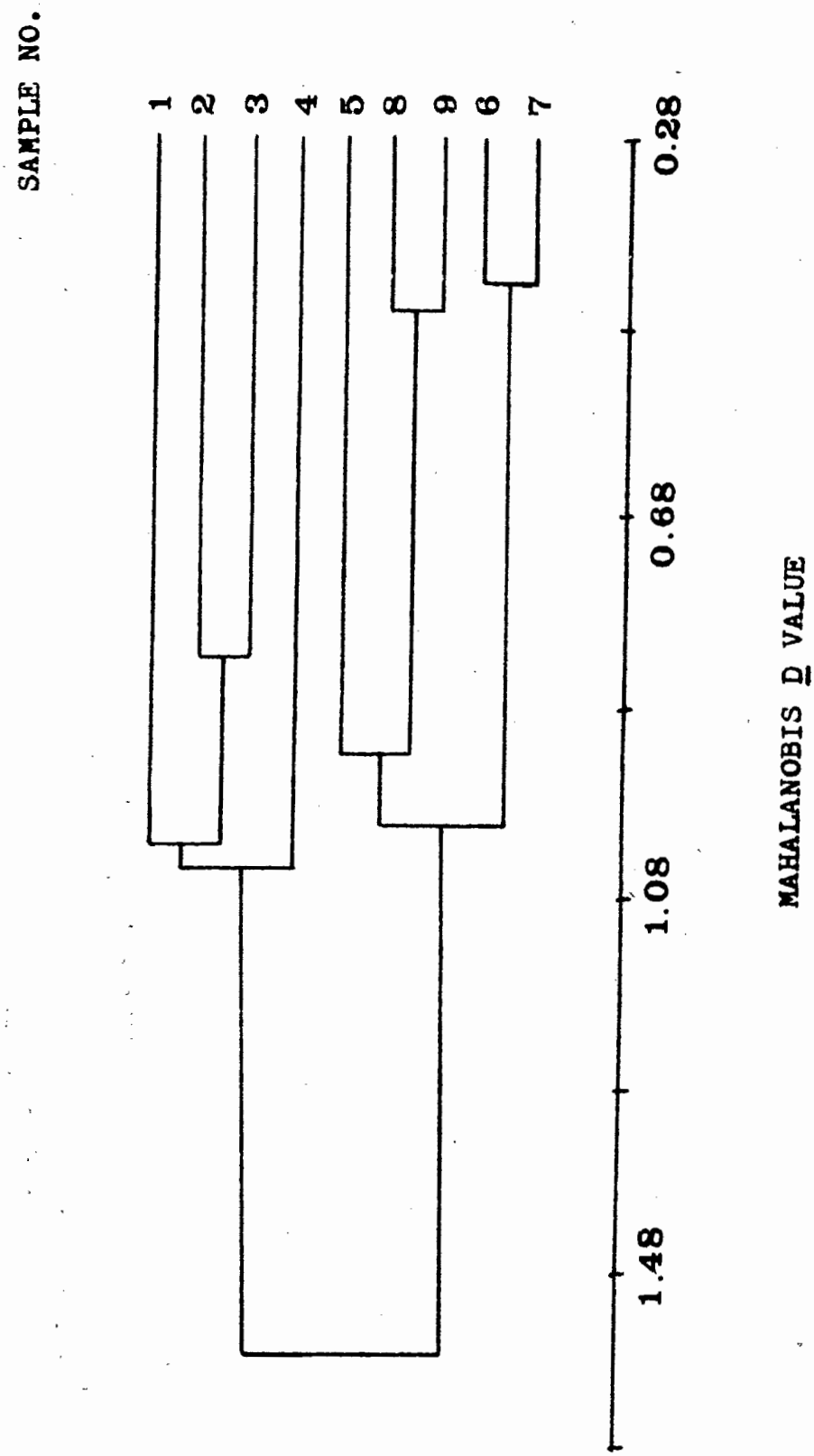
Figure 11. Phenogram for UPGMA cluster analysis of Mahalanobis Generalized Distance, D, (Table VI) for population samples No. 1 to 9 based on 5 pore counts of adult balsam woolly aphid, Adelges piceae.


SAMPLE NO.
1
2
3
4
5
8
9
6
7
0.28
0.68
1.08
1.48
MAHALANOBIS D VALUE

in multi-dimensional hyperspace.

Comparison of the identification tables using the first instar (Table VII) and adult (Table VIII) variables shows patterns of correct and incorrect allocation that complement the hierarchical structure of the phenograms. For many samples of first instar specimens the frequency of incorrect allocations is not greater in adjacent groups; there is a nearly continuous spread of misidentifications over the other groups. This indicates very poor discriminating ability in the variables chosen. The "Maritimes" samples were the only phenetically distinct cluster of the first instar phenogram. They were correctly identified 93% of the time on a group basis.

Misidentifications in the identification table based on the adult continuous variables show trends that support the results of the cluster analysis. Improperly identified specimens were usually placed within the major cluster to which they belonged. If allocations within one of the three major clusters are considered, there is an average correct identification of 87.1% ("British Columbia"), 91.4% ("Intermediate"), and 85.6% ("Maritime").

Table VII. Identification table for 18 population samples of first instar balsam woolly aphid, Adelges piceae. Identification functions based on 21 continuous variables and sample sizes of 40 individuals. Correct identifications are in the diagonal positions, incorrect identifications are in the off-diagonal positions.

	Sample No.																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	17	1	1	2	1		1		4	3	3	3	1	3				
2	7	6		1	6	5	2	2	1	1	2		1	1	4	1		
3	1	3	17	1	2	6	4	1		1	2	2						
4	1	1		15	1	2		5	5	2	4			1	3			
5	1	1	2	3	15	2	2	2	2	3		2		1	3			1
6		1	3	2	2	25	2	1	1	1	1				1			
7		1	3	1	3	1	20	3	1	2	4	1						
8	1		1	3				25	2	1	4	1			1	1		
9	2		1	4				3	19	5	1	1	1		3			
10	3		1	1			2	1	4	14	3	3	1	2	3	1		1
11	3			3			2	1	1	3	22				5			
12	2		2	1	2	4	1		1	1		16	6	1	2	1		
13	1			1		1				1	2		31	1	2			
14	1	2					1			2		1	1	30	2			
15	2		1	3	1	2	1		1	3	2	1	1	1	21			
16					1									1		34	3	1
17								1								1	37	1
18												1		1		2	5	31

Table VIII. Identification table for 18 population samples of adult balsam woolly aphid, Adelges piceae. Identification functions based on 18 continuous variables and sample sizes of 40 individuals. Correct identifications are in the diagonal positions, incorrect identifications are in the off-diagonal positions.

	Sample No.																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	22	2	3	1	6	1	1	2						2				
2	2	22	4	3	1	1	4				1				2			
3	3	1	13	3	2	6	4	1	1		4			1	1			
4	7	4	3	14	2	5	4		1									
5	5	4	1	3	20	1		2	3		1							
6	3	1	7	10	1	8	3			1	2			3	1			
7	1	1	3	6	1	2	21				3				1			1
8						1		21	9	2	1	1	2	2	1			
9					5			7	21	1	2	2		2				
10						1		2	1	26	2	1	6		1			
11			1		1		4		5	1	17	2	1	5	3			
12			1						1	2	1	27	3	3	1		1	
13								3	2	6		2	25	2				
14	1					2		1	4	2	2	1	3	22	1			1
15		1					2	1				3			31		1	1
16	2					1						1				20	4	12
17			1									2				2	34	1
18	1				1	1				2	1				5	1	4	24

The adult continuous variables provide the most stable classification and show a geographic pattern of group association. In contrast, the first instar variables only add weight to the definition of the "Maritime" cluster.

If the adult discriminatory variables provide the most interpretable classification of North American samples of BWA, it is necessary to have a correct measure of their predictive power. A simple validation procedure can be used to correct for the upward bias inherent in calculations of the proportion of correct identifications that use the same individuals to develop the identification functions as are used to test the discriminatory power of the functions. Frank, Massy & Morrison (1965) state that a realistic estimate of predictive power can be obtained by splitting each sample into two groups; one group is used to calculate the identification functions and members of the other group are identified on the basis of these functions.

The procedure was applied to the 18 samples of 18 adult continuous variables. The results are shown in Table IX which shows a proportion of correct identification

Table IX. Identification table for 18 population samples of adult balsam woolly aphid, Adelges piceae. Identification functions based on 18 continuous variables and sample sizes of 20 individuals. Table shows allocations for 18 samples of 20 individuals each that were not used to calculate the original identification functions. Correct identifications are in the diagonal positions, incorrect identifications are in the off-diagonal positions.

Sample No.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	14	1	1		1			2						1				
2	1	9	2	2	1	1	3					1						
3		1	6	1	2	4	3		1		2							
4	3	1	1	3	5	2	3	1	1									
5	1	2	1	1	6	2			3		3			1				
6	1	1	3	5	1	4	1			1	1			1	1			
7	1	1	1			5	10											2
8						2		6	9				2	1				
9					4			3	9		1	1		2				
10						1		3		11	3	1	1					
11		1					1		5	1	9	1		1	1			
12									1	4		11	1	2	1			
13								1	1	4		1	11	2				
14		1				1		1	2	1		1	2	10	1			
15		1			1		1	1				1			14		1	
16			1	1			1									10		7
17												1				3	14	2
18	1				1		1			1	1	1				2	4	8

of 45.6% on a sample by sample basis. Again, a large proportion of misidentifications fall within each of the three provisional groups. If these provisional groups are pooled the result is a rate of correct identification of 84.3%, 90.0%, and 80.0% (average, 85.6%) for the "British Columbia", "Intermediate", and "Maritime" clusters, respectively.

4. RESULTS: ANALYSIS OF WITHIN-POPULATION VARIATION

4.1 Univariate trends in the data

For the mean and standard error of each morphological character measured in all samples collected at Fellow's Creek, B.C. refer to Appendix 1 (first instar) and Appendix 2 (adult).

No trends in differences between the means of the first instar characters of BWA from the four trees are evident. There are, however, definite changes in the mean values for many variables over the four samples taken on the same tree. For example, body length starts with a relatively high value (0.3929 mm), drops slightly over the next two collecting dates (0.3893, 0.3870mm), and then increases to a relatively high value (0.4083 mm). Other characters, such as tarsal hair length, show first a gradual increase then a decline back to the original level. Labial segment II - width increases over the four sample times.

Examination of the means of the adult continuous variables revealed no consistent trends among the four trees. The first of the samples taken from the

same tree shows a lower mean value for 14 of the 18 variables measured when compared to the second sample, which suggests the presence of a seasonal trend.

Examination of the means of the 5 pore counts did not reveal any consistent difference betwen the two seasonal samples. Tree No. 4 shows higher means for pore counts II, III, IV, and V when compared to other trees.

4.2 Multivariate analysis of the samples

Discriminant function analysis and cluster analysis of Mahalanobis D values where made on the within-site (Fellow's Creek) sets of first instar continuous variables, adult continuous variables, and adult pore counts. Mahalanobis D values are given in Table X and the results of the UPGMA cluster analysis of these matrices are shown in Figure 12.

Most Mahalanobis D values calculated between pairs of first instar samples are non-significant or are only significant at the 5% level. No consistent trend with respect to sample times on the same or on different trees are evident in the corresponding phenograms. None of

Table X. Matrices of Mahalanobis D values for within-population (Fellow's Creek, British Columbia) samples of balsam woolly aphid, Adelges piceae: (a) first instar, 21 continuous variables; (b) adult, 18 continuous variables; (c) adult, 5 pore counts. Statistical significance as in Table III.

Sample No.

(a)

	1	2	3	4	5	6	7
1	0.000						
2	(1.225)	0.000					
3	1.585	(1.349)	0.000				
4	1.634	1.688	2.148	0.000			
5	1.537	(1.328)	(1.470)	1.648	0.000		
6	2.024	(1.552)	(1.289)	1.938	(1.411)	0.000	
7	1.891	2.036	1.720	2.202	1.889	1.689	0.000

(b)

	1	2	3	4	5
1	0.000				
2	2.147	0.000			
3	1.755	1.914	0.000		
4	2.974	2.588	1.756	0.000	
5	3.261	3.171	1.762	1.769	0.000

(c)

	1	2	3	4	5
1	0.000				
2	(0.430)	0.000			
3	(0.632)	(0.418)	0.000		
4	(0.507)	(0.489)	(0.349)	0.000	
5	(0.674)	(0.743)	(0.668)	(0.382)	0.000

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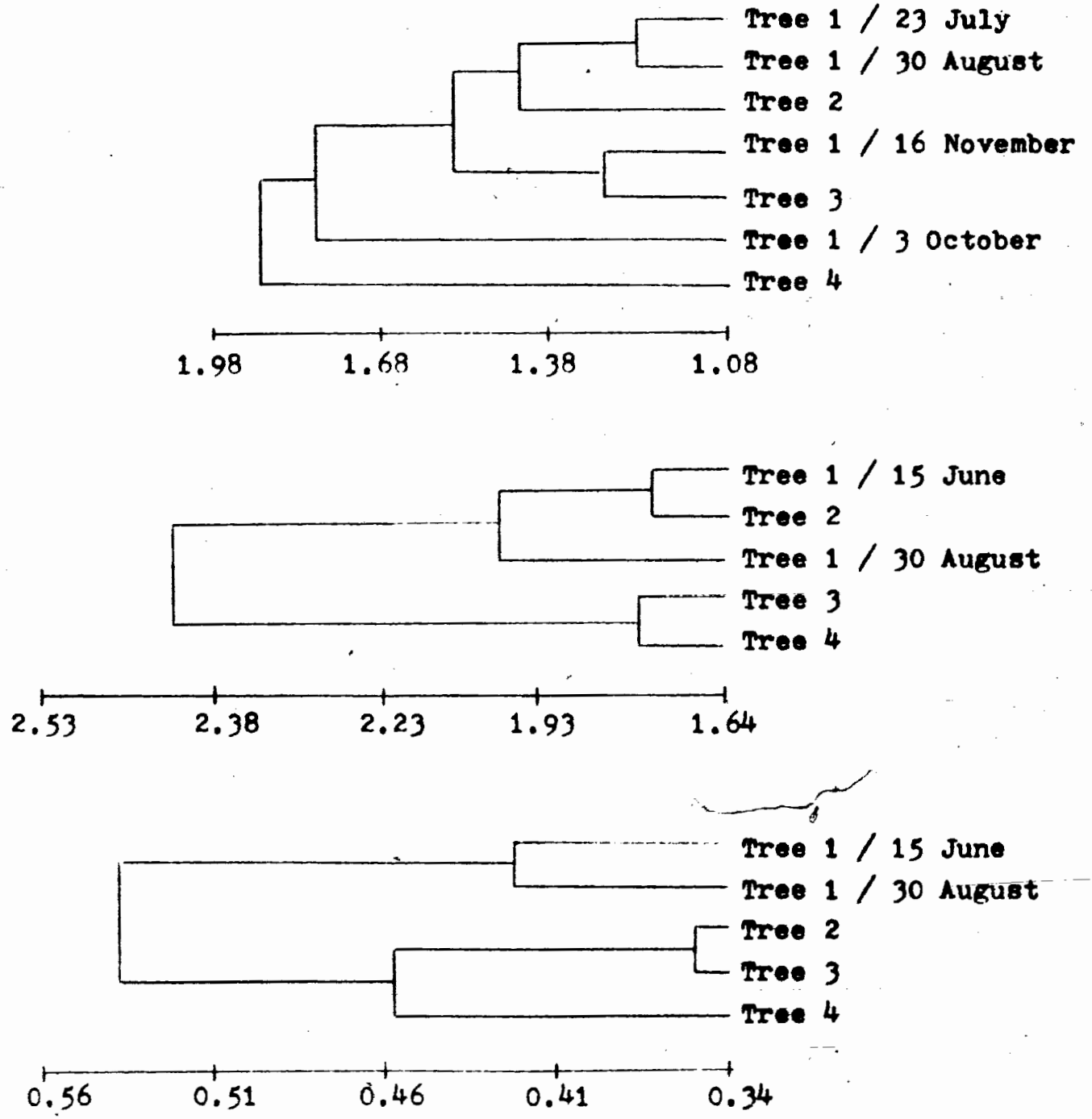
Figure 12. Phenograms for UPGMA cluster analysis of Mahalanobis Generalized Distance, D, (Table VII) for within-population (Fellow's Creek, British Columbia) samples of balsam woolly aphid, Adelges piceae; (a) first instar, 21 continuous measurements; (b) adult, 18 continuous measurements; (c) adult, 5 pore counts.



MAHALANOBIS D VALUE

the D values computed for comparisons of adult pores are significantly different at the 5% level.

However, all D values based on adult continuous variables are significantly different at the 1% level. No trends in the two main clusters shown were detected when compared for severity of attack by the aphid, general condition of the tree, or cardinal direction of the collection site of the sample. One possible association is the separation of Trees No. 1 and 2 from Trees No. 3 and 4. This corresponds to the relative locations of the trees; the two trees of each pair were within 20 m of each other but the two pairs were approximately 300 meters apart.

The within-site samples of the first instar and the adult stages were included with their respective between-site samples as a test of the influence of within-population variation on the determination of systematic differences between the population samples. Mahalanobis D values were calculated and subjected to UPGMA cluster analysis.

The first instar within-site samples stayed as a distinct cluster and did not bring about any changes in the hierarchy established by analysis of the between-site samples alone. The within-population

adult pore samples behaved in a similar fashion. The within-site sets of adult continuous measurements stayed well within the main inter-locality cluster of groups 1 to 7. However, trees No. 2, 3 and 4 stayed as a cluster but separated from tree No. 1.

It should be noted that some authors consider significance testing in association with Mahalanobis Generalized Distance to be unimportant (Blackith and Reyment 1971; Morrison 1969). The argument is that one can find significant differences in generalized distances simply by increasing the sample size and the number of variables. Because generalized distances are a function of these properties they are used only in a comparative manner. Statements about statistical significance are simply that and are only used to give strength to a descriptive statement and to compare the discriminatory power of sets of variables.

This situation is exemplified by the results of the discriminant function analysis of the within-population samples. Projection of the group centroids based on the adult continuous measurements onto the first two discriminant axes did not result in a separation into two distinct groups as did the phenogram.

Although there was a significant difference at the 1% level between tree No. 3 and tree No. 4 there was actually a great deal of overlap between the individual specimens when these individual specimens were projected onto the first two discriminant axes and viewed in a multivariate sense. No interpretable groupings were found in the first instar or adult pore data sets when centroids were projected onto the first two discriminant axes.

5. TAXONOMY OF NORTH AMERICAN POPULATIONS OF BWA

As the analysis of the continuous variables of adult BWA gives the most stable and geographically explainable results, taxonomic considerations will be based primarily upon that analysis. The analysis of the first instar variables and the adult pore counts provides additional evidence. Examination of certain qualitative attributes of the cleared specimens such as the shape of the wax pores and the amount of pigmentation reveals trends similar to those shown in the analysis of the quantitative attributes. In particular, the adult samples show some marked differences in accordance with the three major clusters as determined by the morphometric analyses.

Despite published criticisms of the subspecies designation the subspecies is a convenient category for classifying population samples of a species (Mayr 1963, 1969, 1970; Simpson 1961). This study shows that BWA consists of several distinguishable morphological forms that are associated with different geographic regions. Therefore, a more definite nomenclatural system is proposed than used in the past. Three subspecies are proposed [6], namely Adelges piceae piceae, A. piceae

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6 The three subspecies will be formally named and described elsewhere.

canadensis, and A. piceae occidentalis.

The nominate subspecies A. piceae piceae corresponds morphologically to A. piceae forma typica (Merker & Eichhorn 1956; Pschorn-Walcher & Zwölfer 1958) found in Europe. Specimens from Oregon and Washington were described as this form in the literature (Pschorn-Walcher 1960, 1964; Pschorn-Walcher & Zwölfer 1960). The nominate subspecies is represented in North America by the "Intermediate" group of this study.

A. piceae canadensis corresponds to A. piceae forma canadensis of Merker & Eichhorn (1956). This subspecies is represented by the Maritime samples (Nos. 16 to 18), which were grouped together by the UPGMA cluster analysis of both the first instar and the adult stages.

A. piceae occidentalis, which is represented by samples 1 to 7, does not correspond to any previously described form of A. piceae. It is more similar to A. piceae piceae than to A. piceae canadensis, but it possesses sufficient distinguishing characteristics to enable its separation from the former.

The distinguishing characteristics of each subspecies are described below. Biometric data for each subspecies are given in Table XI (first instar stage) and Table XII (adult stage).

5.1 Adelges piceae piceae

Adult specimens of A. piceae piceae tend to be smaller than those of subspecies canadensis and occidentalis when comparing the means (Table XII) for the variables measured. The head region is more darkly pigmented than in subspecies occidentalis but not as darkly as and not as uniformly as in subspecies canadensis. Plates on the abdominal tergites are usually distinctly sclerotized. The pore fields are relatively flat and the pores are not as closely clumped together as in specimens of subspecies occidentalis (Figure 13). There is a tendency, particularly in the first three mesial abdominal pore fields, for the pores to spread out laterally. These pores are often larger and more irregular in shape than those in other pore fields.

Specimens of the first instar stage of this

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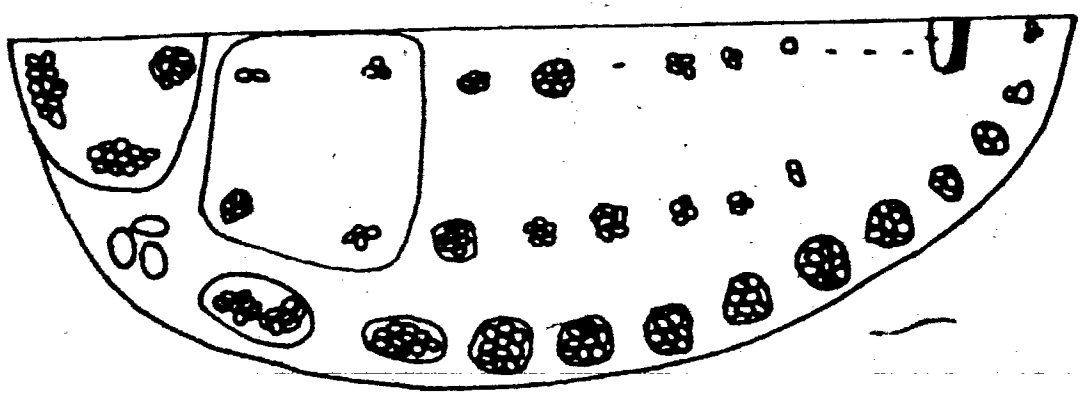
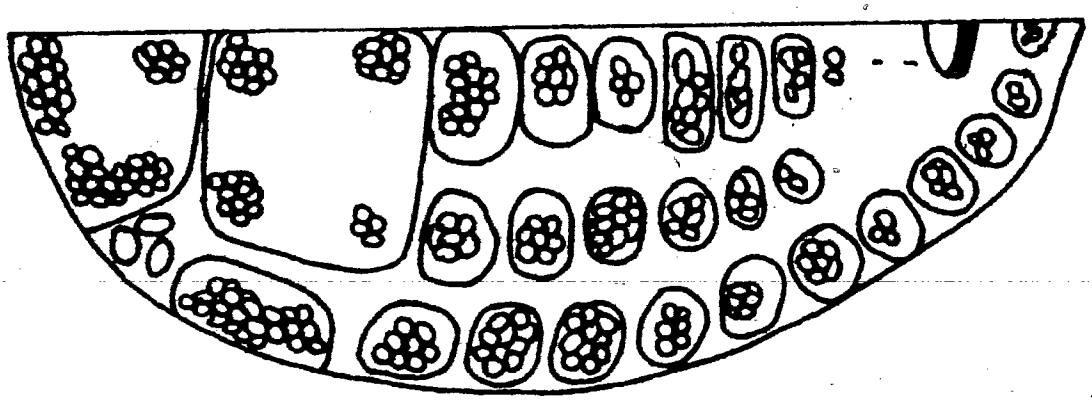
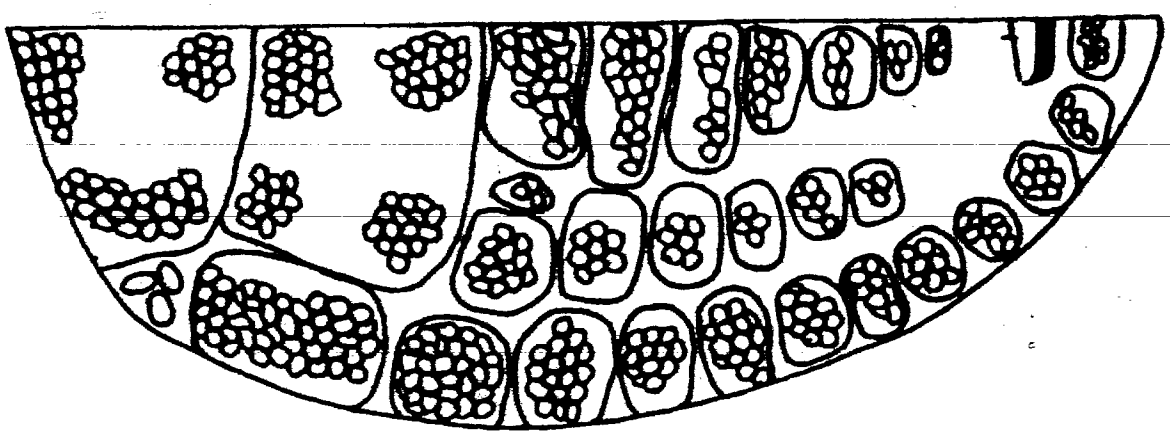
Figure 13. Diagrammatic representation of the sclerotized plates and the distribution of the wax pores on one side of the dorsal surface of the adult balsam woolly aphid, Adelges piceae: (a) A. piceae canadensis; (b) A. piceae piceae; (c) A. piceae occidentalis.



(c)



(b)



(a)

Table XI. Biometric data for the first instar stage of the three subspecies of the balsam woolly aphid, Adelges piceae, found in North America. For each subspecies, the mean ± standard deviation (mm x 10^{-4}) is given for each variable measured, based on the following sample sizes: piceae, n = 320; canadensis, n = 120; occidentalis, n = 280.

VARIABLE	SUBSPECIES					
	piceae		canadensis		occidentalis	
1. Body -length	3862	224	4192	231	3900	244
2. Body -width	2170	127	2357	164	2215	163
3. Antennal segment II -length	168	13	181	14	169	14
4. Antennal segment II -width	223	18	218	21	218	19
5. Antennal segment III -length	599	31	672	40	590	30
6. Antennal segment III -width	188	18	180	18	188	17
7. Apical seta -length	398	26	435	26	397	22
8. Femur -length	448	21	482	24	451	16
9. Femur -width	283	22	284	27	278	24
10. Tibia -length	568	24	611	33	565	23
11. Tibia -width	260	23	253	21	263	20
12. Tarsus -length	257	12	270	18	255	12
13. Tarsus -width	146	13	146	13	146	14
14. Tarsal hair -length	210	12	222	15	210	13
15. Labial segment I -length	384	12	417	26	379	20
16. Labial segment I -width	306	29	316	34	301	30
17. Labial segment II -length	345	22	374	28	341	21
18. Labial segment II -width	517	53	547	62	510	53
19. Labial clamp -width	120	9	139	12	116	10
20. Ocellus -diameter	107	5	104	6	106	5
21. Stylet -length	11960	121	14490	230	11750	135

Table XII. Biometric data for the adult stage of the three subspecies of the balsam woolly aphid, Adelges piceae, found in North America. For each subspecies, the mean ± standard deviation (mm x 10^{-4}) (pore counts, x 10) is given for each variable measured, based of the following sample sizes: piceae, n = 320; canadensis, n = 120; occidentalis, n = 280.

VARIABLE	SUBSPECIES					
	piceae		canadensis		occidentalis	
1. Antennal segment II -length	156	14	168	12	156	13
2. Antennal segment II -width	212	23	230	29	244	23
3. Antennal segment III -length	346	31	370	32	336	32
4. Antennal segment III -width	166	18	181	22	183	20
5. Femur -length	548	50	692	60	595	50
6. Femur -width	295	31	367	46	347	29
7. Tibia -length	650	56	808	100	667	53
8. Tibia -width	235	17	272	24	260	19
9. Tarsus -length	282	24	327	26	291	21
10. Tarsus -width	125	9	143	14	142	8
11. Labial segment I -length	504	49	614	63	518	44
12. Labial segment I -width	352	38	416	46	390	42
13. Labial segment II -length	456	39	520	36	464	40
14. Labial segment II -width	541	63	611	58	591	65
15. Labial clamp -width	114	8	124	11	122	10
16. Ocellus -diameter	113	9	118	12	114	7
17. Ovipositor -length	797	99	786	258	842	173
18. Anal plate -length	447	44	465	43	492	42
19. Pore count 1	46	19	63	24	39	19
20. Pore count 2	62	28	87	37	47	24
21. Pore count 3	80	32	102	44	61	25
22. Pore count 4	68	30	91	47	52	23
23. Pore count 5	62	29	76	40	46	21

subspecies have a smaller general body size than subspecies canadensis. Most of the other linear measurements (Table XI) are also considerably smaller. This subspecies is more heavily pigmented than subspecies occidentalis, but it is usually less heavily pigmented than subspecies canadensis. As a result, the pore fields are more distinct; that is, it is possible to count the wax pores in the central pore fields of the dorsal surface of some specimens under the light microscope.

5.2 Adelges piceae canadensis

Adult specimens are larger (Table XII) than those of subspecies piceae or subspecies occidentalis. This subspecies is also much more darkly pigmented than the others and always has distinct sclerotized plates on the abdominal tergites. It has relatively high pore numbers for pore counts 1 to 5 (Figure 13-a). The pore fields over the entire dorsal surface are usually flat. The pores are often irregularly shaped. Pore fields in the mesial rows of the thorax and abdomen are often spread out laterally. In some specimens a separate group of pores is present between the mesial and pleural rows in the mesothorax, metathorax, and the first three abdominal segments.

The first instar stage of this subspecies also shows darker pigmentation and a larger general body size and associated linear dimensions than the other subspecies. Specimens are very heavily pigmented with relatively narrow bands of light integument visible between the heavily sclerotized dorsal plates. The wax pores in all pore fields, including those in the distal abdominal segments, are clearly visible under the light microscope. The relatively dark sclerotization and high pore number in specimens of the first instar stage collected in the Maritime region has been recognized by other workers (Eichorn 1956, 1957; Merker & Eichhorn 1956; Pschorn-Walcher & Zwölfer 1958).

5.3 Adelges piceae occidentalis

Many linear measurements are intermediate between subspecies piceae and subspecies canadensis. Exceptions are the larger ovipositor and anal plate (Table XII) in this subspecies. Adults are very lightly sclerotized. Often there is little pigmentation except for a narrow band around each pore field. The pores are round to slightly oval in shape. The pores are smaller and more clumped than in subspecies piceae or canadensis (Figure 13).

Usually the whole pore field is raised above the surrounding integument of the dorsal plate.

Two samples of the adult stage of this subspecies, namely, Glenora Road (Sample No. 2) and Land's End Road (Sample No. 3), are extremely lightly sclerotized, even in the head region. Some specimens have no wax pores in the mesial row; each pore field is represented only by a single seta.

The first instar stage of this subspecies is very lightly pigmented in comparison to the other subspecies. It was not possible to count the wax pores of the central pore fields in nearly all cleared specimens. Overall size measurements and other linear measurements are smaller than those of subspecies canadensis but differ only insignificantly from those of subspecies piceae.

5.4 Key to the subspecies of Adelges piceae in North America

The following key is based on morphological characteristics of cleared specimens (see Methods

and Materials). Because of the variability present in this species, a sample of 30 to 40 specimens is usually required to enable a local population to be identified adequately. All measurements are in millimeters.

1. Adult lightly pigmented, including head region; pore fields often raised above dorsal surface; pores closely clumped together; pore fields in central gland areas of first instar stage indistinct. - - - - - - - - - - A. piceae occidentalis

1'. Adult stage darkly pigmented; pore fields flat; pores not clumped; pores in central pore fields of first three abdominal segments often spread out laterally; pores in these areas often irregularly shaped. Pore fields in central gland areas of first instar stage usually visible. - - - - - - - 2.

2. Mean measurement values of adult specimens fall within the following ranges: femur length (0.0632 - 0.0752), femur width (0.0321 - 0.0413), tibia length (0.0708 - 0.0908), tibia width (0.0248 - 0.0296), tarsus length (0.0301 - 0.0353), labial segment I - length (0.0551 - 0.0677). - - - - - - - - - - - - - A. piceae canadensis

2'. Mean values for measurements of adult specimens situated within the following ranges: femur length (0.0498 - 0.0598), femur width (0.0264 - 0.0326), tibia length (0.0594 - 0.0706), tibia width (0.0218 - 0.0252), tarsus length (0.0258 - 0.0306), labial segment I - length (0.0455 - 0.0553). - - - - - - - - - - - - - - - - - A. piceae piceae

6. DISCUSSION

6.1 Multivariate morphometric analysis

It is not uncommon for classifications based upon separate sets of larval and adult morphological variables of the same species to differ in their structure (Rohlf 1963; Sneath & Sokal 1973). In fact, this is to be expected because different morphs have different developmental processes and are affected differently by the environment.

The first instar variables do not discriminate well between the populations. The only prominent grouping in the phenogram is that consisting of the Maritime samples with the remaining samples showing little explainable relationship among themselves. Although a great deal of distortion of phenetic associations may occur when cluster analysis and phenograms are used, ordination of the samples on the major discriminant axes did not produce a more readily interpretable separation of the groups than did the cluster analysis.

The inability of the first instar variables to discriminate well between the samples may be due in part to the non-synchrony of the samples and the large amount of developmental variability within and between populations (Atkins 1972; Bryant 1971, 1974). This time-related heterogeneity may cause many of the variables to be unstable discriminators. In contrast, the stable separation of the Maritime group may be a consequence of the greater size of the specimens; they can be distinguished from specimens belonging to other samples in spite of the presumed seasonal variation between these samples.

Seasonal morphometric trends have been noted in other aphid species (Bodenheimer & Swirski 1957; Woodford & Lerman 1974). Heryford & Sokal (1971) observed similar trends in Pemphigus populitransversus Riley on cottonwood (Populus deltoides), and Varty (1964) observed seasonal variation in the size of Betulaphis quadrituberculata (Kalt.) on birch (Betula sp.). Specimens collected in the spring and fall were on the average larger than specimens collected during the summer.

Most authors postulate that such seasonal changes are determined by changes in local climates and/or changes in the physiology and nutritive status of the host tree (Heryford & Sokal 1971; Woodford & Lerman 1974). Murdie (1969) has shown that temperature has an important influence on the size of the pea aphid, Acyrthosiphon pisum Harris, as measured by different body dimensions. Temperature differences have been found to cause developmental variability in BWA (Atkins 1972).

In addition, as the first instar stage is often present in large numbers and crowded together on the stem, differences in density between the samples may have introduced a substantial component of morphological heterogeneity. For example, Murdie (1969) has shown that size and correlated morphometric characters in aphids are influenced by crowding.

Use of the first instar morph for identification is advantagous because it is available for study

throughout the year, including the winter. The adult stage is available only during the spring and summer; its chief advantages are that the diagnostic features (qualitative and quantitative) are easily determined under the light microscope and that there may be less age-related morphological variability.

On the basis of the data from Fellow's Creek, it does not appear that within-locality variability of adult morphometric characters due to different sampling times or to differences between trees has a major effect upon the discrimination of the systematic groups identified in this study. Different altitudes and different host plants do not appear to have any major influence on the systematic groupings that were determined.

This study shows that comparative multivariate morphology is a useful approach to the study of adelgid systematics. The multivariate techniques provide a clearer summary of the systematic relationships between populations of BWA than do the univariate tests of qualitative and quantitative data alone. The results of the morphometric analyses, in

conjunction with observations of major qualitative differencess between the main systematic groups, provide a distinct picture of systematic differences between populations of BWA that can be interpreted in a meaningful way.

Most European authors have suggested that the first instar is the only morph that gives a stable separation of the Abies-attacking species of Adelges. However, it would appear that when multivariate statistical techniques are employed, the adult morph gives the most reliable classification of population samples of North American BWA. Further analysis of geographic variation in the other species of adelgids on Abies will aid in developing a robust classification of these species and help in determining their systematic relationship to the other species of Adelges.

6.2 Colonization history and morphological divergence

Insufficient knowledge of the genetic and environmental components of observed morphological variation in North American BWA makes it hazardous to speculate about

the underlying causes of the established morphometric trends. However, in view of the known or inferred colonization history of BWA on this continent, it is perhaps possible to explain the observed systematic differences as the result of BWA being introduced from the same or from different source areas in Europe. It is possible, also, that subsequent morphological divergence through selection by geographically localized factors has taken place in some instances.

It must be remembered that the biological species concept (Mayr 1963) is not precisely applicable to obligatory parthenogenetic species such as BWA. Recently, some authors (Dobzhansky 1972; Scudder 1974) pointed out that it is most productive to recognize that there are many different kinds of species each with different biological properties and evolutionary strategies.

Steffan (1964) recognized the presence of anholocyclic parthenogenetic species, or agamospecies, in the Adelgidae. Because genetic exchange within an agamospecies is limited, genetic changes of selective

advantage are maintained in a restricted set of environmental conditions and may result in the evolution of new, morphologically distinct forms. Available evidence suggests that BWA is a polytypic agamospecies. Introduction of BWA from Europe into North America and subsequent selection in relatively isolated, apomictic situations has resulted in the evolution of a number of distinct morphological forms.

Present morphological trends could be the result of the interaction between the place of origin of founder populations, the size of the founder population, the time of colonization, the effects of selection, the number of subsequent introductions into a given area, and the spread of the aphid into new zones of infestation. Published accounts (Annand 1928; Balch 1952; Silver 1959) of the initial findings of BWA on the east and west coasts of North America indicate that the three main morphological subdivisions of BWA are the result of nursery stock being introduced from Europe at different times and from different locations. Examination of the records of the agencies concerned with the importation of nursery stock may clarify this further.

The fact that A. piceae canadensis has been found both in Scotland and on the east coast of North America suggests that this form may have arrived in North America from Scotland. Populations of A. piceae piceae in North America probably originated in continental Europe with separate introductions having occurred in North Carolina and in the Washington-Oregon area.

Similarities between the North Carolina populations and populations geographically remote from them could indicate that all these populations came from the same source population, or that one was colonized by the other, perhaps through the movement of nursery stock. Subsequent local selection may not have had enough time to alter the phenotypes to the extent that they would be morphologically separable.

Subspecies occidentalis is morphologically distinct from the other population samples. This could be the result of a single introduction of material into British Columbia with subsequent spread and local geographic variation occurring due to selection pressures peculiar to each area.

In addition to the three major groups defined in this study, there is evidence of a component of finer, geographic variation as shown by the gradients of change in some of the morphological variables. For example, sample 11 shows affinities with samples 1 to 7 rather than with samples 8 to 15 in some variables. Because taxonomic considerations should be based on the most stable combination of the variables and not on examinations of variation in any particular variable sample 11 is placed with subspecies piceae.

Investigations into the biology or control of BWA should take into account the observed systematic differences between populations in North America. The morphological differences between the British Columbia and Maritime populations are considerable. These differences may well be associated with other, biological properties that would make the results of biological investigations in any one area not applicable to other areas. Therefore, the results of this study support Atkins' (1972) suggestion that populations of BWA should be scrutinized closely for ecological variants resulting from continued spread from a point of entry

into new environments. This may be of particular interest in British Columbia where BWA is presently confined to the southeastern corner of the province despite the fact that much habitat is available in the form of A. lasiocarpa in subalpine regions of the province. Investigations of these possible differences may show one subspecies to be a greater threat to A. lasiocarpa than the others.

APPENDIX 1

Measurement data (mean ± standard error, in mm x 10^{-4}) of first instar balsam woolly aphid, Adelges piceae used in the study. The letters A to G represent the within-site (Fellow's Creek, British Columbia) samples and the numbers 1 to 18 represent the between-site samples. The within-site samples are as follows:
A - Tree 1, 1973-7-23; B - Tree 1, 1973-8-30;
C - Tree 1, 1973-10-05; D - Tree 1, 1973-11-16;
E - Tree 2, 1973-8-30; F - Tree 3; 1973-8-30; and
G - Tree 4, 1973-8-30. Collection data for samples No. 1 to 18 are given in Table 1.

APPENDIX 1

Sample No.	Body -Length		Body -Width		Antennal Segment II - Length		Antennal Segment II - Width	
A	3929	38	2213	26	181	4	226	3
B(1)	3893	25	2219	16	179	2	230	2
C	3870	31	2159	21	179	2	228	2
D	4083	29	2326	26	178	2	222	3
E	3942	26	2240	20	179	2	220	3
F	3873	26	2232	17	179	2	227	2
G	3937	27	2210	18	182	2	228	3
2	3935	41	2226	28	169	2	217	3
3	3877	34	2181	24	163	2	216	3
4	3793	37	2177	22	169	2	224	2
5	4067	43	2326	32	170	2	218	3
6	3894	38	2184	24	161	2	216	3
7	3839	37	2194	25	173	2	205	3
8	3703	29	2145	17	171	2	215	3
9	3838	22	2198	16	171	2	230	2
10	3876	27	2152	19	170	2	223	2
11	3660	26	2096	16	162	2	217	3
12	4007	24	2211	19	170	2	229	2
13	3806	24	2182	21	164	2	226	2
14	4181	25	2278	19	171	2	224	3
15	3826	29	2101	18	168	3	223	3
16	4204	36	2254	23	179	2	211	3
17	4189	36	2432	19	183	2	224	3
18	4182	38	2384	27	181	2	220	4

APPENDIX 1 (continued)

Sample No.	Variable (Mean ± SE, in mm x 10^{-4})							
	Antennal Segment III-Length		Antennal Segment III-Width		Apical Seta -Length		Femur -Length	
A	612	5	189	3	399	3	458	2
B(1)	620	4	195	3	409	3	460	3
C	628	4	193	2	410	4	468	3
D	623	4	189	2	409	4	461	3
E	626	5	189	3	401	4	469	3
F	627	5	193	2	408	3	469	2
G	617	4	188	2	412	3	464	2
2	595	3	188	2	403	3	454	2
3	570	4	189	3	392	3	445	3
4	595	4	193	2	395	3	445	2
5	593	5	185	3	396	3	454	3
6	570	5	190	2	389	3	451	2
7	589	4	189	3	393	4	450	2
8	597	3	187	3	396	4	446	2
9	603	6	191	2	410	2	450	3
10	603	6	188	3	397	4	455	4
11	590	5	184	3	385	4	443	3
12	602	5	196	2	407	6	446	3
13	598	7	190	3	374	3	422	4
14	622	4	191	3	413	3	453	3
15	593	4	191	3	401	3	443	3
16	644	5	176	2	425	4	469	2
17	681	6	184	3	436	4	476	2
18	691	6	180	3	445	4	502	4

APPENDIX 1 (continued)

Sample No.	Variable (Mean ± SE, in mm x 10^{-4})							
	Femur -Width		Tibia -Length		Tibia -Width		Tarsus -Length	
A	292	3	565	5	274	3	260	2
B(1)	291	3	576	4	274	3	259	2
C	292	3	574	5	273	3	263	2
D	287	3	576	3	270	3	260	2
E	289	3	576	5	275	3	259	2
F	292	3	578	5	274	2	266	2
G	293	3	571	5	272	3	260	2
2	278	3	571	3	264	3	257	2
3	274	4	551	4	262	3	250	2
4	291	2	560	4	265	2	257	2
5	278	4	567	4	263	3	254	2
6	273	4	564	3	263	3	256	2
7	261	4	567	3	251	4	252	2
8	274	4	552	4	249	3	248	2
9	295	2	565	3	264	3	257	1
10	287	3	577	4	258	3	259	2
11	279	4	567	3	250	4	254	2
12	284	4	570	2	268	3	256	2
13	281	4	559	4	264	4	252	2
14	279	4	591	3	263	3	267	1
15	285	3	564	4	262	3	260	2
16	270	4	594	4	247	3	262	2
17	298	3	602	4	258	3	266	2
18	286	4	637	5	253	3	282	3

APPENDIX 1 (continued)

Sample No.	Variable (Mean ± SE, in mm x 10^{-4})							
	Tarsus -Width		Tarsal Hair -Length		Labial Segment I-Length		Labial Segment I-Width	
A	157	2	213	2	385	3	316	4
B(1)	152	2	217	2	389	3	324	4
C	150	2	220	2	388	3	317	4
D	148	2	214	2	387	3	318	5
E	148	2	213	2	387	2	322	4
F	149	2	216	2	393	2	320	4
G	152	2	218	2	392	3	292	4
1	146	2	214	2	384	3	309	6
3	142	2	204	2	371	3	287	4
4	151	2	211	2	377	2	304	3
5	147	2	210	2	382	4	310	5
6	142	2	208	2	368	4	293	4
7	139	2	206	2	381	3	282	3
8	142	2	210	2	372	2	284	4
9	148	2	215	2	384	3	308	4
10	145	2	209	2	387	4	301	4
11	143	2	206	2	374	3	294	4
12	148	2	209	2	391	3	306	4
13	148	2	201	2	387	4	304	5
14	145	2	215	2	398	3	323	5
15	151	2	210	2	378	3	324	4
16	142	2	214	2	392	4	302	6
17	150	2	222	2	413	3	328	5
18	147	2	228	2	430	3	320	5

APPENDIX 1 (continued)

Sample No.	Variable (Mean ± SE, in mm x 10^{-4})							
	Labial Segment II-Length		Labial Segment II-Width		Labial Clamp -Width		Ocellus Diameter	
A	357	4	533	11	120	1	108	1
B(1)	358	3	541	8	121	1	108	1
C	360	3	548	9	122	2	109	1
D	363	3	559	7	121	1	107	1
E	361	4	557	8	120	1	105	1
F	362	3	535	9	119	1	108	1
G	361	3	539	7	116	2	108	1
2	349	3	512	9	119	2	107	1
3	338	3	499	7	111	1	106	1
4	329	2	509	8	116	1	106	1
5	345	4	519	9	120	1	106	1
6	331	2	499	8	113	1	105	1
7	340	2	492	7	110	1	106	1
8	335	3	505	8	116	1	104	1
9	347	3	537	7	122	1	109	1
10	346	3	520	9	120	2	108	1
11	337	4	504	9	115	1	106	1
12	358	3	519	8	121	2	106	1
13	354	4	510	10	121	2	106	1
14	344	2	534	8	125	1	109	1
15	336	2	508	7	119	2	108	1
16	356	2	518	10	133	2	102	1
17	376	4	582	8	144	2	103	1
18	389	5	542	9	142	2	106	1

APPENDIX 1 (continued)

Sample No.	Variable (Mean ± SE, in mm x 10^{-4})	
	Stylet Length	
A	1250	17
B(1)	1270	20
C	1279	16
D	1253	18
E	1273	17
F	1274	18
G	1279	16
2	1220	17
3	1100	17
4	1206	22
5	1227	22
6	1059	11
7	1146	21
8	1245	20
9	1219	19
10	1231	18
11	1112	17
12	1256	16
13	1157	19
14	1222	15
15	1124	13
16	1227	25
17	1624	20
18	1495	30

APPENDIX 2

Measurement data (mean ± standard error, in mm x 10^{-4}) (pore counts, x 10) of adult balsam woolly aphid, Adelges piceae, used in the study. The letters A to E represent the within-site (Fellow's Creek, British Columbia) samples and numbers 1 to 18 represent the between-site samples. The within-site samples are as follows: A - Tree 1, 1973-6-15; B - Tree 1, 1973-8-30; C - Tree 2, 1973-8-30; D - Tree 3, 1973-8-30; and E - Tree 4, 1973-8-30. Collection data for samples No. 1 to 18 are given in Table 1.

APPENDIX 2

Sample No.	Variable (Mean ± SE, in mm x 10^{-4})							
	Antennal Segment II-Length		Antennal Segment II-Width		Antennal Segment III-Length		Antennal Segment III-Width	
A	148	2	226	3	336	4	175	2
B(1)	149	2	245	4	328	6	191	3
C	154	2	231	4	343	6	181	2
D	159	2	244	3	375	5	193	2
E	156	2	247	4	355	4	197	3
2	160	2	262	3	361	5	194	3
3	156	2	238	4	327	5	182	3
4	157	2	248	3	338	3	183	2
5	149	2	235	3	329	5	176	3
6	156	2	241	4	327	6	178	3
7	162	2	242	3	338	4	180	3
8	149	2	199	3	330	5	162	3
9	145	2	204	3	328	4	163	2
10	163	2	208	3	356	4	157	2
11	157	2	229	4	328	5	174	3
12	160	2	210	3	374	4	171	2
13	152	1	198	3	350	4	159	3
14	154	2	223	4	343	4	171	3
15	168	2	220	3	362	4	170	3
16	172	2	251	4	382	5	195	3
17	167	2	211	4	360	4	170	2
18	166	2	229	4	367	6	176	2

APPENDIX 2 (continued)

Sample No.	Variable (Mean ± SE, in mm x 10^{-4})							
	Femur -Length		Femur -Width		Tibia -Length		Tibia -Width	
A	564	6	319	6	645	4	242	3
B(1)	569	8	336	8	640	6	260	3
C	560	6	330	6	651	4	257	3
D	573	7	354	8	689	5	269	3
E	548	4	347	4	659	4	273	3
2	634	9	367	4	720	9	269	3
3	598	8	356	4	670	7	259	3
4	602	6	348	3	673	6	263	2
5	563	6	320	4	636	6	247	3
6	582	6	347	3	647	6	258	2
7	619	7	355	5	685	7	267	3
8	527	5	287	5	612	7	231	2
9	530	6	292	4	621	7	236	3
10	547	6	280	4	645	6	231	2
11	549	7	316	4	646	7	239	3
12	561	4	298	5	688	6	240	2
13	525	4	272	4	641	5	225	2
14	513	7	310	5	615	7	240	3
15	636	5	307	5	731	7	240	2
16	701	10	398	5	832	11	288	3
17	690	7	344	7	828	8	260	3
18	687	11	360	6	790	14	271	3

APPENDIX 2 (continued)

Sample No.	Variable (Mean ± SE, in mm x 10^{-4})							
	Tarsus -Length		Tarsus -Width		Labial Segment I-Length		Labial Segment I-Width	
A	274	3	134	3	492	6	364	6
B(1)	279	3	149	3	478	6	372	8
C	277	3	139	3	470	5	362	5
D	294	3	148	4	481	5	378	6
E	286	3	154	3	466	4	367	7
2	307	3	144	2	548	5	399	6
3	289	3	139	2	533	8	399	5
4	293	3	146	2	509	5	382	6
5	288	3	135	2	498	5	373	6
6	283	3	141	2	514	5	397	6
7	302	3	142	2	547	7	409	7
8	268	3	124	1	466	6	334	5
9	274	3	123	1	484	5	345	6
10	284	3	125	1	495	6	335	5
11	280	4	129	2	529	7	367	6
12	296	3	126	1	526	6	363	6
13	272	3	119	1	480	4	338	6
14	271	3	124	2	488	6	362	6
15	314	3	135	1	569	6	379	5
16	341	4	153	2	647	13	439	7
17	315	3	137	2	595	6	416	6
18	326	4	141	2	600	7	395	7

APPENDIX 2 (continued)

Sample No.	Variable (Mean ± SE, in mm x 10^{-4})							
	Labial Segment II-Length		Labial Segment II-width		Labial Clamp -Width		Ocellus Diameter	
A	436	5	564	8	116	2	109	1
B(1)	450	7	565	10	123	2	116	1
C	438	4	559	7	118	1	110	1
D	432	5	609	9	122	2	113	1
E	418	4	566	10	120	2	109	1
2	483	5	607	8	124	2	117	1
3	475	8	600	10	122	2	115	1
4	456	5	575	11	121	2	113	1
5	443	5	568	10	114	1	110	1
6	456	5	602	10	123	1	111	1
7	484	6	625	10	125	1	115	1
8	429	6	532	9	109	1	110	1
9	444	4	519	10	109	1	110	1
10	459	5	511	8	114	1	115	1
11	469	6	562	12	116	1	113	1
12	479	5	561	10	114	1	115	1
13	440	4	505	7	112	1	105	1
14	431	5	554	9	116	1	112	1
15	497	5	588	8	121	1	119	1
16	534	7	636	10	132	2	119	1
17	518	5	613	8	121	1	116	1
18	509	4	584	8	122	1	116	2

APPENDIX 2 (continued)

Sample No.	Variable (Mean ± SE, in mm x 10^{-4})			
	Ovipositor -Length		Anal Plate -Length	
A	815	10	456	6
B(1)	822	11	469	7
C	823	7	447	4
D	827	9	462	4
E	790	7	437	3
2	932	10	514	6
3	904	12	518	7
4	903	8	484	5
5	825	8	467	6
6	840	14	480	6
7	918	9	513	5
8	781	8	434	5
9	785	10	445	4
10	810	10	438	5
11	818	10	473	6
12	790	6	434	7
13	766	8	414	5
14	781	6	434	5
15	925	10	508	6
16	941	14	483	7
17	833	8	443	5
18	884	9	469	6

APPENDIX 2 (continued)

Sample No.	Variable (Mean ± SE)									
	Pore Count									
	1		2		3		4		5	
A	41	2	46	2	59	3	51	3	40	3
B(1)	39	2	47	3	58	3	47	3	39	3
C	35	2	48	3	56	3	48	3	38	3
D	36	2	46	3	55	4	52	5	43	4
E	36	2	51	3	61	3	56	3	46	3
2	32	3	33	3	47	3	43	3	42	3
3	27	3	28	4	44	4	34	3	30	3
4	31	2	44	3	60	4	53	4	48	3
5	44	3	61	4	76	4	72	4	63	3
6	49	2	60	3	70	3	57	2	50	2
7	52	2	55	4	66	3	55	3	47	3
8	50	3	70	3	81	4	65	3	62	3
9	55	2	72	3	78	3	63	3	58	4
10	48	3	60	4	78	4	66	4	56	4
11	32	3	48	5	64	6	55	5	52	4
12	53	2	76	3	94	3	78	4	69	4
13	55	2	77	3	104	4	89	4	88	4
14	40	2	47	3	63	4	54	4	44	3
15	35	4	46	6	76	8	71	7	63	6
16	73	5	104	6	130	7	120	8	96	7
17	49	2	72	6	76	5	62	4	54	4
18	67	3	86	5	100	5	89	6	80	5

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