MORPHOMETRIC ANALYSIS OF CHARACTER VARIATION AND TAXONOMIC DISCRIMINATION AMONG A COMPLEX OF SPECIES OF THE GENUS CINARA (HOMOPTERA: APHIDOIDEA: LACHNIDAE)

by

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Morphometric analysis of character variation and taxonomic discrimination among a complex of species of the genus Cinara (Homoptera: Aphidoidea: Lachnidae)

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ABSTRACT

Morphological variation among the species of a taxonomic complex of aphids of the genus Cinara Curtis (Homoptera: Aphidoidea: Lachnidae) on western North American pines was studied using techniques of univariate and multivariate statistical analysis. This morphometric approach was used to describe trends in variation, to establish species boundaries, and to test the discriminatory ability of a set of morphological characters.

Within-sample and between-sample variation of a single species, C. nigra (Wilson), was characterized first. Correlation analysis and principal component analysis of a suite of 52 characters in one sample and 32 characters in 19 geographic samples of this species revealed the presence of components of variation other than just size variation. Geographic variation in the 19 population samples was analyzed using discriminant function analysis. Variation in the magnitude and composition of the main components of variation within and between samples was demonstrated.

Morphometric trends within 9 species of Cinara were characterized by the use of principal component analysis. Patterns of morphometric variation were shown to be complex and unique for many species; functional groups of characters exhibited different internal relationships and different degrees of association with the main components of variation. Information on the covariation among

the characters studied was used to select a set of characters for discrimination among the species of Cinara. Discriminant function analysis and cluster analysis of Mahalanobis Generalized Distances were used to establish species boundaries among samples of the 9 species and to identify those variables which discriminated best between the species. It was shown that nearly one half of the 32 variables used were necessary to discriminate between the species; these variables were from all of the functional groups of characters.

Descriptive and distributional information and a taxonomic key to the species of Cinara on lodgepole pine (Pinus contorta Douglas ex Laudon) were developed. Extensive geographic sampling allowed for an interpretation of the distributions and hostplant preferences of these species to be made within the context of the systematic relationships of North American pines.

The application of multivariate morphometrics to Cinara taxonomy in particular and to aphid biosystematics in general is discussed, including the potential contribution of this approach to the phylogenetic reconstruction of the Aphidoidea.

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1. GENERAL INTRODUCTION

Aphids of the genus Cinara Curtis (Homoptera: Aphidoidea: Lachnidae) are a common component of the insect fauna of coniferous forests, particularly in the north temperate zone. Species of this genus feed on bark, roots, cones and other parts of coniferous trees. The ecology and economic importance of most species of Cinara are poorly understood. However, some Cinara aphids have been found to cause seed loss, to increase susceptibility to secondary disease and drought, and to reduce growth (Johnson 1965). Further investigation of the ecological and economic importance of Cinara aphids will depend on a sound knowledge of the taxonomy, host-plant relations, and geographic distributions of species of this group.

As is the case with many aphid genera, the taxonomy of species of the genus Cinara is generally considered to be difficult (Eastop 1972). Over 200 species have been described as feeding on conifers belonging to the families Pinaceae and Cupressaceae. A number of these species are known only from their original descriptions, while others have never been observed except at their type localities (Voegtlin 1976). Examination of the taxonomic literature concerning Cinara species indicates that some previously used taxonomic characters are of limited use for discriminating between species (Bradley 1961, Fedde 1967, Voegtlin 1976). For example, Palmer's (1952) widely used key to 39 species of western North American Cinara species relied much on morphological

measurements without considering size variation and its effect on these variables.

The purpose of this study is to describe morphological character variation in some aphids of the genus Cinara, to evaluate the degree to which morphological characters define species boundaries, and to quantify the ability of these characters to discriminate between species. Within-sample and between-sample variability of a single species and variability between species are characterized using techniques of univariate and multivariate morphometrics (Dunn and Everitt 1982, Neff and Marcus 1980, Pimentel 1979, Sneath and Sokal 1973). These techniques are now widely used in biosystematic studies to describe patterns of morphological variation and to quantify the discriminatory ability of taxonomic characters. For example, Foottit (1979) used multivariate morphometric techniques to compare 18 population samples of Adelges piceae Ratzeburg (Homoptera: Aphidoidea: Adelgidae) collected in North America and to cluster these into 3 distinct groups; these 3 groups were subsequently recognized as 3 subspecies (Foottit and Mackauer 1983).

Approximately 150 species of Cinara have been described from North America (Smith and Parron 1978). However, I studied a more limited group of Cinara species associated with a restricted host-plant range in order to examine morphological character variation in detail.

Lodgepole pine, Pinus contorta Douglas ex Loudon, is the main host plant that was studied as its distribution is restricted to western North America, a fact that allowed extensive sampling for geographic variation throughout much of its range. The growth form and habitat preference of

P. contorta allow for relatively thorough searching of its vegetative parts for aphids as compared to other conifer hosts such as Picea. In addition, the geographic variation in many morphological and biochemical characters of P. contorta itself have been studied extensively (Wheeler and Guries 1982a, b; Wheeler et al. 1983).

Compared to the Cinara species found on pines in eastern North America, the 45 species described from western pines (Appendix 1) are generally considered to be monophagous or restricted to a very few host-plant species (Fedde 1967). However, this may be the result of a lack of thorough sampling and of inadequate taxonomic data. The use of P. contorta is advantageous in that it overlaps in distribution with 2 other pine species, namely P. monticola Douglas ex D. Don and P. ponderosa Douglas ex P. and C. Lawson. Local, mixed stands of P. contorta and these other species could be searched to determine if Cinara species are entirely restricted to individual pine species.

The aphid and host-plant system is described in more detail in Chapter 2. The principles and practice of the multivariate morphometric techniques used in this study are discussed in Chapter 3. Chapter 4 provides details on the univariate and multivariate analyses of character variation within and between samples of a single species of Cinara (C. nigra (Wilson)), and Chapter 5 is concerned with similar analyses between a number of species of Cinara. In Chapter 6 the morphs of the species studied are described and distributions, feeding site and host-plant preferences are summarized. In Chapter 7, the implications of the morphometric approach to aphid systematics in general and to Cinara

taxonomy in particular are considered, including the application of these techniques to the phylogenetic analysis of the family Lachnidae and to the creation of generic and sub-generic divisions within the tribe Cinarini Börner.

2. BIOLOGY AND DISTRIBUTION OF THE APHIDS AND THEIR HOST PLANTS

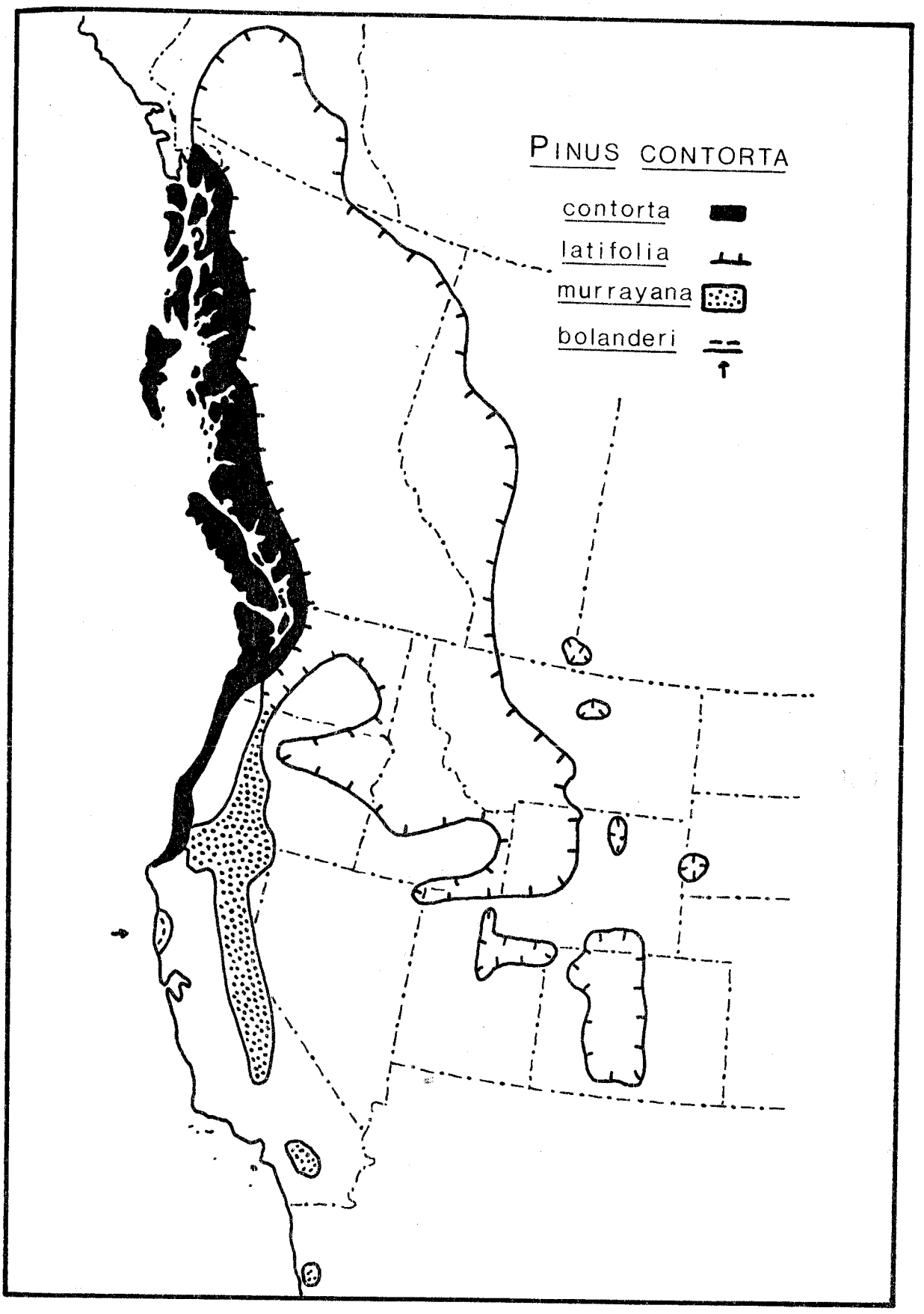
2.1 The *Pinus* Species

Lodgepole pine (*Pinus contorta* Douglas ex Laudon) is one of the most widespread and variable North American conifers (Figure 1). It exhibits considerable morphological variation and occurs over a wide range of climatic and edaphic conditions from southeastern Alaska and the Yukon Territory to Baja California, and from the Pacific Coast to the Rocky Mountains of Colorado with outlying populations as far east as the Black Hills of South Dakota (Critchfield 1957, Mirov 1967).

2.1.1 Biology

Lodgepole pine is a monoecious, wind-pollinated species. It is characterized generally as a shade-intolerant, deep-rooted, hardy, initially fast-growing but relatively short-lived (100 to 175 years) pioneer successional species (Pfister and Daubenmire 1975). *P. contorta* reaches 25 to 75 m in height with a long and narrow crown, except in dense stands where foliage is only present on the top portion. The needles are 2.5 to 7.5 cm in length and grouped in fascicles of 2. The ovulate cones of *P. contorta* are 2 to 5 cm in length. The cones may be serotinous, requiring high temperatures (45 C) to cause the opening and the release of seeds (Preston 1961, Fowells 1965). As a result, fire has

Figure 1. Geographical distribution of the four subspecies of Pinus contorta Doug. ex. Loud. (Re-drawn from Critchfield (1957) and Wheeler and Guries (1982a, b)).


PINUS CONTORTA
contorta
latifolia
murrayana
bolanderi

been an important factor in the reproduction and distribution of P. contorta. Trees of the interior range of the species are characterized by cones which persist for a number of years while coastal trees have non-persistent cones (Critchfield 1957).

The ecology of P. contorta has been reviewed by Pfister and Daubenmire (1975). It is an extremely adaptable species, exhibiting a broad ecological amplitude. It is found in 9 of the biogeoclimatic zones of British Columbia (Krajina 1969). Lodgepole pine grows at altitudes from sea-level up to 3500 m in the Rocky Mountains. It grows in a wide variety of soil conditions throughout its geographic range although it prefers well-drained, sandy or gravelly loams.

As a result of its wide ecological amplitude, P. contorta is found in association with a number of conifer species, among them the pines, P. ponderosa Dougl. ex Laws. and Laws. and P. monticola Dougl. ex Don. The 3-needle pine, P. ponderosa grows from southern British Columbia to the Mexican border. The 5-needle pine, P. monticola, is found from southern British Columbia to central California and adjacent parts of Nevada. It is also found on a wide variety of sites ranging from peat bogs to dry, sandy and rocky soils (Little 1971, Mirov 1967). The distribution in British Columbia and the ecological characteristics of the above-mentioned pine species have been reviewed by Krajina et al. (1982). As all three of these pines have wide ecological amplitudes, they were found in different combinations in mixed and adjacent stands throughout many of the regions surveyed during this study.

2.1.2 Taxonomy

The taxonomic treatment of P. contorta has varied with respect to the number and type of categories used to subdivide the species. Based on morphological features of the needles and cones, Critchfield (1957) divided P. contorta into 4 subspecies (Figure 1) and reviewed the morphological and ecological differences between them. P. contorta bolanderi consists of small, isolated populations on the California coast. P. contorta contorta extends from the west coast of Alaska to northern California including Vancouver Island and the Queen Charlotte Islands. P. contorta murrayana extends from the Cascade Mountains in Oregon south to the Siskyou, Sierra Nevada, and San Bernadino Mountains in California. P. contorta latifolia occupies the greater part of the range of lodgepole pine, extending from the Yukon Territory, Alberta, much of interior British Columbia southeast into the Rocky Mountains. Little (1971) considered only 2 varieties of P. contorta, namely, var. contorta and var. latifolia. In the Pacific Northwest, Hitchcock and Cronquist (1973) recognized only 2 varieties (var. contorta and var. latifolia); they synonymized var. murrayana with var. latifolia. Using multivariate analysis of morphological features, Jeffers and Black (1963) confirmed the general division of P. contorta into coastal and inland provenances.

The monoterpene composition of the shoot cortical oleoresin of trees collected throughout the range of P. contorta was analyzed by Forrest (1980). He found that his division of the range into chemically

distinct regions corresponded in general with the divisions into subspecies of Critchfield (1957). The only exception was ssp. murrayana which appeared to intergrade with ssp. latifolia. Wheeler and Guries (1982 a, b) analyzed morphological and allozyme variation throughout the range of P. contorta and found that their results also supported Critchfield's (1957) taxonomic subdivisions. However, they suggested that ssp. murrayana should be restricted to populations in the Sierra Nevada and in the southern California mountain ranges. Based on the analysis of genetic distances calculated from the allozyme data, Wheeler and Guries (1982b) concluded that geographic isolation of the subspecies was nearly complete; the subspecies exhibited only moderate genetic affinities and, in most cases, gene exchange between them was very limited. Provenance testing has also supported the division of P. contorta into 4 subspecies; the subspecies have been shown to differ in life-history characteristics, tree dimensions and form, and other morphological and phenological characteristics (Wheeler and Guries 1982a).

2.1.3 History

Literature documenting the historical development of the pines in western North America is reviewed by Mirov (1967). There is evidence that a land bridge connected the Old and New Worlds during the Cretaceous and the early and middle Tertiary periods which allowed the migration of pines between the two areas. During the early Tertiary, the pines spread south to Mexico by 2 routes, along the old western coastal mountain

ranges and along the eastern Appalachian and Ozark uplands. Subsequently the western and southern regions of North America became secondary centers of speciation (Mirov 1967). Quaternary glaciation severely restricted the ranges of some species of Pinus, while others may have survived in unglaciated refugia in Alaska, the Yukon, and islands off the Pacific Northwest coast. The final disappearance of the ice after the last glacial maximum took place about 12,000-10,000 years B. P. This was followed by the development of a lodgepole pine parkland along coastal areas from southeastern Alaska to the Pacific Northwest (Wheeler and Guries 1982a, b).

The rapid appearance of P. contorta in the palynological record of much of the northern coastal regions, within 1,000 years of the last glacial retreat, suggests the possibility of a glacial refugium for ssp. contorta in south Alaska (Wheeler and Guries 1982b). There is evidence (Wheeler and Guries 1982a, b), based on allozyme data, that showed the Yukon and northern British Columbia populations to be a cohesive unit, which was distinct from the southern population of ssp. latifolia. However, more recent work (MacDonald and Cwynar 1985), using a fossil pollen based reconstruction, has shown that ssp. latifolia migrated northward from refugia south of the continental glacial limits.

Lodgepole pine is generally considered to be most closely related to Pinus banksiana Lamb. (Critchfield 1957, Wheeler et al. 1983), which is now distributed across Canada and the northeastern United States from the Michigan River basin to the Atlantic coast (Little 1971). Yeatman (1967) has reviewed the biogeography and history of P. banksiana. This

species and P. contorta probably differentiated from a common progenitor during the late Tertiary (Dancik and Yeh 1983). Natural hybrids are formed between the two species in some areas of Alberta, British Columbia, and the Northwest Territories where their ranges overlap; these hybrids are of recent origin, dating from the post-glacial migrations of the two species.

2.2 The Cinara Species

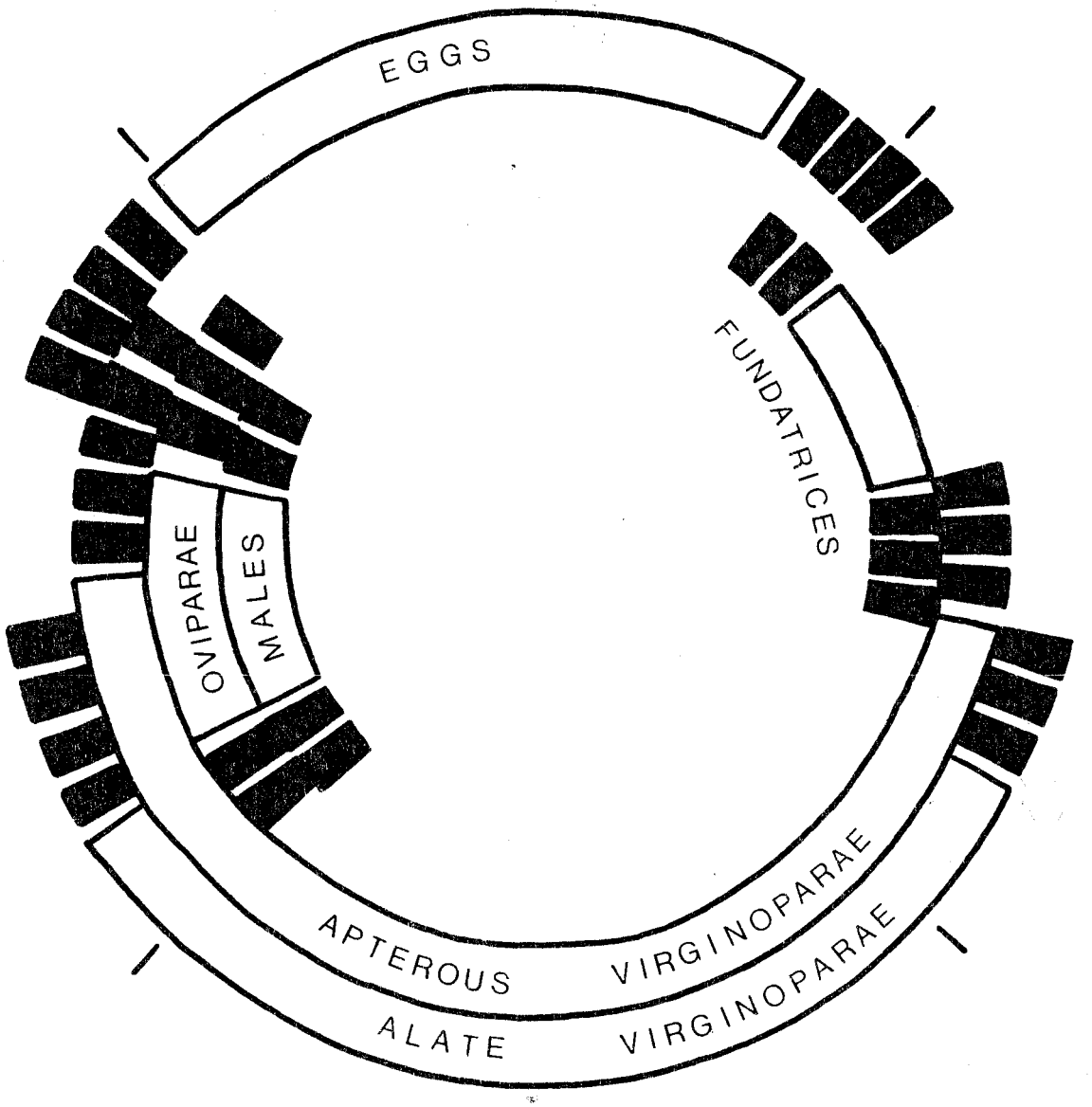
2.2.1 Life Cycle and Morphological Forms

Life history studies of Cinara species, particularly the North American fauna, have been carried out for only a few species. Exceptions are the studies of Bradley (1961) and Bradley and Hinks (1968) on Cinara in Canada, Fedde's (1965, 1967) studies of the species feeding on pines in South Carolina, and Voegtlin's (1976) work on Cinara on conifers in the Sierra Nevada mountains of California.

The general life cycle of aphids of the genus Cinara is shown in Figure 2. Aphids of this genus are autoecious, that is, they do not migrate between primary and secondary hosts. The life cycle is holocyclic, that is, sexual forms are produced every year. However, anholocyclic life cycles that do not include a sexual generation, are known for some species of Cinara. For example, Voegtlin and Dahlsten (1982) found C. ponderosae (Williams) to be anholocyclic in the foothills region of the Sierra Nevada mountains of California. In some species,

Figure 2. Diagram showing the general life history of Cinara aphids. The darkened, broken sections indicate periods of least abundance. Based on Carter and Maslen (1982).

WINTER



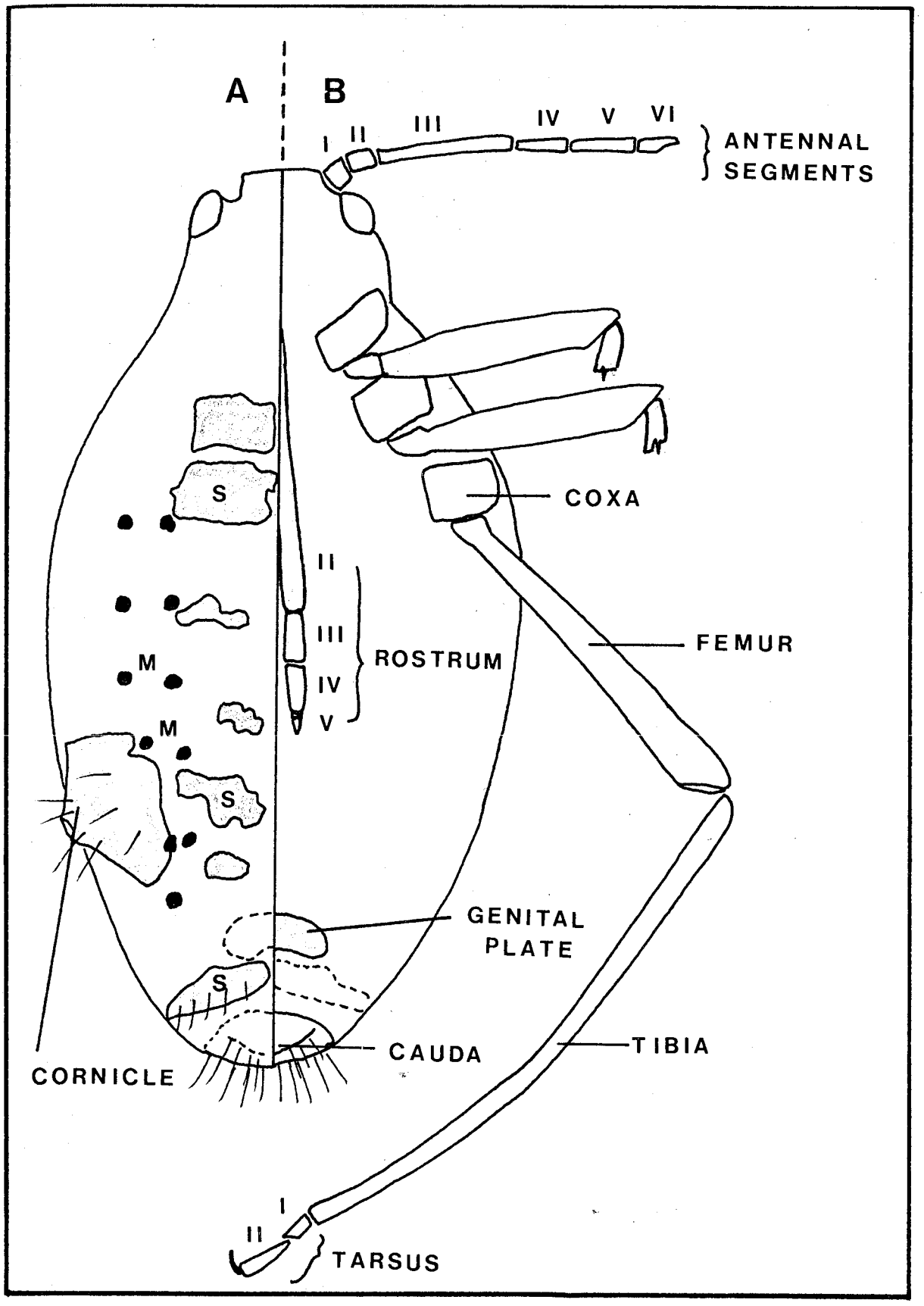
SUMMER

such as the widely distributed C. piceae (Panzer), the oviparous morph is commonly found although the male sexual morph is unknown (Eastop 1972).

In the early spring, nymphs hatch from overwintering eggs and develop into apterous (wingless) females which are termed fundatrices, or stem mothers. The fundatrix reproduces viviparously. A number of generations follow during the summer; all individuals are female and viviparous (virginoparae). Both apterous and alate (winged) individuals are produced. As there is no host alternation, these winged aphids disperse to other trees, usually of the same species, and start new colonies. Bradley (1961) observed that some individuals will start new colonies on the tree on which they developed. Cinara species vary in the extent of alate production; alates may account for up to 80 to 90 percent of the second generation of virginoparae. In the fall, female sexual aphids (oviparae) and male aphids are produced; these mate and produce overwintering eggs. The eggs of most species of Cinara are laid on needles, with the exception of species that feed on Larix, a deciduous conifer; here the eggs are laid on the bark of twigs (Bradley 1961). The number of summer generations varies, depending on local climatic effects.

Morphological features of the apterous viviparous morph are shown in Figure 3. The apterous fundatrix of Cinara is similar morphologically to the summer apterous virginoparae. However, the fundatrix is usually darker, has a larger abdomen and shorter appendages and lacks a mesosternal tubercle even in those species in which it is present in the virginoparae. The virginoparae are often the most distinct morph of the species due to their development of sclerotized areas on the dorsum of

Figure 3. Diagram showing the general morphological features of the adult virginoparous morph of Cinara: A, dorsal view; B, ventral view; M, muscle attachment plates; S, sclerotized areas on the dorsum of the abdomen.


A
B
I
II
III
IV
V
VI
ANTENNAL SEGMENTS
COXA
FEMUR
S
M
M
S
II
III
IV
V
ROSTRUM
GENITAL PLATE
S
CAUDA
TIBIA
CORNICLE
I
II
TARSUS

the abdomen, the muscle-attachment plates, the siphunculi (cornicles), and at the bases of the setae. The alate virginoparae have smaller bodies and reduced abdominal sclerotization but longer appendages, longer setae, and more numerous sensillae on the antennae than do the apterous virginoparae. The oviparae are similar to the virginoparae but, in some species, the oviparae have a pericaudal wax ring, which is a posterior area of the dorsum of the abdomen covered with a secretion of white wax. In some species, the hind tibiae of the oviparous morph are darker, thickened, and bear small, round, pseudosensorial pits. The genital plate of the oviparae is larger and the setae on it are more dense than in the virginoparae. The male is the smallest morph with respect to body size, but it has disproportionately long appendages and many sensoria on the antennae. It is apterous in some species and alate in others.

2.2.2 Host Preferences and Feeding Sites

Aphids of the genus Cinara live on Coniferae, usually on Pinaceae and Cupressaceae. With the exception of a few species, most native North American conifers serve as host-plants for Cinara aphids. The majority of Cinara species living on Pinaceae are specific to one species or to a small number of closely related species of Abies, Larix, Picea, or Pinus (Bradley 1961, Eastop 1972). As was mentioned in Chapter 1, it is believed that there is a larger proportion of Cinara species having multiple host ranges in eastern North America than in western North America (Fedde 1967). However, the general perception of Cinara aphids

being monophagous or extremely restricted to a narrow range of host species appears to be that of the western North American workers only (Fedde 1967, Gillette and Palmer 1924, Hottes 1928, Palmer 1952). This situation may simply be the result of incomplete host records.

Cinara aphids may feed on new growth shoots, small branches (Figure 4-b), roots, and on the main stem of large, mature trees. In western Canada, C. nigra (Wilson) is usually found on the main stem of young trees (Figure 4-a). Some species prefer branches devoid of needles and sites on the branches that are adjacent to the main stem while other species are only found among the needles. Most species of Cinara feed directly on the bark of the tree, however, some species such as C. brevispinosa (Gillette and Palmer) may feed on the needle fascicles (Figure 4-c), and C. oregonensis (Wilson) feeds on the green cones of P. contorta. Cinara species are usually restricted to a particular feeding site at the start of the summer. However, some species show a tendency to gradually move as a colony to other feeding sites on the same tree as the season progresses, presumably to exploit new food sources or acquire protection from such factors as weather (Bradley 1959, 1961).

Bradley (1959) found that as many as 6 species of Cinara could occur on the same tree. The extent of multiple-species infestations on the same tree was found to be closely related to the presence of larger numbers of species of Cinara in a stand of trees and their particular population trends (Fedde 1967). Bradley (1959) also found that while there may be a number of species of Cinara on the same tree, they were found only rarely in mixed colonies.

Figure 4. Feeding sites of *Cinara* species: A (top left), *C. nigra* feeding on the main stem of *Pinus contorta*; B (top right), *C. contortae* feeding on a side branch; C (bottom left), yellowing of needles due to *C. brevispinosa* feeding on the needle fascicles; D (bottom right), *C. medispinosa* feeding on cankers resulting from attack by the western gall rust, *Endocronartium harknessi*.

Among species of Cinara the distribution of individuals within colonies is variable, ranging from dense clusters to extremely dispersed individuals. Some species such as C. pergandei (Wilson) are more or less solitary; the virginoparae move away from the nymphs after they are deposited (Bradley 1961). Some species always occur as small colonies of less than 100 individuals due to dispersal by alates and adult apterae. Other species form large, dense colonies along the main trunk and adjoining branches as adjacent colonies are amalgamated into one as the population grows.

Some species of Cinara are known to be associated with the lesions and cankers of pine-rust fungi belonging to the order Uredinales (Basidiomycetes) (Ziller 1974). Tissot and Pepper (1967) described 2 new species of Cinara (C. cronartii and C. westi) which were found feeding on the lesions of the rust Cronartium fusiforme Hedgc. and Hunt on P. taeda L. in the southeastern United States. The aphids were found feeding beneath the loose bark of the lesions. Other species of Cinara, normally found at other feeding sites on a tree, have been found to feed on rust-fungus lesions on P. contorta and P. banksiana in Quebec, Ontario, Manitoba and Alberta. The western gall rust, Endocronartium harknessi (J. P. Moor) Y. Hiratsuka, which is found on P. banksiana and P. contorta, is the most common and destructive stem rust of hard pines (Section Diploxylon) in western Canada (Ziller 1974). It commonly attacks nursery plantings and managed forests and small, native ornamentals; these are some of the situations most extensively exploited by Cinara. Cankers of this fungus (Figure 4-d) were frequently found

throughout the area sampled during this study. The frontispiece shows C. contortae Hottes feeding on cankers of E. harknessi on P. contorta.

The occurrence and location of Cinara aphids on their host plants is greatly influenced by the presence and behaviour of ants (Hymenoptera: Formicidae) (Bradley and Hinks 1968, Carter and Maslen 1982). There is a mutualistic association between the aphids and the ants. The ants feed on the anal excretory products, or honeydew, of the aphids, removing it as it is produced. This behaviour keeps the aphid feeding site clean and prevents outbreaks of fungal growth in the colony. Being rich in sugars, honeydew serves as an important food source for ants (Way 1963). In addition, the presence of ants in aphid colonies tends to discourage attacks by predators and parasites (Bradley and Hinks 1968, Tilles and Wood 1982).

This mutualistic association with ants is advanced to a level in Cinara that these aphids show morphological adaptations to this life history strategy. They have a reduced cauda while a relatively long cauda, necessary to expel the honeydew droplets, is present in many non-myrmecophilous aphids (Blackman 1974). Cinara aphids essentially possess a "trophobiotic organ" (Wilson 1971) in the form of a ring of setae in the caudal area; the setae retain the droplet of honeydew while the ant imbibes it (Way 1963).

2.2.3 Previous Taxonomic Studies

European studies which are of particular interest to students of Cinara taxonomy are those of Pintera (1966), Eastop (1972), and especially Börner (1938, 1939, 1949, 1952, 1957). The latter divided the European species into a number of genera and subgenera. Fedde (1967) chronologically enumerated the species of Cinara described in North America since the first species, C. strobi, was described by Fitch (1851). A number of aphid taxonomists have specialized in the study of Cinara, the most notable being H. F. Wilson, C. P. Gillette, M. A. Palmer, F. C. Hottes, and G. A. Bradley (Smith 1972).

Many studies of Cinara in North America have been, by necessity, regional in nature. Exceptions to this trend are the more extensive, host-plant related, studies such as Pepper and Tissot's (1973) work on the Cinara found on pines of eastern North America and some of Hottes' works, such as his (1961) review of and key to the species on Picea.

Different Cinara taxonomists have favoured the use of particular characters. For example, Oestlund (1942) devised a phylogenetic scheme based partly on the frequency of occurrence of the sensoria on the antennal segments. However, in quantitatively comparing the morphology and biology of C. carolina Tissot and C. melaina Boudreaux, Fedde (1967) found that sensorial counts were unstable; in addition to varying between left and right antennae on individual specimens, sensorial counts also varied between summer generations of the same aphid species. He concluded from his study that counts of antennal sensilla should be used as descriptive supplements rather than as diagnostic characters.

Many workers have used ratios of morphological features, particularly those of the antennal segments, to designate new species (Eastop 1972). However, when analyzed quantitatively, these characters also proved to be unstable. Bodenheimer and Swirski (1957) found that lengths of antennal segments and ratios of these lengths were poor criteria for separating species of aphids due to the effects of seasonal variation and the effect of individual size variation on these characters. Fedde (1967) found that ratios did not enhance the discrimination between C. carolina and C. melaina. When ratios are employed, the relationships between the component measurements, which are used to calculate the ratios, are often obscured. It should be noted that ratios, as derived variables, have other disadvantageous properties, among them the loss of precision and the compounding of measurement errors as well as the creation of unusual statistical distributions (Atchley et al. 1976, Atchley and Anderson 1978, Pimentel 1979).

Bradley (1959, 1961) attempted to separate species based on the overall length of the rostrum. He found a significant positive relationship between the length of the rostrum and the feeding site, and hence the bark thickness. He suggested that information on the feeding site of Cinara aphids would help to separate morphologically similar species. However, in some species, the feeding sites are known to change with season, and the limits of variability of the rostrum measurement, particularly the influence of body size on this measurement are not known. In addition, no information is available on if and in what manner the individual segments of the rostrum vary and covary.

Bradley (1961) thought that subspecies are likely to exist in Cinara. However, he recognized infraspecific differences only if indicated by differences in rostrum length. A number of subspecies were erected by Hottes (1955) on the basis of differences in the length and number of setae. Each putative subspecies was described from a sample from a single locality and not compared on a geographic basis to the overall range of variation of the characters throughout each species.

It is clear that the taxonomic difficulties which have arisen in the study of North American Cinara aphids are due in large measure to the lack of critical evaluation of the taxonomic characters previously used and to the lack of any quantitative evaluation of classification schemes of Cinara species (Bradley 1961, Fedde 1965, 1967, Pepper and Tissot 1973). One of the greatest problems in evaluating the taxon designations of other workers, particularly in a morphologically variable group such as the Aphididae, is the frequent absence of statements of sample size and of measures of the variation of characters. Quantitative assessment of individual and geographic variation in morphological characters and observations of biological phenomena of potential systematic use, such as differences in feeding site preferences, are needed to discriminate between species. The grouping of Cinara species into more tractable generic and/or subgeneric categories would help to bring order into the morphological and biological diversity of this group of aphids.

3. GENERAL METHODS AND MATERIALS

3.1 Field and Laboratory Techniques

During the summers of 1979 to 1982 field trips were undertaken throughout the range of P. contorta, that is, British Columbia including Vancouver Island, western Alberta, Washington, Oregon, northern California, Idaho, Montana, and western Wyoming. Collections were made at sites containing 1 or 2 trees to sites of many acres containing hundreds of trees. Trees ranging in age from 1- to 2-years-old to maturity were examined. At the larger sites, between 75 and 100 trees were examined in order to determine accurately the number of aphid species present and the distribution of their feeding sites. All potential feeding sites were searched. Beating was employed to locate solitary and difficult-to-locate species such as C. pergandei. In many cases, colonies of the aphids were first located by the observation of ant activity on the tree. In addition, various species of Diptera and Hymenoptera are attracted to the honeydew produced by the aphids; their flight activity aided in the location of aphid colonies.

For each collection, records were made of the date, the location, the host-plant species, and the nature and position of the feeding site on the tree. If more than one possible Cinara species was found within a single colony, on a single tree, or on different trees within a single site, this was also noted. Any indications of variation in the feeding

site of a species, aphid coloration, or damage to the host plant were also recorded. In total, 529 collections of aphids were made. These collections ranged in size from a few individuals, in the case of newly alighted alate aphids with their nymphs and relatively solitary species, to colonies consisting of hundreds of individuals in the case of some stem- and canker-dwelling species.

Aphid colonies were removed from the tree along with the substrate they were feeding on (including stems and cankers) with pruning shears and placed in plastic cages covered with mesh (Mackauer and Bisdee 1965). The aphids were then removed from the plant material and stored in 70% ethanol; the aphids do not become brittle at this concentration of ethanol. As Cinara aphids are extremely fragile insects, they were handled with a small brush, in order to avoid damaging appendages.

The aphids from each collection were examined under a dissecting microscope. The adult summer apterous viviparous morph was selected as the morph to be used for all morphometric analyses as it is the most abundant morph and the one upon which the majority of the descriptions of Cinara species have been based. The adult stage can be separated from the other instars, particularly the similarly sized fourth instar, by the presence of an anal plate.

The aphids were cleared of pigments and internal tissue by boiling in a 10% potassium hydroxide solution and in chloralphenol according to the method of Hille Ris Lambers (1950) and mounted in Hoyer's medium on microscope slides. The aphids were mounted with the ventral side up to facilitate the measurement of rostral features. In some cases the dorsal

surface of the abdomen was dissected away from the remainder of the aphid in order to make observation and counting of the dorsal setae easier. Some cleared specimens were floated in glycerine to enable the observation of some structures, particularly those of the thorax, which would normally be distorted by the mounting procedure.

For all samples, 1 to 5 specimens were mounted for tentative, and, following the morphometric analyses, for final identification. Larger series of from 30 to 50 specimens were mounted from those samples selected for morphometric analysis.

All continuous characters were measured using a Leitz Oknor micrometer eyepiece[1]. The exceptions were the character body-length, which was measured with a calibrated eyepiece on a dissecting microscope, and the characters length-of-the-hind-tibia and length-of-the-second-rostral-segment, which were measured by tracing their projected image using a calibrated map measure. All setal counts were made using a compound microscope. In addition to the measurements and counts taken, notes were made on the amount, pattern, and colour of the sclerotized surfaces of the aphid and of other morphological features such as the size and shape of the mesosternal tubercle.

Additional material, including type material, of all Cinara species found on the species of Pinus under study, was obtained for comparison from the Canadian National Collection (Ottawa), the Agriculture Canada

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

Research Station (Vancouver, British Columbia), the United States National Museum (Systematic Entomology Laboratory, Beltsville, Maryland), the Frost Entomological Museum (University Park, Pennsylvania), and the University of Minnesota (St. Paul).

3.2 Statistical Methods

3.2.1 Univariate and Multivariate Morphometrics

Numerical techniques provide an objective, operational approach for the examination of data for systematic patterns. Univariate analysis of descriptive statistics can be used to compare the central tendencies and variation of samples. Statistics such as the mean and coefficient of variation allow an initial evaluation of the variables and samples under study and aid in the selection and deletion of variables in subsequent morphometric analyses. The precision and accuracy of the measurement procedure can be tested using univariate methods. For each variable measured in each population sample (Chapter 4) and each species sample (Chapter 5), the descriptive statistics which were calculated included the mean, the standard error, the standard deviation, and the coefficient of variation (Sokal and Rohlf 1981). The homogeneity and normality of the data were determined by calculating the measures of kurtosis ($\underline{g}1$) and skewness ($\underline{g}2$) (Zar 1974) and D'Agostino's $\underline{D}_A$ statistic (D'Agostino 1971).

Often the response of an organism to selective forces will manifest itself as the adaptation of a number of features to many interdependent

biological and environmental factors. Morphologically, responses may occur in a multidimensional fashion, rather than as a change in a single character. (Blackith 1960, Blackith and Reyment 1971, Gould and Johnston 1972, Sokal and Rinkel 1963). In addition, populations and/or species may overlap when characters are studied individually but they may become distinct entities when all of the characters are studied jointly. From a taxonomic point of view, classifications are based on a wide range of characters; when classifications are based on a few characters, they are often unstable and taxa boundaries may change easily with the addition of other characters (Blackith and Reyment 1971, Sneath and Sokal 1973). For these reasons, the techniques of multivariate morphometrics were used to analyze the variation and interaction of morphological variables at the population and species levels of aphids of the genus Cinara.

Morphometrics is a term for the study and the quantitative characterization of morphological form and pattern (Pimentel 1979). Multivariate, or multi-dimensional, statistical analyses involve the simultaneous analysis of more than one variable (Neff and Marcus 1980). These techniques describe and summarize patterns of variation and delineate groups of OTU's[2] that share these recognized patterns of variation. This approach is particularly useful in the study of

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2 OTU = Operational Taxonomic Unit. This is the lowest rank of taxon used in a given study (Sneath and Sokal 1973); they represent the population samples in Chapter 4 and the species samples in Chapter 5.

geographic variation where the variation and interaction of characters may be clinal in nature (Thorpe 1976). General reviews of the application of multivariate statistics to studies of biological variability are provided by Blackith and Reyment (1971), Clifford and Stephenson (1975), Oxnard (1978), Pimentel (1979), and Sneath and Sokal (1973).

3.2.2 Ordination and Cluster Analysis

When multivariate statistics are used to analyze a data set in order to determine patterns of variation from which taxonomic structure can be determined, it is best to use both of the two general morphometric approaches, namely cluster analysis of similarity measure and an ordination technique (Sneath and Sokal 1973). This strategy allows one approach to compensate for some of the disadvantages of the other. By grouping the most similar OTU's together, cluster analysis imposes a hierarchical order on the data, which may be taxonomically interpreted. Ordination techniques do not impose structure on the data and provide a more meaningful taxonomic representation in situations where the variation under study is in the form of a continuum. By using ordination techniques, such as multiple discriminant analysis and principal component analysis, one may gain a better understanding of taxonomic relationships and of the relationships between the characters that determine these patterns because trends in variability can be associated with the morphological attributes that cause them.

Cluster analysis refers to a group of methods for identifying natural groups in data, that is, for determining sets of similar entities from a previously unpartitioned set of entities (Everitt 1974, Sneath and Sokal 1973). There are many algorithms for cluster analysis but they often impose different structures upon the data due to their different computational peculiarities (Sokal 1977). The method of cluster analysis used in this study was the UPGMA (unweighted pair group using arithmetic averages) method (Sneath and Sokal 1973). When compared with other methods of cluster analysis, the UPGMA method produces a phenogram[3] with the least loss of the information present in the original matrix of OTU's (Sokal and Rohlf 1962). Sneath and Sokal (1973) provide an example of the calculation of UPGMA cluster analysis.

3.2.3 Multiple Discriminant Analysis

Multiple discriminant analysis, which includes discriminant function analysis and generalized distance analysis, is a multivariate statistical technique which combines variables in a linear fashion so as to maximize the separation of groups. Fisher (1936) originally developed the discriminant function to solve the problem of maximizing the difference between 2 groups. The method was later generalized for the analysis of situations involving many groups. Most aspects of multiple

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3 Phenogram. A diagram of phenetic relationships, i.e., those based on similarity (Sneath and Sokal 1973).

discriminant analysis are dealt with by Lachenbruch (1975), Morrison (1976), Nie et al. (1975), and Pimentel (1979). Albrecht (1980) provides an overview of the interpretation of multiple discriminant analysis.

In calculating the linear combination of the variables to produce the discriminant functions, emphasis is placed on those variables which maximize the among-groups (OTU's) variance relative to the within-group variance. As a result, the original set of variables is transformed into a set of functions, each independent of the other, of which the first discriminant function accounts for the largest amount of total, independent, variation and the second discriminant function accounts for the largest proportion of the remaining variation; this process is carried out until all of the variation among groups has been accounted for. It is often the case that most of the variation, and potential discrimination, can be obtained with less than the maximum possible number of discriminant functions.

Two kinds of variation matrices, containing measures of the amount of absolute variation within and among the variables, are manipulated in order to calculate the discriminant functions. After the variances and covariances between the variables in each group have been calculated, they are averaged over all of the groups to produce the pooled within-groups variance-covariance matrix, $\underline{W}$. The sample means are then used to calculate the among-groups variance-covariance matrix, $\underline{A}$. The following equation

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

is solved. The result is a set of roots (λ's) which are the discriminant functions. Each discriminant function is orthogonal, that is, it represents a pattern of variation which is uncorrelated with that of other discriminant functions. The discriminant functions can be expressed in the following form

$$DF_i = di_1 Z_1 + di_2 Z_2 + \cdots + di_p Z_p \qquad (2)$$

where DF_i is the score on discriminant function i, the values $di_1, \ldots, di_p$ are the discriminant function coefficients and the values $Z_1, \ldots, Z_p$ are the standardized values of the original p discriminating variables. The discriminant function coefficients are weighted according to the variance structure of the original p variables. They are calculated so that differences between the group means are maximized, that is, the independent variables with large discriminating power have large weights. The mathematical derivation of these coefficients is described in detail in Cooley and Lohnes (1971) and in Seal (1964).

Each discriminant function can be interpreted as an axis in geometric space and all of the samples involved in the analysis can be positioned along each discriminant axis (ordination). These mean discriminant scores for each sample on the discriminant functions are the sample centroids. The centroids can be plotted on any pair of axes and examined for systematic trends; usually only those positions on the axes accounting for the major trends in variation are of interest.

Each discriminant axis has an eigenvalue associated with it which is the variance of the sample means on that discriminant axis. A measure of the total variance in the p discriminating variables is provided by the sum of the eigenvalues. Therefore, a measure of the relative discriminatory ability and the amount of variability accounted for by each discriminant function is given when each eigenvalue is expressed as a percentage of the sum of the eigenvalues. The discriminant function coefficients can be standardized by scaling each coefficient for an independent variable by multiplying it by the pooled standard deviation of that variable. The standardized discriminant function coefficients can then be used as a measure of the importance of each variable to a particular discriminant function. Irrespective of sign, the magnitude of the standardized coefficient indicates the contribution of a particular variable to discrimination among groups along each axis.

Single specimens can be allocated into a number of a priori groups on an objective basis by using discriminant functions in order to provide a quantitative check on the discriminatory power of particular sets of variables. This is carried out by computing a set of separate identity functions for each a priori group. Probabilities of membership in each group are determined from the function scores; an individual specimen is allocated into the group with which it shares the highest probability, that is, the group with the closest sample centroid in multivariate space. As the actual group membership of each specimen to be allocated is known beforehand, this can be compared with the results of the above procedure and summarized in the form of an identification table.

When the allocation procedure is based on the use of specimens that were also used in the calculation of the identity functions of the *a priori* groups there is an upward bias in the calculated percentage of correct allocations. The degree of bias is determined by the number of variables, the number of samples, and the sample sizes of the groups. The amount of bias can be checked by allocation of a number of specimens which were not used to calculate the identity functions of the groups (Frank *et al*. 1965, Morrison 1969). If the amount of bias is not too great, allocation procedures provide a means of characterizing the extent of phenetic overlap between groups (Foottit 1979).

3.2.4 The Mahalanobis Distance

The Mahalanobis Generalized Distance (D^2 statistic) (Mahalanobis 1936) can be derived from the discriminant functions and be used as a measure of statistical distance and phenetic dissimilarity between any 2 groups. As D^2 is based on the discriminant function it eliminates the effect of correlation between characters and allows the use of that discriminatory information which is unique to a given character (Blackith and Reyment 1971). In a study of the properties of a number of different types of distance functions, Atchley *et al*. (1982) found that the D^2 statistic was the best at describing the actual level of differentiation between groups, particularly if correlated characters were involved. While ordination of sample centroids will often show systematic patterns, not all of the significant variation is usually accounted for in any one

projection on two or three axes. The $\underline{D}^2$ statistic provides an estimate of phenetic dissimilarity which uses all of the discriminatory information in the variables.

The $\underline{D}^2$ statistic is calculated for all pairwise comparisons between all of the samples under study. This is done by multiplying the vector of discriminant function coefficients of the discriminant function calculated for any pair of samples by the vector of the difference between the means of the discriminatory variables for that pair of samples. As the value of $\underline{D}^2$ gets larger, it indicates that a given pair of samples is phenetically more and more dissimilar; a $\underline{D}^2$ value of zero would indicate that a pair of samples is identical. The square root of $\underline{D}^2$, or $\underline{D}$, can be used as a measure of taxonomic distance in Euclidean space; a matrix of $\underline{D}$ values can therefore be subjected to cluster analysis, the results of which can be represented in the form of a phenogram. Matrices of $\underline{D}$ values often are too large to be accurately inspected for taxonomic structure. Cluster analysis will order the OTU's into a hierarchical form that can be interpreted taxonomically.

3.2.5 Principal Component Analysis

While multiple discriminant analysis maximizes the distinction between *a priori* groups, principal component analysis is used to find relationships among variables and among individuals in a sample assuming no *a priori* division of the OTU's into separate groups. Principal component analysis does not incorporate any analysis of within-groups

variation to weight the separation of OTU's; it is used as a dimension-reducing technique to summarize trends in data. Jeffers (1964) provides a review of the stages involved in conducting a principal component analysis. Isebrands and Crow (1975) provide a useful review of the uses and interpretation of principal components.

Principal component analysis transforms the original variables into a set of composite variables, each of which is uncorrelated with the others. Each linear transformation is of the form

$$\begin{aligned} Z_1 &= a_1x_1 + b_1x_2 + c_1x_3 + \ldots r_1x_n \\ Z_2 &= a_2x_1 + b_2x_2 + c_2x_3 + \ldots r_2x_n \\ &\vdots \quad\quad \vdots \quad\quad \vdots \quad\quad \vdots \quad\quad \vdots \\ Z_n &= a_nx_1 + b_nx_2 + c_nx_3 + \ldots r_nx_n \end{aligned} \qquad (3)$$

where the coefficients a_1, b_1, c_1, . . ., r_1, are chosen so that the first transformation (principal component), Z_1, has as large a variance as possible. The second set of coefficients a_2, b_2, c_2, . . ., r_2, is chosen to produce the second component, which is uncorrelated with the first, and which has as large a variance as possible. This is continued until all of the variation is accounted for. Often, the data set will be reduced to a few components which account for the major, independent, patterns of variation and which produce the greatest differentiation among the OTU's in the data set (Seal 1964). In addition to providing information on the correlation of characters, principal component analysis provides axes of variation along which the ordination of OTU's can be carried out.

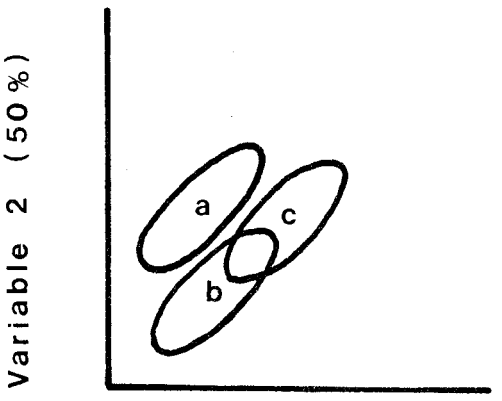
A hypothetical example is shown in Figure 5 to illustrate graphically the difference between principal component analysis and discriminant function analysis. In Figure 5-a, three groups (a, b, c) are measured for two variables (1, 2); the centroid of each group is indicated by the letters a, b, and c. Approximately 50% of the variation is accounted for on each axis. The ellipses encompass the positions of the individual specimens in each group with respect to the variables measured.

As a variance-maximizing technique, principal component analysis (Figure 5-b) can be seen as a rotation of the original axes system so that principal axis I takes up a maximum amount of the variation in the data. Then rotation around this fixed axis is carried out to produce the second principal axis. This procedure would be carried out further to produce more axes if more variables were involved. Multiple discriminant analysis also performs a variance-maximizing rotation where it rotates the original coordinate axes so that they become parallel with the major axes of within-groups dispersion (Figure 5-c). Then it adjusts for the effect of within-group variability in the characters by scaling the distances between groups with a value equal to one standard deviation of the within-groups variation. This has the effect of changing the distances between group centroids. The last step is to perform another variance-maximizing rotation along the major axes of between-groups dispersion (Figure 5-d). When the original measurements are plotted (Figure 5-a), it is obvious from the overlap of the ellipses that groups b and c are more similar to each other than to group a but that the

Figure 5. Graphical representation of the analysis of a hypothetical data set by principal component analysis and discriminant analysis. The percentages refer to the amount of variation in the data which is represented by an axis of discrimination. See text for details. After Albrecht (1976, 1980).

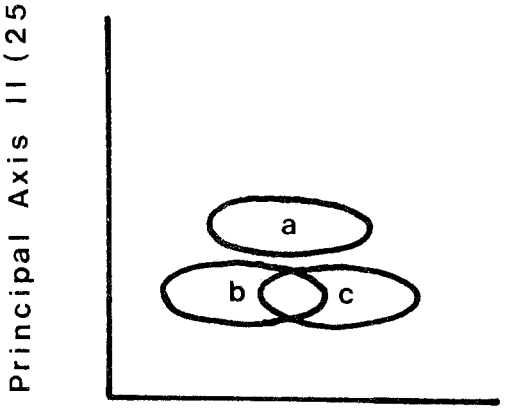
A

ORIGINAL DATA



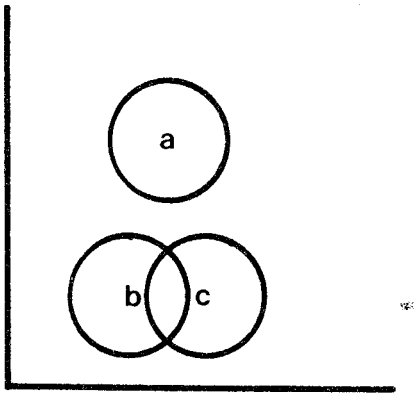
B

PRINCIPAL COMPONENTS ANALYSIS



C

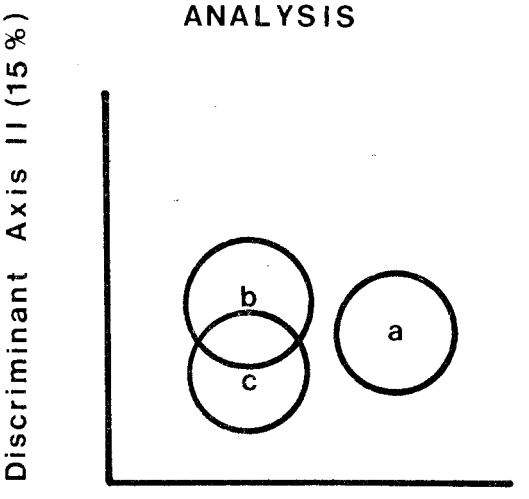
DISCRIMINANT ANALYSIS



Rotation To Maximize Between-Group Variation ⟹

D

DISCRIMINANT ANALYSIS



centroids of groups b and c are further from each other than each is from group a. With standardization of the within-groups dispersions, groups b and c are brought closer together and group a is now further away from them; in other words, between-group differences have been maximized. In a final step in discriminant function analysis, the rescaled, standardized axes are rotated so as to be parallel with the major and minor axes of between-groups dispersion (Figure 5-d).

Multivariate statistical techniques assume that the samples undergoing analysis have a multivariate normal distribution and that the variance-covariance matrices of the a priori groups are equal. Both assumptions are difficult to achieve with biological material. However, departures from normality by any single character will not invalidate these techniques (Pimentel 1979), in fact these techniques are robust and tend to minimize irregularities due to violations of the above assumptions (Blackith and Reyment 1971, Lachenbruch 1975). In addition, multivariate normality only becomes important if statistical tests are to be made (Pimentel 1981). For these reasons, I did not carry out any transformations of the data.

All statistical analyses for this project were carried out on Simon Fraser University's IBM 4341 computer. The Statistical Package for the Social Sciences (SPSS) (Nie et al. 1975) was used for computing the descriptive statistics and for all aspects of multiple discriminant analysis with the exception of the calculation of the Mahalanobis Generalized Distances which were computed using a program written by J.

A. Ludwig of New Mexico State University (Zimmerman and Ludwig 1974). All principal component analyses, cluster analyses, and the development of phenograms were carried out with the NT-SYS system of multivariate statistical programs for numerical taxonomic studies (Rohlf et al. 1971).

4. MORPHOMETRIC VARIATION WITHIN ONE SPECIES: CINARA NIGRA (WILSON).

4.1 Introduction

This chapter is concerned with the analysis and description of variation and covariation of morphological characters within and between samples of a single species of Cinara. By examining the morphometric characteristics of a large set of variables from different body areas of a single species it was hoped that a tractable set of characters that included a maximum amount of information content and hence, discriminatory ability, for the subsequent analysis of species differences could be identified.

No quantitative analysis of morphological character variation has been carried out for the genus Cinara. As was discussed in Chapter 1, this genus is considered to be taxonomically difficult; particularly in North America, there are a large number of Cinara species which are morphologically similar though their biology is known to differ (Fedde 1965). Many of the taxonomic characters previously used to separate species are likely to be influenced by size variation. In addition, most species of Cinara are extremely hirsute, making the choice of and measurement of setal characters operationally difficult. By the simultaneous examination of potential characters from more than one functional and/or operational character group and by the reduction of highly correlated characters it was hoped that stable taxonomic patterns, little influenced by the choice of character, would result.

As was mentioned previously, techniques of morphometric analysis were selected for the study of morphological character variation. A number of morphometric studies have been carried out on geographic samples of aphids. However, most of these works (Sokal et al. 1980, Sokal and Riska 1981; Wool 1977, Wool and Manheim 1983) have centered on the analysis of variation in aphid systems where galls are produced. As a result, some partitioning of the genetic and environmental components of morphological variation is obtained. However, many aphid taxa do not fall into this category and, in fact, some taxa are totally parthenogenetic. My interest was to use morphometrics as an exploratory tool in aphid taxonomy, that is, to describe and quantify the morphological variation in field collections of aphids, to search for taxonomic characters, and to quantify the degree to which these characters could discriminate between species in the face of the many factors which influence the morphology of aphids.

Preliminary examination of the material collected during this study indicated the presence of several morphologically distinct groups. However, many of the preliminary groupings of samples into putative species groups showed considerable morphological variability, even in gross morphological characters such as the pigmentation patterns on the dorsum of the abdomen; this situation made it difficult to determine the limits of species boundaries. For this initial characterization of within-species variation a morphologically distinct species of Cinara, the identity of which was not in doubt, was required in order that samples of other, subsequently determined species, were not included in the initial analysis of variation.

I chose Cinara nigra (Wilson) for this analysis because it has a distinctive, large sclerotized patch on the dorsal surface of the abdomen (Figure 35). No other Cinara species found on pine in western North America has this character. C. nigra is found in relatively large colonies consisting of hundreds of individuals located on the main stem of five- to ten-year-old Pinus contorta (Figure 3.). Occasionally, colonies were also found on the underside of side branches. As a result, there usually were enough adult apterous specimens available from each sample to meet the sample size requirements of the morphometric analyses.

C. nigra is interesting in that it belongs to a group of four species (including C. canatra Hottes and Bradley, C. gracilis (Wilson) and C. russellae Pepper and Tissot found in North America; these four species are morphologically similar in shape and in the presence of the above-mentioned dorsal pigmentation pattern in the apterous viviparae and the oviparae. C. gracilis and C. russellae are readily separated from C. canatra and C. nigra on the basis of differences in the number of setae on certain structures. C. canatra resembles C. nigra but can be separated from it on the basis of its more extensive pigmentation pattern and lower number of setae on most appendages (Pepper and Tissot 1973). Although Bradley (1961) states that the distribution of C. canatra extends into British Columbia, I was not able to locate it during the course of this study. Until this study was carried out, C. nigra was thought to be confined to Pinus banksiana Lamb. in Wisconsin and Michigan (Pepper and Tissot 1973). Identification of C. nigra was confirmed by comparison of my material with Wilson's type material in the University of Minnesota collection (see also Cook 1982).

4.2 Character Selection: Variation Within One Sample

A sample collected 20 km west of Edson, Alberta, on August 11, 1980, was chosen for the analysis of character variation and covariation within a single sample. Twenty adult virginoparae were used to gather measurement data. Based on the characters used by Bradley (1961), Eastop (1972), Voegtlin (1976) and on my own work (Foottit 1979), a series of continuous measurements was taken in order to estimate differences in size and shape. In addition, the number of setae on certain structures were counted in an attempt to sample other components of variation, which were independent of size and shape. Although, from my previous work (Foottit 1979, Foottit and Mackauer 1980), it was found that some width measurements varied due to distortion from the slide-mounting procedure, these data were included in the initial analyses. In general, characters were selected which could be measured precisely within a reasonable amount of time and with a reasonable amount of effort. Continuous characters were chosen so they would sample size and shape variation over as large a portion of the aphid body as possible.

The 52 continuous variables and setal counts which were chosen initially are listed in Table I. The operational dimensions or locations of most of the continuous measurements and counts on the aphid body are shown in Figure 6. Some of the variables are discussed below.

The body width was not measured across the abdomen as this dimension is influenced greatly by the amount of pressure applied to the

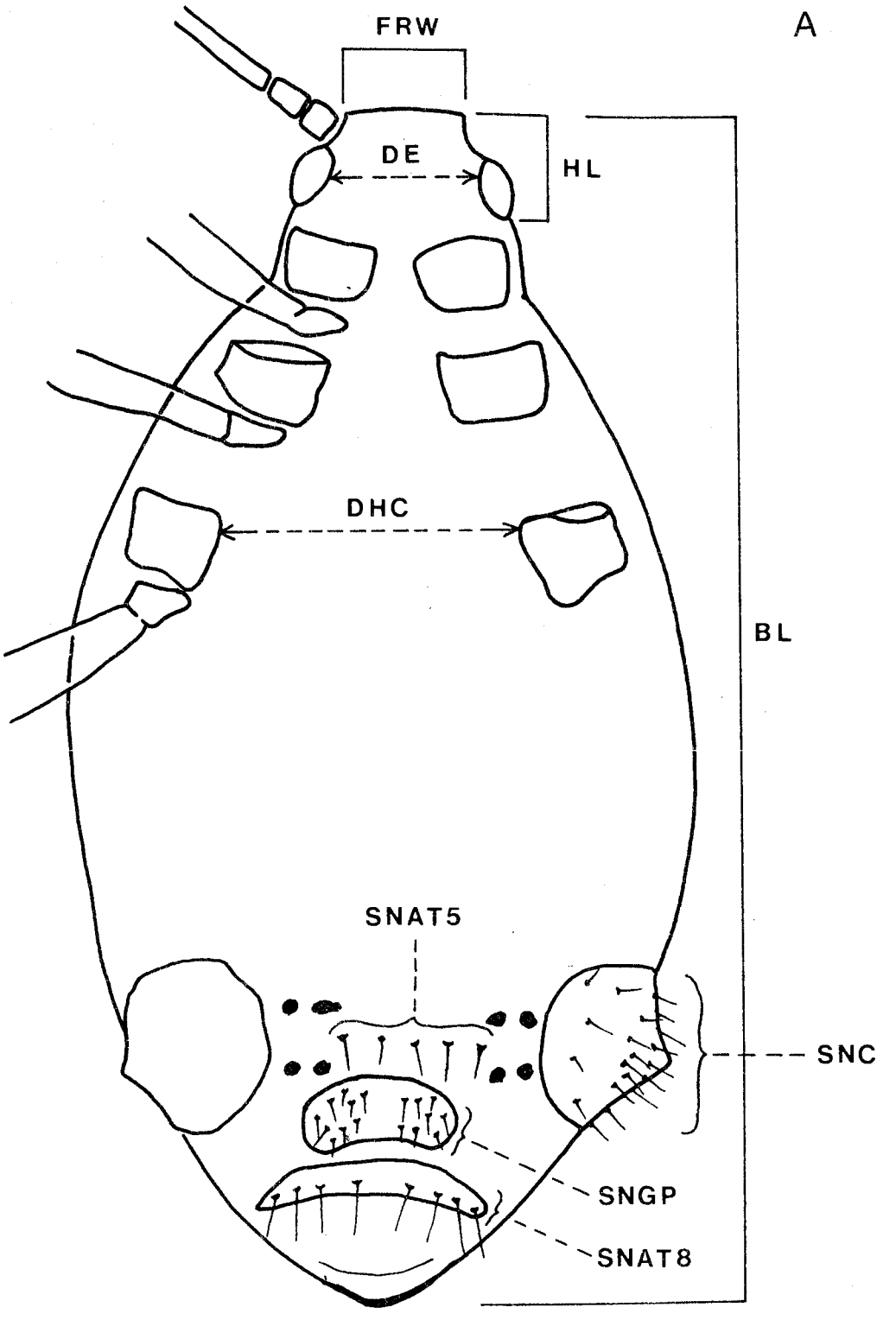
Table I. Continuous variables and setal counts for the adult apterous viviparous morph of *Cinara nigra*.

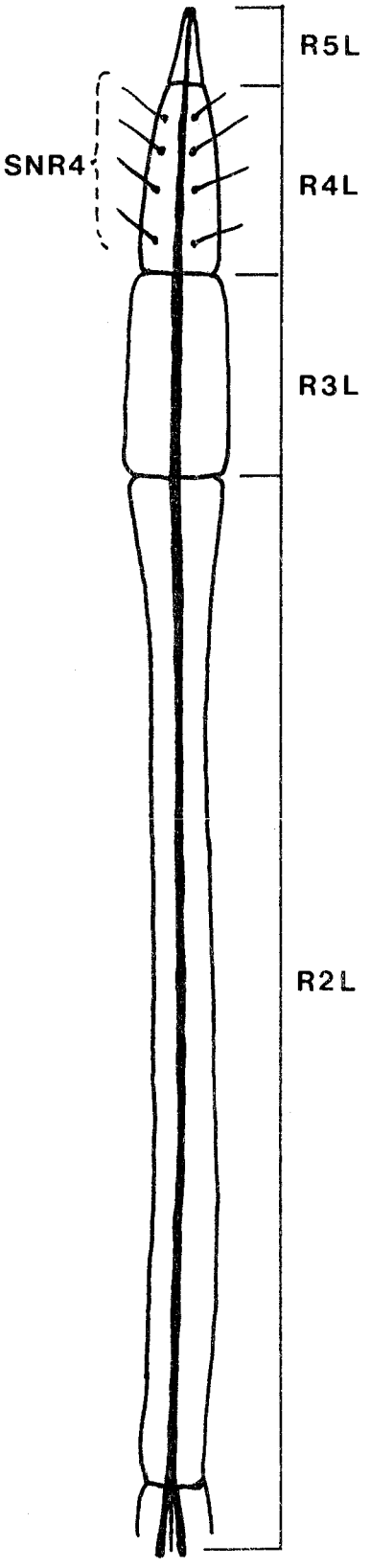
Variable Name	Abbreviation	Variable Name
1	BL	Body length
2	DE	Distance between eyes
3	DHC	Distance between hind coxae
4	FRW	Frons width
5	HL	Head length
6	A1L	Antennal segment I, length
7	A1W	Antennal segment I, width
8	A2L	Antennal segment II, length
9	A2W	Antennal segment II, width
10	A3L	Antennal segment III, length
11	A3W	Antennal segment III, width
12	A4L	Antennal segment IV, length
13	A4W	Antennal segment IV, width
14	A5L	Antennal segment V, length
15	A5W	Antennal segment V, width
16	A6BL	Antennal segment VI, base, length
17	A6BW	Antennal segment VI, base, width
18	A6PTL	Antennal segment VI, proc. term., length
19	R5L	Rostrum segment V, length
20	R4L	Rostrum segment IV, length
21	R3L	Rostrum segment III, length
22	R2L	Rostrum segment II, length
23	CL	Hind leg, coxa, length
24	CW	Hind leg, coxa, width
25	FL	Hind leg, femur, length
26	FW	Hind leg, femur, width
27	TL	Hind leg, tibia, length
28	TW	Hind leg, tibia, width
29	TS1W	Hind leg, tarsus segment I, width
30	TS1VL	Hind leg, tarsus segment I, ventral length
31	TS1DL	Hind leg, tarsus segment I, dorsal length
32	TS2L	Hind leg, tarsus segment II, length
33	TS2W	Hind leg, tarsus segment II, width
34	SLH	Setal length, head
35	SLA3	Setal length, antennal segment III
36	SLT	Setal length, hind leg, tibia
37	SLTS2	Setal length, hind leg, tarsus segment II
38	SLCO	Setal length, cornicle
39	SLCA	Setal length, cauda
40	SLGP	Setal length, genital plate

Table I. cont'd

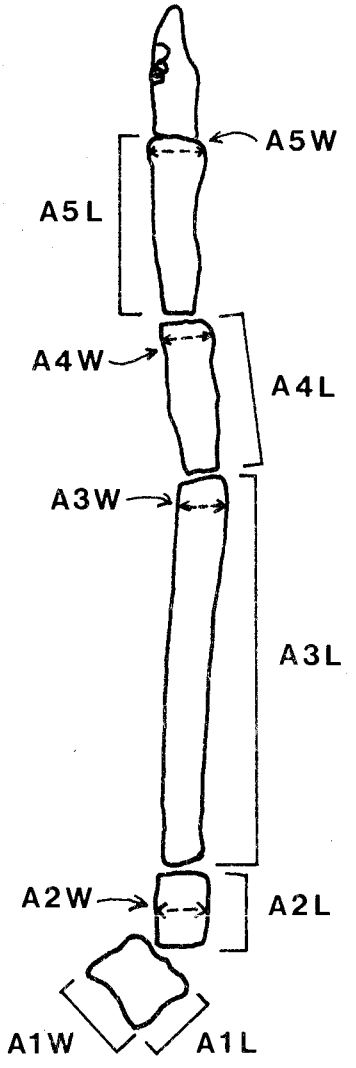
Variable	Abbreviation	Variable Name
41	SLAT8	Setal length, abdominal tergite VIII
42	SLAT5	Setal length, abdominal tergite V
43	SNA6SA	Setal number, antennal segment VI, subapical setae
44	SNA6B	Setal number, antennal segment VI, base
45	SNA5	Setal number, antennal segment V
46	SNA2	Setal number, antennal segment II
47	SNR4	Setal number, rostrum segment IV, accessory setae
48	SNGP	Setal number, genital plate
49	SNAT5	Setal number, abdominal tergite V
50	SNAT8	Setal number, abdominal tergite VIII
51	SNC	Setal number, cornicle
52	SNT	Setal number, 0.2 mm of hind tibia

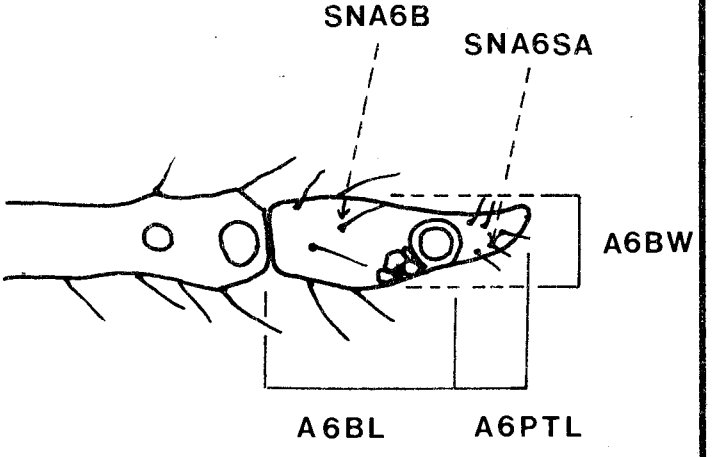
Figure 6. Operational dimensions of continuous variables measured and location of the setal counts on Cinara nigra. Abbreviations of the variables are as indicated in Table I. Additional structures are named where setal length measurements and setal counts were taken. See text for additional information on the locations of and procedures for measurement. a) ventral projection, b) rostrum and antennal dimensions, c) hind-leg dimensions.

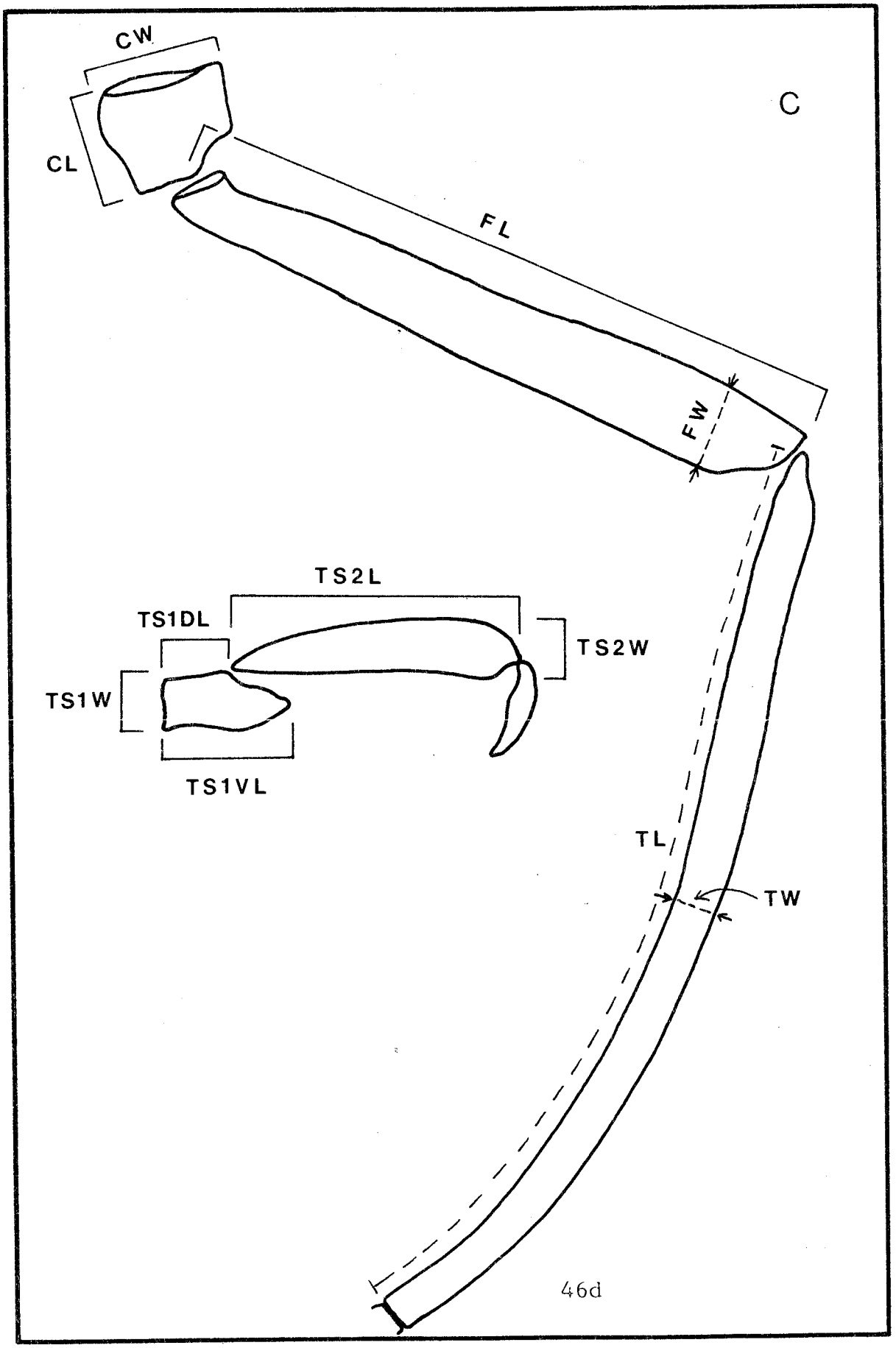

A
FRW
DE
HL
DHC
BL
SNAT5
SNC
SNGP
SNAT8


R5L
SNR4
R4L
R3L
R2L

B


A5W
A5L
A4W
A4L
A3W
A3L
A2W
A2L
A1W
A1L


SNA6B
SNA6SA
A6BW
A6BL
A6PTL


C
CW
CL
FL
FW
TS2L
TS1DL
TS2W
TS1W
TS1VL
TL
TW

cover slip during mounting. Tibia length (TL) was measured by tracing along the curve of the appendage, rather than in a straight line from distal end to proximal end. It was felt that the former gave a more accurate representation of the true length variation of this appendage as it was not influenced by the degree to which the tibia was curved or positioned by the mounting procedure.

The exact termination of the membranous base of the first segment of the rostrum is difficult to determine and thus was not included in the measurement of the rostrum by other workers (Bradley 1961, Voegtlin 1976). For this reason, I measured only segments II, III, IV and V. The second segment of the rostrum telescopes within the first segment of the rostrum. The result is that the apical end of the first segment is turned inward forming a tube that partly covers the second segment (Hottes 1954). Therefore, for added accuracy, the complete stylet groove was measured as an indicator of the length of the second segment, even though the stylet groove appears to be included in part of the first segment.

The count of the number of accessory setae on rostrum segment IV (SNR4) includes all of the setae along each side of the stylet groove but not the setae on the distal margin of the segment. The number of setae on abdominal tergite V (SNAT5) includes all setae between the cornicles and between the anterior and posterior muscle attachment plates on that tergite. The number of setae on 0.2 mm of the hind tibia (SNT) was taken by focusing the microscope in and out of the dorsal and ventral projection of the mid-section of the tibia and by counting all setae

within a 0.2 mm section as delimited by the scale on the micrometer eyepiece. The length of the setae on the hind tibia (SLT) was taken on the dorsal surface of the mid-section of the tibia; this procedure has been used by other workers (Voegtlin 1976). The setae counted and measured on the eighth abdominal tergite (SNAT8, SLAT8) were those found within the dark, sclerotized patch on that sclerite.

The precision of measurement of each variable was checked by measuring one specimen 10 times for all variables. The test specimen was measured at intervals among the other 19 specimens. In cases where a variable was measured on an appendage that was present on both the left and the right side of the aphid body, this variable was measured on both sides. These bilaterally measurable variables were also subjected to a check of precision of measurement.

Descriptive statistics were first calculated for all precision measurements of each variable ($n = 10$). The coefficient of variation was low, ranging between 0.0 and 3.5, in all variables with the exception of the length of antennal segment I (AlL) ($V = 9.6$). Variable AlL varied among specimens in the way it was orientated; this made it difficult to determine precisely the reference points for measurement and resulted in a high coefficient of variation.

No significant differences were found between measurements or counts taken on the left and on the right side of the aphid body when the data were compared by paired t-tests ($p \leq 0.01$) (Sokal and Rohlf 1981). Therefore, in all further work, measurements were taken only on the right side of the ventral projection of the aphid.

Descriptive statistics were then calculated for all remaining measurements and counts (n = 20, 52 variables). Nine of the variables had non-normal distributions as determined by D'Agostino's $\underline{D}_A (p \leq 0.1)$ (D'Agostino 1971). In the case of the number of sub-apical setae on the sixth antennal segment, this non-normality was the result of the almost invariate nature of this count in this sample. The other cases of non-normality were distributed throughout the character set and were not associated with any particular functional group of variables, such as measurements of the hind leg or of the antennae. Summary statistics for the 49 variables which were subsequently retained after the analysis of this first sample are given in Appendix 2 (Sample No. 11).

The coefficient of variation (V) can be used as a measure of the relative amounts of variation in population samples, as it is independent of the unit of measurement and of the magnitude of the sample means (Sokal and Rohlf 1981). In this sample the coefficient of variation ranged considerably (3.1 - 22.8) over the variables that were measured. The values of V for the continuous measurements were consistently low: body size measurements, 4.0 - 9.3; antennal segment measurements, 4.2 - 8.9; rostrum segment measurements, 3.1 - 3.3; and hind leg measurements, 3.4 - 9.3. The range of values of V for the setal length measurements was larger than that of the continuous measurements. However, with the exception of the high value for variable SLAT5 (22.8), the setal length measurements showed a relatively narrow range of values (9.5 - 13.3). The setal counts were often highly variable as shown by the values of V; they showed a relatively wide range of values (8.1 - 17.9) for this measure of variability.

Correlation coefficients between the 52 variables were calculated (Table II). Examination of the correlations of the variables within functional groups showed that some trends were apparent:

a). Body size measurements. All measurements, except the distance between the eyes (DE), were correlated with the body length (BL).

b). Rostrum measurements. Individual segments of the rostrum differed in their covariation among themselves and with the overall size of the aphid. The lengths of the third (R4) and fourth (R4) rostrum segments were highly correlated with size while R5 and R2 were only slightly correlated with body size. Previous workers (Bradley 1961, Voegtlin 1976) have not included the first segment in the measurement of the rostrum and have used a total measurement. Based on this analysis, it would appear that important information is lost by combining the rostrum segments into one measurement.

c). Antennal measurements. Antennal segments II, III, IV, and V were highly, positively correlated with overall size as indicated by the body length measurement. These segments also showed a strong positive correlation among themselves in many cases. This may be a reflection of the development of the antennal segments in aphids; these are the segments which differentiate last during the development of the aphid (Sokal 1952). Antennal segment VI was not strongly correlated with general size nor with most other antennal segment measurements. It is for this reason that this character has proven useful in taxonomic discrimination of aphid species (Eastop 1972).

Table II. Correlation coefficients between 52 variables calculated from a sample of 20 specimens of Cinara nigra collected 20 km west of Edson, Alberta, 9 August 1980. See Table I for abbreviations of variable names. Significant values are underlined (Critical value = .444 (p = .05)).

(a). Body Size Measurements

Variable

	BL	DE	DHC	FRW	HL
BL	1.00				
DE	0.21	1.00			
DHC	0.70	0.24	1.00		
FRW	0.50	0.58	0.56	1.00	
HL	0.47	0.32	0.14	0.33	1.00

(b). Rostrum Measurements

Variable

	R5L	R4L	R3L	R2L	Body Length
R5L	1.00				0.22
R4L	0.68	1.00			0.50
R3L	0.04	0.33	1.00		0.59
R2L	-0.22	-0.22	0.51	1.00	0.18

Table II - (c). Antennal Measurements

Variable	A1L	A1W	A2L	A2W	A3L	A3W	A4L	A4W	A5L	A5W	A6BL	A6BW	A6PTL	Body Length
A1L	1.00													0.38
A1W	0.54	1.00												0.24
A2L	-0.03	-0.11	1.00											0.49
A2W	0.28	0.29	0.74	1.00										0.66
A3L	0.26	0.16	0.56	0.66	1.00									0.73
A3W	0.52	0.09	0.54	0.39	0.49	1.00								0.46
A4L	0.18	0.10	0.54	0.55	0.70	0.38	1.00							0.55
A4W	0.39	0.42	0.48	0.60	0.46	0.58	0.72	1.00						0.61
A5L	0.19	0.15	0.60	0.65	0.64	0.42	0.84	0.74	1.00					0.62
A5W	0.34	0.22	0.43	0.33	0.42	0.72	0.14	0.34	0.15	1.00				0.28
A6BL	0.05	0.18	0.28	0.26	0.31	0.13	0.08	0.09	0.34	0.05	1.00			0.26
A6BW	0.06	0.03	0.27	0.14	0.14	0.40	-0.30	0.12	-0.11	0.61	-0.12	1.00		0.01
A6PTL	0.36	0.22	0.34	0.20	0.15	0.46	0.42	0.57	0.33	0.15	-0.08	0.32	1.00	0.28

Table II - (d). Hind Leg Measurements

Variable	CL	CW	FL	FW	TL	TW	TS1W	TS1VL	TS1DL	TS2L	TS2W	Body Length
CL	1.00											0.74
CW	0.83	1.00										0.79
FL	0.88	0.80	1.00									0.82
FW	0.47	0.62	0.58	1.00								0.60
TL	0.85	0.73	0.95	0.60	1.00							0.75
TW	0.40	0.45	0.63	0.69	0.66	1.00						0.52
TS1W	0.45	0.42	0.49	0.22	0.52	0.25	1.00					0.63
TS1VL	0.56	0.39	0.69	0.37	0.62	0.47	0.53	1.00				0.58
TS1DL	0.66	0.72	0.65	0.59	0.63	0.67	0.35	0.39	1.00			0.67
TS2L	0.60	0.51	0.64	0.36	0.69	0.41	0.75	0.59	0.42	1.00		0.72
TS2W	0.16	0.27	0.42	0.52	0.41	0.50	0.15	0.52	0.50	0.15	1.00	0.39

Table II - (e). Setal Length Measurements

Variable	SLH	SLA2	SLT	SLTS2	SLCO	SLCA	SLGP	SLAT8	SLAT5	Body Length
SLH	1.00									-0.15
SLA3	0.46	1.00								-0.17
SLT	0.45	0.40	1.00							-0.10
SLTS2	0.39	0.38	0.47	1.00						-0.46
SLCO	0.11	0.15	-0.10	0.22	1.00					-0.26
SLCA	0.32	0.49	0.26	0.04	0.42	1.00				0.17
SLGP	0.34	0.41	0.35	0.55	-0.23	0.05	1.00			0.01
SLAT8	0.51	0.76	0.33	0.38	0.45	0.62	0.36	1.00		-0.20
SLAT5	0.24	-0.18	-0.20	0.08	0.54	0.08	-0.26	0.14	1.00	-0.21

Table II - (f). Setal Counts

Variable	SNA6SA	SNA6B	SNA5	SNA2	SNR4	SNGP	SNAT5	SNAT8	SNC	SNT	Body Length
SNA6SA	1.00										-0.17
SNA6B	0.26	1.00									0.08
SNA5	-0.28	-0.20	1.00								-0.27
SNA2	-0.06	-0.04	0.04	1.00							-0.14
SNR4	-0.01	0.29	-0.18	0.49	1.00						-0.12
SNGP	0.06	0.05	-0.23	-0.04	-0.09	1.00					0.63
SNAT5	-0.20	-0.32	-0.20	0.18	0.36	0.39	1.00				0.24
SNAT8	-0.24	0.05	0.00	-0.04	-0.04	0.47	0.32	1.00			0.26
SNC	-0.05	-0.42	0.36	0.04	-0.39	0.27	0.03	0.32	1.00		-0.01
SNT	-0.14	-0.10	0.17	0.27	0.21	0.08	0.07	0.34	0.10	1.00	-0.16

d). Hind leg measurements. With the exception of the width of the second tarsal segment (TS2W), all hind leg dimensions were highly correlated with overall size and showed a great deal of internal positive correlation as well.

e). Setal length measurements. No consistent internal pattern or relationship with overall size was apparent except that many setal lengths were slightly negatively correlated with size in this sample. No trends of internal correlation were apparent. There was a low level of internal correlation; over 70% of the correlation coefficients were non-significant ($p = 0.05$).

f). Setal counts. Most counts of setae showed little correlation among each other and little correlation with size, indicating that they represent independent components of variation. The exception is the count of the number of setae on the genital plate (SNGP) which showed a significant, positive correlation with body length indicating that this sclerotized region is itself influenced by overall size.

The product-moment correlation matrix of all variables was subjected to a principal components analysis. The scores, or contributions of the variables (see Chapter 3), on the first three principal components, which account for 48.7% of the total variation in the data, are shown in Table III. Examination of the scores of the variables and of the projections of the individual specimens onto the major principal axes, that is, axes I x II, I x III, and II x III, (Figure 7) , revealed some general trends in the data.

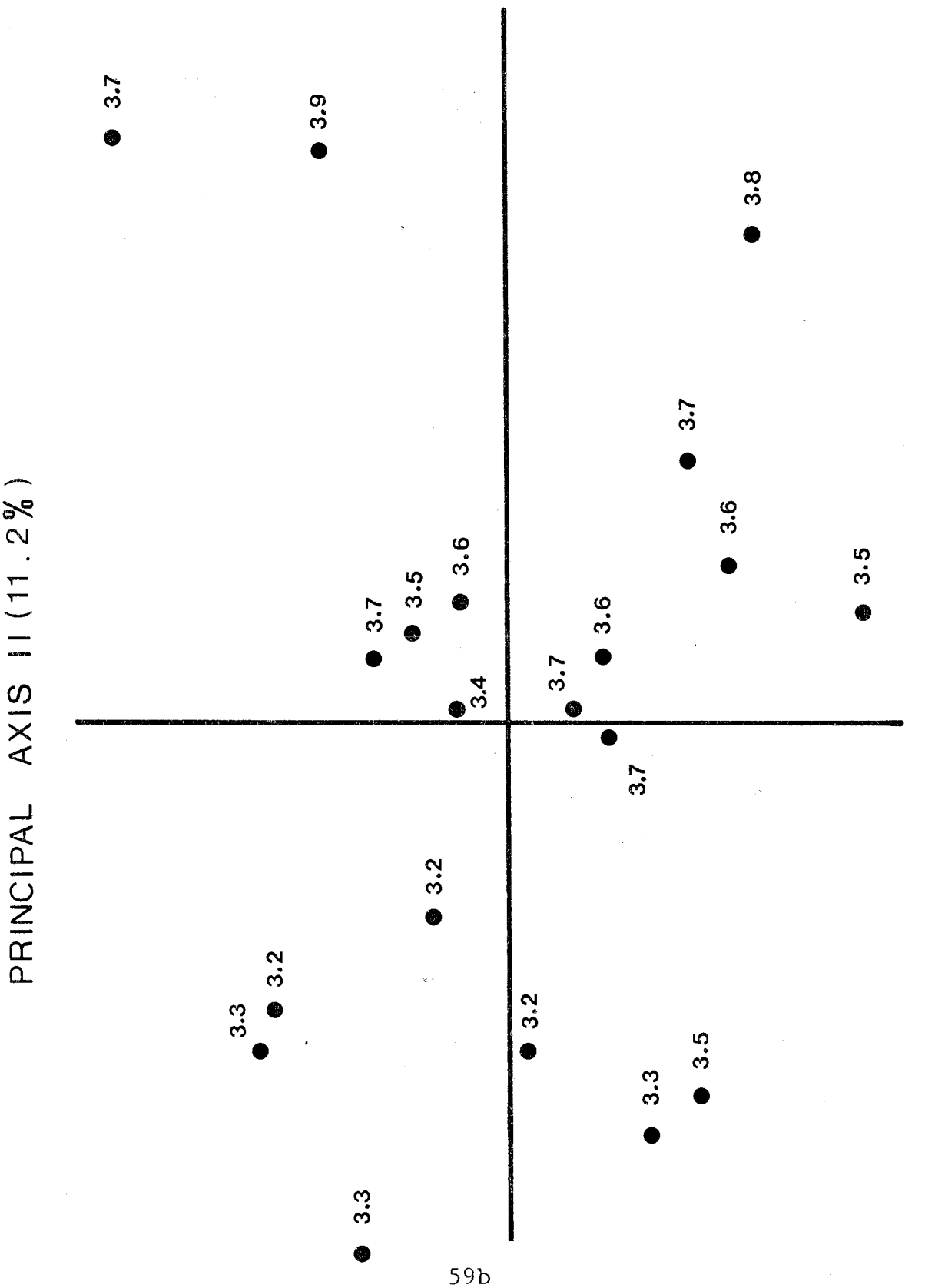
Table III. Contributions of 52 variables to the first three principal components calculated from 20 specimens of Cinara nigra collected at a site 20 km west of Edson, Alberta, 11 August 1980. See Table I for full names of variables.

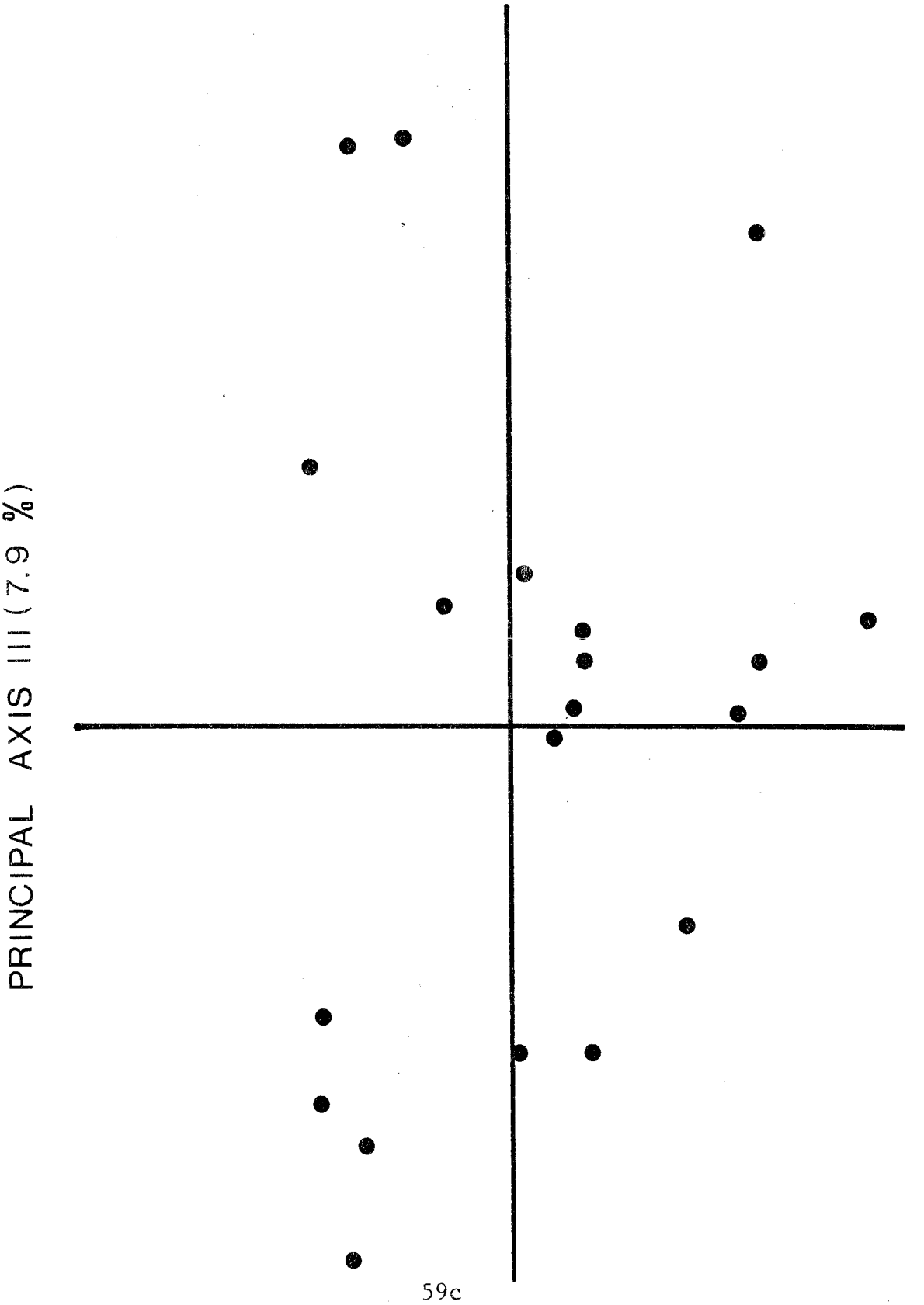
	VARIABLE	PRINCIPAL COMPONENT		
		I	II	III
1.	BL	0.849	-0.217	0.132
2.	DE	0.381	0.372	-0.322
3.	DHC	0.675	0.143	0.003
4.	FRW	0.721	0.384	-0.010
5.	HL	0.481	-0.214	0.320
6.	A1L	0.438	-0.078	-0.452
7.	A1W	0.231	-0.148	-0.263
8.	A2L	0.719	0.380	0.013
9.	A2W	0.832	-0.164	-0.096
10.	A3L	0.841	-0.081	0.088
11.	A3W	0.632	0.305	-0.382
12.	A4L	0.719	0.128	0.325
13.	A4W	0.716	0.020	0.030
14.	A5L	0.790	0.033	0.350
15.	A5W	0.513	0.301	-0.571
16.	A6BL	0.264	-0.108	0.199
17.	A6BW	0.217	0.369	-0.350
18.	A6PTL	0.364	0.565	0.002
19.	R5L	0.305	-0.310	0.511
20.	R4L	0.619	0.040	0.436
21.	R3L	0.697	0.034	-0.258
22.	R2L	0.345	-0.009	-0.445
23.	CL	0.791	-0.198	-0.012
24.	CW	0.824	-0.192	0.002
25.	FL	0.900	-0.185	-0.051
26.	FW	0.718	-0.231	-0.197
27.	TL	0.892	-0.162	0.062
28.	TW	0.629	-0.312	-0.179
29.	TS1W	0.510	-0.283	0.260
30.	TS1VL	0.592	-0.354	-0.069
31.	TS1DL	0.690	-0.378	0.045
32.	TS2L	0.660	-0.177	0.111
33.	TS2W	0.515	-0.182	-0.010
34.	SLH	-0.243	-0.736	-0.101
35.	SLA3	-0.369	-0.694	-0.133

Table III. cont'd

	VARIABLE	PRINCIPAL COMPONENT I	II	III
36.	SLT	-0.141	-0.487	-0.098
37.	SLTS2	-0.609	-0.325	0.111
38.	SLCO	-0.235	-0.085	-0.335
39.	SLCA	0.047	-0.653	-0.488
40.	SLGP	-0.217	-0.582	0.501
41.	SLAT8	-0.418	-0.685	-0.221
42.	SLAT5	-0.127	0.093	-0.328
43.	SNA6SA	-0.204	0.242	0.169
44.	SNA6B	-0.096	-0.247	0.127
45.	SNA5	-0.042	0.299	-0.380
46.	SNA2	-0.152	-0.230	-0.603
47.	SNR4	-0.342	-0.429	-0.201
48.	SNGP	0.655	-0.241	-0.150
49.	SNAT5	0.172	-0.408	0.067
50.	SNAT8	0.271	-0.636	-0.070
51.	SNC	0.305	0.110	-0.282
52.	SNT	-0.120	-0.245	-0.595
	Relative Percentage of Variability	29.2 %	11.2 %	7.9 %

Figure 7. Diagram showing a principal component ordination of 20 specimens of Cinara nigra based on the analysis of 52 morphological variables. A, projection of specimens onto the first and second principal axes, with the value (in mm) for the body length measurement positioned to the right of the mark indicating the location of each specimen; B, projection of the specimens onto the first and third principal axes; C, projection of the specimens onto the second and third principal axes, with the value (in mm) for the setal length measurement on the head positioned to the right of the mark indicating the location of the specimen.


PRINCIPAL AXIS I (29.2%)
A
PRINCIPAL AXIS II (11.2%)
3.7
3.9
3.8
3.7
3.6
3.5
3.7
3.5
3.6
3.4
3.6
3.7
3.7
3.2
3.2
3.3
3.2
3.5
3.3
3.3


PRINCIPAL AXIS I (29.2%)
B
PRINCIPAL AXIS III (7.9 %)

PRINCIPAL AXIS III (7.9 %)

C

PRINCIPAL AXIS II (11.2%)

.054
.061
.053
.075
.058
.063
.062
.072
.073
.067
.066
.080
.064
.067
.067
.068
.076
.063
.076
.059

The first principal component, which accounted for 29.2% of the total variation in the sample, was a general size factor. Most of the continuous measurements of the body dimensions (Variable No. 1-33) had relatively high, positive values, indicating an increase in magnitude along this axis. This was contrasted by the negative values for most of the setal length measurements and some of the setal counts; in general, these variables were not significantly correlated with size, as shown by their relatively low scores. The presence of a size factor is evident in Figure 7-a, which shows the ordination of the individual specimens in the sample onto the first two principal axes. There is clearly a trend involving a change in the size of individual specimens along the first principal axis.

The second principal component (11.2% of total variation) exhibited two trends in variation, namely, negative scores for all leg dimensions and relatively high, negative scores for most setal length measurements. This is shown in Figure 7-c (principal axes II and III), where, for example, the individual values for SLH were plotted. The scores of most of the setal length characters on various body structures showed relatively large decreases in magnitude of their component scores on principal component II indicating that they may be influenced by ontogenetic changes in these structures.

The third principal component (7.9% of total variation) represented shape variation as was shown by the contrasts of positive and negative values for the length and width dimensions of many structures, such as the antennal segments. Projection of the specimens onto principal axes I

and III (Figure 7-b) showed a trend where the smallest and largest individuals usually had positive values on principal axis III while most medium-sized individuals showed negative scores on this axis, thus indicating that this shape variation along axis III was under the influence of size.

As the group of variables selected represented different components of variation, it was decided that the majority of the variables would be retained for further analysis. But the measurements of the length and width of antennal segment I (AlL, AlW) and of the width of the hind coxa (CW) were eliminated due to their relatively high variability. This was thought to be the result of their distortion due to the slide-mounting procedure.

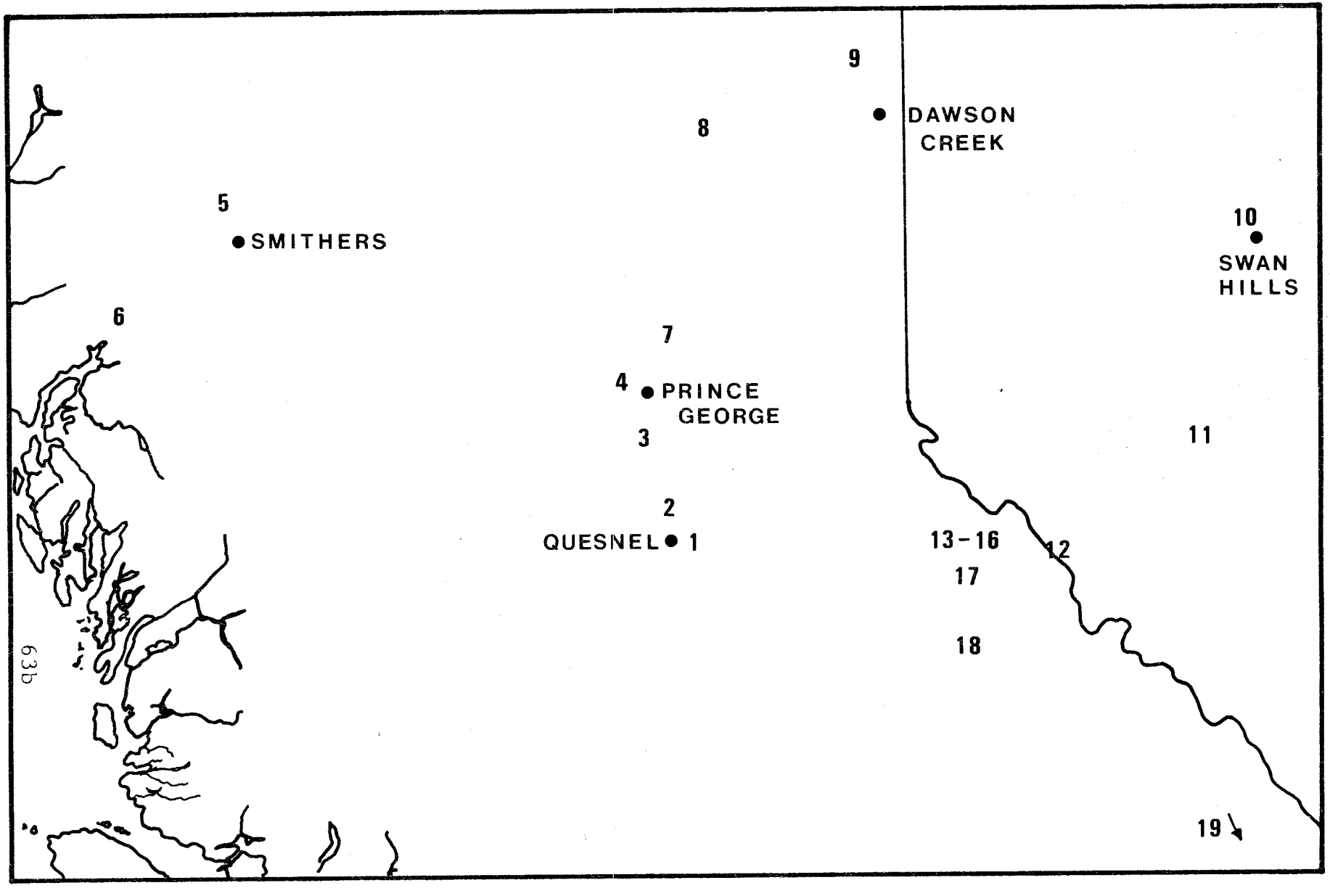
4.3 Variation Within and Between Geographic Samples.

Geographic variation among the morphological characters of C. nigra was examined next. Nineteen population samples (each with n = 20) including sample No. 11 which was already investigated, were analyzed. The collection data for these samples are given in Table IV and their geographical distribution is shown in Figure 8. This species appears to be restricted to Pinus contorta in the mid- to northern and mountainous regions of British Columbia and Alberta. With the exception of the sample from Sparwood, B. C. (No. 19), all samples were collected during a two-week period in 1980, thus minimizing the effect on the analysis of

Table IV. Collection data of population samples of *Cinara nigra* used in the study. All samples were collected by R. Foottit. All samples are from British Columbia unless noted otherwise.

Sample Number	Location and Date of Collection
1	15 km East of Quesnel, Hwy 26, 30 July 1980
2	10 km North of Quesnel, Hwy 97, 31 July 1980
3	12 km North of Hixon, Hwy 97, 31 July 1980
4	5 km West of Prince George, Hwy 16, 31 July 1980
5	46 km Northwest of Smithers, Hwy 16, 3 August 1980
6	Lakelse Lake, 19 km South of Terrace, Hwy 25, 3 August 1980
7	31 km North of Prince George, Hwy 97, 5 August 1980
8	45 km South of Chetwynd, Hwy 97, 6 August 1980
9	18 km South of Taylor, Hwy 97, 7 August 1980
10	5 km North of Swan Hills, Alberta, Hwy 33, 9 August 1980
11	20 km West of Edson, Alberta, Hwy 16, 11 August 1980
12	2 km East of Mt. Robson Provincial Park, Hwy 16, 12 August 1980
13	Tête Jaune, 12 August 1980
14	Tête Jaune, 12 August 1980
15	Tête Jaune, 12 August 1980
16	Tête Jaune, 12 August 1980
17	Valemount, 13 August 1980
18	26 km South of Valemount, Hwy 5, 13 August 1980
19	Sparwood, 9 July 1982

Figure 8. Distribution in British Columbia and Alberta of the 19 population samples of Cinara nigra used in the study. Population No. 19 was collected at Sparwood in the south-eastern corner of British Columbia.


9
DAWSON CREEK
8
5
SMITHERS
10
SWAN HILLS
6
7
4
PRINCE GEORGE
3
11
2
QUESNEL
1
13-16
12
17
18
63b
19

temporal variation in the phenology of the colonies. The samples from Tête Jaune, B. C. (Nos. 13-16) were collected within 1 km of each other; these samples were used in order to see if the morphometric techniques would recognize microgeographic affinities in the samples.

The 49 continuous measurements and counts that were identified from the previous analysis were taken on the specimens of the other 18 population samples. To avoid bias, the samples were not measured in any particular geographic sequence. Including the initial sample, a total of 18,620 measurements were taken. Descriptive statistics for all variables were calculated and are shown for all samples in Appendix 2.

Analysis of the normality of the samples using D'Agostino's $\underline{D}_A$ ($p \leq 0.01$) showed that 12.2% of the variable by sample distributions were non-normal. No samples showed consistently higher non-normality rates among the character set. As in the initial sample that was analyzed, the count of the number of subapical setae on antennal segment VI (SNA6SA) was consistently non-normal. However, considering the variable nature of biological data, I did not consider that the rate of non-normality among the characters was sufficiently high to affect the results of the subsequent morphometric analysis. Therefore, no transformations of the data were carried out.

The sample means of each variable were tested for significant differences and geographic trends using a one-way analysis of variance and the Student-Newman-Keuls range test ($p \leq 0.01$) (Sokal and Rohlf 1981). All variables were significantly different among localities with the exception of three setal counts. These were the number of setae on

the base of antennal segment VI (SNA6B), on antennal segment II (SNA2), and on abdominal tergite V (SNAT5). With the exception of one or two samples, these variables showed an almost complete overlap of their ranges. No geographic trends in the samples, when each variable was considered separately, were evident; geographically adjacent samples occasionally had similar values.

Values of the coefficient of variation revealed trends in variability that were similar to those shown in the analysis of the initial sample. None of the 19 population samples were consistently more variable, with respect to the values of V, than the other samples. There was an overall range of values from 0.1 to 27.8 with the continuous measurements generally showing lower values than the setal length measurements and the setal counts. The values of V for the continuous measurements were as follows: body size measurements, 2.2-9.2; antennal segment measurements, 2.3-10.5; rostrum segment measurements, 2.0-11.4; and hind leg measurements, 1.8-15.7. Tibia width was consistently more variable (7.5-15.7) than the other hind leg dimensions. If this variable is excluded, the other hindleg measurements show a range of variability (1.8-9.8) similar to that of the other continuous measurements. Values of V for the setal length measurements ranged from 3.7 to 15.9, excluding the variable SLAT5, which was consistently more variable (12.5-27.8). The setal counts showed a wide range of variability (0.1-19.8).

4.3.1 Correlation and Principal Component Analyses

For each of the 19 samples, a matrix of correlation coefficients was calculated for all combinations of variables. Each correlation matrix was inspected for trends as in the analysis of the original population sample collected at Edson, Alberta. It was found that the correlations of many pairs of variables varied considerably from sample to sample with respect to sign and magnitude. For example, over the 19 samples, the correlation of R5L with the other rostrum segment variables ranged from negative values, to weak and to significantly ($p = 0.05$) positive values. The correlation of some of the variables with body length was not consistent over the 19 samples.

Rather than present all correlation tables for all 19 samples, and in order to quantify any cumulative patterns over the 19 samples, I tabulated the total numbers (out of 19) of significant ($p = .05$) correlation coefficients for each functional or operational set of variables (Table V). Examination of these tabulations revealed some trends among the variables:

a). Body size measurements. The measure of the distance between the hind coxae (DHC) was most frequently and head length (HL) the least frequently significantly correlated with body length.

b). Rostrum measurements. There was a low number of significant correlations among the segments. With the exception of R4L the rostrum segments showed a low frequency of significant correlations with body length.

Table V. Total numbers of significant ($p = 0.05$) correlation coefficients between 49 variables for each of 19 population samples of Cinara nigra. The subtotals of significant negative correlations are in brackets. See Table I for for full names of variables.

(a) Body Size Measurements

Variable	BL	DE	DHC	FRW	HL
BL	--				
DE	9	--			
DHC	13	5	---		
FRW	9	11	8	--	
HL	5	2	2 (1)	4	--

(b) Rostrum Measurements

Variable	R5L	R4L	R3L	R2L	Body Length
R5L	---				2
R4L	6	---			10
R3L	3	8	---		4
R2L	2	3	2	---	3

Table V - (c). Antennal Measurements

Variable	A2L	A2W	A3L	A3W	A4L	A4W	A5L	A5W	A6BL	A6BW	A6PTL	Body Length
A2L	---											7
A2W	5	---										8
A3L	11	6	---									15
A3W	7	9	10	---								14
A4L	9	9	15	10	---							12
A4W	7	10	10	11	10	---						8
A5L	5	8	13	11	14	6	---					12
A5W	3	2	5	5	2	5	1	---				5
A6BL	5	1	3	2	3	1	3	0	---			2
A6BW	6 (1)	7 (1)	6 (1)	6	5	6	2	6	1	---		5
A6PTL	1	1	3 (1)	2	2	2	2	2	2(1)	2	---	3

Table V - (d). Hind Leg Measurements

Variable	CL	FL	FW	TL	TW	TS1W	TS1VL	TS1DL	TS2L	TS2W	Body Length
CL	--										16
FL	17	--									17
FW	13	11	--								10
TL	18	19	6	--							14
TW	10	11	19	8	--						5
TS1W	9	8	6	6	11	--					7
TS1VL	13	17	8	13	9	6	--				10
TS1DL	6	8	6	6	4	0	6	--			6
TS2L	13	13	4	14	7	5	14	2	--		8
TS2W	6	5	12	4	16	9	3	4	0	--	4

Table V - (e). Setal Length Measurements

Variable	SLH	SLA3	SLT	SLTS2	SLCO	SLCA	SLGP	SLAT8	SLAT5	Body Length
SLH	---									1
SLA3	2	---								1(1)
SLT	2	1	---							2(1)
SLTS2	2	2	6	---						3(2)
SLCO	2	1	0	1	---					1
SLCA	2	2	1	0	0	---				5(2)
SLGP	2	3	1	4	1	5	---			1
SLAT8	4	1	2	0	5	2	1	---		3(2)
SLAT5	1	1	2	2	1	0	0	1	---	3(1)

Table V - (f). Setal Counts

Variable	SNA6SA	SNA6B	SNA5	SNA2	SNR4	SNGP	SNAT5	SNAT8	SNC	SNT	Body Length
SNA6SA	--										0
SNA6B	0	--									0
SNA5	0	1	--								4
SNA2	0	2	1	--							2
SNR4	0	0	0	2	--						1
SNGP	0	1	2	1	6(1)	--					5
SNAT5	0	1(1)	0	0	0	1	--				2
SNAT8	0	3(2)	2	0	0	2	0	--			2
SNC	0	3(3)	1	0	1	1	0	0	--		1
SNT	0	1(1)	1	1	1(1)	3	0	0	1	--	2

c). Antennal measurements. Antennal segments 3 to 5 showed a relatively high frequency of significant correlations with body length and a relatively high rate of internal correlation of dimensions compared to the dimensions of the distal antennal segment 6.

d). Hind leg measurements. The frequency of significant correlations of these variables with body length was very high for the proximal segments, less so for the tarsal dimensions. The length dimensions were more frequently correlated with body length than the width dimensions. The frequency of internal correlations was high for most dimensions.

e). Setal length measurements. There was a low frequency of significant internal correlation and a low frequency of significant correlation with body length.

f). Setal counts. There was none or only a low frequency of significant correlation either among the counts or with body length.

For each of the 19 samples, the matrix of correlation coefficients between all variables was subjected to a principal component analysis. The contribution of each variable to each principal axis was calculated. In addition, each specimen was projected onto the first three principal axes (I x II, I x III, II x III). The results of these analyses were inspected for trends as in the analysis of the initial sample.

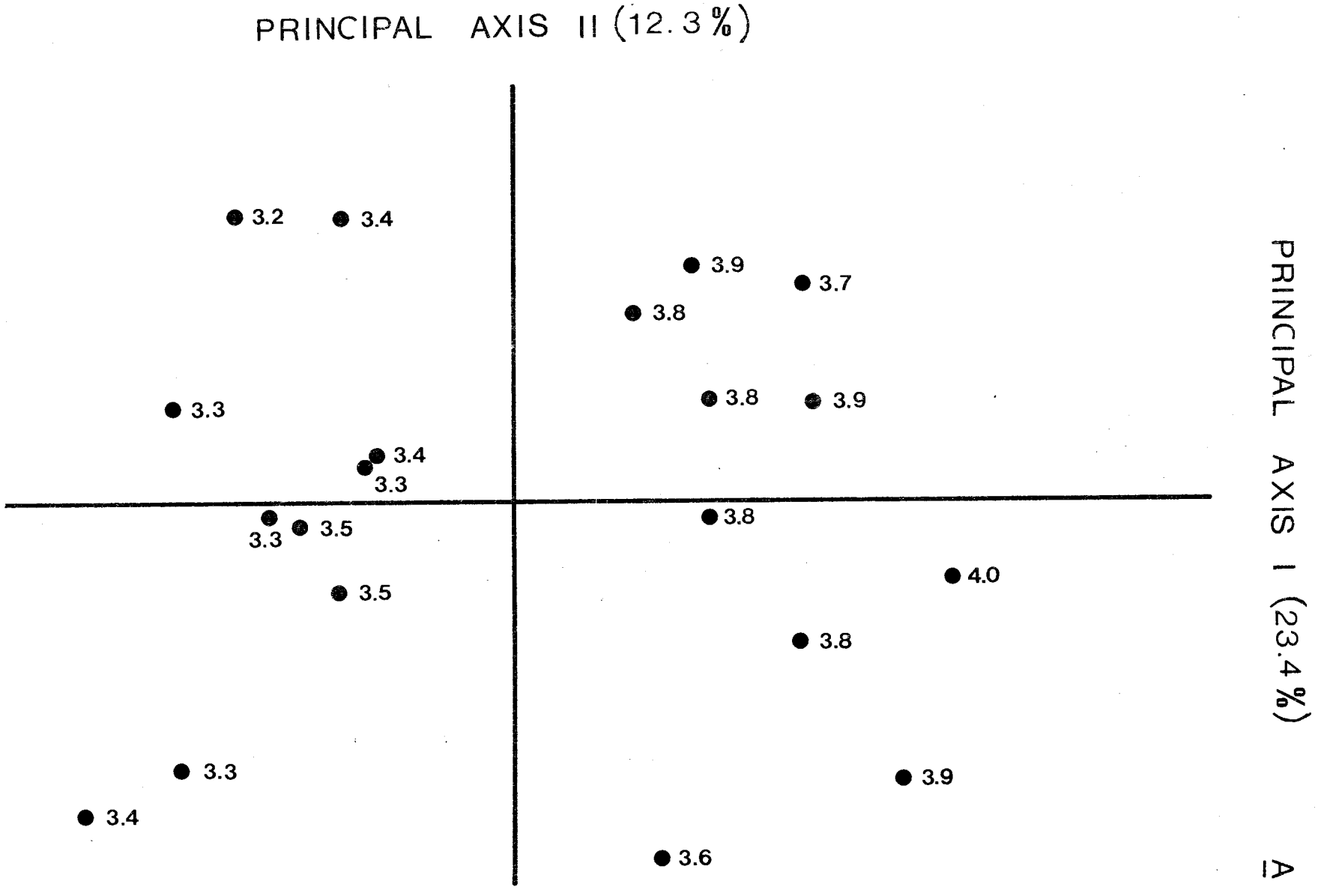
The presence of a size factor (17.2 - 36.9% of total variation) was evident in all of the samples. The continuous measurements showed high positive scores on the first principal component, the exceptions being some of the terminal antennal and tarsus dimensions. There was considerable variability in the sign and magnitude of the scores on the first component for the setal length measurements and setal counts.

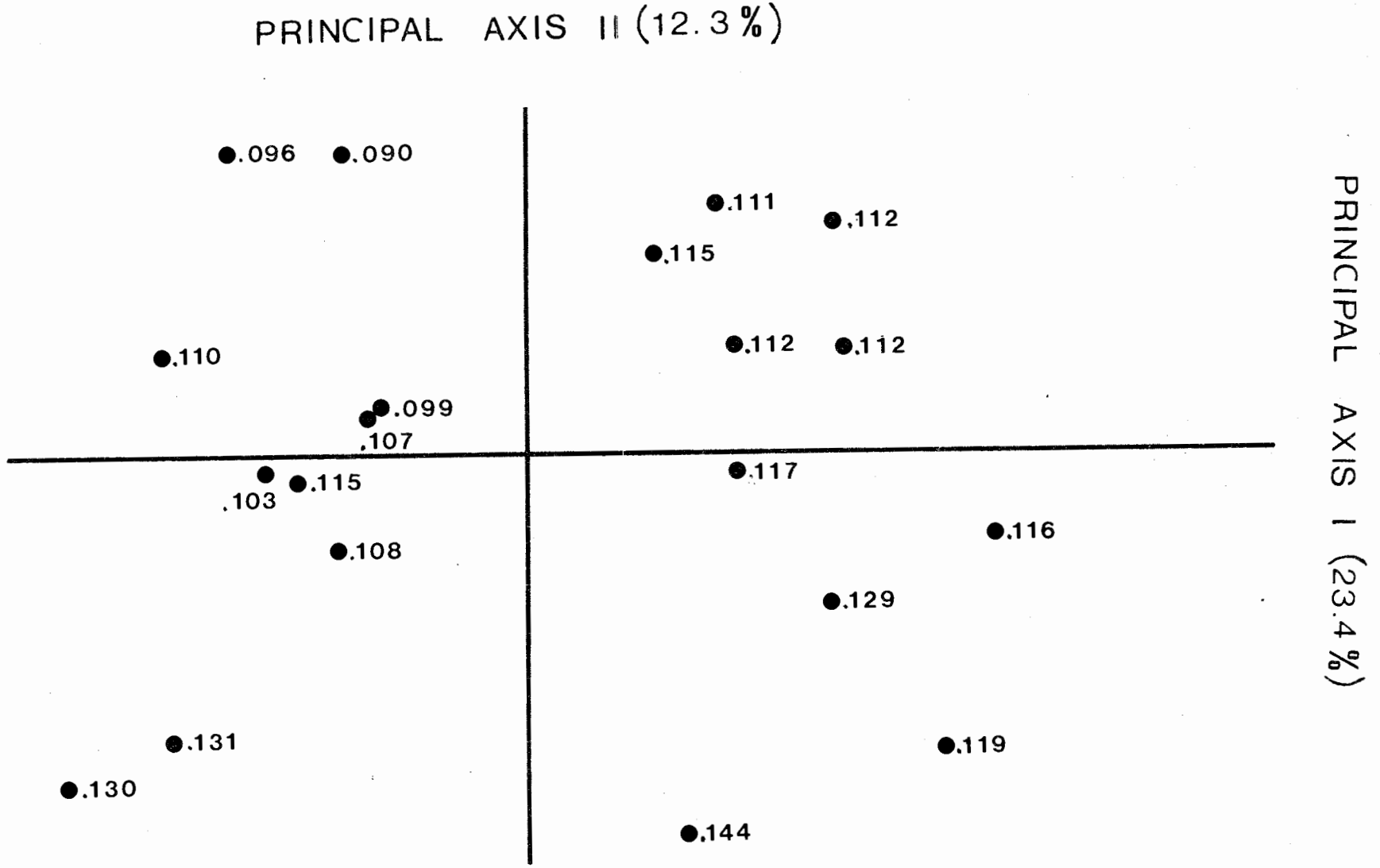
For most samples, the trend of negative scores for the leg dimensions and setal counts was apparent on the second component. In the second and the third components there were many contrasts of sign of the scores for length and width dimensions and for groups of measurements of closely situated structures; this indicated the presence of shape and size-related shape variation.

There were similar patterns in the projections of the individual specimens onto the principal axes computed for each sample. Most consistent was the continuous orientation of specimens according to size along principal axis I. The exception to this trend was evident in Sample No. 2 where there was a clear separation of the specimens in this sample into 2 size groups (Figure 9-a). Re-examination of the specimens did not reveal any taxonomic differences between the 2 subgroups; in particular, no characters of the closely related C. canatra were evident. Embryos were present in specimens of both subgroups, indicating that neither subgroup represented a earlier generation. It is likely that Sample No. 2 was from a mixed colony, consisting of the clonal offspring from at least two different virginoparae.

Examination of the contributions of the variables to the first three principal components calculated for Sample No. 2 (Table VI) (45.6% of total variation) showed morphometric patterns that were similar to those shown in the analysis of Sample No. 11 and the other geographic samples. Principal component I consisted of large positive scores for many continuous variables while negative scores on this component were shown by the distal antennal segments, setal length measurements and some

Figure 9. Diagrams showing the principal component ordinations of 20 specimens of Cinara nigra, collected 10 km N of Quesnel, British Columbia (31 VII 1980), based on the analysis of 49 morphological variables. A, projection of specimens onto the first and second principal axes, with the value (in mm) for the body length measurement positioned to the right of the mark indicating the location of each specimen; B, projection of the specimens onto the first and second principal axes, with the value (in mm) for the femur length measurement positioned to the right of the mark indicating the location of each specimen.


PRINCIPAL AXIS II (12.3%)
PRINCIPAL AXIS I (23.4%)
3.2
3.4
3.9
3.7
3.8
3.3
3.8
3.9
3.4
3.3
3.3
3.5
3.8
4.0
3.5
3.8
3.3
3.9
3.4
3.6


PRINCIPAL AXIS II (12.3%)
.096
.090
.111
.112
.115
.110
.112
.112
.099
.107
.103
.115
.117
.116
.108
.129
.131
.119
.130
.144
PRINCIPAL AXIS I (23.4%)

B

Table VI. Contributions of 49 variables to the first three principal components calculated from 20 specimens of Cinara nigra collected at a site 10 km N of Quesnel, British Columbia, 31 July 1980. See Table I for full names of variables.

VARIABLE	PRINCIPAL COMPONENT I	II	III
1. BL	0.911	-0.075	0.078
2. DE	0.734	0.131	0.262
3. DHC	0.788	0.316	0.104
4. FRW	0.752	0.257	0.167
5. HL	-0.135	0.100	-0.133
6. A2L	0.578	0.202	-0.417
7. A2W	0.187	-0.590	0.427
8. A3L	0.855	-0.151	-0.126
9. A3W	0.670	-0.115	-0.361
10. A4L	0.384	-0.580	-0.313
11. A4W	0.537	-0.326	0.229
12. A5L	0.516	0.188	0.145
13. A5W	-0.315	0.155	0.358
14. A6BL	-0.151	-0.275	-0.618
15. A6BW	-0.278	-0.049	0.637
16. A6PTL	-0.333	-0.242	0.259
17. R5L	-0.194	0.166	-0.113
18. R4L	0.109	-0.293	0.413
19. R3L	0.197	0.504	-0.153
20. R2L	0.246	-0.215	-0.483
21. CL	0.863	-0.248	-0.189
22. FL	0.936	-0.095	-0.066
23. FW	0.089	-0.779	0.219
24. TL	0.933	-0.088	-0.107
25. TW	0.230	-0.784	0.188
26. TS1W	0.411	-0.595	0.389
27. TS1VL	0.613	-0.283	-0.164
28. TS1DL	0.424	-0.256	-0.412
29. TS2L	0.441	-0.270	-0.287
30. TS2W	-0.145	-0.745	0.284

Table VI. cont'd

VARIABLE	PRINCIPAL COMPONENT I	II	III
31. SLH	-0.259	-0.564	-0.051
32. SLA3	-0.478	-0.170	-0.345
33. SLT	-0.491	-0.500	0.036
34. SLTS2	-0.577	-0.292	-0.538
35. SLCO	-0.496	-0.366	0.090
36. SLCA	-0.529	-0.036	-0.186
37. SLGP	-0.516	-0.159	-0.437
38. SLAT8	-0.460	-0.168	-0.134
39. SLAT5	-0.346	-0.651	-0.076
40. SNA6SA	0.007	0.202	-0.274
41. SNA6B	-0.209	-0.350	0.161
42. SNA5	-0.416	0.417	0.323
43. SNA2	0.053	0.007	-0.298
44. SNR4	-0.378	0.122	0.210
45. SNGP	0.003	-0.238	-0.133
46. SNAT5	-0.350	-0.415	-0.579
47. SNAT8	0.068	0.066	-0.510
48. SNC	0.147	-0.192	0.608
49. SNT	-0.426	0.128	-0.058
Relative Percentage of Variability	23.4	12.3	9.9

setal counts; these latter groups of variables were negatively correlated with BL in this sample. Principal component II showed relatively high negative scores for some of the leg, antennal, and setal length measurements. Principal component III consisted of contrasts of sign and magnitude for many variables; the largest scores were shown by the antennal segment VI dimensions and some setal counts (SNAT5, SNAT8, SNC).

The presence of 2 size groups within Sample No. 2 allowed for further analysis of the components of variation within C. nigra. For example, while FL had a large score (0.936) on principal axis I, some variation in this measurement was not associated with the overall size factor. Figure 9-b shows the values of FL for the specimens projected onto axes I and II. There is a clear negative gradient of this variable (and other leg dimensions) along axis II. This trend occurred in both subgroups and was independent of the overall size separation along principal axis I.

4.3.2 Overall Patterns of Character Variability

This section deals with the analysis of overall patterns of variation in the 19 samples of C. nigra. This analysis was carried out in order to determine if the sample size used (n = 20) was large enough to sample adequately all of the major trends in variation. Descriptive statistics were calculated for all 49 variables measured on the total of 380 specimens. The mean, standard deviation and the range are given in Chapter 6.

The overall range of values for the coefficient of variation was reduced (4.0 - 18.2) as were the ranges for the functional and/or operational groups of measurements. The values of V for the continuous measurements were as follows: body size measurements, 5.4 - 10.9; antennal segment measurements, 4.3 - 8.3; rostrum segment measurements, 4.0 - 4.9; and hind leg measurements, 4.6 - 10.2 (without TL, 14.4). If the value for SLAT5 (18.2) is omitted, the values of V for the setal length measurements ranged from 7.3 to 12.4. The setal counts showed a much reduced range of variability (9.1 - 16.2).

Correlation coefficients between all 49 variables for all samples combined (n = 380), were calculated and are shown in Table VII. When each sub-group of variables was examined it was evident that internal correlation between the variables was high and usually statistically significant. All continuous body measurements were positively correlated with body size and in most cases there was high, significant internal correlation as well. All dimensions of antennal segment VI still showed lower internal correlation among themselves and had the lowest correlation with BL. With the exception of the variable SLAT5, the setal length measurements showed high internal correlation as well as significant correlation with BL. The setal length measurements were significantly correlated with the structures they arise upon, for example the correlation coefficient for SLT with TL was 0.32.

The exception to the general trend mentioned above was the series of counts of setae, which had low or negative correlation with body size in many cases, and also showed many low, non-significant internal

Table VII. Correlation coefficients between 49 variables calculated from 19 population samples (n = 20) of Cinara nigra. Total sample size equals 380. See Table I for abbreviations of variable names. Significant values are underlined (Critical value = .101 (p = .05))

(a). Body Size Measurements

Variable	BL	DE	DHC	FW	HL
BL	1.00				
DE	0.76	1.00			
DHC	0.75	0.55	1.00		
FRW	0.70	0.65	0.56	1.00	
HL	0.58	0.44	0.42	0.57	1.00

(b). Rostrum Measurements

Variable	R5L	R4L	R3L	R2L	Body Length
R5L	1.00				0.27
R4L	0.28	1.00			0.69
R3L	0.34	0.51	1.00		0.49
R2L	0.18	0.38	0.33	1.00	0.42

Table VII-(c). Antennal Measurements

Variable	A2L	A2W	A3L	A3W	A4L	A4W	A5L	A5W	A6BL	A6BW	A6PTL	Body Length
A2L	1.00											0.61
A2W	0.50	1.00										0.61
A3L	0.65	0.64	1.00									0.72
A3W	0.65	0.66	0.70	1.00								0.72
A4L	0.61	0.58	0.73	0.69	1.00							0.71
A4W	0.57	0.61	0.64	0.73	0.63	1.00						0.63
A5L	0.58	0.54	0.68	0.66	0.74	0.56	1.00					0.66
A5W	0.38	0.50	0.47	0.54	0.41	0.52	0.41	1.00				0.46
A6BL	0.35	0.22	0.27	0.31	0.37	0.23	0.37	0.17	1.00			0.31
A6BW	0.38	0.50	0.42	0.49	0.40	0.44	0.33	0.50	0.15	1.00		0.43
A6PTL	0.16	0.13	0.17	0.17	0.18	0.21	0.17	0.14	-0.09	0.17	1.00	0.12

Table VII-(d). Hind Leg Measurements

Variable	CL	FL	FW	TL	TW	TS1W	TS1VL	TS1DL	TS2L	TS2W	Body Length
CL	1.00										0.86
FL	0.90	1.00									0.81
FW	0.68	0.66	1.00								0.66
TL	0.83	0.92	0.56	1.00							0.73
TW	0.71	0.71	0.83	0.63	1.00						0.63
TS1W	0.67	0.65	0.60	0.62	0.70	1.00					0.60
TS1VL	0.75	0.80	0.60	0.76	0.62	0.58	1.00				0.70
TS1DL	0.57	0.54	0.48	0.47	0.45	0.38	0.54	1.00			0.54
TS2L	0.74	0.78	0.58	0.74	0.63	0.59	0.73	0.43	1.00		0.69
TS2W	0.50	0.44	0.60	0.41	0.66	0.71	0.40	0.28	0.41	1.00	0.45

Table VII-(e). Setal Length Measurements

Variable	SLH	SLA2	SLT	SLTS2	SLCO	SLCA	SLGP	SLAT3	SLAT5	Body Length
SLH	1.00									0.27
SLA3	0.42	1.00								0.28
SLT	0.38	0.30	1.00							0.33
SLTS2	0.34	0.29	0.44	1.00						0.28
SLCO	0.42	0.38	0.41	0.38	1.00					0.40
SLCA	0.41	0.34	0.35	0.30	0.41	1.00				0.35
SLGP	0.49	0.39	0.37	0.40	0.46	0.42	1.00			0.55
SLAT3	0.49	0.40	0.43	0.33	0.51	0.39	0.50	1.00		0.33
SLAT5	0.08	0.01	0.02	0.05	0.01	-0.01	0.05	0.10	1.00	-0.11

Table VII-(f). Setal Counts

Variable	SNA6SA	SNA6B	SNA5	SNA2	SNR4	SNGP	SNAT5	SNAT8	SNC	SNT	Body Length
SNA6SA	1.00										-0.03
SNA6B	0.01	1.00									0.09
SNA5	0.08	0.12	1.00								0.39
SNA2	0.08	0.06	0.16	1.00							0.05
SNR4	-0.05	0.03	0.02	0.17	1.00						0.02
SNGP	0.14	0.04	0.31	0.24	0.12	1.00					0.50
SNAT5	0.05	-0.06	0.21	0.06	-0.01	0.05	1.00				-0.04
SNAT8	0.06	-0.01	0.22	0.05	0.04	0.21	0.63	1.00			0.21
SNC	0.15	-0.02	0.34	0.13	0.07	0.46	-0.03	0.15	1.00		0.47
SNT	0.01	-0.02	0.28	0.08	0.00	0.44	0.02	0.21	0.42	1.00	0.34

correlations as well. The exception to the above was those counts which were highly correlated with BL. This indicates that this group of variables accounts for a number of components of variation that are independent of size.

The correlation matrix (49 variables, n = 380) was then subjected to a principal component analysis in order to determine the strongest, overall patterns of variability in C. nigra. The component scores for each variable on the first 3 principal components are given in Table VIII.

The first principal component, the general size component (36.2% of total variation), was characterized by high positive scores for the continuous body dimensions and setal lengths with the exception of SLAT5. Some setal counts (SNA5, SNGP, SNC, SNT) had high scores on the first principal component; these variables were significantly correlated with body size as shown in the correlation analysis (Table VII-f).

The second principal component (7.0% of total variation) was largely a dimension influenced by decreases in the magnitude of the setal length measurements. The third principal component (3.0% of total variation) consisted of shape variation, particularly in the antennal and leg dimensions, as was shown in the analysis of the smaller samples. There were also some relatively high scores for some of the setal counts. No patterns among the variable scores were evident on the remaining principal components.

Table VIII. Contributions of 49 variables to the first three principal components calculated from 380 specimens of Cinara nigra. See Table I for full names of variables.

VARIABLE	PRINCIPAL COMPONENT I	II	III
1. BL	0.884	-0.070	-0.030
2. DE	0.818	0.047	0.051
3. DHC	0.649	0.038	-0.083
4. FRW	0.726	0.119	-0.075
5. HL	0.575	-0.119	-0.187
6. A2L	0.714	0.234	0.124
7. A2W	0.762	0.086	-0.192
8. A3L	0.831	0.203	-0.036
9. A3W	0.831	0.184	-0.039
10. A4L	0.827	0.056	0.112
11. A4W	0.741	0.188	-0.085
12. A5L	0.778	0.119	0.230
13. A5W	0.586	0.124	-0.082
14. A6BL	0.365	0.010	0.300
15. A6BW	0.540	0.182	-0.061
16. A6PTL	0.190	0.276	0.137
17. R5L	0.336	-0.086	0.209
18. R4L	0.737	0.023	-0.038
19. R3L	0.581	0.045	0.204
20. R2L	0.508	0.104	0.224
21. CL	0.921	0.028	-0.029
22. FL	0.915	0.228	-0.007
23. FW	0.757	-0.158	-0.343
24. TL	0.847	0.286	0.035
25. TW	0.797	-0.068	-0.297
26. TS1W	0.749	-0.014	-0.229
27. TS1VL	0.820	0.135	0.087
28. TS1DL	0.576	-0.002	0.014
29. TS2L	0.814	0.053	0.054
30. TS2W	0.583	-0.123	-0.453

Table VIII. cont'd

VARIABLE	PRINCIPAL COMPONENT I	II	III
31. SLH	0.280	-0.654	0.129
32. SLA3	0.274	-0.544	0.075
33. SLT	0.360	-0.544	0.068
34. SLTS2	0.254	-0.568	0.026
35. SLCO	0.396	-0.590	0.079
36. SLCA	0.348	-0.537	0.137
37. SLGP	0.546	-0.510	0.044
38. SLAT8	0.331	-0.659	0.151
39. SLAT5	-0.127	-0.210	-0.260
40. SNA6SA	0.040	0.189	0.333
41. SNA6B	0.122	-0.067	0.225
42. SNA5	0.522	0.103	0.204
43. SNA2	0.132	0.103	0.491
44. SNR4	0.052	0.023	0.350
45. SNGP	0.625	0.071	0.127
46. SNAT5	-0.019	-0.169	0.191
47. SNAT8	0.265	-0.001	0.065
48. SNC	0.628	0.052	0.124
49. SNT	0.488	-0.212	-0.163
Relative Percentage of Variability	36.2	7.0	3.5

4.3.3 Discriminant Function Analyses

The 19 population samples were analyzed using multiple discriminant function analysis, as described in Chapter 3, in order to determine if there were geographic patterns among the samples. The standardized discriminant function coefficients for the first four discriminant functions (68.2% of total variation), which represent the contributions of the variables to discrimination between the samples on the discriminant axes, are given in Table IX. The projection of the sample centroids onto the first two discriminant axes, which represent 50.7% of the total variation, is shown in Figure 10.

Discriminant function I, which accounted for nearly 34% of the total variation, was largely influenced by size variation; the highest contribution to this function was made by the variable body length (BL). Examination of Figure 10 shows that the samples are aligned along this axis with respect to general size (see values for BL in Appendix 2). The length of the femur (FL) was a strong contributor to discrimination along axis II. It is evident from the examination that there are a number of size and size-related shape influences upon discrimination along each axis. A clear example is the contrast in the absolute values and signs of the contributions of the measurements of antennal segments II to V compared to the dimensions of antennal segment VI. This is particularly noticeable when discriminant functions II and IV are compared (Table IX).

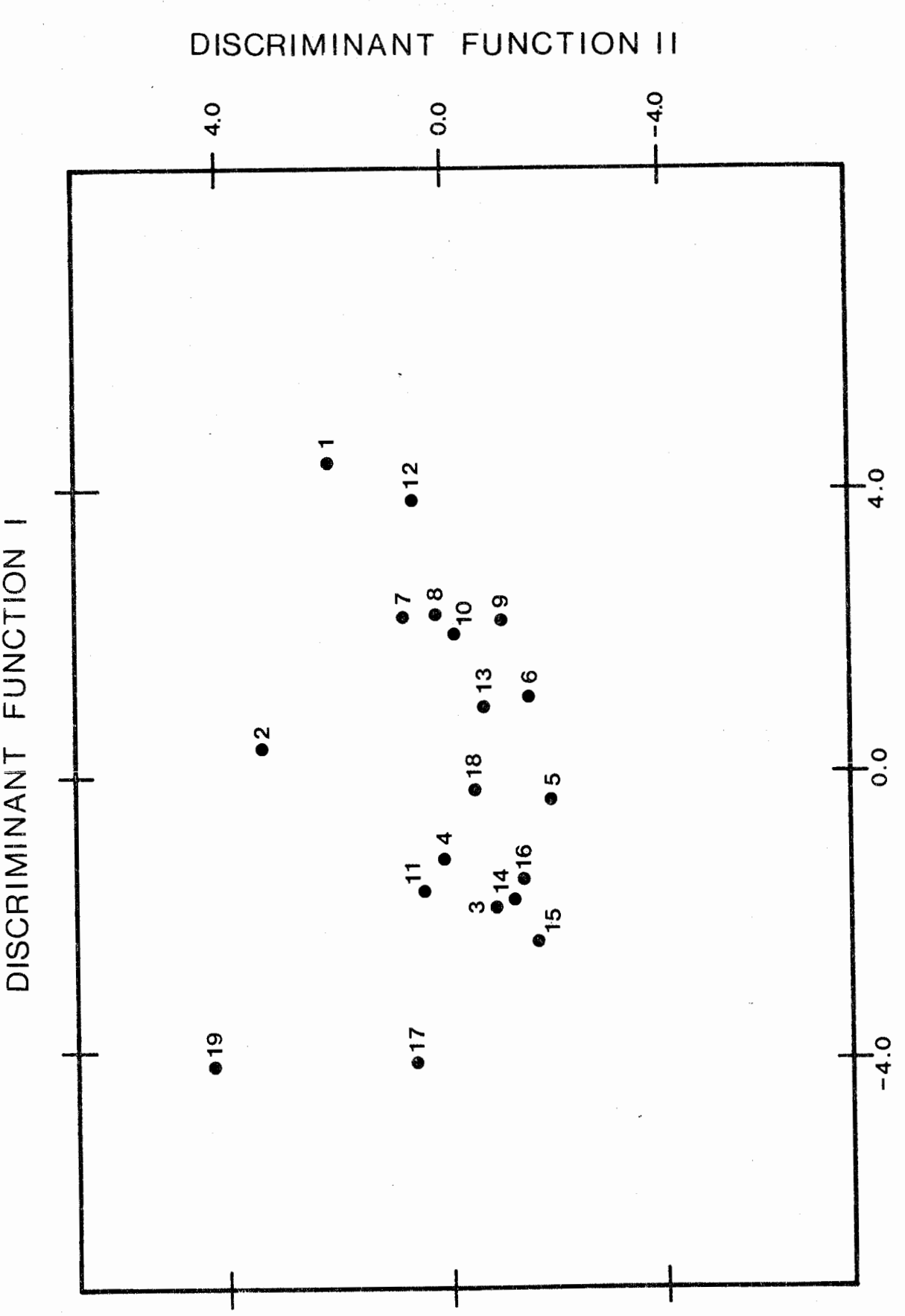
Table IX. Standardized discriminant function coefficients for the first four discriminant functions calculated from 19 population samples (n = 20) of 49 variables of *Cinara nigra*. See Table I for full names of variables.

	VARIABLE	DISCRIMINANT FUNCTION			
		I	II	III	IV
1.	BL	0.561	-0.381	-0.055	0.277
2.	DE	0.157	-0.205	0.194	-0.040
3.	DHC	0.094	0.127	-0.342	-0.007
4.	FRW	0.194	-0.052	-0.271	-0.003
5.	HL	0.110	-0.024	-0.320	-0.462
6.	A2L	0.194	0.019	0.105	-0.077
7.	A2W	0.037	-0.006	0.413	-0.006
8.	A3L	-0.322	-0.300	0.386	-0.607
9.	A3W	-0.003	0.012	0.117	-0.234
10.	A4L	-0.178	-0.287	0.126	0.004
11.	A4W	0.059	0.118	0.052	-0.026
12.	A5L	0.063	-0.129	0.099	0.458
13.	A5W	-0.053	-0.024	0.040	-0.224
14.	A6BL	-0.127	-0.029	-0.208	0.159
15.	A6BW	0.032	-0.011	-0.180	0.251
16.	A6PTL	-0.139	0.065	-0.136	0.116
17.	R5L	-0.056	0.067	0.010	-0.021
18.	R4L	-0.024	0.086	-0.236	0.169
19.	R3L	-0.121	-0.396	-0.016	0.263
20.	R2L	0.123	0.048	-0.132	0.181
21.	CL	0.267	-0.038	-0.148	-0.226
22.	FL	0.006	0.841	-0.327	-0.060
23.	FW	0.143	-0.493	0.460	-0.333
24.	TL	-0.054	0.308	-0.333	0.180
25.	TW	-0.217	0.155	-0.427	-0.176
26.	TS1W	-0.019	0.062	0.206	-0.211
27.	TS1VL	-0.019	0.231	-0.060	0.041
28.	TS1DL	-0.062	-0.148	-0.144	0.311
29.	TS2L	0.054	0.167	0.140	0.098
30.	TS2W	0.062	0.091	0.092	0.198
31.	SLH	0.102	-0.071	0.393	0.079
32.	SLA3	0.115	0.011	0.021	0.069
33.	SLT	0.064	-0.153	-0.237	0.138
34.	SLTS2	0.057	-0.046	0.031	0.235
35.	SLCO	0.125	-0.227	-0.009	0.149

Table IX. cont'd

	VARIABLE	DISCRIMINANT FUNCTION I	II	III	IV
36.	SLCA	0.081	-0.164	-0.102	-0.022
37.	SLGP	0.208	-0,062	0.108	-0.149
38.	SLAT8	0.339	-0.130	0.114	-0.073
39.	SLAT5	-0.125	-0.119	-0.147	-0.206
40.	SNA6SA	0.075	0.244	0.018	-0.131
41.	SNA6B	0.076	0.004	0.026	-0.135
42.	SNA5	0.098	0.211	-0.057	-0.192
43.	SNA2	-0.193	0.057	0.145	0.042
44.	SNR4	0.006	-0.001	0.012	-0.038
45.	SNGP	-0.021	0.196	0.122	0.374
46.	SNAT5	-0.110	-0.036	0.081	0.030
47.	SNAT8	-0.072	0.121	0.088	-0.133
48.	SNC	0.118	0.409	0.274	0.193
49.	SNT	0.186	0.213	0.315	0.051
	Relative Percentage of Variability	34.0	16.7	10.1	7.4

Figure 10. Centroids of 19 population samples of Cinara nigra projected onto the first and second discriminant axes; based on the analysis of 49 morphological variables. See Table IV for the collection data corresponding to the sample numbers.


DISCRIMINANT FUNCTION II
DISCRIMINANT FUNCTION I
4.0
0.0
-4.0
4.0
0.0
-4.0
1
12
7
8
10
9
13
6
2
18
5
4
11
16
14
3
15
19
17

Mahalanobis Generalized Distances ($\underline{D}$ values) (Chapter 3) were calculated for all pairwise comparisons of samples, using the 49 variables measured for the 19 population samples. The resulting matrix of $\underline{D}$ values was subjected to a cluster analysis (UPGMA) (Figure 11). As was the result with the previous analysis, no geographic pattern in clusters of samples was evident, except that some geographically adjacent samples were grouped together. However, even the geographically local samples from Tête Jaune (No.'s 13 - 16) were not grouped.

Allocation of individual specimens into the 19 population samples, using identification functions calculated from the specimens in each sample, was carried out. The results of this analysis are shown in Table X. Although there is an upward bias in the procedure, when the analysis is carried out in the manner described in Chapter 3, this approach gave a useful picture of the degree of phenetic overlap betweeen the samples. Nearly 92% of the specimens were allocated into the correct samples. Incorrectly allocated specimens were often placed in geographically close samples. This is particularly noticeable in the case of the geographically adjacent samples from Tête Jaune, B. C. (No.'s 13-16).

The associations, as shown in the phenogram (Figure 11), if examined from the top to the bottom, resemble closely the sequence along the first discriminant function (Figure 10), that is, a sequence based roughly on decreasing overall size. Thus, while the variables used in this analysis are generally useful for discriminating between samples, there are no apparent geographically defined clusters, other than local affinities between adjacent samples.

Figure 11. Phenogram for the UPGMA cluster analysis of Mahalanobis Generalized Distances, D, calculated for 19 population samples of Cinara nigra, based on the analysis of 49 morphological variables. See Table IV for the collection data corresponding to the sample numbers.

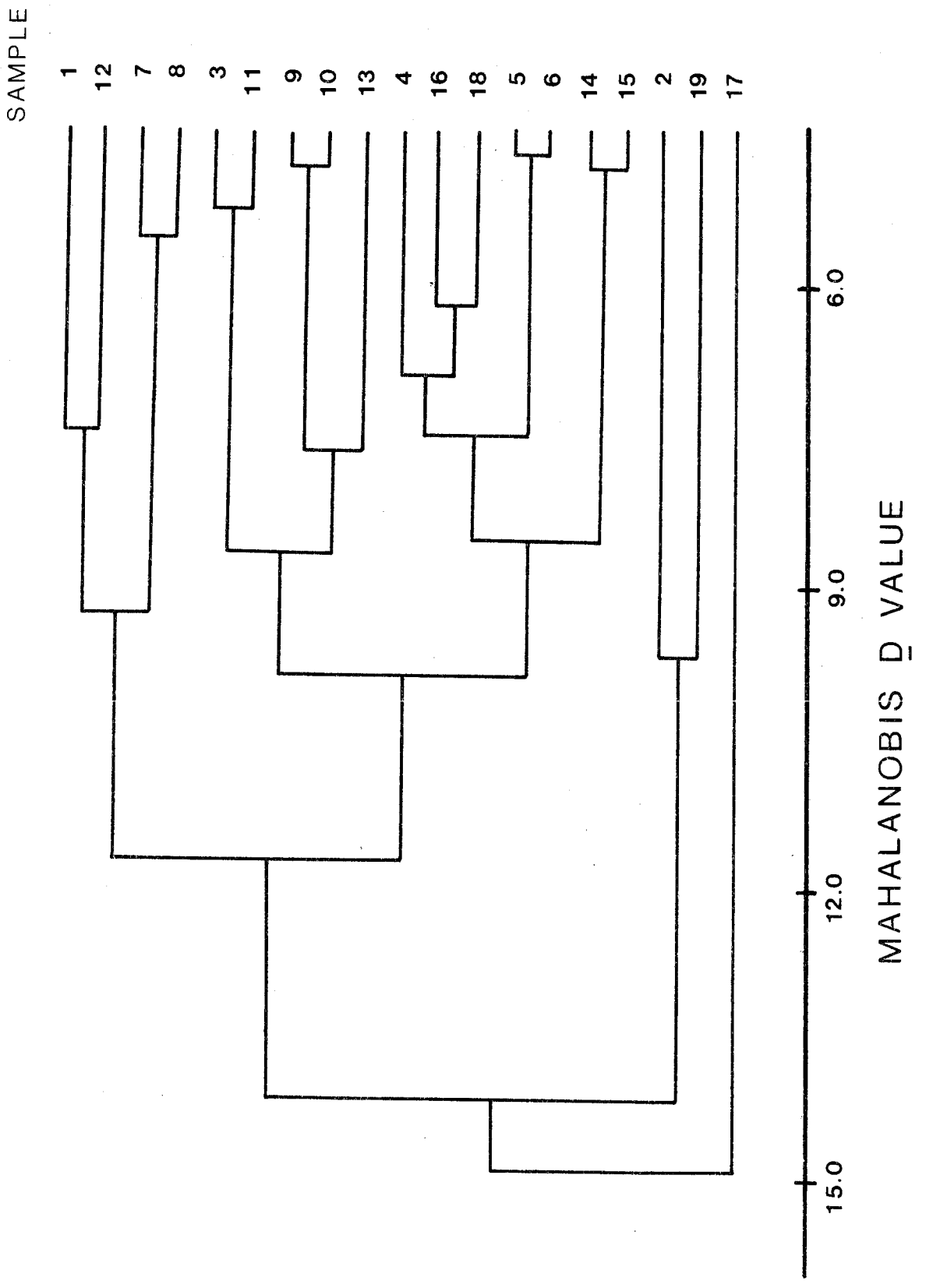

SAMPLE
1
12
7
8
3
11
9
10
13
4
16
18
5
6
14
15
2
19
17
6.0
9.0
12.0
15.0
MAHALANOBIS D VALUE

Table X. Identification table for 19 population samples of Cinara nigra. Identification functions based on 49 variables (n = 20). The numbers of correct identifications are shown 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	19
1	20																		
2		20																	
3			19						1										
4		1	1	15				1						1		1			
5					20														
6			1			18								1					
7							19			1									
8							1	18		1									
9				1					16	2								1	
10			1				1		2	16									
11											20								
12									1			19							
13													20		1				
14				1										16	2	1			
15				1										1	14	3			
16																20			
17																	20		
18																1		19	
19																			20

4.4 Reduction of the Number of Variables

On the basis of the analyses described above, I reduced the number of variables from 49 to 32. This gave a more tractable data set for the analysis of species differences (Chapter 5) without a great deal of loss of information content or discriminatory ability. As a result, some variables that where highly correlated with other variables were eliminated. Variables that proved difficult to accurately measure or count were also eliminated from further analysis.

a). Body size measurements. The measurements of body length (BL) and frons width (FRW) were retained from those variables measured as size and head dimensions, respectively. Other related measurements were highly correlated with these.

b). Rostrum measurements. The rostrum measurements were retained as these are important in the biological determination of species differences, particularly feeding site differences. They showed independent patterns of variation.

c). Antennal measurements. All antennal measurements were kept except the width measurements of segments II to V; these were always highly correlated with the length measurements of these segments.

d). Hind leg measurements. The following measures of features on the hind leg were retained: femur length (FL), femur width (FW), tibia length (TL), the ventral length of tarsal segment I (TS1VL) and the length of tarsal segment II (TS2L). Other leg dimensions were highly correlated

with these variables. The width of the tibia (TW) was not retained as it had a relatively high coefficient of variation (7.5 - 15.7) (Appendix 2) when compared to other continuous measurements. This was likely the result of variation in the plane on which the tibia was projected on the slide.

e). Setal length measurements. Setal length measurements on antennal segment III (SLA3), on the genital plate (SLGP), on abdominal tergite V (SLAT5), and on the hind tibia (SLT), were retained. The other variables were dropped due to a high correlation with other setal measurements, to high variability, or to difficulty in obtaining an accurate measurement. The latter was a particular problem with the longer setae such as those on the head, cornicle and the cauda. These setae tended to be curved, bent and even broken in some specimens.

f). Setal counts. All setal counts were retained. Based on the analyses presented above it is evident that these variables represent a number of components of variation which are independent of size and which could be taxonomically useful.

In order to compare the discriminatory ability of the reduced character set with that of the original character set, allocation of the individual specimens into the 19 population samples, using identification functions calculated from 32 variables, was carried out. The result was that 82% of the specimens were correctly allocated (Table XI). This value compares with nearly 92% correct allocation with the use of all 49 variables, a fact indicating that much of the discriminatory ability of the original data set was retained.

Table XI. Identification table for 19 population samples of Cinara nigra. Identification functions based on 32 variables (n = 20). The numbers of correct identifications are shown 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	19
1	18											1	1						
2		18		1								1							
3			16	2										1	1				
4		1	2	13				1	1					1				1	
5			1		17	2										1			
6			1		1	15								1		1		1	
7							17	2	1										
8						1		18		1									
9									15	2	1			1				1	
10		1	1				1		3	13								1	
11			1								18		1						
12	1							2				17							
13			1						1				16		1	1			
14			1	1							1			15	1	1			
15			1										1		15	2		1	
16				1											1	18			
17																	20		
18					1			1	1				1	1		1		14	
19																			20

As was discussed in Chapter 3, there is an upward bias in the allocation procedure when the same specimens are used both in order to calculate the identification functions and to allocate individuals into their respective groups. I estimated the degree of bias by reducing the size of each sample to 15 specimens, selected at random, and used the remaining 5 specimens from each sample as "unknowns" to be allocated, and carried out the allocation procedure using the two data sets consisting of 49 and 32 variables, respectively. The result was that when 49 variables were used to calculate the identification functions, 64% of the "unknowns" were correctly allocated and when 32 variables were used, 62% of the "unknown" specimens were correctly allocated. This indicated that there had been little loss in the discriminatory ability of the data set due to a reduction in the number of variables employed in the analysis. The reduction in correct allocations from 92% to 64% (when 49 variables used) and from 82% to 62% (when 32 variables used), when unknown specimens were allocated, does not reflect just the upward bias discussed above. As the number of specimens used to calculate the identity functions was reduced this also would have an effect and diminish the discriminatory power of the identity functions.

4.5 Discussion

4.5.1 Correlation and Covariation Patterns.

Within populations of aphids, correlation among the measurable characters can be due to the forced correlation of functional parts of the body, response to environmental factors, the pleiotrophic action of the same gene complex, or a combination of the above (Sokal, Bird and Riska 1980, Sokal and Riska 1981). Examination of the matrix of correlation coefficients between characters enables the evaluation of the redundancy of information in a character set, that is, the determination of the extent to which each character supplies unique information. Of particular biological relevance are the magnitude and sign and not necessarily the statistical significance of the correlation coefficients (Thorpe 1976). Common epigenetic control of characters will be evident in relatively high intra-locality correlations. It was in this sense that I used the correlation coefficient to compare the relationships between the characters within and among the population samples of C. nigra.

It has been shown for many insect groups, and for aphids (Eastop 1972) and scale insects (Blair, Blackith and Boratynski 1964, Boratynski 1952) that ratios of characters, such as "antennal formulae" have proved unreliable in separating species. For

example, aphid taxonomists have used the ratio of the fifth and sixth antennal segments to separate species (Eastop 1972). In this study and in the work of Sokal (1952, 1962), it was shown that the sixth antennal segment exhibits considerable morphogenetic independence, being much less correlated with overall size than the other antennal segments. A ratio of this segment with the fifth antennal segment, which is under the influence of size variation, would obviate the unique information of the sixth segment.

In a study of the correlation of antennal segments of the hemipteran Pyrrhocoris apterus, Alpatov and Boschko-Stepanenko (1928) showed that there was greater correlation between adjacent segments than alternate ones and that the correlation decreased from the proximal to the distal segments. Sokal (1952, 1962) found this to hold for antennal segments and hind leg segments of the aphid Pemphigus populitransversus. This was also the case with C. nigra; this is particularly evident in the correlation tables calculated from the combined samples (n = 380) (Table VII).

It has been stated (Blackith 1960, Sokal 1962) that there are only two or three biologically meaningful components of morphological variation in insects. However, this impression may simply be the result of not selecting enough characters, types of characters, and geographic samples to adequately represent the variation which is present. With the exception of studies on the geographic variation of gall-forming aphids (Sokal et al 1980, Sokal

and Riska 1981, Wool 1977) and my work on Adelges piceae (Foottit 1979), other taxonomic studies of aphids in which morphometric techniques have been used have dealt with a relatively small number of characters. The number of characters that were analyzed ranged from 8, used to separate species of Amphorophora (Blackman, Eastop and Hills 1977), to 16 used to separate morphs of Metopolophium dirhodum (Walker)(Hand 1986).

There are relatively few additional studies where morphometric variation within an aphid species has been studied. Not only did these studies usually test a relatively small number of characters, the characters that were chosen were almost exclusively continuous measurements; no setal counts and few setal length measurements have been considered. For example, Hampson and Madge (1986) used 9 variables, all of which were body dimensions, to examine variation in clones of Phorodon humuli (Schrank) and Jeffers (1967) used mostly continuous measurements to examine variation within a sample of an unnamed species of Adelgidae.

This study has shown that while there is a major component of size-related variation in samples of C. nigra, there are other components of morphological variation present as well. Some of this variation is in the form of shape changes, which may or may not be related to size changes (allometry). Some components of variation, particularly those represented by some of the setal counts, are independent of size variation, as shown in both the correlation analyses and the principal component analyses. Finally, there are

strong, internal correlations of characters of related function, such as those of the hind leg, which are correlated with separate components of variation, and which represent adaptation to particular modes of living. Any or all of these sources of variation may prove useful in the establishment of species boundaries.

4.5.2 Geographic Variation.

The lack of geographically-defined clusters of the population samples of C. nigra, with the exception of some relatively localized sample pairs, could be due to a number of factors. However, the most important one is the overriding effect of size variation which in itself could be due to a number of non-genetic factors which are likely to be relatively localized.

Individual size in aphids is a consequence of the interaction of nutrition and temperature on the growth and development rate (Dixon 1985). Additional factors, such as crowding, are known to also have an effect on aphid size (Murdie 1965). When a change in body size of an organism occurs, this in turn results in concomittant changes in many developmental and morphological relationships of an organism (Strauss 1985). Size and shape covary, that is there is a changing relationship between the two components of variation (Gould 1966). Many of the variables or functional groups of variables which showed patterns of variation on the

principal components subsequent to the main, size component were likely due to shape changes in response to size variation.

In a study of gall-forming aphids in relation to climate, Wool (1977) found a strong size effect on the first principal component. This was the result of a geographic pattern where the largest aphids were located in areas of lower and more variable temperatures. In the larger aphids, the surface area to volume ratio is smaller; they therefore lose less heat energy in these climatic conditions.

Other studies of the geographic variation of aphids have found a similar lack of geographic patterns as was found in C. nigra. In an analysis of geographic variation in Pemphigus populitransversus, Sokal and Riska (1981) concluded that there was a lack of demonstrable and interpretable pattern in the morphological characters that were studied. From this work and the analysis of other Pemphigus species over much of the North American continent, they concluded that within a given locality there was considerable stochastic fluctuation of characters from one year to the next.

4.5.3 Character Selection.

The quantitative approach followed in this study allowed for a thorough analysis of the relationships among the variables considered for use in the taxonomic analysis of the Cinara species (Chapter 5). The morphometric techniques allowed for the

elimination of some highly correlated, redundant variables and those variables which proved to be unstable due to difficulties of measurement. This resulted in a more manageable data set without the loss of a great deal of information content necessary for the analysis of species relationships.

Examination of the correlation coefficients of the characters within the samples and for all samples of C. nigra combined revealed some important relationships with respect to the choice of a character set for the subsequent analysis of the Cinara species. Functional groups of characters, such as the antennal measurements and the hind leg dimensions, showed relationships of high internal correlation which allowed for the reduction of the character set without an excessive loss of information content.

The reduced character set is still a relatively large one when compared to the character sets of other aphid studies. The exception has been that of Sokal and his colleagues (Sokal et al. 1980, Sokal and Riska 1981) who have recommended the use of a large number of variables. I believe that it is important to include characters which sample as many body areas and components of variation as possible, for maximum information content. This is particularly important in the early stages of a biosystematic study of a group. The data set can be reduced, particularly for practical reasons, on an objective basis as the relationships among the variables becomes known.

Allocation procedures, involving the calculation of

identification functions, are a useful, objective means of evaluating the effect of the selection of different characters and the reduction in the number of characters on taxonomic discrimination. This technique also serves to portray the degree of phenetic overlap among the OTU's. This analysis showed that there was a slight loss of information content when the variable number was reduced from 49 to 32.

The results of this study support the claim (Neff and Marcus 1980, Pimentel 1979) that principal component analysis is a useful dimension-reducing technique. Common components of variation were revealed with population samples of C. nigra and the complexity of the variation was assessed. While the largest component of variation was size variation, there were other, some even independent, components of variation in the morphology of C. nigra.

The analysis demonstrated that there was variation in the magnitude and composition of the components of variation among the 19 samples of C. nigra and that the relationships of the functional groups of variables varied spatially. These results indicate that a species of aphid, even when it is characterized using techniques of multivariate analysis, has to be represented on the basis of geographical samples and on the basis of characters selected from a wide range of the holomorph.

Clearly, it is operationally impractical to measure 380 specimens of each Cinara species. However, the major components of variation which were shown in the analysis of the large (n = 380)

data set were also evident in the smaller (n = 20) samples. That is, the major size effect on the first component, the negative response of the hind leg dimensions and setal length measurements on the second component, the mixture of shape responses of the antennal and rostrum dimensions and of the setal counts, were all estimated by the smaller samples. In fact, it is evident that the best approach towards the morphometric characterization of a species of Cinara is not to emphasize a large sample but it is to emphasize some estimate of the geographic variation, whether it is stochastic variation or a recognizable geographic pattern.

A number of potentially useful taxonomic characters were identified, such as the dimensions of the sixth antennal segment, the measurements of the segments of the rostrum, and many of the setal counts. Many of these characters are of potential taxonomic value at the species level. In Chapter 5 the ability of these characters to discriminate between species of Cinara is tested.

5. MORPHOMETRIC VARIATION AND DISCRIMINATION BETWEEN SPECIES.

5.1 Introduction.

This chapter is concerned with the analysis of morphometric variation within and among species of Cinara. As was discussed in Chapter 4, there have been few studies of the morphometrics of taxonomic discrimination among species of aphids. Previous work has involved discrimination only between pairs of species or between morphs of the same species (see, for example, Blackman, Eastop and Hills 1977, Hand 1986). In addition to the characterization of morphometric trends within species of Cinara, the ability of the previously identified character set to discriminate between 9 species of Cinara is established. The use of a multivariate morphometric approach in this study allowed for the quantitative assessement of taxonomic discrimination and for the development of a clearer definition of the species boundaries than has been previously available in the literature on Cinara.

5.2 Methods and Materials

Samples of each putative species to be analyzed were selected after preliminary identification of a few specimens from each collection made in the field. Samples were selected so as to

include adequate sample sizes of the apterous morph, to include some geographic variation in the material to be studied, and, where possible, to include differences in feeding sites within the samples of the species. Of course, some species have uniform feeding sites; for example, C. parvicornis Hottes is confined to the new growth tips of the branches.

One species, C. oregonensis (Wilson), was not included in these analyses. While it is a morphologically distinct species, I did not collect it during the time I carried out the field surveys for material. Museum specimens of this species were not of adequate number and quality for the collection of morphometric data.

Among the geographic samples of Cinara species, I detected some morphological variation in the taxonomic characters previously used to distinguish between the species. Specifically, there were difficulties in separating all samples of C. medispinosa (Gillette and Palmer) and C. murrayanae (Gillette and Palmer) on the basis of the descriptive literature that was available on these species and on the basis of reference material in collections (Canadian National Collection, United States National Museum). Therefore, in addition to representative samples of "typical" C. medispinosa and "typical" C. murrayanae I included a sample of what appeared to be C. murrayanae without its characteristic dorsal pigmentation and which had setae which were intermediate in length between the "typical" forms of these two species.

Among the material of another species, C. contortae Hottes, there were samples which differed with respect to certain

morphological characteristics, including size and pigmentation differences, to the extent that it could be questioned whether or not these were the species C. contortae. Therefore, I grouped representative material into three categories, namely, "typical" C. contortae, "small, thin" C. contortae, and C. contortae with reduced dorsal pigmentation. The latter group was found feeding only on cankers.

Other taxa represented in the morphometric analyses were species, particularly C. nigra, C. pergandei (Wilson), and C. brevispinosa (Gillette and Palmer), which are comparatively well-defined. Also included were two species of Cinara from other Pinus host plants, namely, C. kuchea Hottes from Pinus monticola and C. ponderosae (Williams) from Pinus ponderosa. These above-mentioned species would serve as useful comparisons or "controls" against which the discriminatory ability of the variables could be tested. In addition, the morphometric variability patterns of these relatively well-defined species would serve as reference points against which the variability patterns of the species with doubtful boundaries could be compared.

Instead of representing each species by one sample, I decided to, where possible, group under each species or morphological category 5 sub-samples of 5 specimens each. This approach would, as a result, include some of the geographic heterogeneity in body size and associated features as this factor would likely have a substantial effect on the species discrimination process. In addition, single specimens could be taken from each sub-sample for

use in the allocation test of "unknown" specimens, and still leave a sample size (n = 20) that would be large enough for computation of the identification functions. The exceptions were C. murrayanae (reduced pigmentation) where only 4 sub-samples of 5 specimens each were available and C. parvicornis where 3 sub-samples of 4 specimens each and 1 sub-sample of 3 specimens were available.

In total, 286 specimens of the Cinara species were measured for the 32 morphological variables, as identified in Chapter 4, for a total of 9,152 measurements. To avoid bias, the samples and sub-samples were not measured in any particular geographic or species-based sequence. The collection data for the 12 main species or representative types, and their sub-samples, are given in Table XII.

Descriptive statistics were calculated for all 32 variables for all 12 species or representative samples. The mean, the standard error and the coefficient of variation for each variable for each sample are given in Appendix 3.

The ranges of values of the coefficient of variation for the groups of variables were similar to those for C. nigra, with a few exceptions. Of the continuous measurements, the variable A6PTL showed a wide range of values (6.7 - 20.0) as this structure was more variable in some species than in others. The other variable showing a wide range of values for the coefficient of variation was SLAT5; this measurement also showed high values in the population samples of C. nigra. No species or sample showed consistently high or low values for the coefficient of variation.

Table XII. Collection data for samples and sub-samples of *Cinara* species collected on *Pinus contorta*, *P. monticola* and *P. ponderosa* .

Sample No.	Location	Date	Feeding Site
1.	*Cinara nigra* (n = 5 x 5)		
1-1	15 km E Quesnel, B. C.	30.VII.1980	Main stem
1-2	46 km NW Smithers, B. C.	3.VIII.1980	Main stem
1-3	5 km N Swan Hills, Alta.	9.VIII.1980	Main stem
1-4	Tête Jaune, B. C.	12.VIII.1980	Branch
1-5	Sparwood, B. C.	9.VII.1982	Main stem
2.	*Cinara pergandei* (n = 5 x 5)		
2-1	2 km N Nakusp, B. C.	22.VI.1980	Branch
2-2	15 km E Quesnel, B. C.	30.VII.1980	Branch
2-3	20 km N Swan Hills, Alta.	9.VIII.1980	Branch
2-4	18 km E Princeton, B. C.	1.VII.1981	Branch
2-5	20 km E Castlegar, B. C.	10.VII.1982	Branch
3.	*Cinara brevispinosa* (n = 5 x 5)		
3-1	7 km S Hixon, B. C.	31.VII.1980	Needles
3-2	2 km E Mt. Robson Prov. Park, B. C.	12.VIII.1980	Needles
3-3	3 km N Bowser, B. C.	7.VII.1981	Needles
3-4	West Yellowstone, MT.	6.VII.1982	Tip
3-5	Sparwood, B. C.	9.VII.1982	Tip

Table XII cont'd.

Sample No.	Location	Date	Feeding Site
4.	*Cinara parvicornis* (n = 1 x 3, 3 x 4)		
4-1	58 km E Edson, Alta.	10.VIII.1980	Tip
4-2	Mt. Robson Prov. Park, B. C.	12.VIII.1980	Tip
4-3	58 km E Edson, Alta.	10.VIII.1980	Tip
4-4	20 km N Chetwynd, B. C.	6.VIII.1980	Tip
5.	*Cinara contortae* - "typical" (n = 5 x 5)		
5-1	Christian Valley, B. C.	21.VI.1980	Canker
5-2	Bowser, B. C.	9.VII.1981	Stem
5-3	Priest Lake, ID.	29.VI.1982	Canker
5-4	5 km S Cascade, ID.	2.VII.1982	Canker
5-5	MacDonald Pass, 32 km W Helena, MT.	7.VII.1982	Tip
6.	*Cinara contortae* "small, thin" (n = 5 x 5)		
6-1	Bandit Springs, OR.	3.VIII.1975	Branch
6-2	Westbridge, B. C.	21.VI.1980	Branch
6-3	McLeese Lake, B. C.	29.VII.1980	Canker
6-4	McLeese Lake, B. C.	29.VII.1980	Branch
6-5	Fraser Lake, B. C.	1.VIII.1980	Main stem

Table XII cont'd.

Sample No.	Location	Date	Feeding Site
7.	*Cinara contortae* "reduced pigmentation" (n = 5 x 5)		
7-1	3 km S Newport, WA.	29.VI.1982	Canker
7-2	Seeley Lake, MT.	7.VII.1982	Canker
7-3	6 km S West Glacier, MT.	8.VII.1982	Canker
7-4	Burns Bog, Delta, B. C.	29.VII.1982	Canker
7-5	Port Coquitlam, B. C.	9.IX.1982	Canker
8.	*Cinara medispinosa* (n = 5 x 5)		
8-1	McLeese Lake, B. C.	29.VII.1980	Canker
8-2	Houston, B. C.	4.VIII.1980	Branch
8-3	Bowser, B. C.	7.VII.1981	Canker
8-4	10 km S West Yellowstone, MT.	6.VII.1982	Tip
8-5	11 km E Stagleap Prov. Park, B. C.	10.VII.1982	Branch
9.	*Cinara murrayanae* "typical" (n = 5 x 5)		
9-1	7 km S Swan Hills, Alta.	10.VIII.1980	Main stem
9-2	Pitt Meadows, B. C.	4.X.1981	Canker
9-3	Sparwood, B. C.	9.VII.1982	Canker
9-4	29 km E Castlegar, B. C.	10.VII.1982	Canker
9-5	Seeley Lake, MT.	8.VII.1982	Main stem

Table XII cont'd.

Sample No.	Location	Date	Feeding Site
10.	*Cinara murrayanae* "reduced pigmentation" (n = 4 x 5)		
10-1	20 km W Edson, Alta.	11.VIII.1980	Main stem
10-2	Mt. Robson Prov. Park, B. C.	12.VIII.1980	Main stem
10-3	Burns Bog, Delta, B. C.	2.X.1981	Canker
10-4	Burns Bog, Delta, B. C.	29.VII.1982	Canker
11.	*Cinara ponderosae* (n = 5 x 5) (Host: *Pinus ponderosa*)		
11-1	Goldendale, WA.	30.VI.1979	Main stem
11-2	Princeton, B. C.	3.VII.1981	Tip
11-3	62 km N Spokane, WA.	29.VI.1982	Tip
11-4	27 km N New Meadow, ID.	1.VII.1982	Tip
11-5	11 km E Stagleap Prov. Park, B. C.	10.VII.1982	Tip
12.	*Cinara kuchea* (n = 5 x 5) (Host: *Pinus monticola*)		
12-1	18 km N Shelter Bay, B. C.	22.VI.1980	Main stem
12-2	12 km N Nakusp, B. C.	22.VI.1980	Main stem
12-3	82 km W Revelstoke, B. C.	24.VI.1980	Main stem
12-4	72 km S Valemount, B. C.	13.VIII.1980	Main stem
12-5	Blue River, B. C.	13.VIII.1980	Main stem

Analysis of the normality of the samples using D'Agostino's D ($p \leq 0.01$) showed that over 86% of the sample by variable distributions were normal. This rate of normality was consistent with that calculated for the 19 C. nigra samples (87.8%) of the previous study. None of the 12 main samples showed consistently higher non-normality rates among the 32 variables. The only character that was consistently non-normal over the 12 main samples was the count of the number of subapical setae on sixth antennal segment (SNA6SA), as was the case with the analysis of the geographic samples of C. nigra. Therefore, no transformations of the data were carried out.

5.3 Morphometric Variation Within and Between Samples and Species.

Each sample was analyzed in the same manner as were the samples of C. nigra (Chapter 4). For each sample, a matrix of correlation coefficients was calculated for the 32 variables and inspected for trends. The correlation matrix for each sample was then subjected to a principal components analysis. The contributions (loadings) of the variables to the principal components were inspected for trends as were the projections of the individual specimens onto the major axes of variation.

Morphometric variation within each sample is presented and discussed below. For each sample a table is given which shows the contributions of the variables to the first three principal

components; these three components accounted for the major trends in variation. Also given are diagrams showing the ordination of the specimens of each sample onto the first three principal axes (I x II, I x III, II x III). The specimens of each sub-sample within each sample are connected by polygons; the exceptions are those cases where there is considerable overlap of the sub-samples. Where there is clear separation of the sub-samples, the samples are designated with a number corresponding to the number of the sub-sample as indicated in Table XII.

The first sample, of C. nigra, is presented for comparative purposes, as it was the subject of an extensive analysis in Chapter 4. The samples of C. contortae (No.'s 5, 6, 7) and the samples of C. medispinosa and C. murrayanae (No.'s 8, 9, 10) are treated as groups for further analysis. Overall trends in variation are discussed in the final section.

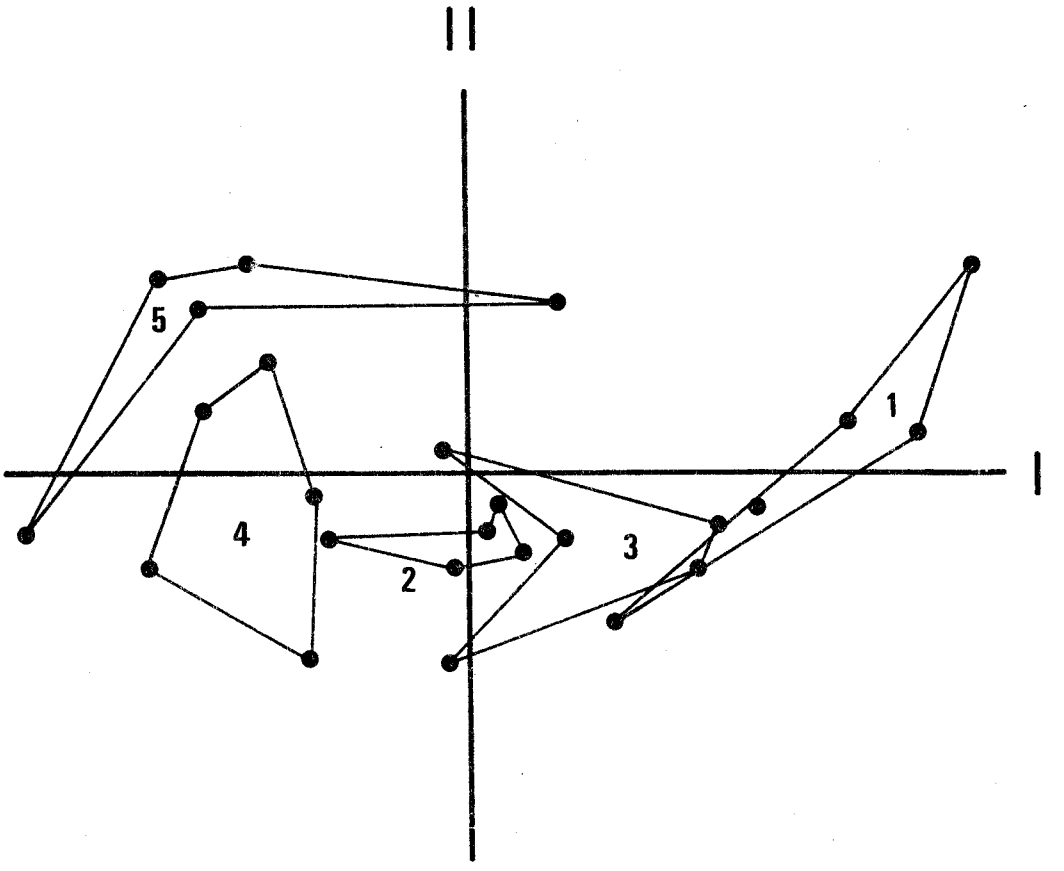
5.3.1 Cinara nigra.

The results of the principal component analysis of the sample of C. nigra are shown in Table XIII and in Figure 12. This species was characterized by a relatively large size component (principal component I, 43.6% of variation) to the extent that the specimens and sub-samples are orientated along this axis of variation on the basis of overall size, as estimated by the variable BL. The second and third principal components showed contrasts of sign and

Table XIII. Contributions of 32 morphological variables to the first three principal components calculated from 25 specimens of C. nigra.

VARIABLE	PRINCIPAL COMPONENT I	II	III
1. BL	0.908	-0.163	0.081
2. FRW	0.821	-0.290	0.143
2. A2L	0.895	0.070	0.095
4. A3L	0.826	0.280	0.315
5. A4L	0.861	0.063	-0.205
6. A5L	0.778	0.024	-0.434
7. A6BL	0.779	-0.014	0.219
8. A6BW	0.634	0.387	0.200
9. A6PTL	0.195	0.521	-0.341
10. R5L	0.500	-0.527	-0.214
11. R4L	0.873	-0.176	-0.065
12. R3L	0.300	-0.355	-0.504
13. R2L	0.503	-0.094	-0.429
14. FL	0.943	0.136	0.047
15. FW	0.826	-0.027	0.248
16. TL	0.861	0.176	-0.166
17. TS1VL	0.831	0.109	-0.193
18. TS2L	0.929	0.034	-0.180
19. SLA3	0.611	-0.608	0.070
20. SLGP	0.677	-0.477	0.205
21. SLAT5	0.442	0.299	0.284
22. SLT	0.626	-0.367	0.099
23. SNA6SA	0.007	0.464	-0.590
24. SNA6B	0.531	0.351	0.362
25. SNA5	0.634	-0.021	-0.248
26. SNA2	-0.215	0.484	-0.423
27. SNR4	0.339	0.097	-0.463
28. SNGP	0.714	0.471	0.204
29. SNAT5	-0.093	0.345	0.290
30. SNAT8	0.377	0.423	0.442
31. SNC	0.539	0.232	-0.367
32. SNT	0.381	-0.074	0.203
Relative Percentage of Variability	43.6	9.7	8.7

Figure 12. Diagrams showing principal component ordination of 25 specimens of Cinara nigra, projected onto the first three principal axes (I x II, I x III, II x III), based on the analysis of 32 morphological variables (Table XIII). See Table XII for collection data. The polygons connect the specimens of each sub-sample; numbers refer to sub-sample designations as in Table XII.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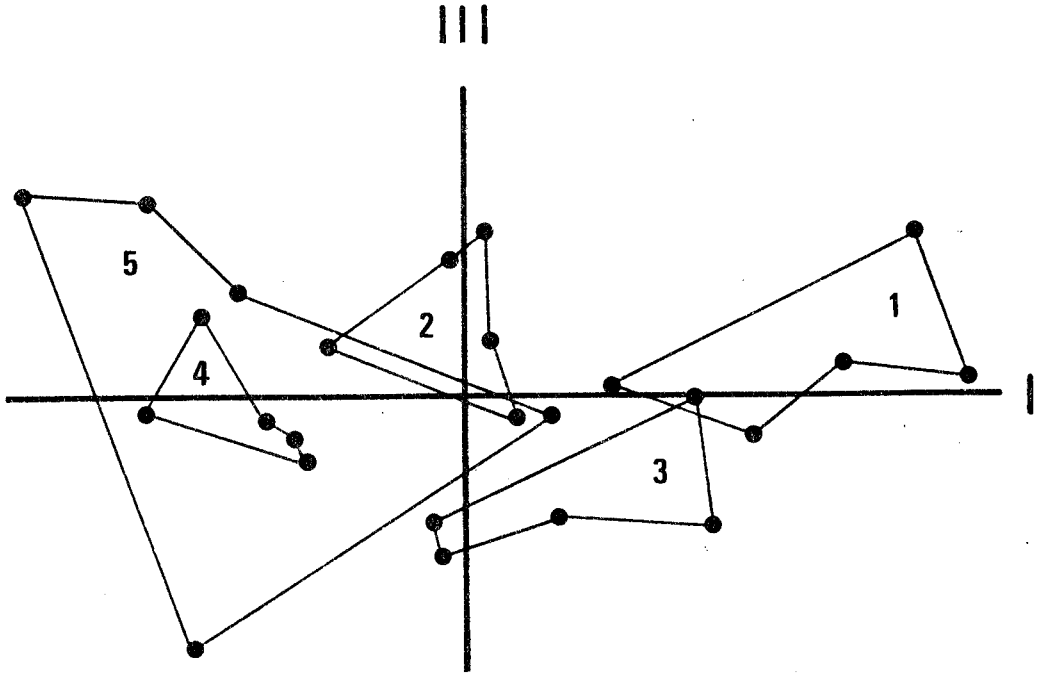
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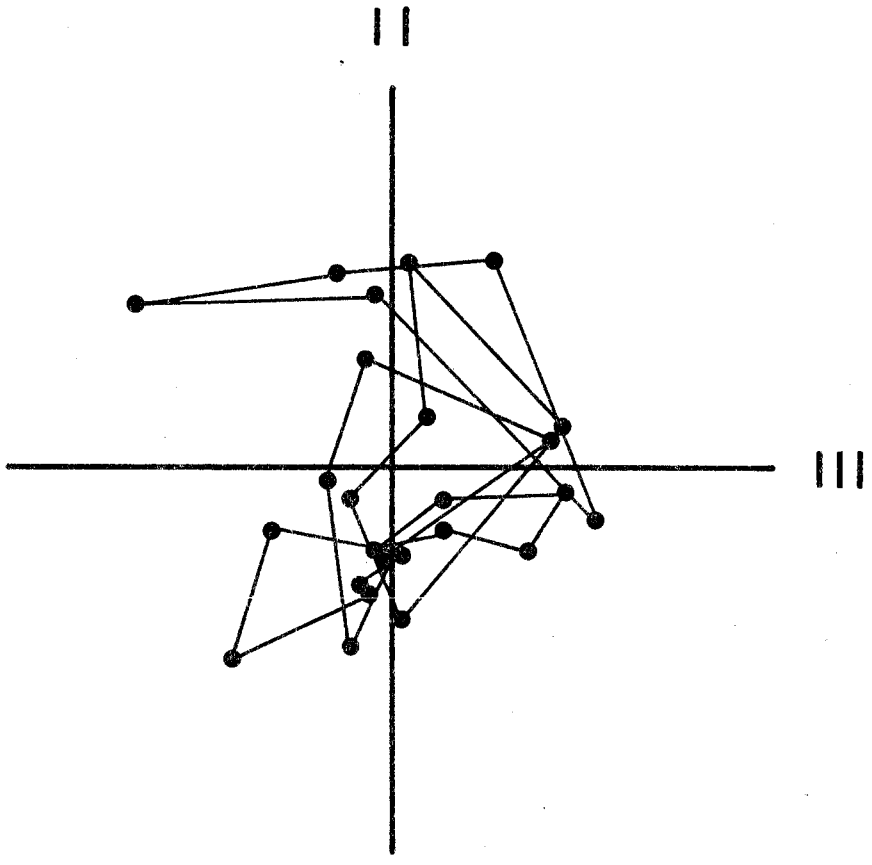
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magnitude of the groups of variables, particularly the tarsus dimensions, antennal dimensions, and the rostrum dimensions. This indicated that there was allometric and shape variation in this species; this was evident in the reorientation of the sub-samples when the plots of principal axes I x II and I x III were compared. No orientation of the sub-samples on a geographic basis was evident.

5.3.2 *Cinara pergandei*

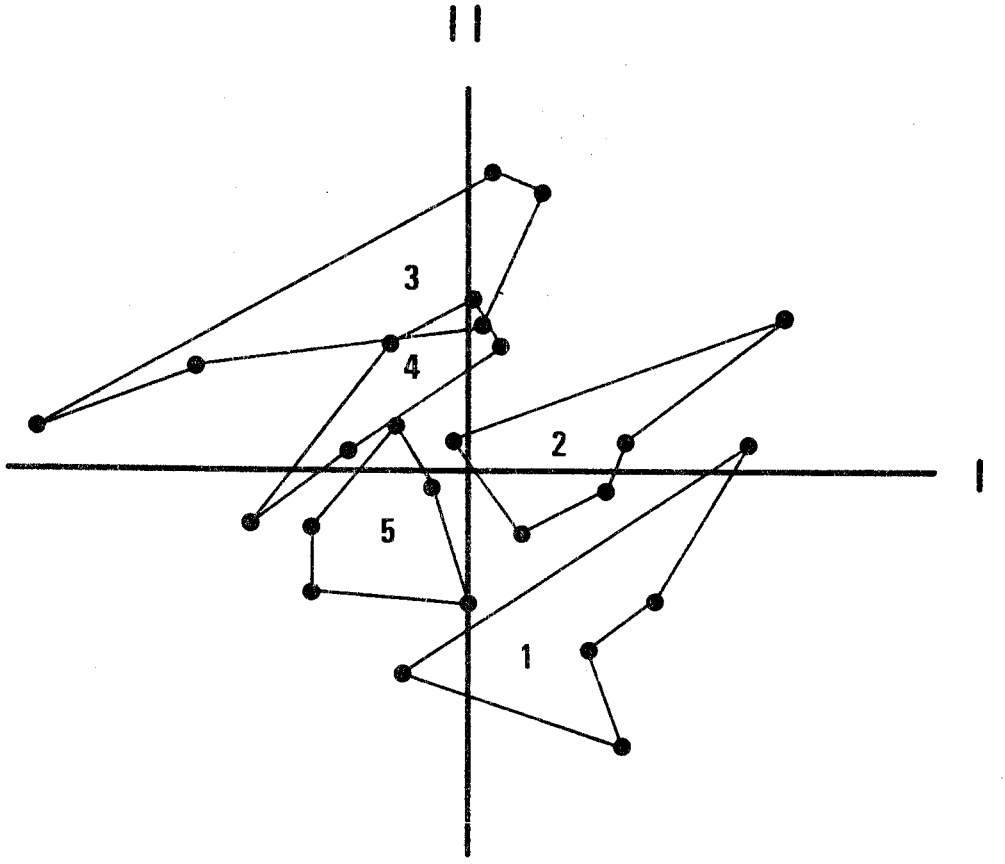
The results of the principal component analysis of the sample of *C. pergandei* are shown in Table XIV and in Figure 13. This species exhibited patterns of variation which were different from those of the other *Cinara* species. The first component accounted for a relatively small amount (19.7%) of the total variation and it did not consist of loadings of uniform sign. Most of the continuous variables increased along this axis, with the exception of R2 and FW, indicating a general increase in size and correlated dimensions. Most of the setal length measurements and setal counts decreased along this axis.

The second component (14.0%) of variation consisted of contrasts of sign of dimensions of the antenna, hind leg and rostrum, indicating changes in shape. The third component was strongly influenced by a decrease in all setal length measurements. Even some of the other, relatively minor, components exhibited patterns of variation. For example, the fifth component (7.0% of

Table XIV. Contributions of 32 morphological variables to the first three principal components calculated from 25 specimens of C. pergandei.

VARIABLE	PRINCIPAL COMPONENT I	II	III
1. BL	0.637	-0.107	0.263
2. FRW	0.602	0.162	-0.230
3. A2L	0.135	0.494	0.367
4. A3L	0.791	-0.066	0.253
5. A4L	0.396	0.775	0.191
6. A5L	0.551	0.719	0.229
7. A6BL	0.523	0.562	-0.257
8. A6BW	0.461	-0.123	-0.383
9. A6PTL	0.592	-0.168	-0.100
10. R5L	0.313	-0.131	-0.019
11. R4L	0.662	-0.112	-0.215
12. R3L	0.102	0.532	-0.403
13. R2L	-0.103	0.014	0.166
14. FL	0.693	-0.075	-0.277
15. FW	-0.188	-0.063	-0.612
16. TL	0.681	0.219	0.045
17. TS1VL	0.536	-0.011	-0.037
18. TS2L	0.769	0.033	0.114
19. SLA3	-0.429	0.417	-0.418
20. SLGP	0.088	0.229	-0.720
21. SLAT5	-0.149	0.483	-0.429
22. SLT	-0.238	0.630	-0.475
23. SNA6SA	-0.093	-0.008	0.305
24. SNA6B	0.420	0.377	0.015
25. SNA5	0.096	0.147	0.483
26. SNA2	-0.300	0.350	0.311
27. SNR4	-0.199	-0.089	-0.377
28. SNGP	-0.405	0.240	0.100
29. SNAT5	-0.567	0.479	0.257
30. SNAT8	-0.131	0.417	0.414
31. SNC	-0.137	0.609	0.438
32. SNT	-0.254	0.591	-0.301
Relative Percentage of Variability	19.7	14.0	11.1

Figure 13. Diagrams showing principal component ordination of 25 specimens of Cinara pergandei, projected onto the first three principal axes (I x II, I x III, II x III), based on the analysis of 32 morphological variables (Table XIV). See Table XII for collection data. The polygons connect the specimens of each sub-sample; numbers refer to sub-sample designations as in Table XII.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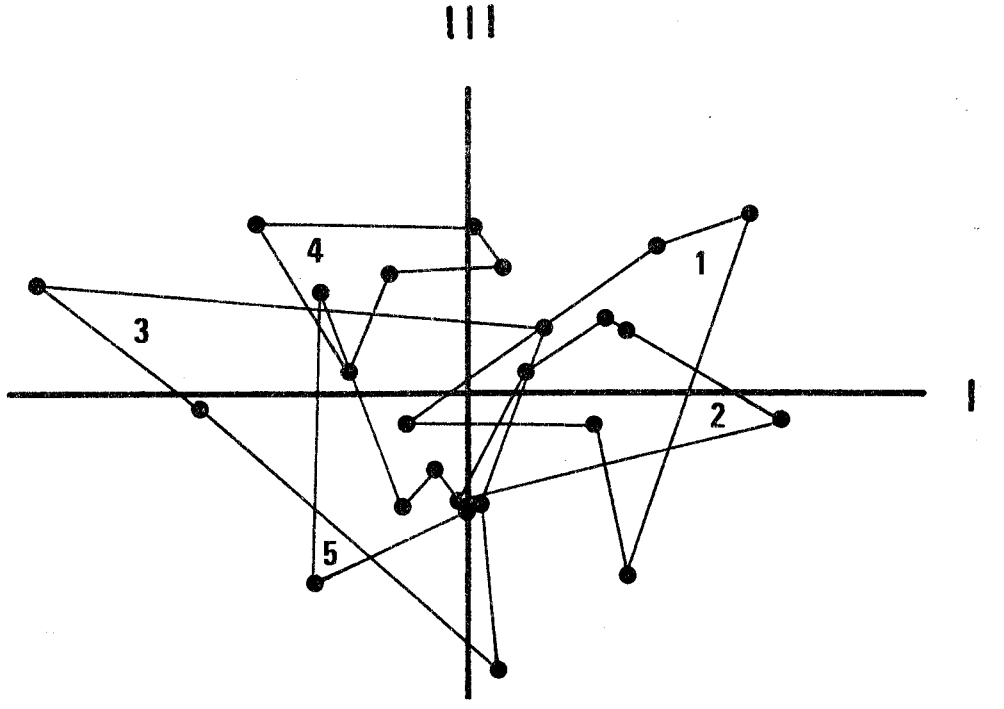
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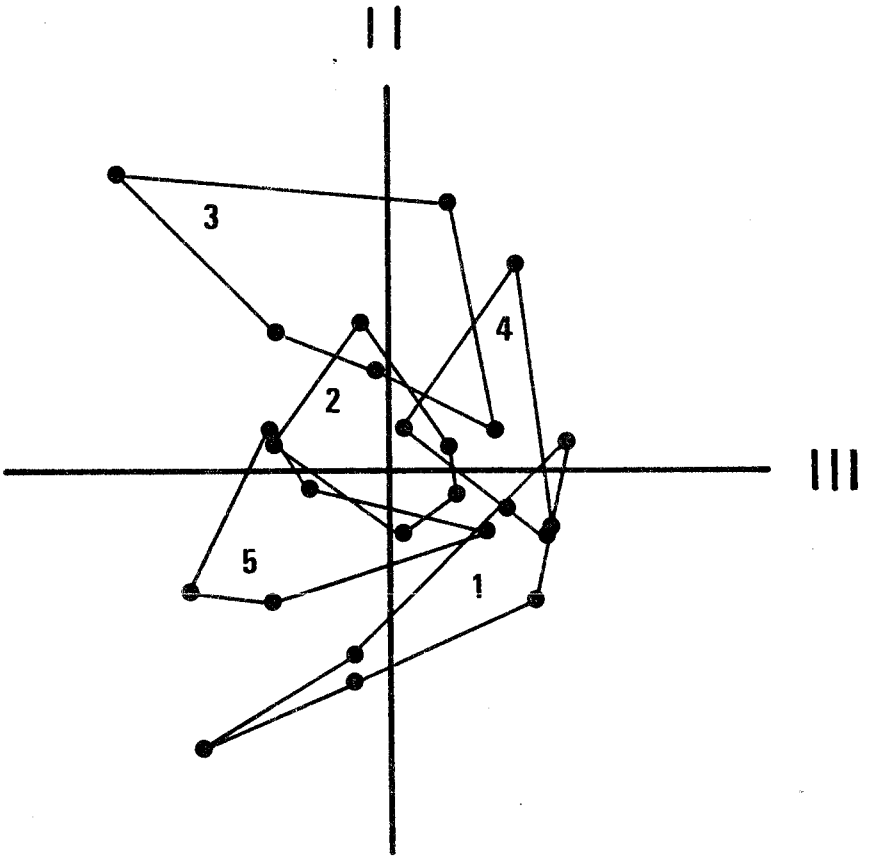
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variation) showed relatively small but consistent decreases of all dimensions of the antennae and hind leg.

The variation along principal axes I and II served to separate the 5 sub-samples (Figure 13), indicating the presence of some geographic variation in these morphometric trends, particularly in the dimensions of the antennae.

5.3.3 Cinara brevispinosa

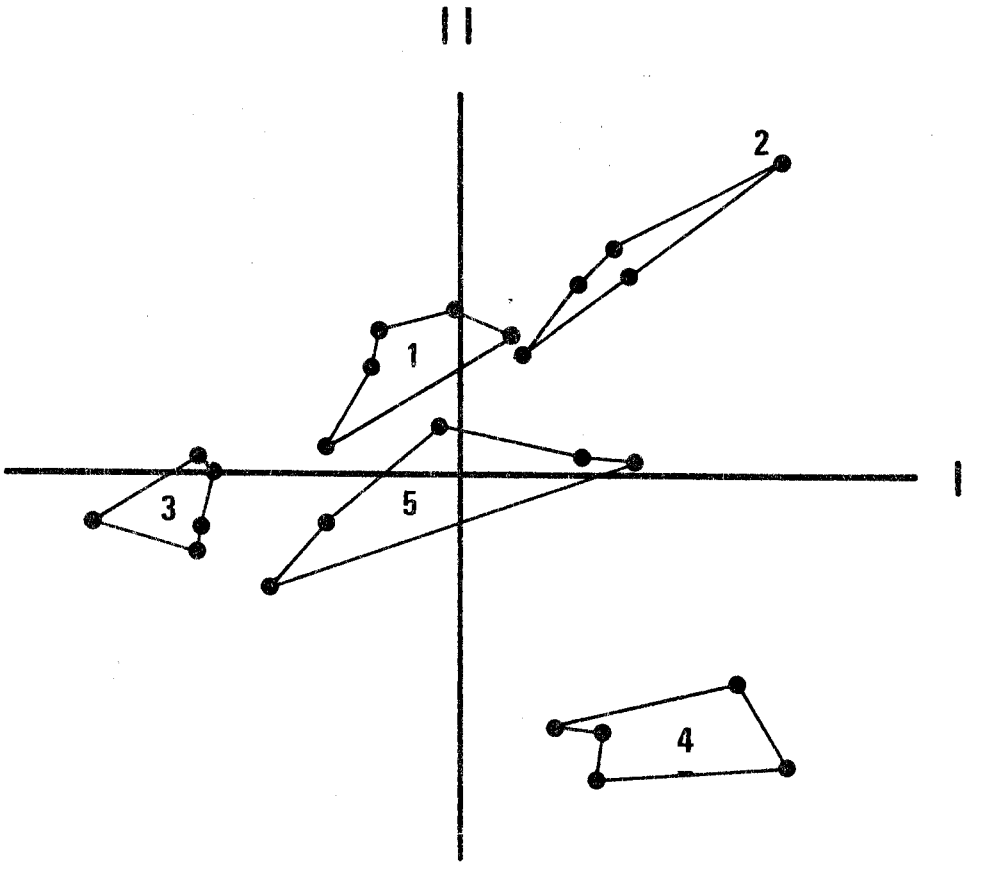
The results of the principal component analysis of the sample of C. brevispinosa are shown in Table XV and in Figure 14. This species was characterized by a relatively moderate size component (principal component I, 27.4% of variation). The continuous measurements, including the setal length measurements showed high, positive contributions on this component, with the exception of the dimensions of antennal segments V to VI. The setal counts on the antennal segments showed weak to negative loadings on this axis, indicating that variation in the antennal variables is partially independent of the general size factor in this species.

The specimens in the sub-samples were oriented along principal axis I (Figure 14) according to overall size as was estimated by the variable BL. However, the sub-samples were also oriented along principal axes II and III. These components exhibited numerous contrasts of sign and magnitude of loadings within functional groups of measurements. There were marked trends with respect to the

Table XV . Contributions of 32 morphological variables to the first three principal components calculated from 25 specimens of C. brevispinosa.

VARIABLE	PRINCIPAL COMPONENT I	II	III
1. BL	0.827	-0.475	0.039
2. FRW	0.818	-0.406	0.018
3. A2L	0.565	-0.033	-0.350
4. A3L	0.852	0.120	0.230
5. A4L	0.031	0.896	0.062
6. A5L	-0.042	0.943	0.102
7. A6BL	0.450	-0.337	-0.627
8. A6BW	-0.278	-0.071	-0.471
9. A6PTL	0.014	0.869	0.273
10. R51	0.196	0.146	-0.540
11. R4L	0.377	-0.022	-0.621
12. R3L	0.729	0.298	-0.269
13. R2L	0.631	-0.332	0.253
14. FL	0.910	0.294	0.135
15. FW	0.635	0.155	-0.294
16. TL	0.807	0.377	0.116
17. TS1VL	0.508	0.666	0.213
18. TS2L	0.636	0.551	-0.177
19. SLA3	0.238	0.172	0.591
20. SLGP	0.738	-0.161	0.230
21. SLAT5	0.691	0.382	0.016
22. SLT	0.622	0.040	0.137
23. SNA6SA	-0.031	0.258	0.058
24. SNA6B	0.172	0.374	-0.317
25. SNA5	-0.112	0.817	0.106
26. SNA2	-0.100	0.223	-0.592
27. SNR4	-0.041	0.489	-0.507
28. SNGP	0.423	-0.094	-0.219
29. SNAT5	0.536	-0.555	-0.295
30. SNAT8	0.530	-0.462	-0.071
31. SNC	0.326	-0.206	0.618
32. SNT	-0.213	0.463	-0.583
Relative Percentage of Variability	27.4	19.8	12.2

Figure 14. Diagrams showing principal component ordination of 25 specimens of Cinara brevispinosa, projected onto the first three principal axes (I x II, I x III, II x III), based on the analysis of 32 morphological variables (Table XV). See Table XII for collection data. The polygons connect the specimens of each sub-sample; numbers refer to sub-sample designations as in Table XII.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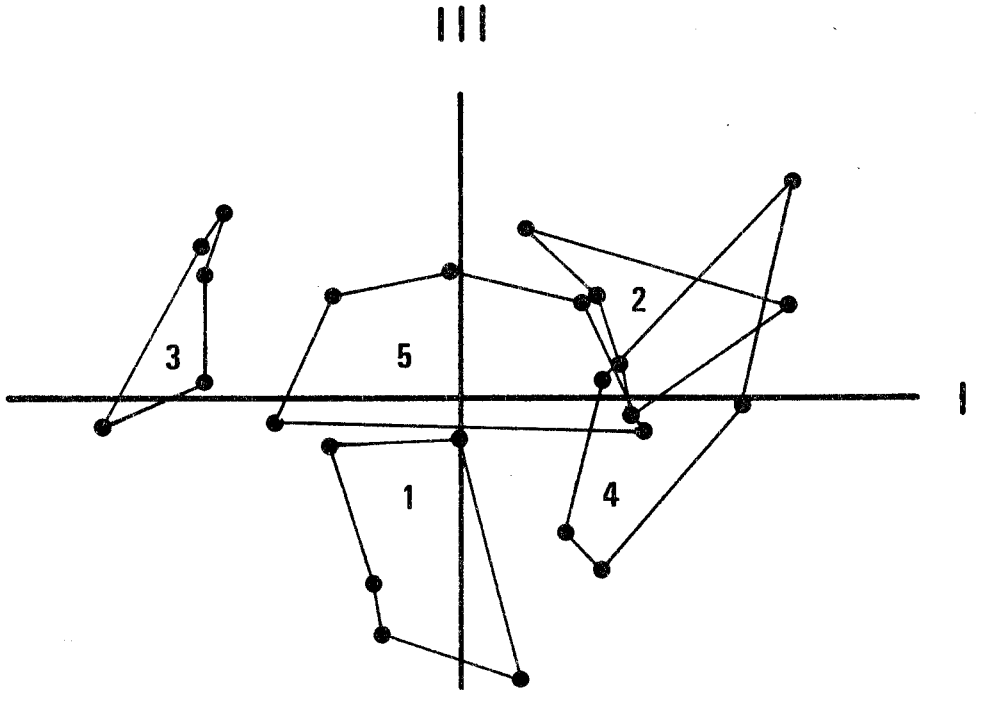
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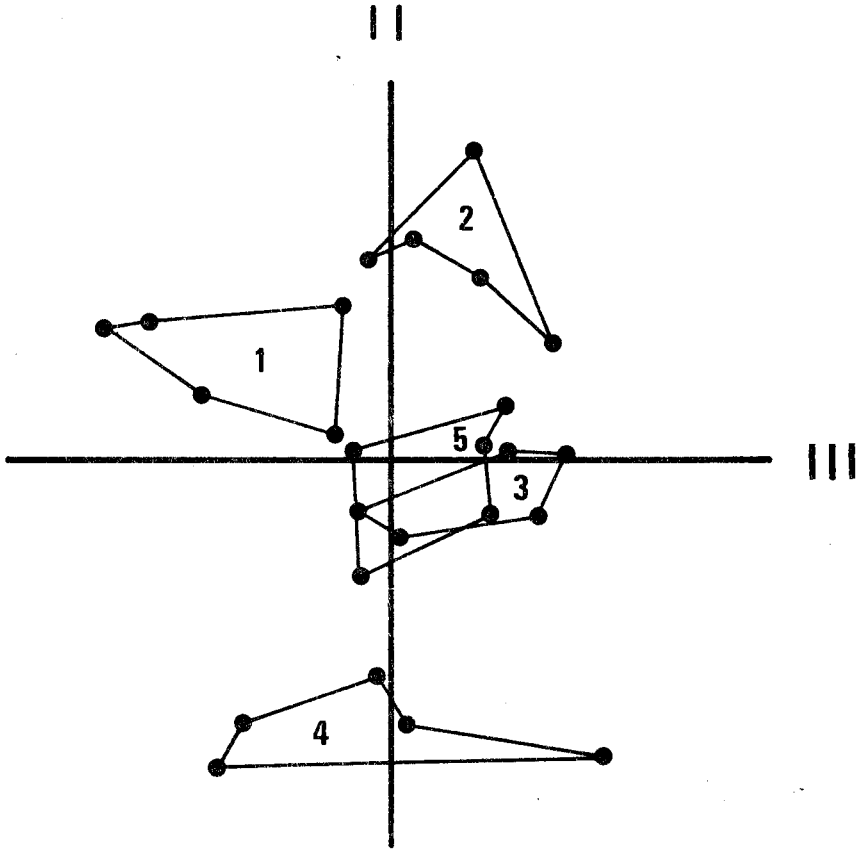
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setal counts on the abdomen (SNGP, SNAT5, SNAT8, SNC) on principal component II and the rostrum dimensions on principal component III.

5.3.4 Cinara parvicornis

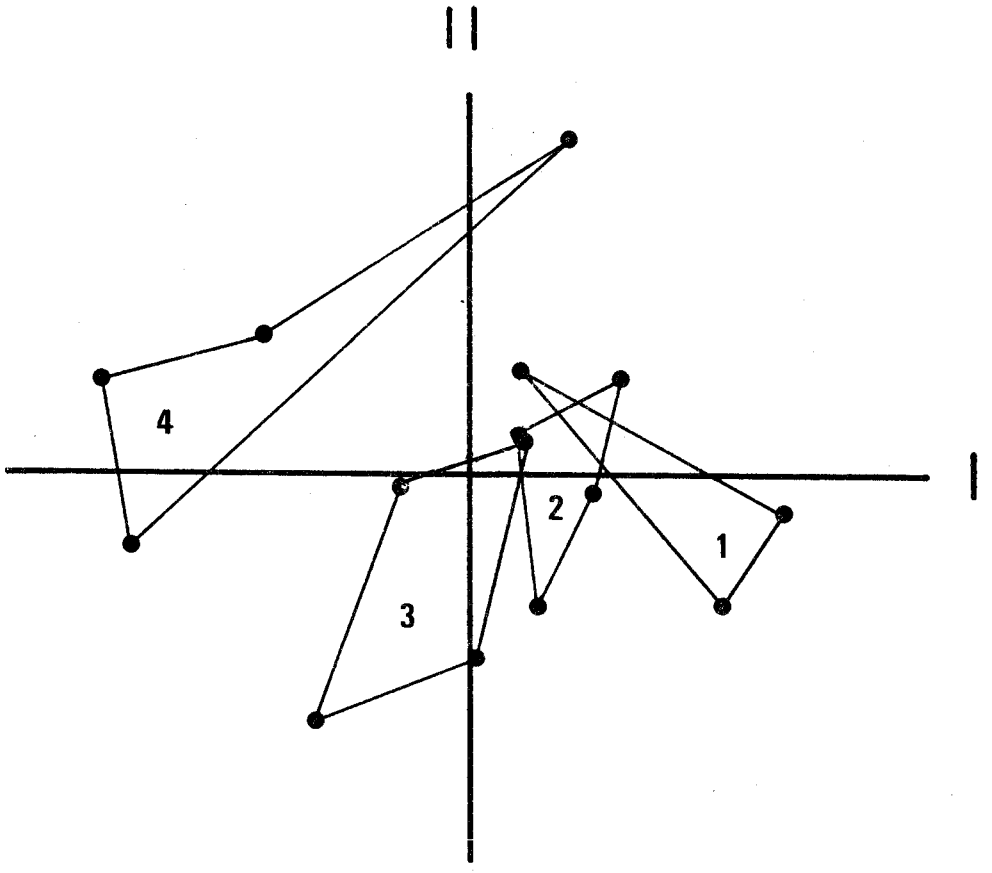
The results of the principal component analysis of the sample of C. parvicornis are shown in Table XVI and in Figure 15. This species exhibited a relatively moderate size component (principal component I, 25.7% of variation) with strong contributions from the leg dimensions. Other groups of variables showed a mixture of loadings, both of sign and magnitude. For example, of the measurements of the rostrum, only the variable R4 was strongly correlated with overall size.

The dimensions of the antenna showed a mixture of contributions to principal components I, II, and III. Only A2L was significantly correlated with BL ($r = 0.71$); it showed a relatively large contribution to PC I. In addition, all setal counts on the antennal segments showed a negative trend on principal component III. The nature of the contribution of the antennal variables to the second and third principal components indicates that each antennal segment has its own independent morphometric characteristics. Examination of the correlation coefficients showed that there was no significant internal correlation among the antennal segments, with the exception of the dimensions of the sixth segment.

Table XVI. Contributions of 32 morphological variables to the first three principal components calculated from 25 specimens of C. parvicornis.

VARIABLE	PRINCIPAL COMPONENT I	II	III
1. BL	0.857	-0.150	0.132
2. FRW	0.530	0.622	-0.254
3. A2L	0.814	-0.090	0.234
4. A3L	0.389	-0.039	0.471
5. A4L	-0.025	0.827	-0.023
6. A5L	0.319	0.386	-0.699
7. A6BL	0.397	-0.043	-0.340
8. A6BW	0.103	0.564	0.180
9. A6PTL	0.019	0.720	-0.169
10. R5L	-0.007	-0.268	0.773
11. R4L	0.814	0.082	0.227
12. R3L	-0.063	0.168	0.182
13. R2L	-0.089	0.666	0.542
14. FL	0.906	-0.191	0.090
15. FW	0.692	0.227	0.100
16. TL	0.912	-0.040	-0.088
17. TS1VL	0.782	0.346	0.004
18. TS2L	0.829	0.081	-0.073
19. SLA3	0.288	0.192	-0.161
20. SLGP	0.059	-0.045	-0.242
21. SLAT5	0.383	-0.715	-0.031
22. SLT	0.207	-0.011	0.678
23. SNA6SA	-0.392	0.073	-0.388
24. SNA6B	0.398	0.604	-0.127
25. SNA5	0.826	0.067	-0.228
26. SNA2	-0.086	0.083	-0.281
27. SNR4	0.071	0.355	0.570
28. SNGP	0.632	-0.467	-0.273
29. SNAT5	-0.291	0.194	0.430
30. SNAT8	-0.008	0.417	-0.147
31. SNC	0.285	-0.583	-0.367
32. SNT	0.422	-0.224	0.506
Relative Percentage of Variability	25.7	14.8	12.1

Figure 15. Diagrams showing principal component ordination of 15 specimens of Cinara parvicornis, projected onto the first three principal axes (I x II, I x III, II x III), based on the analysis of 32 morphological variables (Table XVI). See Table XII for collection data. The polygons connect the specimens of each sub-sample; numbers refer to sub-sample designations as in Table XII.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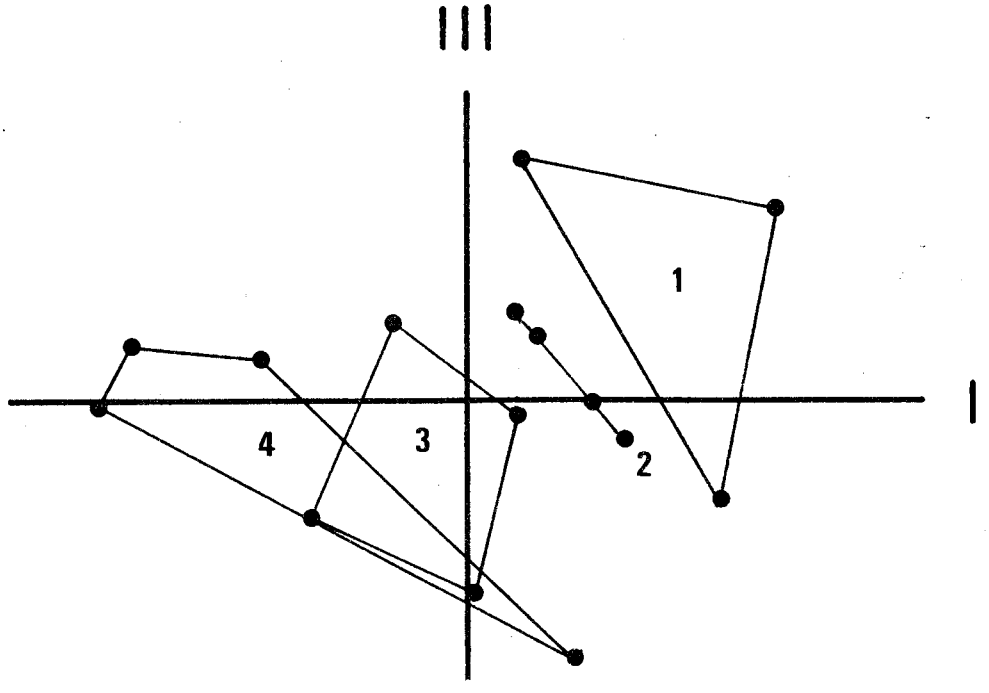
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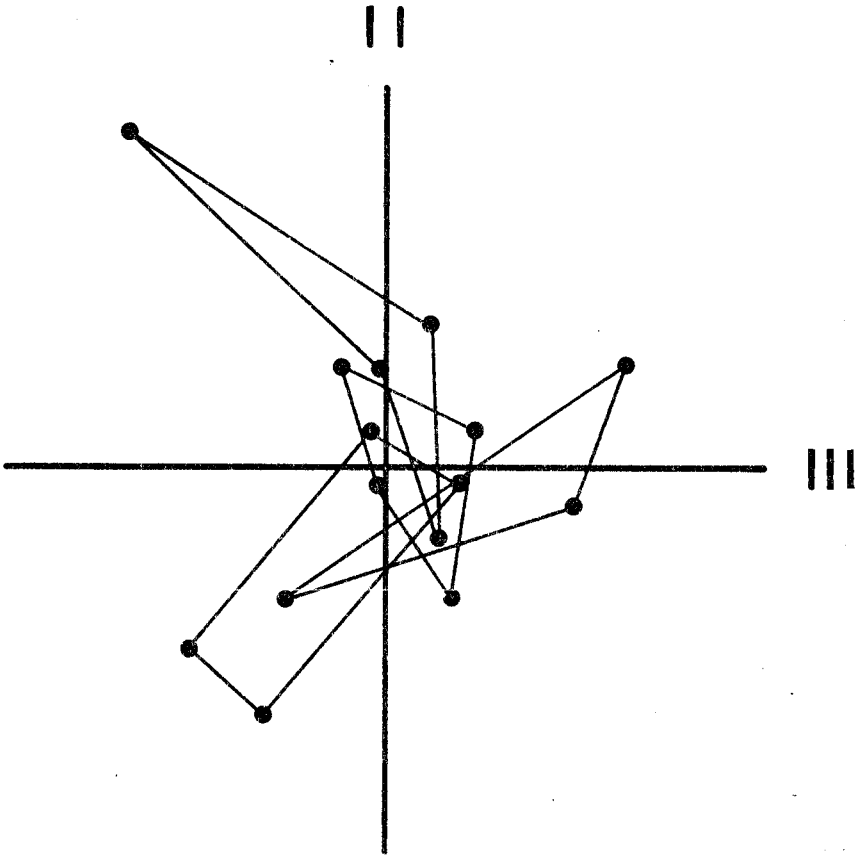
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5.3.5 Cinara contortae - "typical".

The results of the principal component analysis of the sample of C. contortae - "typical" are shown in Table XVII and in Figure 16. This sample was characterized by a relatively large size component (principal component I, 49.4% of variation). All variables had positive, often large, loadings on this component. Specimens in the sub-samples were oriented along this axis with respect to overall size as estimated by the variable BL.

The second principal component was characterized by contrasts in the loadings of antennal segments II to IV compared to V and VI and by reduction in most hind leg dimensions. Principal component III showed a strong negative trend in the rostrum dimensions and in the setal counts on the antennal segments. In comparison with principal component I, these two components accounted for relatively minor amounts of morphometric variation (principal component II, 9.1%; principal component III, 8.6% of variation). The sub-samples were not oriented separately with respect to these axes.

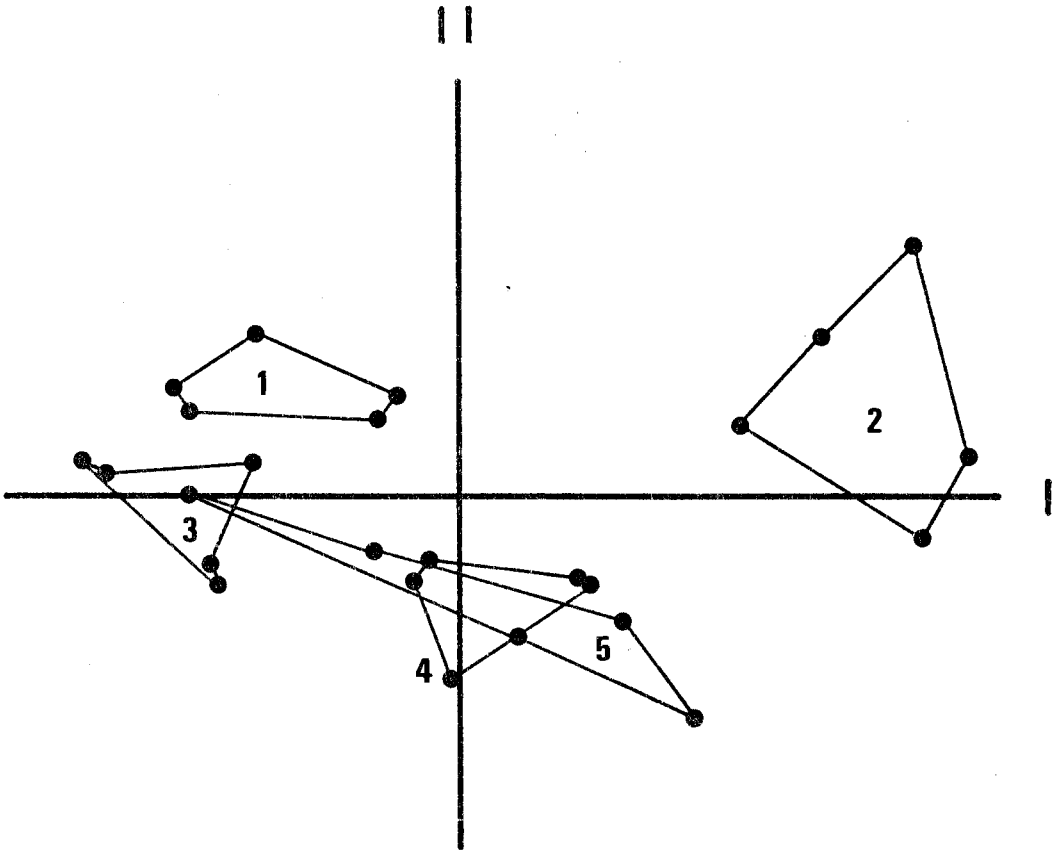
5.3.6 Cinara contortae - "small, thin".

The results of the principal component analysis of the sample of C. contortae - "small, thin" are shown in Table XVIII and in Figure 17. The first principal component exhibited a pattern

Table XVII Contributions of 32 morphological variables to the first three principal components calculated from 25 specimens of C. contortae - "typical".

VARIABLE	PRINCIPAL COMPONENT I	II	III
1. BL	0.728	-0.461	0.103
2. FRW	0.284	-0.760	0.047
3. A2L	0.760	-0.020	0.005
4. A3L	0.677	-0.409	-0.250
5. A4L	0.842	-0.267	0.290
6. A5L	0.950	0.038	-0.103
7. A6BL	0.908	0.107	0.104
8. A6BW	0.708	0.056	-0.373
9. A6PTL	0.683	0.042	-0.489
10. R5L	0.313	0.514	-0.404
11. R4L	0.912	0.013	-0.040
12. R3L	0.905	0.020	-0.122
13. R2L	0.448	-0.512	-0.511
14. FL	0.940	-0.204	0.097
15. FW	0.785	0.115	0.371
16. TL	0.927	-0.182	-0.120
17. TS1VL	0.706	-0.300	0.191
18. TS2L	0.948	-0.031	0.182
19. SLA3	0.814	0.166	0.210
20. SLGP	0.794	0.197	0.162
21. SLAT5	0.215	-0.303	0.762
22. SLT	0.706	0.027	0.185
23. SNA6SA	0.159	0.125	-0.502
24. SNA6B	0.546	0.264	-0.344
25. SNA5	0.731	-0.179	-0.387
26. SNA2	0.317	0.216	-0.069
27. SNR4	0.454	-0.075	-0.278
28. SNGP	0.530	0.626	0.099
29. SNAT5	0.456	0.390	0.424
30. SNAT8	0.802	0.234	0.157
31. SNC	0.811	0.274	0.107
21. SNT	0.472	0.390	0.009
Relative Percentage of Variability	49.3	9.1	8.6

Figure 16. Diagrams showing principal component ordination of 25 specimens of Cinara contortae "typical", projected onto the first three principal axes (I x II, I x III, II x III), based on the analysis of 32 morphological variables (Table XVII). See Table XII for collection data. The polygons connect the specimens of each sub-sample; numbers refer to sub-sample designations as in Table XII.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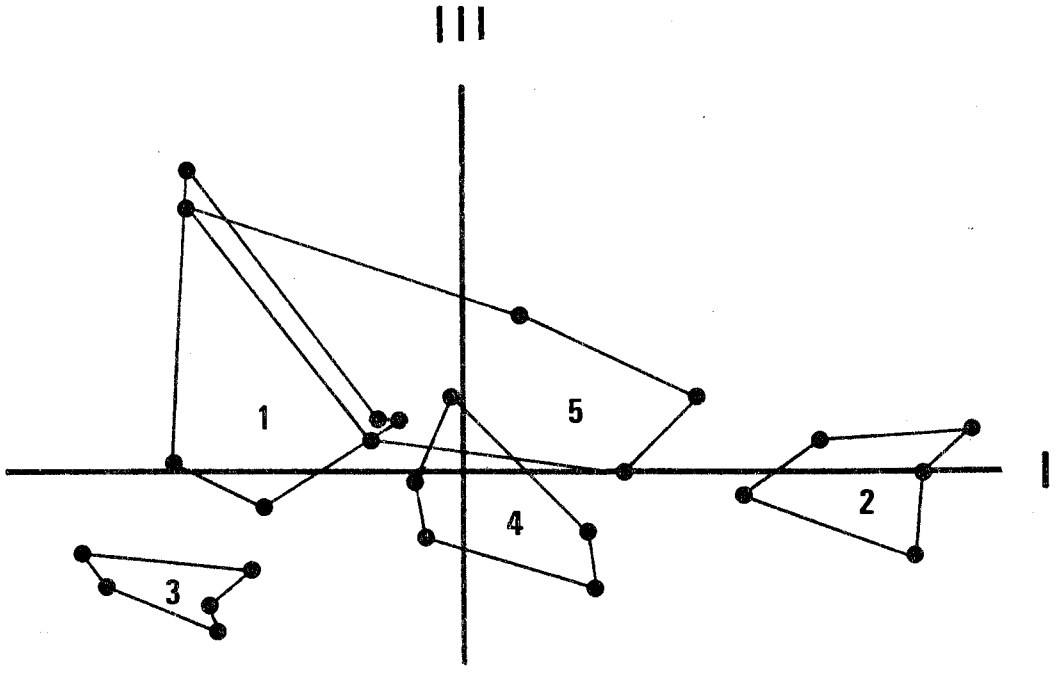
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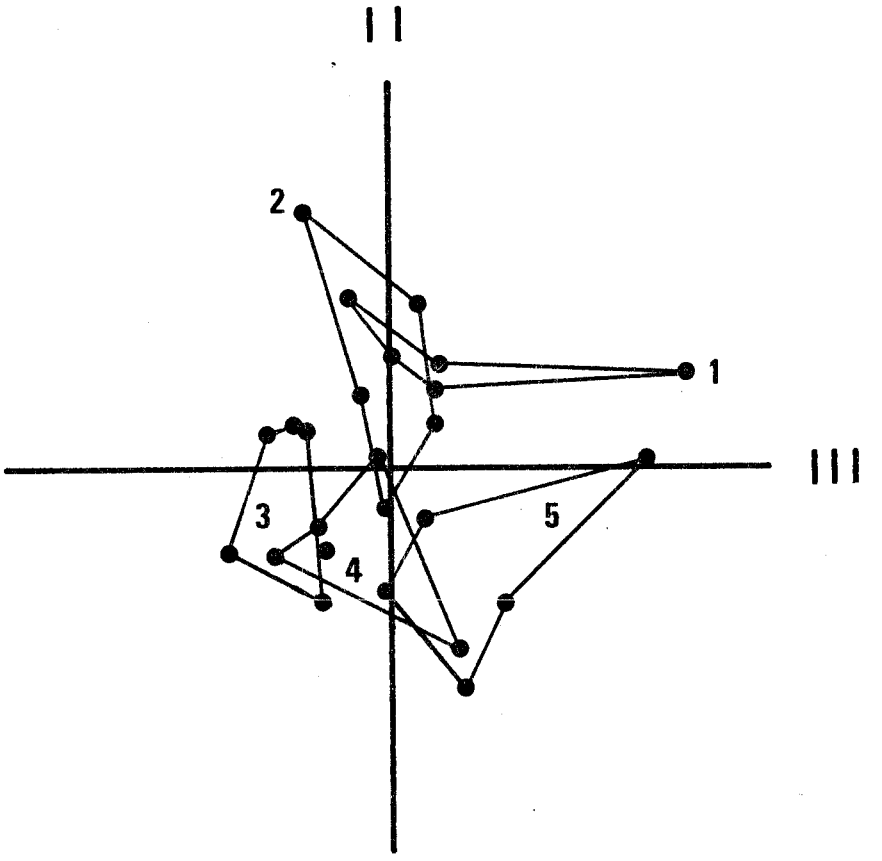
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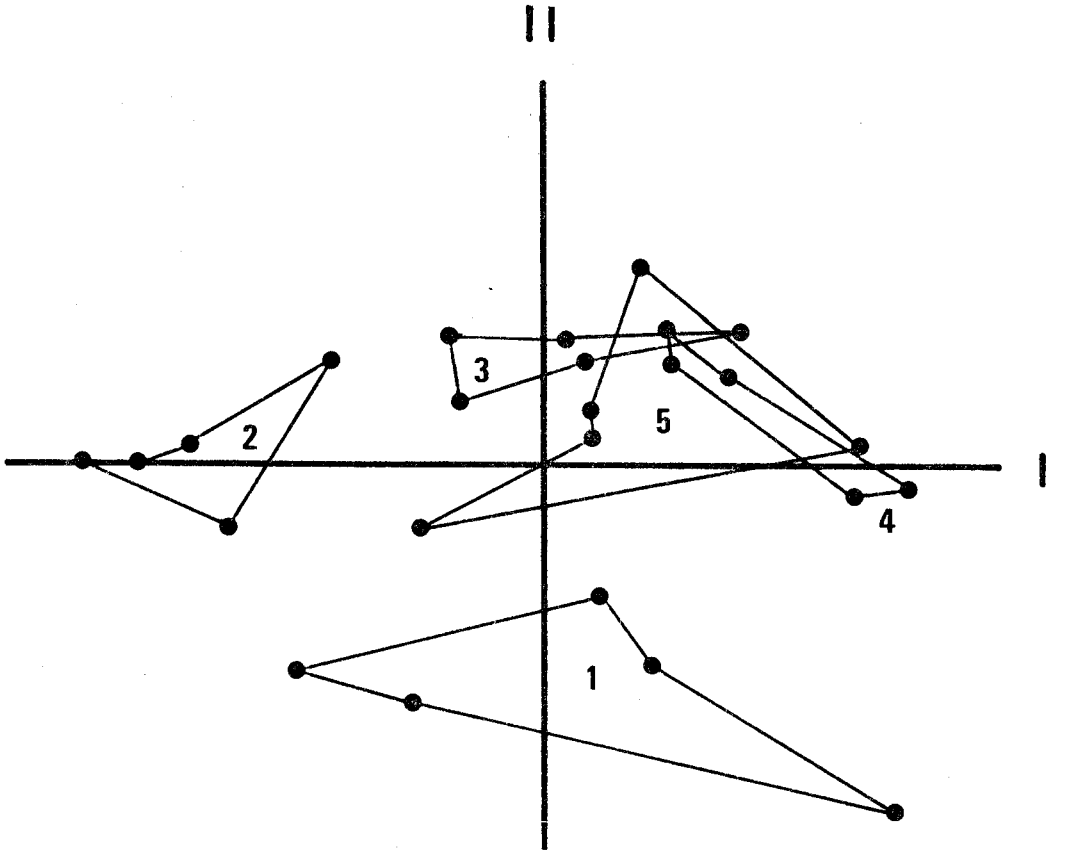
Table XVIII. Contributions of 32 morphological variables to the first three principal components calculated from 25 specimens of C. contortae - "small, thin".

VARIABLE	PRINCIPAL COMPONENT I	II	III
1. BL	0.666	-0.378	0.249
2. FRW	0.466	0.135	0.230
3. A2L	0.580	-0.504	-0.017
4. A3L	0.931	0.120	0.065
5. A4L	0.874	0.011	-0.158
6. A5L	0.882	-0.011	0.014
7. A6BL	0.649	-0.013	-0.241
8. A6BW	0.578	0.170	-0.237
9. A6PTL	0.473	-0.204	-0.610
10. R5L	-0.231	-0.459	-0.228
11. R4L	0.619	-0.077	-0.088
12. R3L	0.530	-0.523	-0.036
13. R2L	0.551	-0.337	-0.434
14. FL	0.855	-0.228	0.291
15. FW	0.528	-0.069	0.441
16. TL	0.936	-0.163	0.122
17. TS1VL	0.729	-0.393	0.174
18. TS2L	0.787	-0.468	-0.103
19. SLA3	0.651	0.647	0.209
20. SLGP	0.700	0.247	0.292
21. SLAT5	0.517	0.467	0.524
22. SLT	0.697	0.445	0.327
23. SNA6SA	-0.250	0.518	-0.342
24. SNA6B	0.600	0.108	-0.496
25. SNA5	0.498	0.341	-0.636
26. SNA2	0.602	0.410	-0.216
27. SNR4	0.533	-0.292	-0.237
28. SNGP	0.483	-0.087	0.320
29. SNAT5	0.451	0.442	-0.044
30. SNAT8	0.555	0.280	-0.261
31. SNC	0.194	0.572	-0.098
32. SNT	0.090	0.597	-0.223
Relative Percentage of Variability	38.2	12.7	8.8

Figure 17. Diagrams showing principal component ordination of 25 specimens of Cinara contortae "small, thin", projected onto the first three principal axes (I x II, I x III, II x III), based on the analysis of 32 morphological variables (Table XVIII). See Table XII for collection data. The polygons connect the specimens of each sub-sample; numbers refer to sub-sample designations as in Table XII.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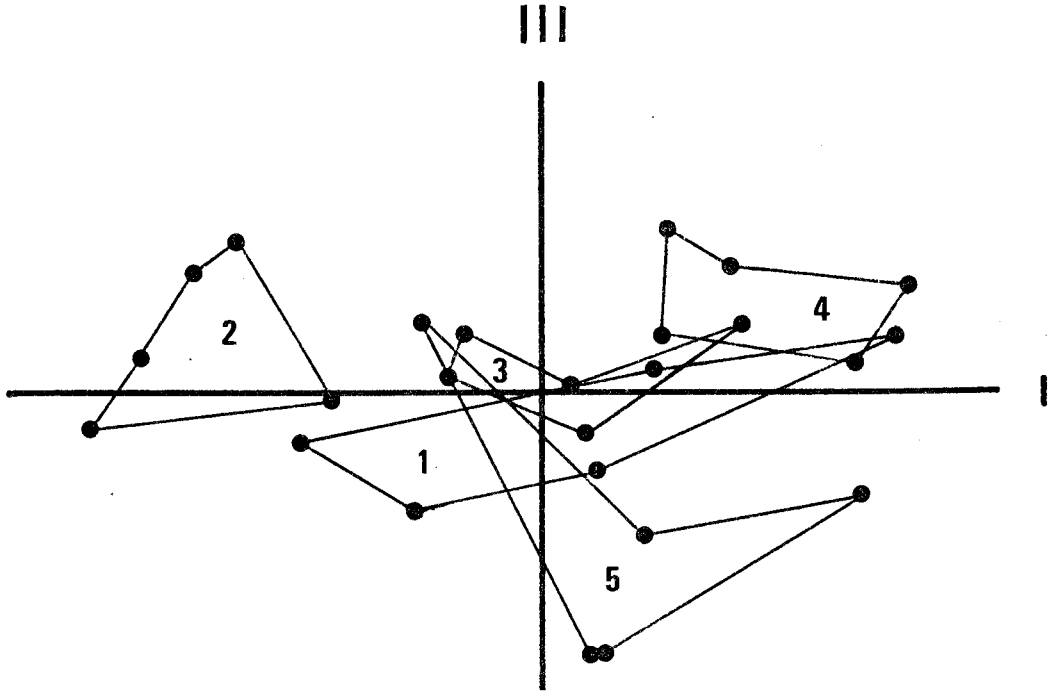
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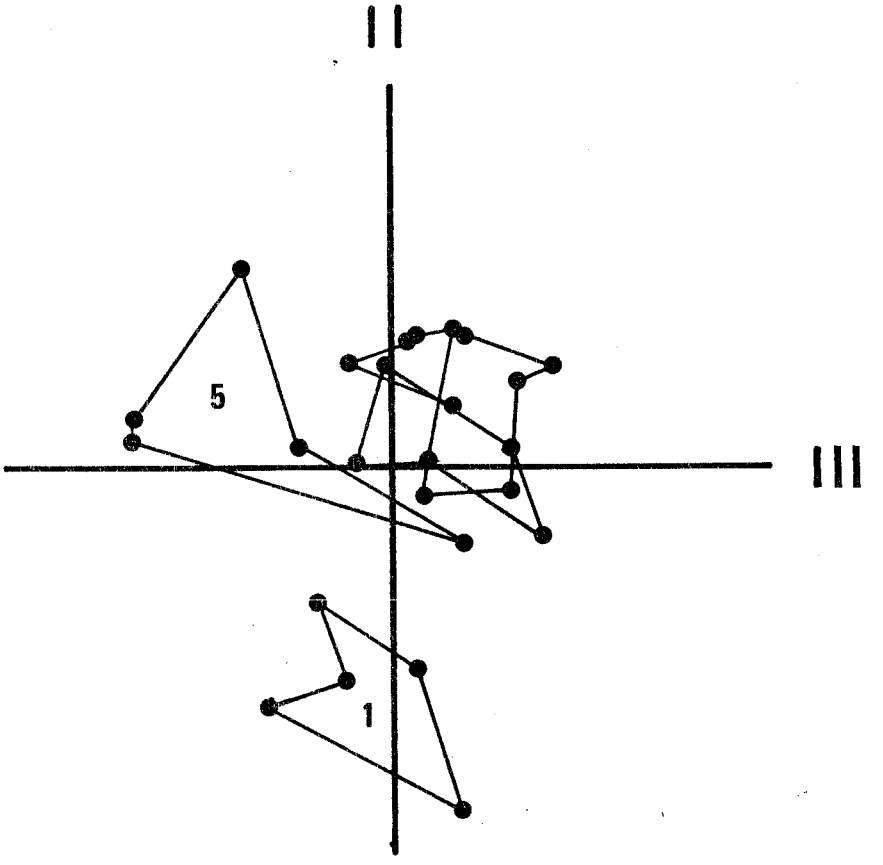
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similar to the previous sample of C. contortae. It was characterized by a relatively moderate size component (38.2% of variation) on which most of the variables exhibited positive loadings, which indicated a general size factor. Specimens in the sub-samples were situated along this axis with respect to overall size as estimated by the variable BL.

The patterns of variation exhibited by principal component II and principal component III were similar to those shown for the previous sample. That is, contrasts of sign and magnitude of the antennal variables, reduction in hind leg dimensions on principal component II and negative trends in rostrum dimensions and in setal counts on the antennal segments on principal component III were exhibited. The difference was that in this sample there was a strong negative trend in the rostrum dimensions on principal component II. Sub-sample No. 5 (Oregon) was consistently separated from the other samples (from British Columbia) along this axis of variation.

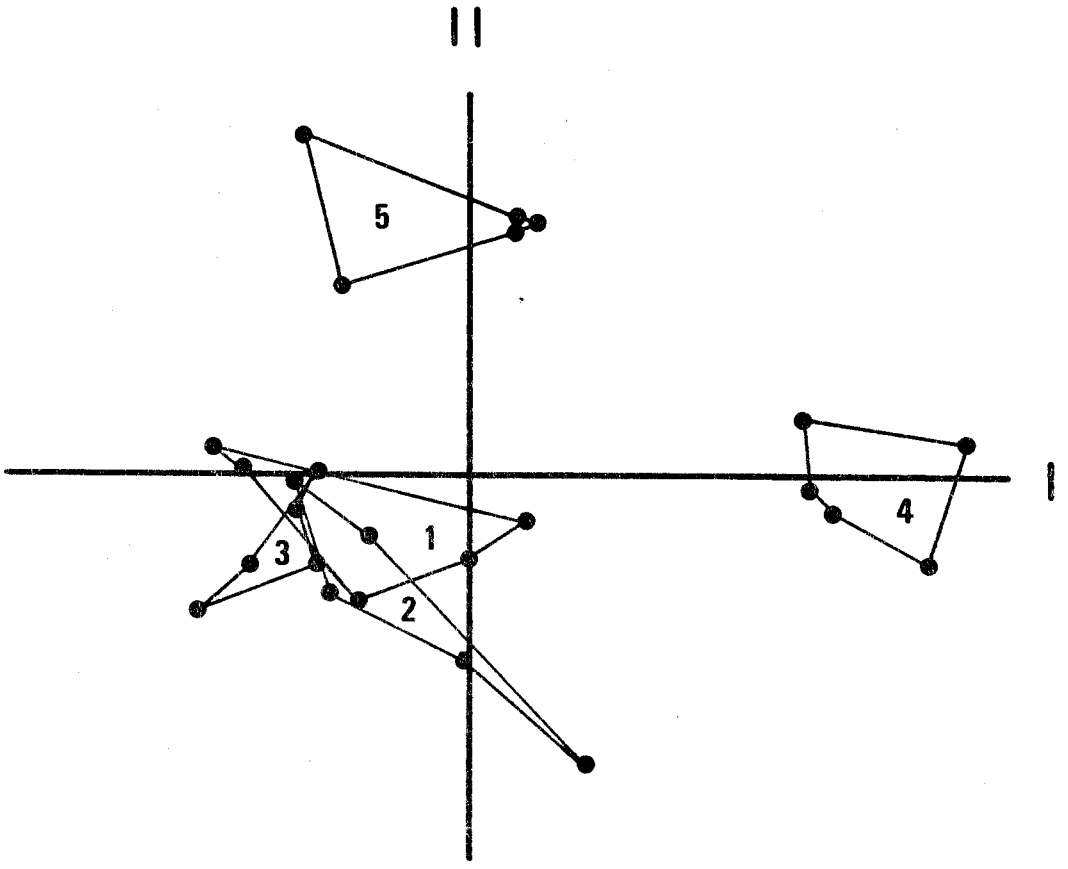
5.3.7 Cinara contortae - "reduced pigmentation".

The results of the principal component analysis of the sample of C. contortae - "reduced pigmentation" are shown in Table XIX and in Figure 18. As was the case with the other two samples of C. contortae, the first principal component was a size component (36.3% of variation) with all variables showing positive loadings on this

Table XIX. Contributions of 32 morphological variables to the first three principal components calculated from 25 specimens of C. contortae - "reduced pigmentation".

VARIABLE	PRINCIPAL COMPONENT I	II	III
1. BL	0.598	-0.667	0.074
2. FRW	0.286	-0.413	-0.332
3. A2L	0.470	-0.649	0.081
4. A3L	-0.063	-0.592	0.510
5. A4L	0.788	-0.350	0.074
6. A5L	0.871	0.268	0.206
7. A6BL	0.682	0.475	-0.254
8. A6BW	0.271	0.341	-0.490
9. A6PTL	0.707	0.155	0.368
10. R5L	0.601	0.429	0.331
11. R4L	0.874	0.297	0.007
12. R3L	0.750	0.433	0.325
13. R2L	0.732	0.340	0.126
14. FL	0.717	-0.594	0.183
15. FW	0.656	-0.535	-0.406
16. TL	0.552	-0.655	0.370
17. TS1VL	0.856	-0.292	0.036
18. TS2L	0.772	-0.291	0.040
19. SLA3	0.608	0.525	-0.018
20. SLGP	0.487	-0.267	-0.217
21. SLAT5	0.264	-0.125	0.056
22. SLT	0.538	-0.168	-0.004
23. SNA6SA	0.181	0.067	0.295
24. SNA6B	0.767	0.259	-0.135
25. SNA5	0.695	0.377	0.156
26. SNA2	0.359	0.594	-0.143
27. SNR4	0.743	0.470	0.065
28. SNGP	0.333	-0.330	-0.559
29. SNAT5	0.069	0.031	-0.540
30. SNAT8	0.656	-0.060	-0.302
31. SNC	0.646	-0.208	-0.433
32. SNT	0.140	0.021	-0.493
Relative Percentage of Variability	36.3	15.9	8.7

Figure 18. Diagrams showing principal component ordination of 25 specimens of Cinara contortae "reduced pigmentation", projected onto the first three principal axes (I x II, I x III, II x III), based on the analysis of 32 morphological variables (Table XIX). See Table XII for collection data. The polygons connect the specimens of each sub-sample; numbers refer to sub-sample designations as in Table XII.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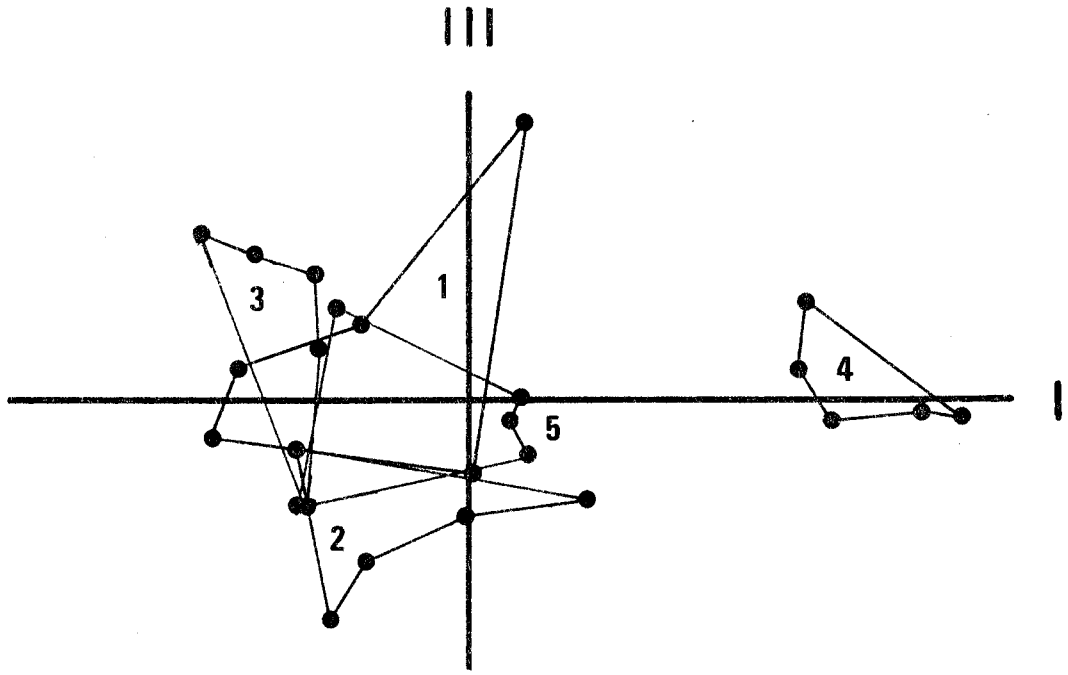
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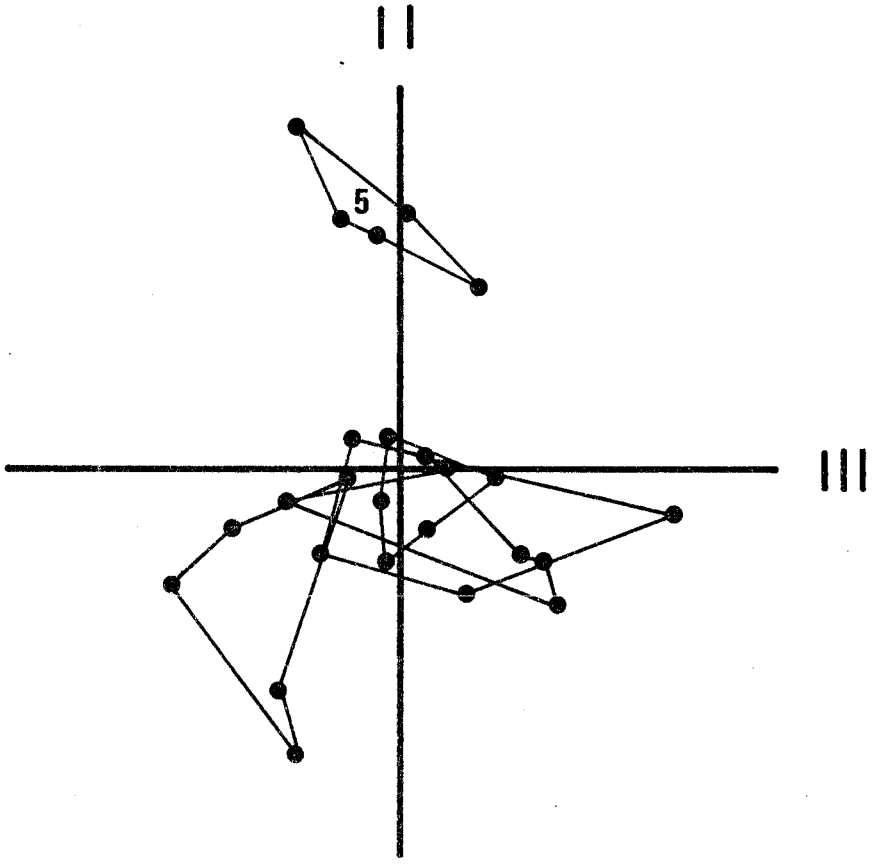
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axis, with the exception of A3L. The second principal component was characterized by a reduction in all dimensions of the hind leg. The lengths of antennal segments II, III and IV decreased in contrast to the dimensions of antennal segments V and VI and to the dimensions of the rostrum. Unlike the previous two samples of C. contortae, this sample did not show a reduction of the rostrum segments on the third principal component. The strongest trend on this component was a reduction of the setal counts on the abdomen and tibia.

Projection of the specimens onto principal axes I, II and III demonstrated some separation of the sub-samples. Principal axis I separated sub-sample No. 4 from the other sub-samples on the basis of overall size. Sub-sample No. 5 separated from the other sub-samples along principal axis II. Specimens in this sub-sample were characterized by smaller sizes of all leg dimensions and the length of antennal segments II, III and IV, as was indicated in the principal component analysis. Sub-sample No. 5 was collected later in the season than were the other sub-samples, however, these specimens were not oviparae. This difference in morphometric characteristics may represent seasonal changes in the form of the aphid.

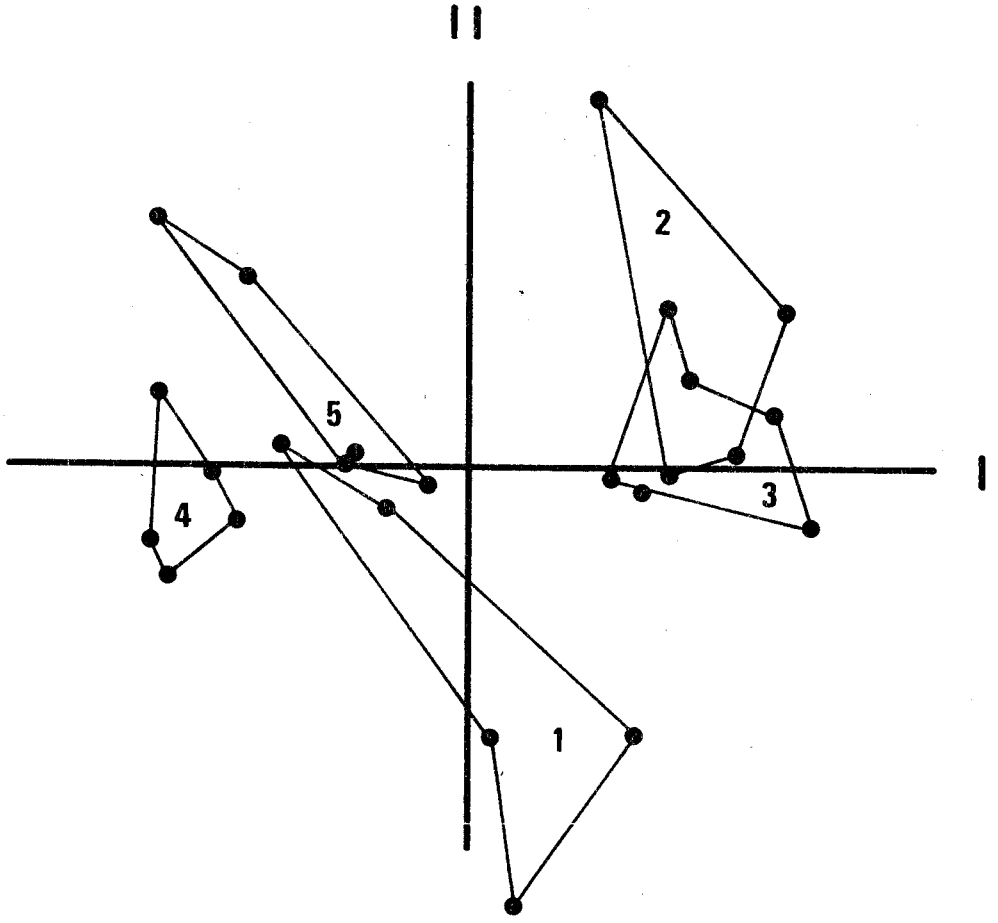
5.3.8 Cinara medispinosa

The results of the principal component analysis of the sample of C. medispinosa are shown in Table XX and in Figure 19. This

Table XX. Contributions of 32 morphological variables to the first three principal components calculated from 25 specimens of C. medispinosa.

VARIABLE	PRINCIPAL COMPONENT I	II	III
1. BL	0.506	-0.481	0.636
2. FRW	0.601	-0.407	0.127
3. A2L	0.057	-0.663	0.161
4. A3L	-0.238	-0.831	-0.298
5. A4L	0.342	-0.650	-0.299
6. A5L	0.800	0.040	-0.347
7. A6BL	0.895	0.211	-0.021
8. A6BW	0.690	0.011	0.065
9. A6PTL	0.583	-0.034	-0.382
10. R5L	0.819	0.178	0.026
11. R4L	0.921	0.136	-0.121
12. R3L	0.746	-0.251	0.345
13. R2L	0.786	0.211	-0.100
14. FL	0.084	-0.902	0.108
15. FW	-0.374	-0.519	0.180
16. TL	0.083	-0.883	-0.024
17. TS1VL	0.517	-0.620	-0.152
18. TS2L	0.743	-0.219	-0.183
19. SLA3	0.465	0.228	0.211
20. SLGP	0.695	0.081	0.145
21. SLAT5	-0.270	-0.624	-0.297
22. SLT	0.060	-0.628	-0.280
23. SNA6SA	-0.042	0.551	0.176
24. SNA6B	0.883	0.320	-0.139
25. SNA5	0.889	0.204	-0.134
26. SNA2	0.493	-0.043	-0.652
27. SNR4	0.570	0.182	-0.407
28. SNGP	0.332	-0.371	0.456
29. SNAT5	0.444	-0.287	0.164
30. SNAT8	0.633	-0.089	0.633
31. SNC	0.797	0.098	0.356
32. SNT	0.497	-0.115	-0.168
Relative Percentage of Variability	35.1	18.8	8.8

Figure 19. Diagrams showing principal component ordination of 25 specimens of Cinara medispinosa, projected onto the first three principal axes (I x II, I x III, II x III), based on the analysis of 32 morphological variables (Table XX). See Table XII for collection data. The polygons connect the specimens of each sub-sample; numbers refer to sub-sample designations as in Table XII.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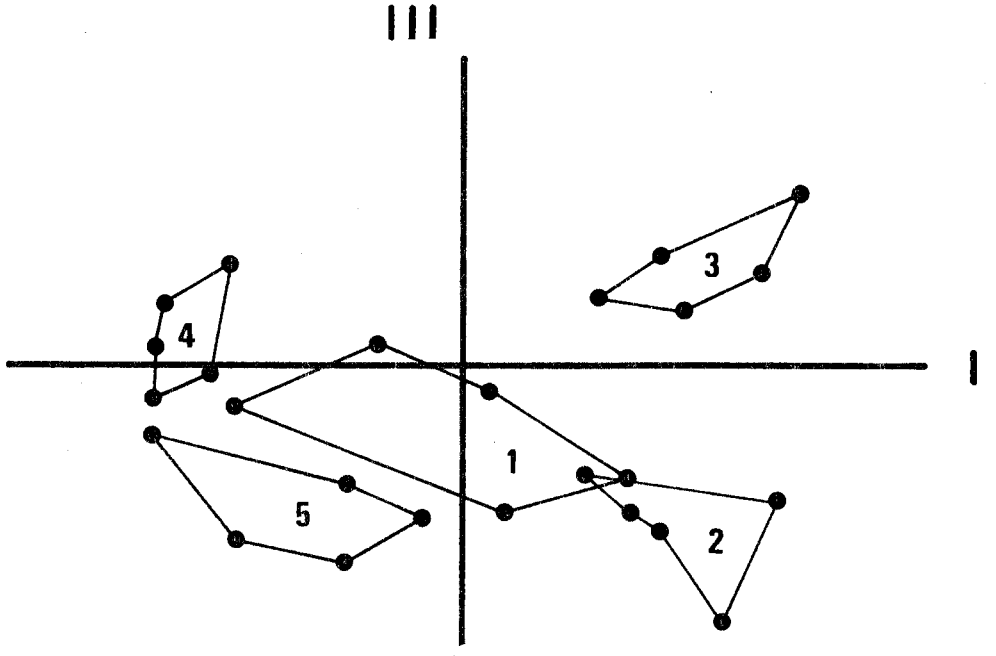
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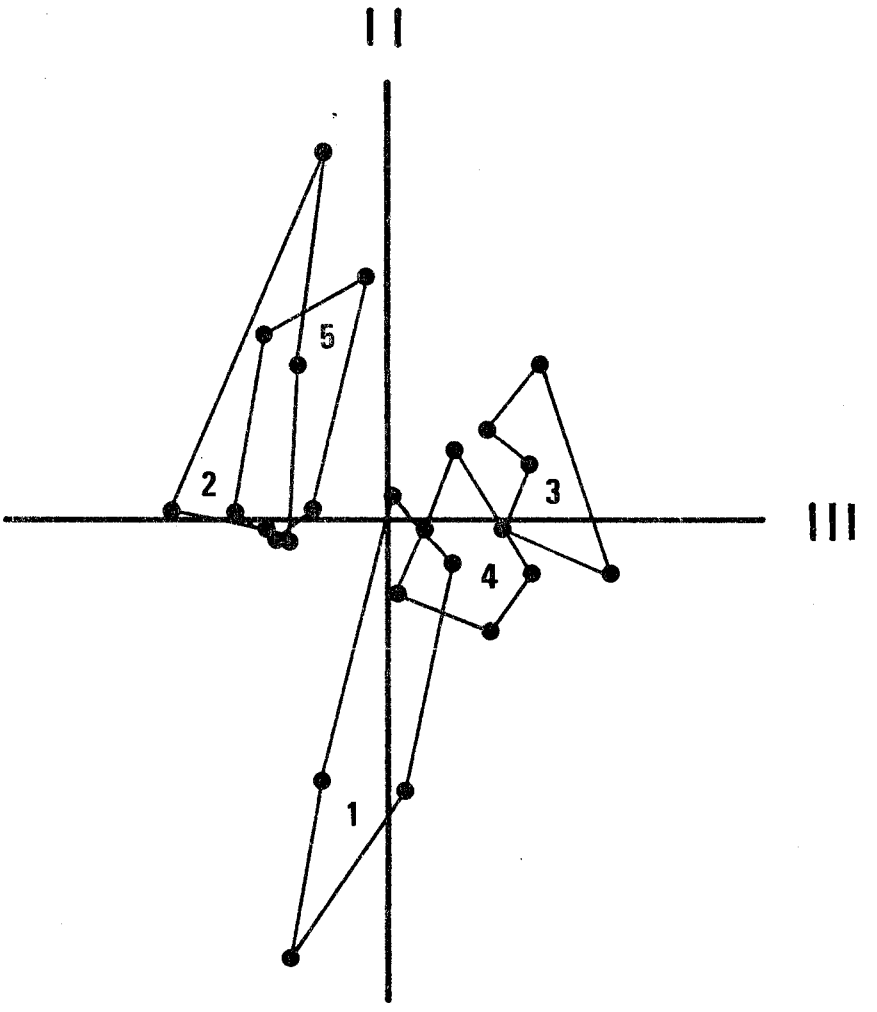
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species was characterized by a moderate size component (principal component I, 35.1% of variation) with relatively low contributions from the femur and tibia dimensions. Antennal segment III and femur width were negatively correlated with size on this component. Principal component II was characterized by relatively large decreases in antennal segments II to IV and in all dimensions of the hind leg. Principal component III was characterized by a mixture of decreases in the tarsal dimensions, some antennal, rostrum dimensions and by decreases in the setal numbers on the antennal segments.

The sub-samples were separated on the basis of size on principal axis I and on the basis of a decrease in antennal and hind leg dimensions on principal axis II. Examination of the ordination of the sub-samples onto axes II and III showed that the sub-samples from branch-feeding sites (No.'s 2 and 5) were separated in morphometric space from the sub-samples from the tip and canker feeding sites.

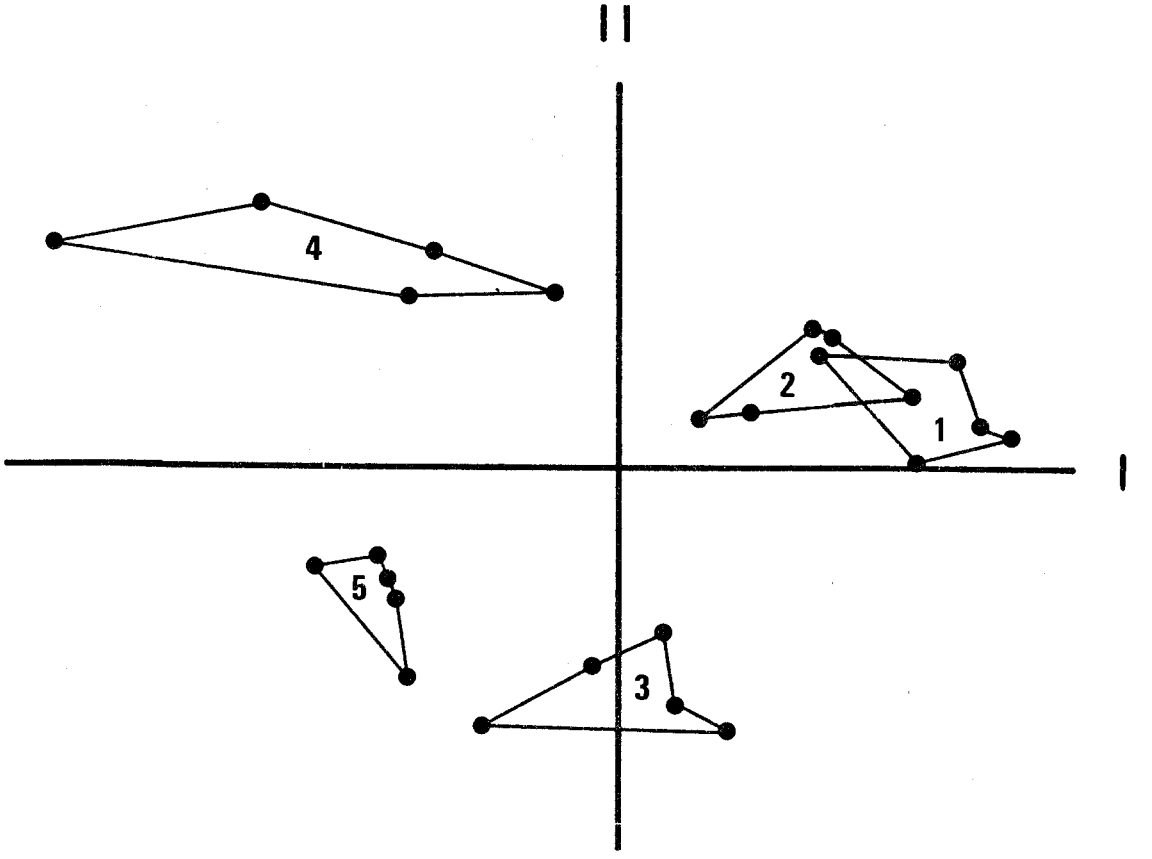
5.3.9 Cinara murrayanae - "typical"

The results of the principal component analysis of the sample of C. murrayanae - "typical" are shown in Table XXI and in Figure 20. This species was characterized by a relatively strong size component (principal component I, 45.6% of variation) with all variables except SNA6SA increasing along this component of

Table XXI. Contributions of 32 morphological variables to the first three principal components calculated from 25 specimens of C. murrayanae - "typical"

VARIABLE	PRINCIPAL COMPONENT I	II	III
1. BL	0.913	-0.056	0.193
2. FRW	0.800	-0.413	0.038
3. A2L	0.696	-0.223	0.463
4. A3L	0.589	0.608	0.140
5. A4L	0.873	0.393	-0.059
6. A5L	0.880	0.186	-0.336
7. A6BL	0.685	-0.302	-0.369
8. A6BW	0.293	-0.787	0.248
9. A6PTL	0.406	-0.618	0.284
10. R5L	0.533	-0.138	0.563
11. R4L	0.765	-0.418	0.365
12. R3L	0.917	-0.248	0.099
13. R2L	0.883	-0.080	0.192
14. FL	0.837	0.471	-0.153
15. FW	0.672	0.542	-0.234
16. TL	0.793	0.507	-0.086
17. TS1VL	0.873	0.197	0.341
18. TS2L	0.959	0.036	-0.137
19. SLA3	0.287	0.198	0.176
20. SLGP	0.617	0.100	-0.141
21. SLAT5	0.752	0.198	0.210
22. SLT	0.694	0.568	0.185
23. SNA6SA	-0.203	-0.173	-0.493
24. SNA6B	0.201	-0.838	-0.041
25. SNA5	0.724	-0.282	-0.411
26. SNA2	0.362	-0.726	-0.071
27. SNR4	0.217	-0.825	0.038
28. SNGP	0.522	0.081	-0.565
29. SNAT5	0.511	-0.459	-0.468
30. SNAT8	0.758	0.249	0.240
31. SNC	0.535	-0.339	-0.364
32. SNT	0.611	-0.099	-0.541
Relative Percentage of Variability	45.6	18.4	9.2

Figure 20. Diagrams showing principal component ordination of 25 specimens of Cinara murrayanae "typical", projected onto the first three principal axes (I x II, I x III, II x III), based on the analysis of 32 morphological variables (Table XXI). See Table XII for collection data. The polygons connect the specimens of each sub-sample; numbers refer to sub-sample designations as in Table XII.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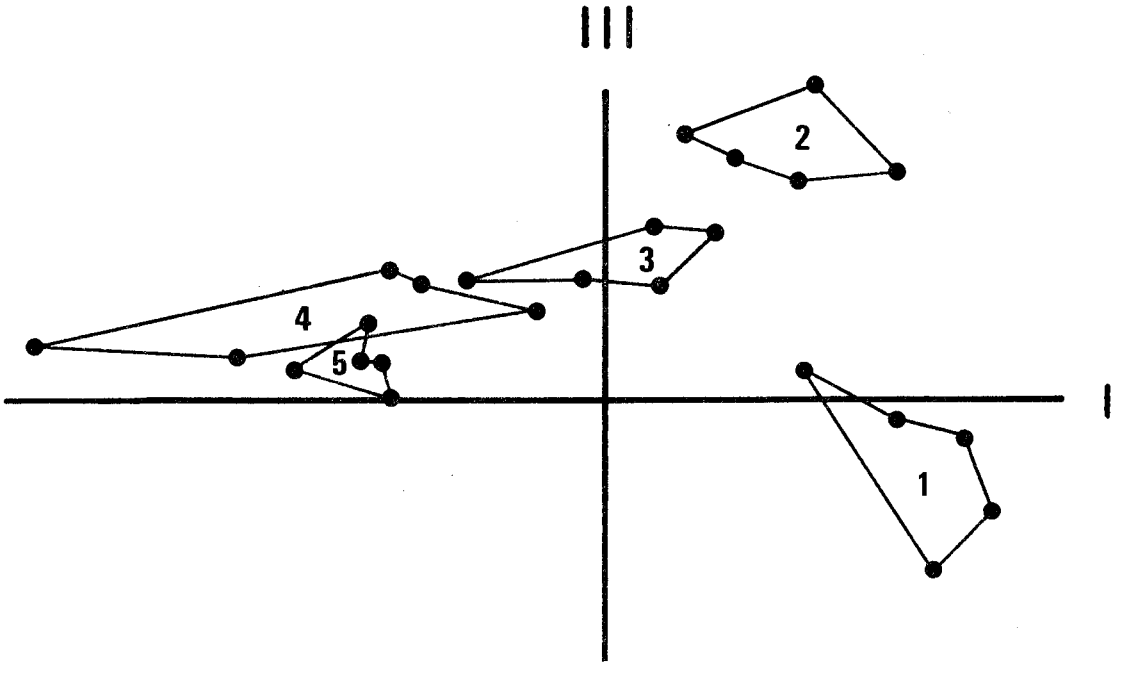
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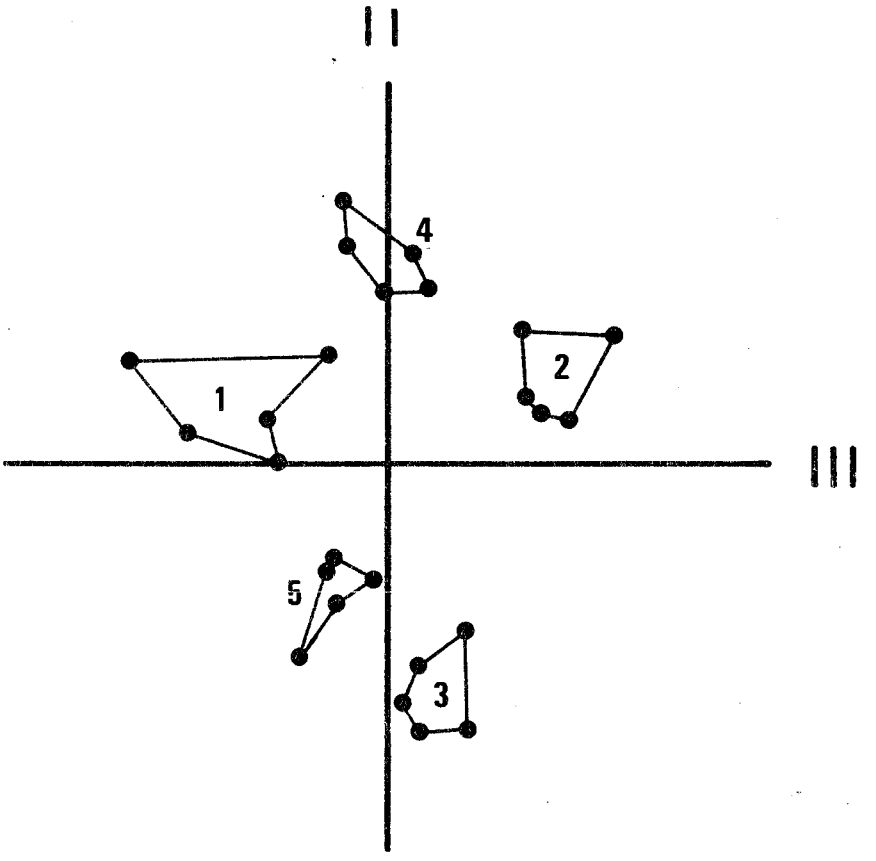
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variation. The second component was characterized by decreases in the dimensions of the sixth antennal segment, all segments of the rostrum and in the setal numbers on the antennal segments and the rostrum. Principal component III consisted of a mixture of changes of sign and magnitude among the groups of characters.

The sub-samples were clearly separated along all three principal axes. No trends with respect to geographic position or feeding site were evident.

5.3.10 Cinara murrayanae - "reduced pigmentation"

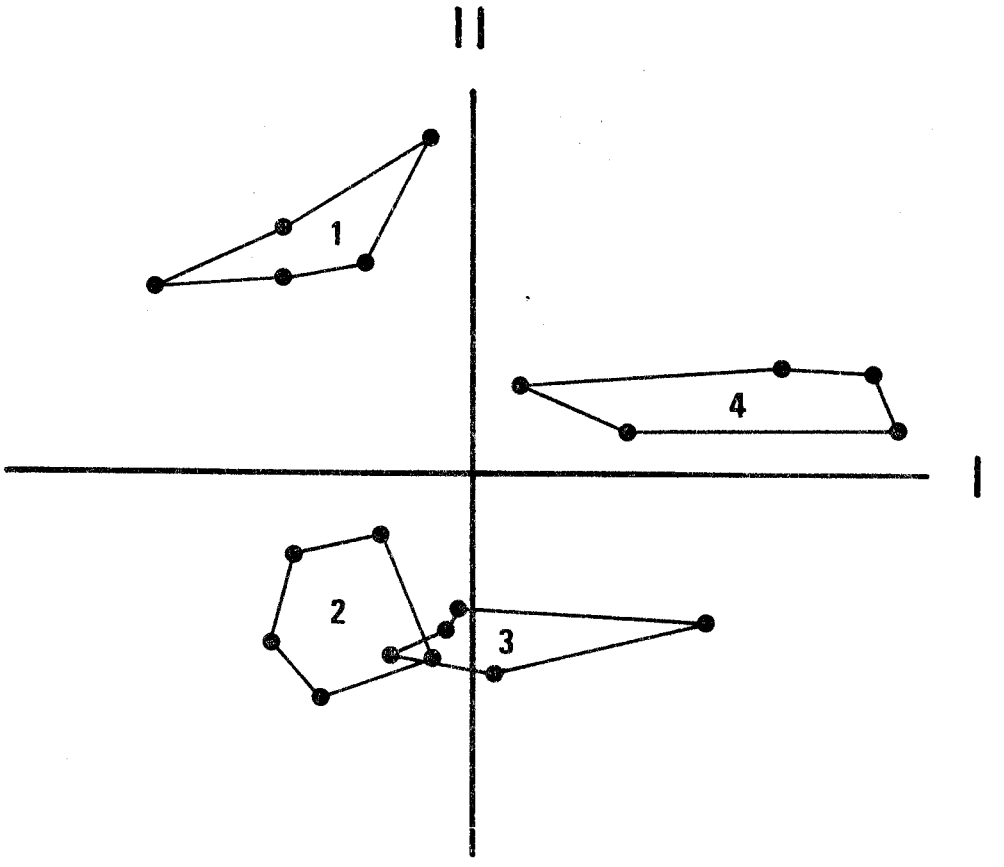
The results of the principal component analysis of the sample of C. murrayanae - "reduced pigmentation" are shown in Table XXII and in Figure 21. This sample exhibited a moderate size component (principal component I, 29.6% of variation); some of the antennal dimensions (A4L, A6BW, A6PTL) and the count of the number of setae on the processus terminalis (SNA6SA) decreased in relation to this component. The second component was a relatively large one (21.1% of variation), consisting of decreases in all rostrum dimensions and most setal length measurements and setal counts. The third component, also relatively large (17.3% of variation), consisted of large increases in A5L, A6PTL and TS2L and decreases in SLA3, SLAT5 and SLT.

The sub-samples were clearly separated along all three principal axes. No trends with respect to geographic position or feeding site were evident.

Table XXII. Contributions of 32 morphological variables to the first three principal components calculated from 20 specimens of C. murrayanae - "reduced pigmentation".

VARIABLE	PRINCIPAL COMPONENT I	II	III
1. BL	0.323	-0.545	0.674
2. FRW	0.450	-0.805	-0.012
3. A2L	0.691	-0.019	0.320
4. A3L	0.785	0.504	-0.063
5. A4L	-0.045	0.745	0.317
6. A5L	0.212	0.585	0.749
7. A6BL	0.730	0.537	0.216
8. A6BW	-0.553	-0.063	0.467
9. A6PTL	-0.289	0.050	0.707
10. R5L	0.419	-0.801	-0.034
11. R4L	0.891	-0.287	-0.135
12. R3L	0.731	-0.192	-0.078
13. R2L	0.020	-0.151	0.432
14. FL	0.831	0.473	0.194
15. FW	0.691	0.376	0.323
16. TL	0.591	0.641	0.321
17. TS1VL	0.568	0.591	-0.316
18. TS2L	0.213	0.068	0.880
19. SLA3	0.708	-0.141	-0.609
20. SLGP	0.654	-0.423	0.010
21. SLAT5	0.536	-0.422	-0.523
22. SLT	0.801	0.167	-0.442
23. SNA6SA	-0.487	-0.064	-0.062
24. SNA6B	0.349	-0.322	0.319
25. SNA5	0.490	-0.286	0.523
26. SNA2	0.194	-0.621	0.509
27. SNR4	0.449	0.522	-0.095
28. SNGP	0.052	0.328	0.331
29. SNAT5	0.111	-0.884	0.179
30. SNAT8	0.837	-0.204	-0.343
31. SNC	0.553	-0.239	0.333
32. SNT	0.080	-0.447	0.590
Relative Percentage of Variability	29.6	21.1	17.3

Figure 21. Diagrams showing principal components ordination of 20 specimens of Cinara murrayanae "reduced pigmentation", projected onto the first three principal axes (I x II, I x III, II x III), based on the analysis of 32 morphological variables (Table XXII). See Table XII for collection data. The polygons connect the specimens of each sub-sample; numbers refer to sub-sample designations as in Table XII.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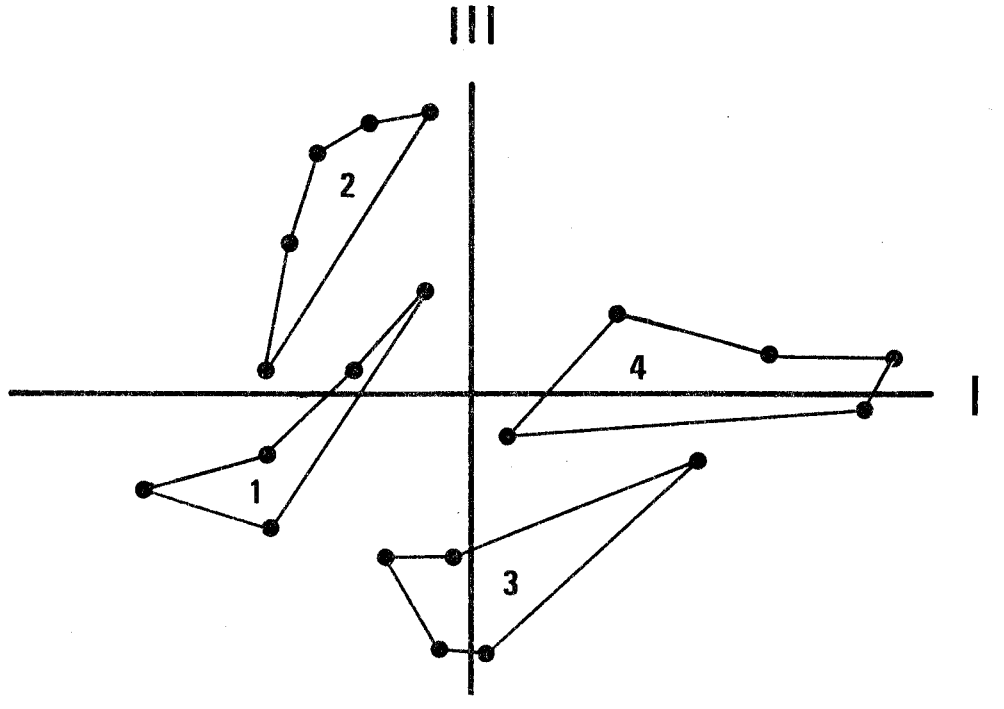
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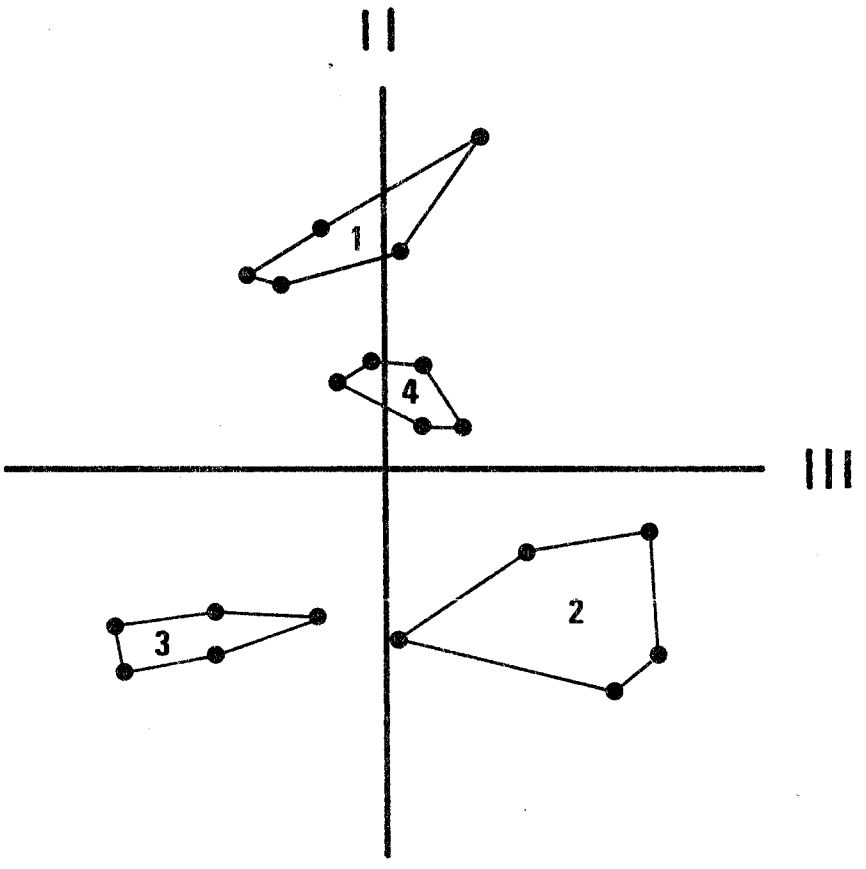
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5.3.11 Cinara ponderosae

The results of the principal component analysis of the sample of C. ponderosae are shown in Table XXII and in Figure 22. This species was characterized by a moderate size component (principal component I, 39.4% of variation) with relatively strong contributions from the continuous variables and only minor contributions from the setal counts. Principal components II and III were relatively small components (9.5% and 7.7% of total variation, respectively). Principal component II was mainly a trend to decreases in setal numbers and rostrum dimensions. The third component consisted of a number of contrasts of sign among the variables.

Specimens in this sample were mainly oriented with respect to overall size. No separation of the sub-samples was evident, even in the projection of the sub-samples onto the second and third axes.

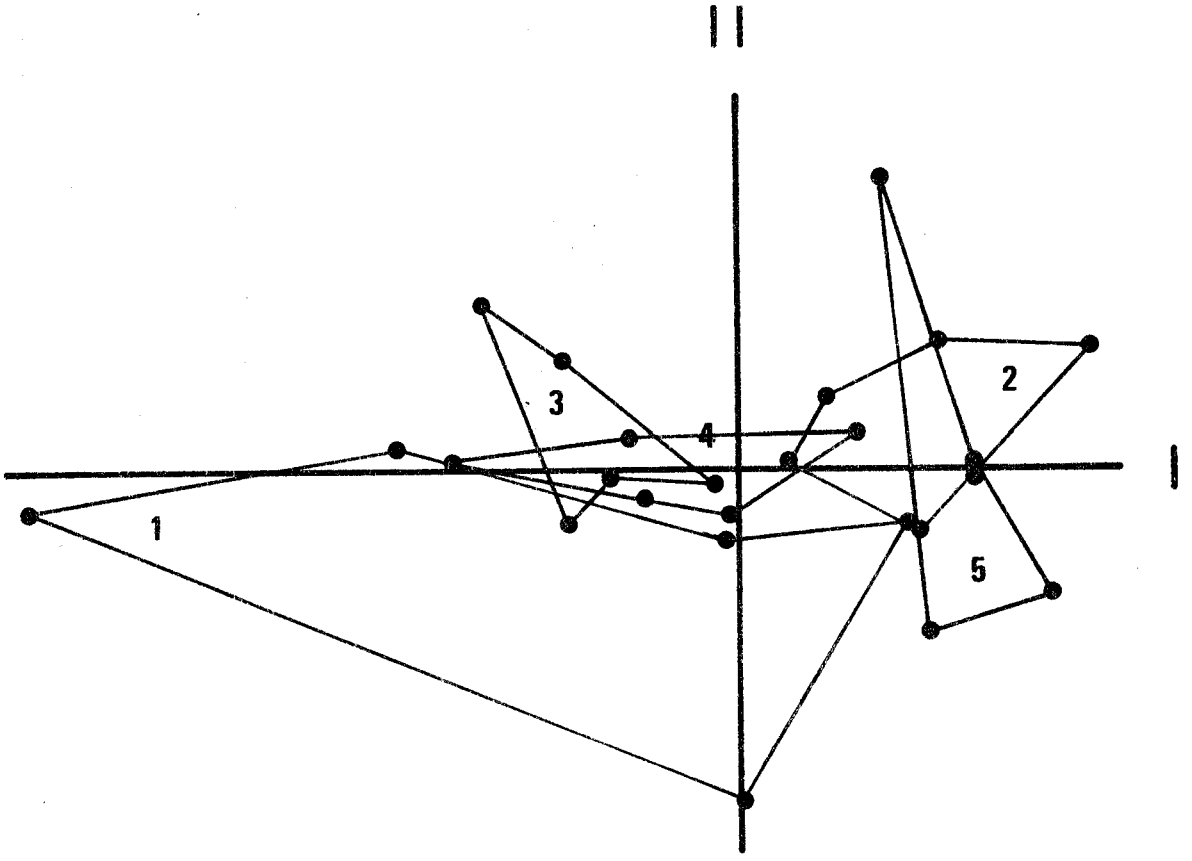
5.3.12 Cinara kuchea

The results of the principal component analysis of the sample of C. kuchea are shown in Table XXIV and in Figure 23. This species exhibited a moderate size component (principal component I, 38.7% of variation) with positive contributions from all variables except A6BW and A6PTL. The second component consisted of changes in

Table XXIII. Contributions of 32 morphological variables to the first three principal components calculated from 25 specimens of C. ponderosae.

VARIABLE	PRINCIPAL COMPONENT I	II	III
1. BL	0.930	-0.021	0.156
2. FRW	0.848	0.231	-0.114
3. A2L	0.839	-0.089	0.194
4. A3L	0.927	0.060	-0.012
5. A4L	0.814	0.141	0.315
6. A5L	0.762	0.048	-0.169
7. A6BL	0.642	-0.094	0.252
8. A6BW	0.757	0.103	-0.265
9. A6PTL	0.515	0.423	-0.276
10. R5L	0.354	0.199	0.117
11. R4L	0.750	-0.173	0.358
12. R3L	0.753	-0.137	-0.082
13. R2L	0.346	-0.284	0.068
14. FL	0.957	0.097	-0.061
15. FW	0.904	0.067	-0.070
16. TL	0.943	0.048	-0.007
17. TS1VL	0.875	-0.091	0.191
18. TS2L	0.747	-0.344	0.328
19. SLA3	0.402	0.362	-0.293
20. SLGP	0.862	0.125	-0.053
21. SLAT5	0.246	0.590	-0.160
22. SLT	0.140	0.519	-0.501
23. SNA6SA	0.006	-0.464	-0.465
24. SNA6B	-0.000	-0.031	-0.292
25. SNA5	0.561	-0.085	-0.418
26. SNA2	0.175	-0.249	0.348
27. SNR4	-0.036	-0.427	0.091
28. SNGP	0.293	-0.278	-0.406
29. SNAT5	-0.184	0.250	0.120
30. SNAT8	0.336	-0.546	0.173
31. SNC	0.308	-0.617	-0.436
32. SNT	0.058	-0.625	-0.609
Relative Percentage of Variability	39.4	9.5	7.7

Figure 22. Diagrams showing principal component ordination of 25 specimens of Cinara ponderosae, projected onto the first three principal axes (I x II, I x III, II x III), based on the analysis of 32 morphological variables (Table XXIII). See Table XII for collection data. The polygons connect the specimens of each sub-sample; numbers refer to sub-sample designations as in Table XII.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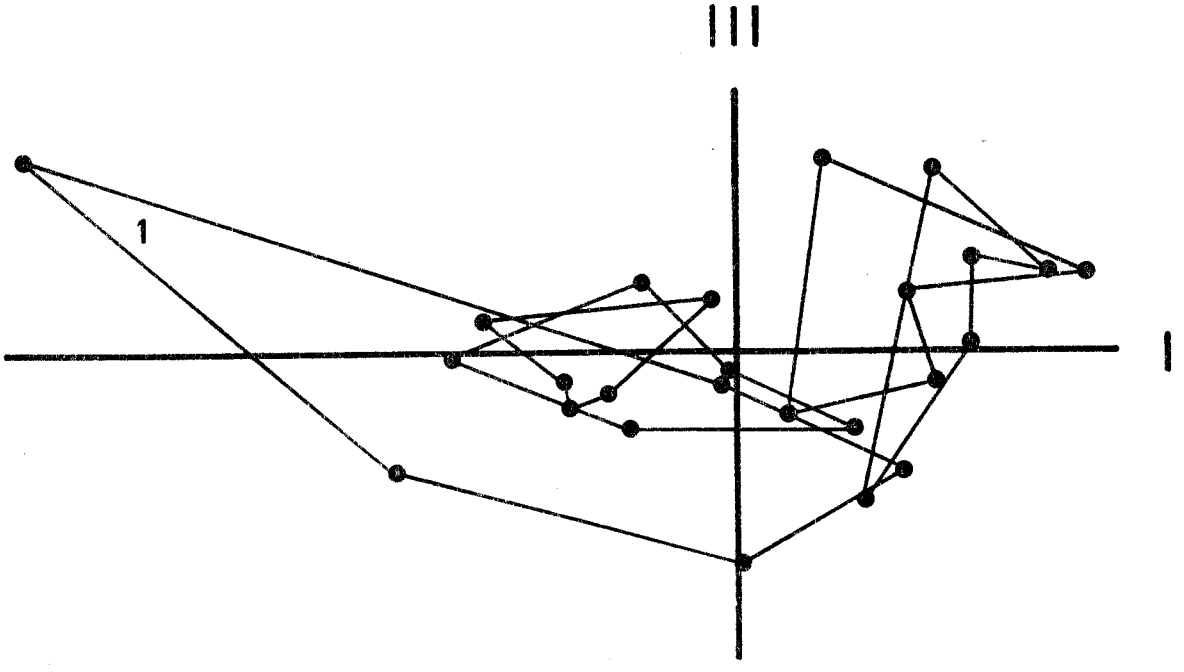
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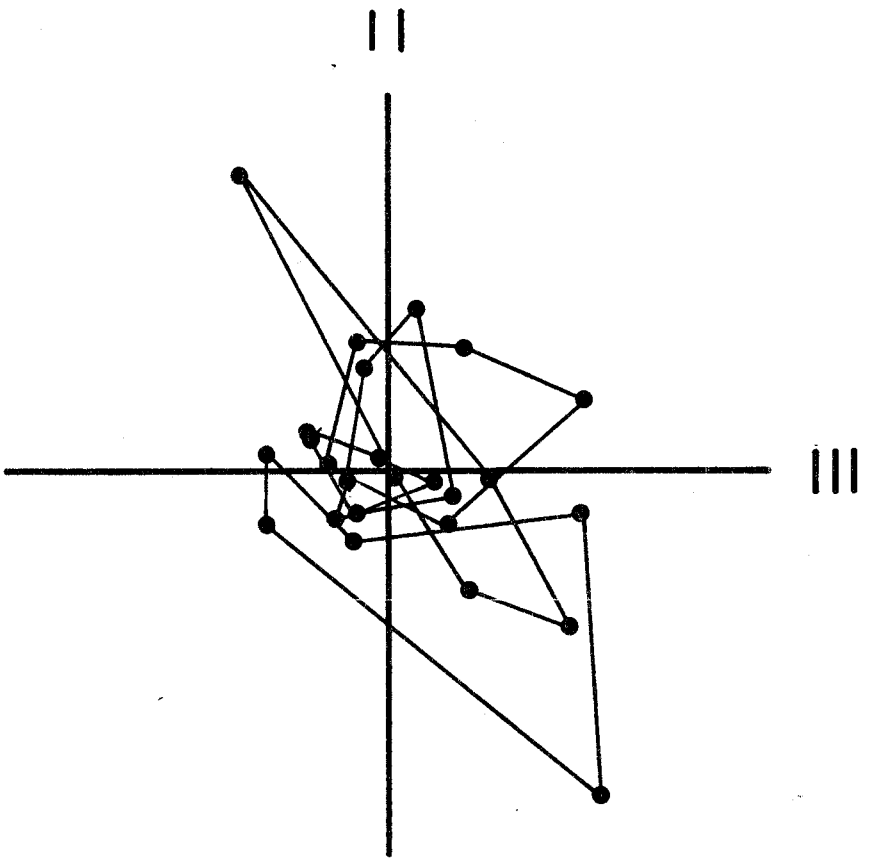
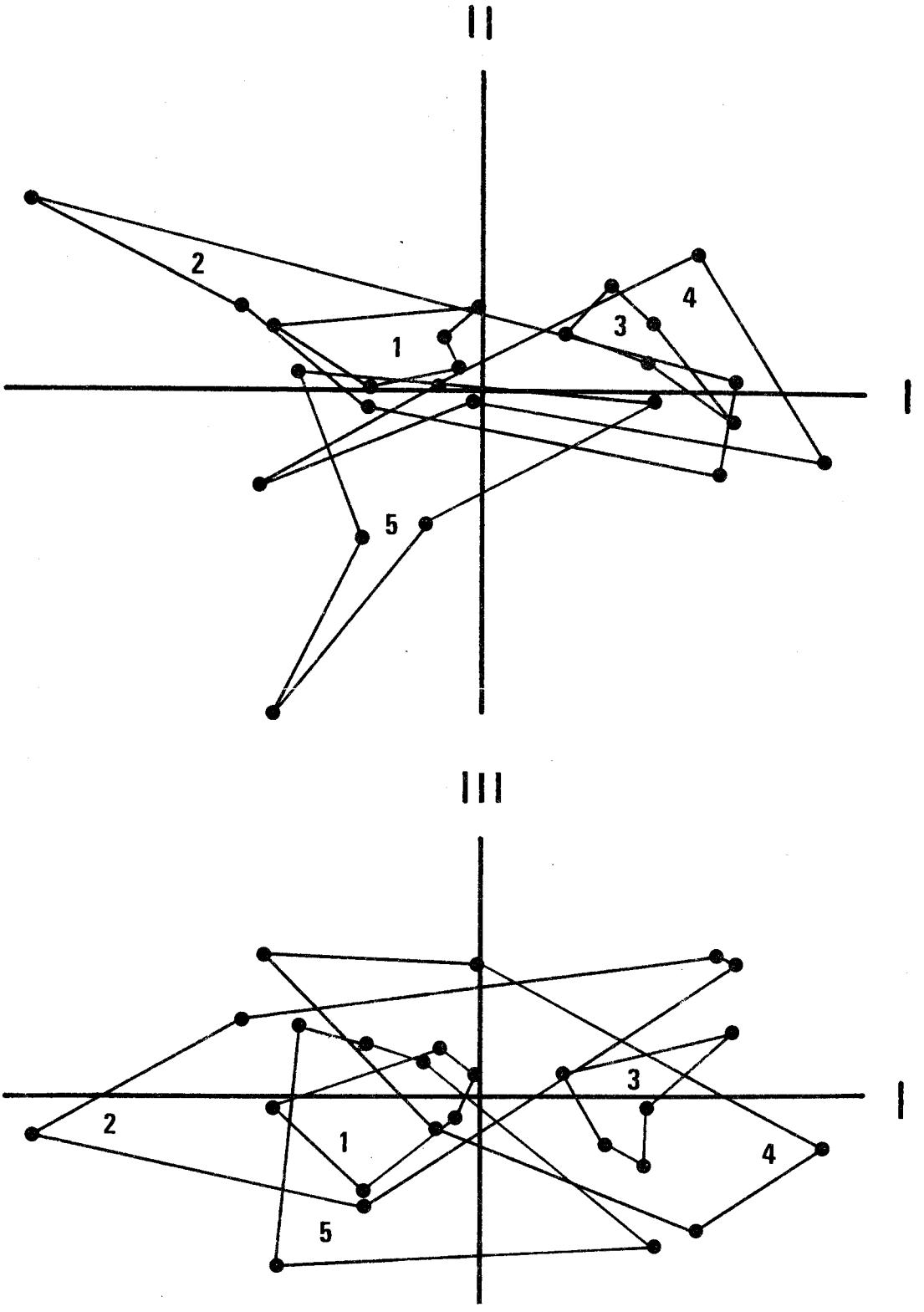

II
III

Table XXIV. Contributions of 32 morphological variables to the first three principal components calculated from 25 specimens of C. kuchea.

VARIABLE	PRINCIPAL COMPONENT I	II	III
1. BL	0.784	-0.130	0.048
2. FRW	0.567	-0.183	0.262
3. A2L	0.876	0.072	-0.017
4. A3L	0.889	0.098	-0.128
5. A4L	0.726	0.023	-0.261
6. A5L	0.667	0.405	0.097
7. A6BL	0.763	0.283	-0.121
8. A6BW	-0.083	-0.309	0.358
9. A6PTL	-0.130	-0.673	0.180
10. R5L	0.418	-0.351	-0.498
11. R4L	0.269	-0.139	0.280
12. R3L	0.545	-0.531	0.018
13. R2L	0.444	0.498	-0.235
14. FL	0.948	-0.055	-0.038
15. FW	0.887	-0.107	0.042
16. TL	0.880	0.109	-0.066
17. TS1VL	0.774	0.012	0.258
18. TS2L	0.815	-0.213	0.375
19. SLA3	0.594	0.092	-0.653
20. SLGP	0.764	0.206	-0.178
21. SLAT5	0.642	-0.097	-0.584
22. SLT	0.360	-0.464	-0.454
23. SNA6SA	0.246	0.463	0.433
24. SNA6B	0.205	0.665	0.200
25. SNA5	0.747	0.389	0.241
26. SNA2	0.088	0.346	-0.107
27. SNR4	0.159	0.038	0.210
28. SNGP	0.794	-0.178	0.101
29. SNAT5	0.501	-0.473	0.308
30. SNAT8	0.348	-0.511	0.126
31. SNC	0.650	-0.349	0.271
32. SNT	0.497	0.264	0.497
Relative Percentage of Variability	38.7	11.0	8.5

Figure 23. Diagrams showing principal component ordination of 25 specimens of Cinara kuchea, projected onto the first three principal axes (I x II, I x III, II x III), based on the analysis of 32 morphological variables (Table XXIV). See Table XII for collection data. The polygons connect the specimens of each sub-sample; numbers refer to sub-sample designations as in Table XII.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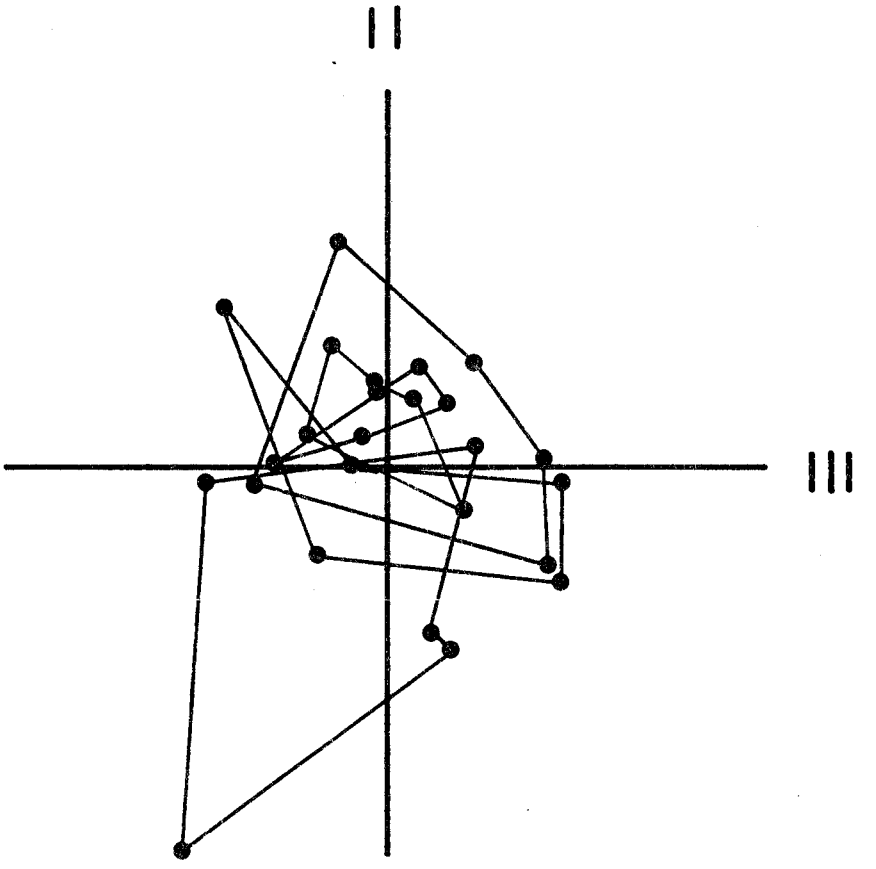
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the dimensions of R5L, R4L and R3L in relation to R2L, a reduction of the number of setae on the abdominal structures and an increase of the number of setae on the antennal segments. Principal component III represented a reduction in setal lengths.

Specimens in this sample were oriented along the size component. No separation of the sub-samples was evident.

5.3.13 Summary of Morphometric Trends.

The main component of variation, as established by the principal component analyses of the samples, was a size component (19.7% to 49.3% of variation). In general, the variables that were measured for all samples exhibited strong, positive contributions to this axis of variation. The exception was C. pergandei (Table XIV) which had a relatively small first component of variation; many variables were negatively correlated with this axis of variation.

The second principal component (9.7% to 21.1% of variation) consisted largely of contrasts of the sign of the antennal dimensions, a reduction of the rostrum segment lengths, and a reduction of the hind leg dimensions in many samples. The third principal component (7.7% to 17.3% of variation) was largely an expression of the contrasts of functional groups of characters and a trend towards a reduction in the numbers of setae.

Each species or sample was characterized by a unique composition of the scores of the functional groups of characters and each functional group of characters exhibited unique patterns of variation across the 12 samples. For example, variation among the antennal segments was of a number of characteristic types. In some species, such as C. contortae (Table XVII) and C. nigra (Table XIII) the entire set of antennal segment measurements increased with overall size while in others, such as C. brevispinosa (Table XV) and C. kuchea (Table XXIV) some antennal segments decreased in relation to this size factor. On the second component of variation, the proximal antennal segments decreased in relation to the sixth antennal segment in some species (C. contortae, for example). In other species, such as C. murrayanae (Table XXI), the opposite occurred.

While the response of the rostrum to overall size variation was consistent in all samples except those of C. pergandei (Table XIV) and C. parvicornis (Table XVI), the segments of the rostrum exhibited a complex pattern of variation on the second and third principal components. Some species, such as C. murrayanae and C. nigra were characterized by negative loadings of all segments. The segments of the rostrum of most samples showed a mixture of responses, that is, each segment of the rostrum exhibited a unique pattern of variation.

The dimensions of the hind leg were also marked by complex variation patterns. In most samples a complete positive response to

overall size by all hind leg dimensions was evident. The segments of the tarsus showed as strong a positive correlation with overall size as did the other segments of the hind leg. As was the case with the antennal and rostrum segments, the scores on the second and third components shown by the segments of the tarsus were varied.

With the exception of C. pergandei, the "operational" groups of characters, that is, the setal length measurements and the setal counts taken on various structures, showed a positive correlation with overall size on the first component. These characters showed a varied pattern of morphometric variation on the second and the third components. However, where these variables were associated with functional areas of the aphid body, they showed trends as a group. For example, variables involving the number of setae on the abdominal area responded as a group in some species such as C. kuchea and C. brevispinosa. The setal numbers on the various antennal segments responded (increases or decreases) as a group in many species and on both the second and third components.

There was no consistent separation of the sub-samples on the basis of feeding site or geographic position. The majority of the sub-samples were separated on the basis of overall size. However, in 4 of the main samples (C. brevispinosa, C. medispinosa, C. murrayanae - "typical", and C. murrayanae - "reduced pigmentation") there was almost complete separation of the sub-samples along all three principal axes of variation. These 4 samples were characterized by relatively large second and third principal

components of variation, although the first component varied considerably in size (19.8% to 45.6% of variation). This indicates that these species have a relatively larger proportion of morphometric variation which is not completely related to size; these species may be useful for the study of geographic variation.

Two samples, those of C. ponderosae and C. kuchea, showed considerable overlap of their respective sub-samples, even along the size component. This indicates that morphological variation in these species is heavily influenced by factors affecting size and that they are relatively size-variable from location to location, as was C. nigra.

5.4 Discrimination Between Samples and Species

As was mentioned previously, I found it difficult to assign all specimens and samples to the species C. contortae, C. medispinosa, and C. murrayanae. In the following analyses I used discriminant function analysis, as discussed in Chapter 3, to determine the relationships among the samples of these species and to identify those variables that, and the degree to which they could, discriminate between the samples and species.

5.4.1 Cinara contortae Samples

The three samples of C. contortae were analyzed using discriminant function analysis in order to determine whether or not

these samples represented discrete taxa or whether they were morphological variants of the one species. The standardized discriminant function coefficients for the 2 discriminant functions that were calculated are given in Table XXV. The individual specimens in each sample were projected onto the discriminant axes; this is shown in Figure 24.

Discriminant function I (55.0% of variation) was largely influenced by size variation; the largest contribution to discrimination along this axis was by the variable BL. Other strong contributions were by those variables associated with the antenna (A4L, A5L, A6BL, and SLA3), the tibia and tarsus (TL, TS1VL, TS2L), and the abdomen (SLGP, SLAT5, SNAT8). Discrimination along this axis separated the "typical" specimens from the "small, thin" specimens of C. contortae.

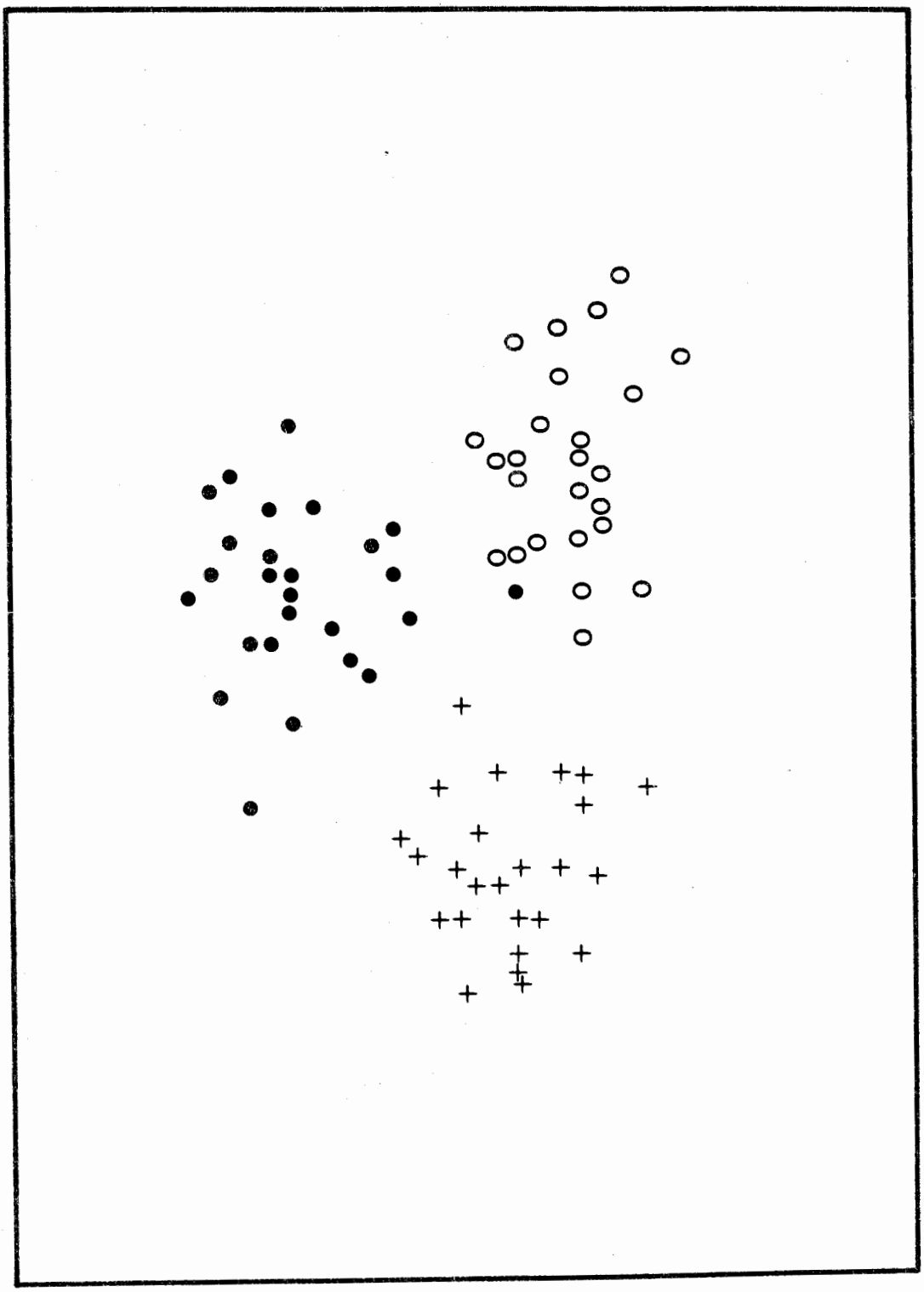
The second discriminant function (45.0% of variation) allowed for the almost complete separation of the "typical" specimens from those characterized by "reduced pigmentation". Nearly one half of the variables that were measured were strong contributors to discrimination along this axis; these variables came from all of the functional and operational groups of measurements, with the exception of the lack of strong contributions from the setal length measurements. The strongest contributions were provided by the antennal segment dimensions, particularly A5L and the setal count taken on this segment (SNA5), some of the hind leg dimensions, R3L, and some of the setal counts taken on the abdomen (SNAT5, SNAT8, and SNC).

Table XXV Standardized discriminant function coefficients for two discriminant functions calculated from 32 morphological variables measured from three samples (n = 3 x 25) of C. contortae.

VARIABLE	DISCRIMINANT FUNCTION I	II
1. BL	1.253	-0.505
2. FRW	0.348	-0.346
3. A2L	-0.203	0.143
4. A3L	0.163	-0.899
5. A4L	-1.011	0.965
6. A5L	-0.791	-1.754
7. A6BL	0.699	0.576
8. A6BW	-0.154	-0.471
9. A6PTL	0.030	-0.994
10. R5L	0.306	0.349
11. R4L	-0.028	-0.317
12. R3L	-0.243	1.201
13. R2L	0.286	0.215
14. FL	-0.132	0.165
15. FW	0.266	1.502
16. TL	0.521	1.565
17. TS1VL	0.511	0.274
18. TS2L	-0.534	-2.074
19. SLA3	0.823	0.196
20. SLGP	0.487	0.306
21. SLAT5	-0.687	-0.037
22. SLT	-0.190	0.118
23. SNA6SA	0.018	-0.390
24. SNA6B	-0.036	0.540
25. SNA5	-0.466	1.074
26. SNA2	0.034	-0.022
27. SNR4	-0.348	0.089
28. SNGP	-0.256	0.118
29. SNAT5	-0.079	-0.556
30. SNAT8	0.720	-0.914
31. SNC	-0.015	-0.549
32. SNT	0.182	0.489
Relative Percentage of Variability	55.0	45.0

Figure 24. Specimens of three samples (n = 3 x 25) of Cinara contortae projected onto the first and second discriminant axes, based on the analysis of 32 morphological variables (Table XXV). See Table XII for the collection data for each sample. (O, C. contortae - "typical"; +, C. contortae - "small, thin"; ●, C. contortae - "reduced pigmentation").

DISCRIMINANT FUNCTION II



DISCRIMINANT FUNCTION I

In order to further investigate the relationships among the variables within the samples, I calculated a correlation matrix, based on the combined specimens (n = 75), and analyzed this using principal component analysis. The results of this analysis showed that nearly one half (47.2%) of the morphometric variation in these combined samples was variation related to size differences. All of the variables, with the exception of SNT, were found to be significantly correlated ($p = 0.01$) with size. There was no clear separation of the specimens of the three samples when an ordination along the first three principal axes was carried out.

From the above analyses I concluded that all three samples represented the taxon C. contortae. While there was separation of the samples, all of the variables which discriminated the most between the samples were strongly influenced by size variation. Neither the "small, thin" sample nor the "reduced pigmentation" sample showed character states that were unique. Variation patterns within the samples, as shown in the principal components analyses of section 5.3 (5.3.5, 5.3.6, and 5.3.7), were evident over all of the samples combined.

It is noteworthy that all of the samples characterized by "reduced pigmentation" were found on cankers. These specimens were distinguished from "typical" C. contortae by differences in the lengths of the antennal segments, particularly A5L, in R3L, the hind leg dimensions (FW, T1, and TS2L) and some of the setal counts, particularly those on the abdomen (SNAT5, SNAT8, and SNC). This may

represent some adaptation or morphological adjustment to this feeding niche. Further sampling may show this to be a geographic subspecies of C. contortae.

5.4.2 Cinara medispinosa and Cinara murrayanae Samples.

Both Palmer (1952) and Bradley (1961) state that C. medispinosa can be separated from C. murrayanae on the basis of the length of the tibial setae of the alate morph. However, while some specimens of the apterous morph can be separated on the basis of this character, a number of specimens were difficult to identify. In addition, some samples were characterized by reduced dorsal pigmention.

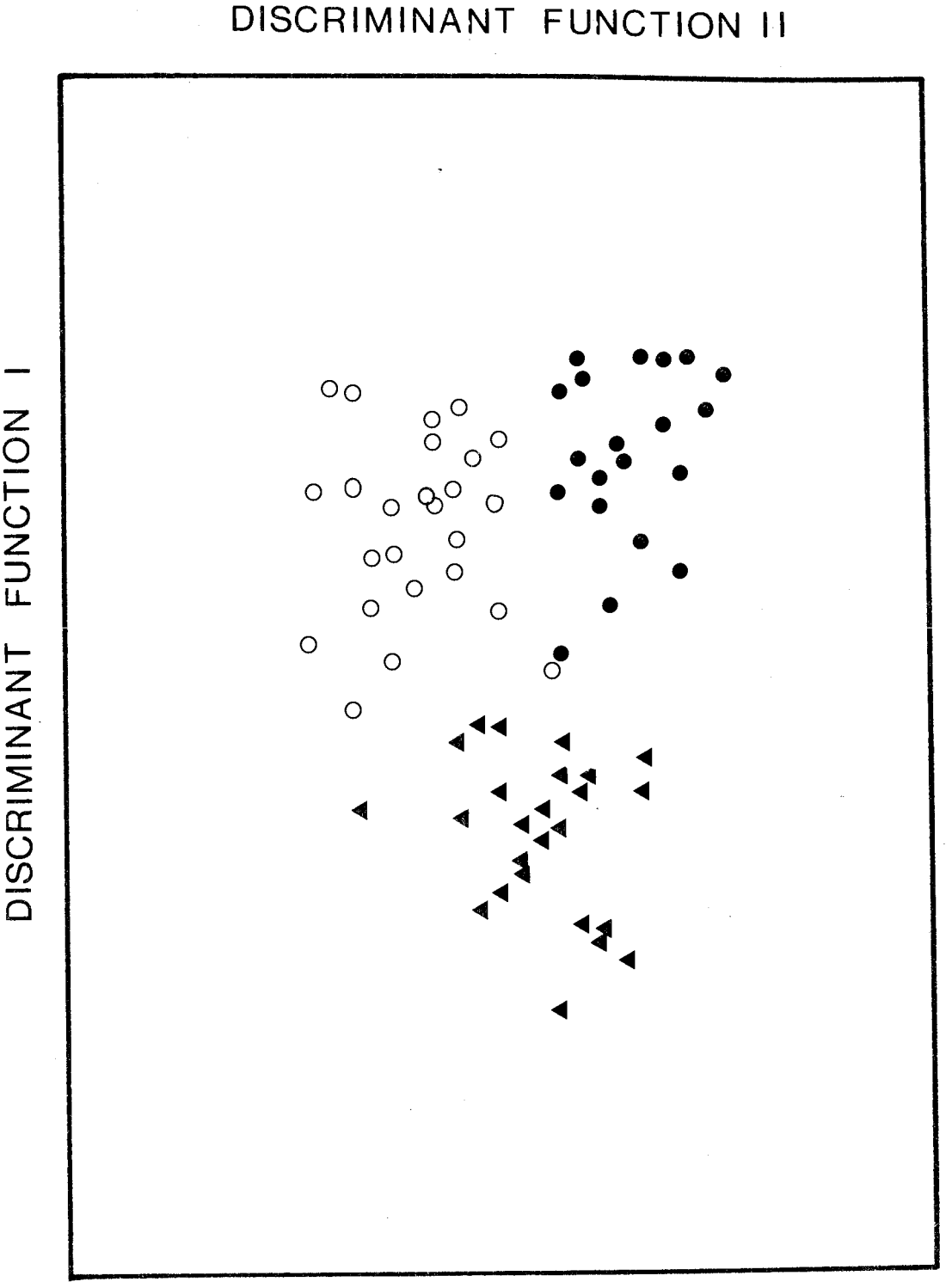
In order to understand more completely the relationships between these two species, a single sample of C. medispinosa and two samples of C. murrayanae ("typical" and "reduced pigmentation") were analyzed using discriminant function analysis. The standardized discriminant function coefficients for the two discriminant functions which were calculated are given in Table XXVI. The individual specimens were projected onto the discriminant axes; this is shown in Figure 25.

Specimens of C. medispinosa were completely separated from specimens of C. murrayanae along the first discriminant axis, which accounted for 66.8% of the total variation. As was known for the alate morph, this analysis showed that the variable SLT was the

Table XXVI. Standardized discriminant function coefficients for two discriminant functions calculated from 32 morphological variables measured from one sample of *C. medispinosa* and two samples of *C. murrayanae*.

VARIABLE	DISCRIMINANT FUNCTION I	II
1. BL	-0.599	0.889
2. FRW	0.099	0.445
3. A2L	0.382	0.125
4. A3L	0.287	1.187
5. A4L	0.172	-0.262
6. A5L	-0.089	0.795
7. A6BL	0.036	0.203
8. A6BW	1.028	-0.571
9. A6PTL	-0.228	0.054
10. R5L	0.541	-0.376
11. R4L	-1.288	-1.308
12. R3L	0.410	-0.723
13. R2L	0.056	0.043
14. FL	-0.975	0.048
15. FW	-0.083	-0.583
16. TL	0.362	-1.438
17. TS1VL	-0.804	1.187
18. TS2L	0.142	0.120
19. SLA3	0.289	0.156
20. SLGP	-0.033	-0.284
21. SLAT5	-0.179	0.133
22. SLT	1.699	0.201
23. SNA6SA	0.261	-0.209
24. SNA6B	0.151	0.735
25. SNA5	-0.111	-0.687
26. SNA2	0.122	0.171
27. SNR4	0.568	0.343
28. SNGP	0.181	0.242
29. SNAT5	0.205	0.168
30. SNAT8	-0.033	-0.536
31. SNC	0.062	0.906
32. SNT	0.305	-0.295
Relative Percentage of Variability	66.8	33.2

Figure 25. Specimens of one sample (n = 25) of Cinara medispinosa and two samples (n = 25, 20) of Cinara murrayanae projected onto the first and second discriminant axes, based on the analysis of 32 morphological variables (Table XXVI). See Table XII for the collection data for the samples. (▲, C. medispinosa; ●, C. murrayanae - "typical"; O, C. murrayanae - "reduced pigmentation").


DISCRIMINANT FUNCTION II
DISCRIMINANT FUNCTION I

strongest contributor to discrimination between these two species. However, additional characters were also identified which were strong contributors to the separation of these species, namely, A6BW, the length of the fourth rostrum segment (R4L) and the count of the number of setae on this structure (SNR4), R5L, and the hind leg dimensions (FL, TS1VL).

The second discriminant function (33.2% of variation) separated most specimens of C. murrayanae - "reduced pigmentation" from those of C., murrayanae - "typical". Discrimination between these two samples was the result of differences in size (BL), antennal segment dimensions (A3L, A5L), rostrum dimensions (R3L, R4L), hind leg dimensions (TL, TS1VL), and setal counts on the antenna (SNA6B, SNA5) and abdomen (SNAT8, SNC). There were only relatively minor differences in the lengths of the setae.

As with the previous analysis, I calculated a correlation matrix, based on the combined specimens (n = 70), and analyzed this using principal component analysis. The results showed a strong first component of size variation (43.5%). Again, all variables were significantly correlated with size ($p = 0.01$). There was no clear separation of the specimens; however, there was partial separation of the "typical" samples of the two species. There was complete overlap of the two C. murrayanae samples.

I concluded that, as was the case with the C. contortae samples, that the "reduced pigmentation" sample was C. murrayanae. Most of the differences between these two samples were due to

variables which were correlated with size (BL), which was an important contributor to discrimination along this axis. The samples of C. medispinosa and C. murrayanae were relatively homogenous taxa, clearly separated by the variable SLT on the first discriminant axis, where BL was not as strong a contributor to discrimination.

5.4.3 Discrimination Between Cinara Species.

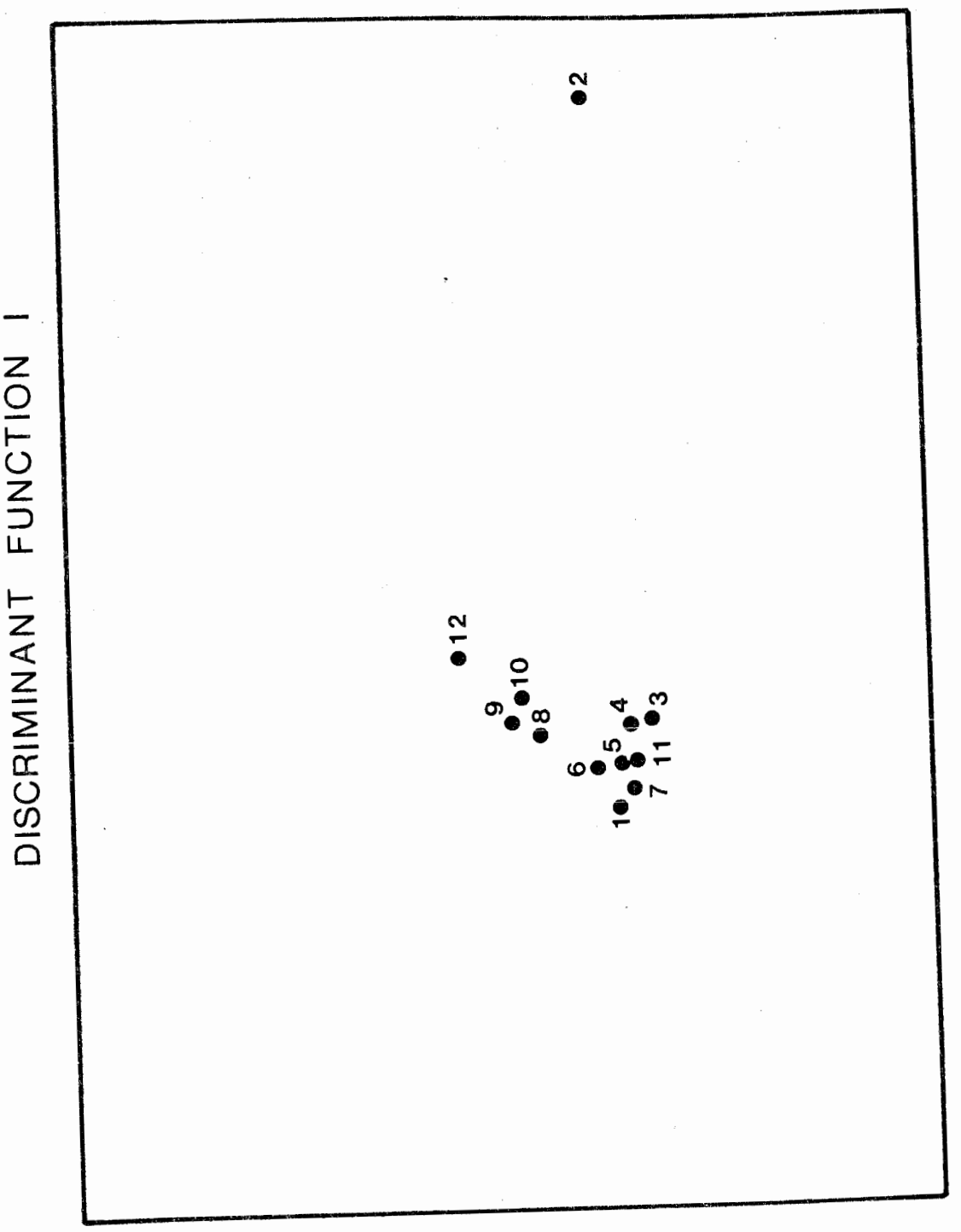
The 12 samples representing the 9 species of Cinara were analyzed using multiple discriminant function analysis. The standardized discriminant function coefficients for the first two discriminant functions (83.2% of variation) are given in Table XXVII. The projection of the sample centroids onto the first two discriminant axes is shown in Figure 26.

The only clear pattern to arise from this analysis is the separation of C. pergandei (Sample No. 2) from the other samples of the Cinara species along the first discriminant axis (72.0% of variation). This species has been placed in the subgenus Cinarella Hille Ris Lambers (Hille Ris Lambers 1948; Eastop 1972, 1976) on the basis of the presence of stalked eyes in the apterae, lack of a mesosternal tubercle, and elongate tarsal segments. It is clear from this analysis that C. pergandei has unique morphological features when compared to the other species of Cinara that were measured. In addition to the character TS1VL, C. pergandei was

Table XXVII. Standardized discriminant function coefficients for the first two discriminant functions calculated from 32 morphological variables measured from 12 samples of 9 species of Cinara.

VARIABLE	DISCRIMINANT FUNCTION I	II
1. BL	0.211	0.161
2. FRW	0.537	-0.070
3. A2L	0.013	0.253
4. A3L	0.106	0.068
5. A4L	-0.201	-0.201
6. A5L	0.223	0.163
7. A6BL	0.826	-0.152
8. A6BW	-0.114	0.048
9. A6PTL	0.480	-0.115
10. R5L	0.135	-0.125
11. R4L	-0.547	-0.490
12. R3L	-0.625	-0.259
13. R2L	-0.275	0.129
14. FL	-0.708	0.065
15. FW	0.128	-0.019
16. TL	-0.304	-0.074
17. TS1VL	0.899	-0.177
18. TS2L	-0.010	0.088
19. SLA3	0.222	0.107
20. SLGP	-0.190	-0.048
21. SLAT5	0.064	0.759
22. SLT	0.259	-0.115
23. SNA6SA	0.183	-0.060
24. SNA6B	-0.366	0.376
25. SNA5	-0.387	-0.111
26. SNA2	0.063	0.288
27. SNR4	0.140	0.363
28. SNGP	0.041	-0.398
29. SNAT5	0.636	-0.102
30. SNAT8	-0.030	0.299
31. SNC	0.245	0.072
32. SNT	-0.178	0.318
Relative Percentage of Variability	72.0	11.2

Figure 26. Centroids of 12 samples of 9 species of Cinara projected onto the first and second discriminant axes, based on the analysis of 32 morphological variables (Table XXVII). See Table XII for the collection data corresponding to the sample numbers.


DISCRIMINANT FUNCTION II
DISCRIMINANT FUNCTION I
2
12
10
9
8
4
3
6
5
11
7
1

separated from the other species by strong contributions from FRW, A6BL, A6PTL, R4L, R3L, FL, and SNAT5.

The presence of C. pergandei in the above analysis so altered the covariance matrix that there was no separation of the other species of Cinara; the analysis simply determined differences between C. pergandei and all of the other species as a group. Therefore, the sample of C. pergandei was removed and the remaining 11 samples representing 8 species were analyzed using multiple discriminant function analysis. The standardized discriminant function coefficients for the first two discriminant functions (65.0% of variation) are given in Table XXVIII. The projections of the sample centroids onto the first two discriminant axes are shown in Figure 27.

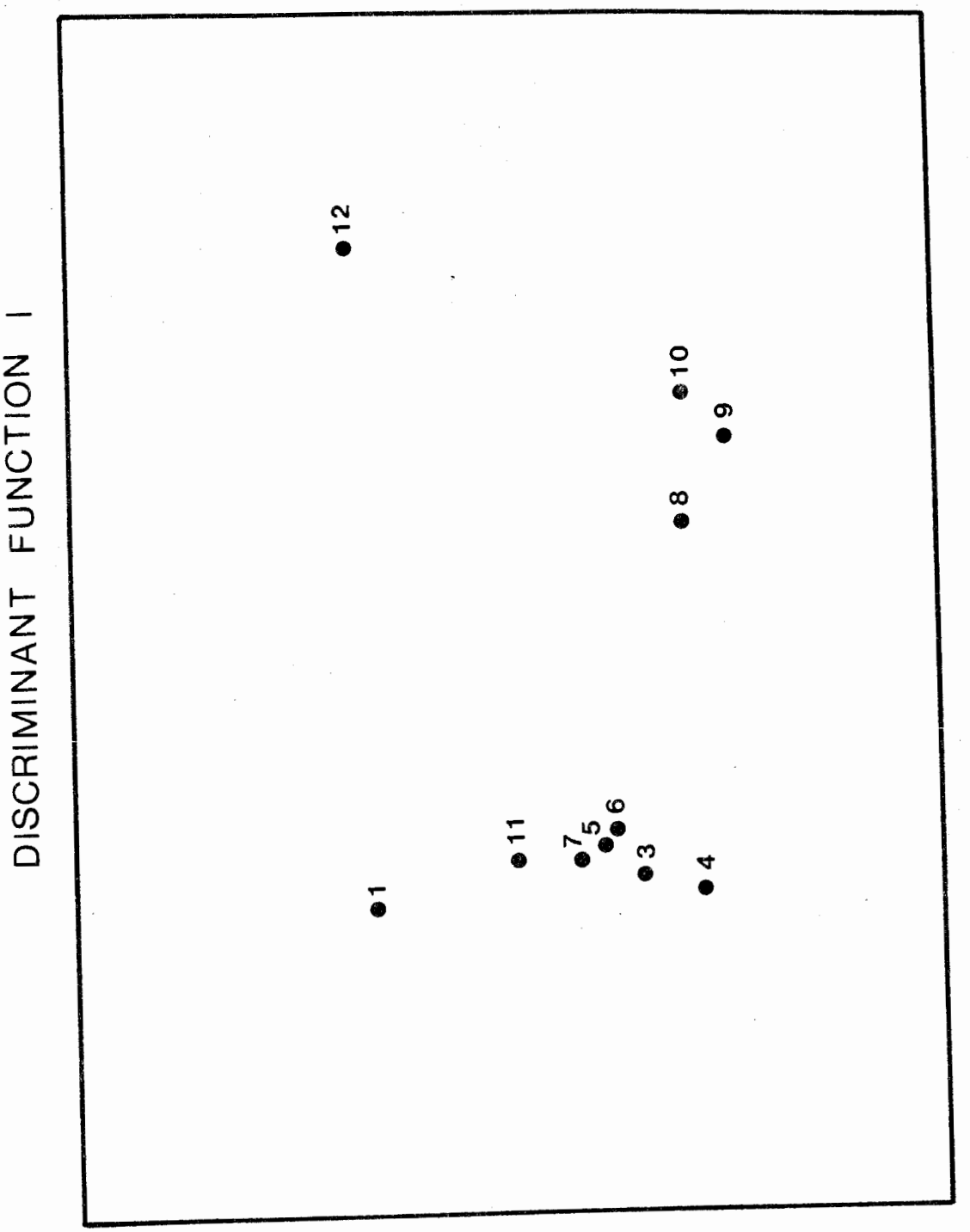
The samples were separated into three groups. C. kuchea (Sample No. 12) was positioned away from the other samples. The C. medispinosa sample (No. 8) and the C. murrayanae samples (No.'s 9 and 10) were grouped together. There was a gradient of the other samples along the second discriminant axis; the samples of C. contortae (No.'s 5, 6, and 7) remained together within this gradient.

Separation of the samples along the first discriminant axis was the result of contributions to discrimination from a number of variables. The main contributors were the variables R4L and SLAT5, that is, the above-mentioned three groups were separated, in part, on the basis of an increase in SLAT5 and a decrease in R4L along the first axis. For example, the position of C. kuchea (Sample No. 12)

Table XXVIII. Standardized discriminant function coefficients for the first two discriminant functions calculated from 32 morphological variables measured from 11 samples of 8 species of Cinara.

VARIABLE	DISCRIMINANT FUNCTION I	II
1. BL	0.128	0.259
2. FRW	0.090	0.250
3. A2L	0.342	0.553
4. A3L	0.078	-0.304
5. A4L	-0.170	-0.368
6. A5L	0.417	-0.020
7. A6BL	0.128	0.219
8. A6BW	0.046	-0.384
9. A6PTL	-0.002	0.076
10. R5L	-0.114	-0.492
11. R4L	-0.723	-0.837
12. R3L	-0.440	0.063
13. R2L	0.071	0.171
14. FL	-0.286	0.189
15. FW	-0.048	-0.091
16. TL	-0.286	-0.118
17. TS1VL	0.177	-0.250
18. TS2L	0.064	0.573
19. SLA3	0.069	0.465
20. SLGP	-0.170	-0.263
21. SLAT5	0.736	-0.576
22. SLT	0.193	0.338
23. SNA6SA	0.063	0.403
24. SNA6B	0.171	0.100
25. SNA5	-0.316	-0.198
26. SNA2	0.253	0.400
27. SNR4	0.358	0.173
28. SNGP	-0.297	-0.125
29. SNAT5	0.184	-0.138
30. SNAT8	0.162	0.282
31. SNC	0.440	-0.392
32. SNT	0.100	0.270
Relative Percentage of Variability	44.0	21.0

Figure 27. Centroids of 11 samples of 8 species of Cinara projected onto the first and second discriminant axes, based on the analysis of 32 morphological variables (Table XXVIII). See Table XII for the collection data corresponding to the sample numbers.


DISCRIMINANT FUNCTION II
DISCRIMINANT FUNCTION I
12
10
9
8
11
7
5
6
3
4
1

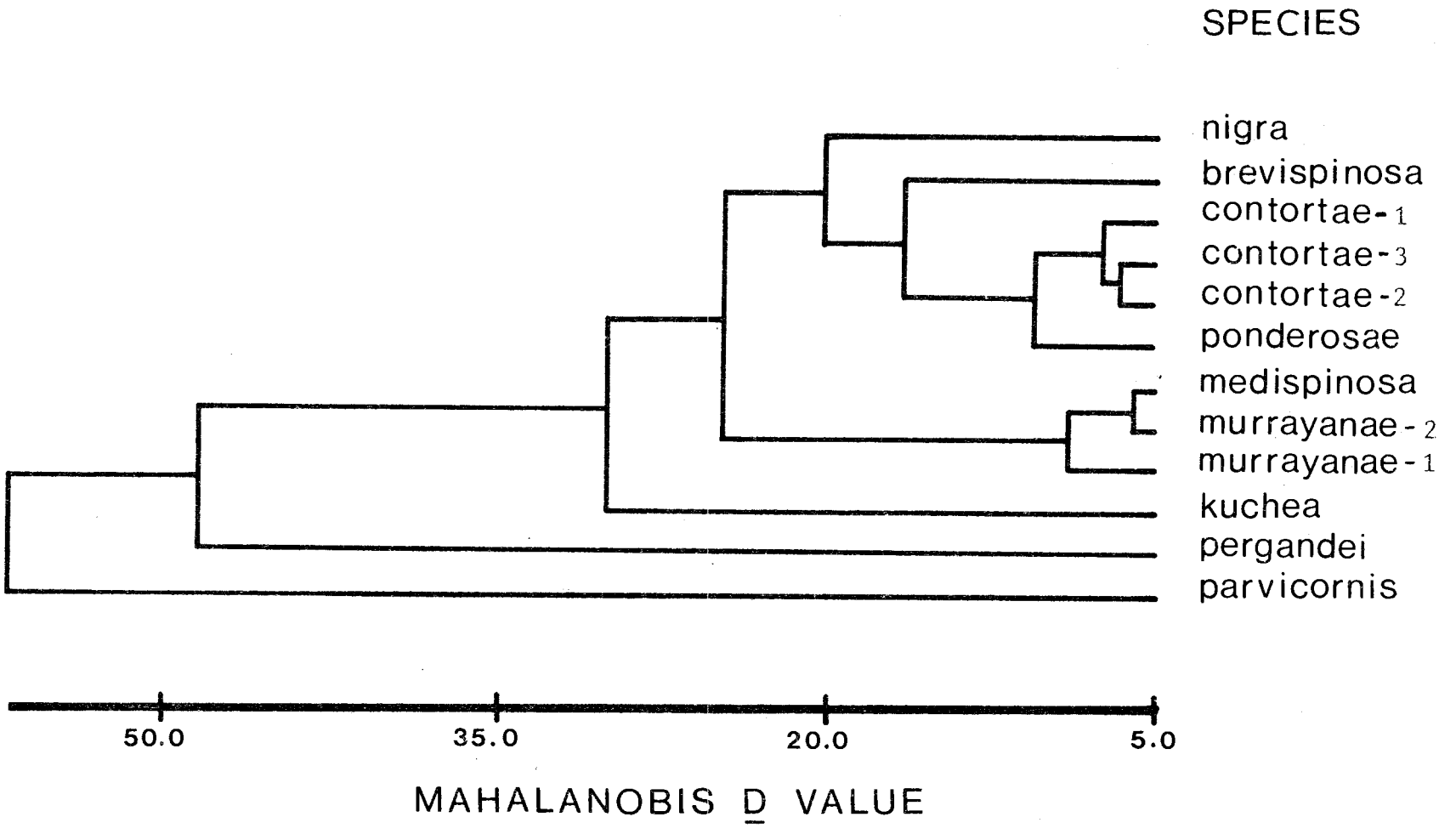
in relation to the other species is determined to large extent by its having relatively long dorsal setae on the abdomen and a relatively short fourth rostrum segment. However, other characters, such as the setal counts, contributed to the separation of these samples.

Separation of the samples along the second discriminant axis was largely due to further reduction of R4L and SLAT5. The samples were also placed along this gradient based on the contributions from other variables, particularly A2L, R5L, TS2L, and SLA3.

No single character served to discriminate between all of the species, in fact separation of these groups along the first and second axis was the result of strong contributions to discrimination from one half of the variables in the data set. Strong contributions were made by some antennal dimensions (A2L, A5L), rostrum dimensions (R3L, R5L), leg dimensions (FL, TL, TS2L), setal length measurements (SLA3), and by some of the setal counts (SNA6SA, SNA2, SNR4, and SNC).

Mahalanobis Generalized Distances (D values) were calculated for all pairwise comparisons of the 12 samples, including the sample of C. pergandei. The resulting matrix of D values was then subjected to a UPGMA cluster analysis and the results summarized in the form of a phenogram (Figure 28). The cophenetic correlation coefficient was 0.801, which indicated that the phenogram closely represented the structure of the matrix of D values (Sneath and Sokal 1973).

Figure 28. Phenogram for the UPGMA cluster analysis of Mahalanobis Generalized Distances, D, calculated for 12 samples representing 9 species of Cinara, based on the analysis of 32 morphological variables. See Table XII for the collection data for each species sample. (contortae: -1, "typical; -2, "small, thin"; -3, "reduced pigmentation"; murrayanae: -1, "typical"; -2, "reduced pigmentation").


SPECIES
nigra
brevispinosa
contortae-1
contortae-3
contortae-2
ponderosae
medispinosa
murrayanae-2
murrayanae-1
kuchea
pergandei
parvicornis
50.0
35.0
20.0
5.0
MAHALANOBIS D VALUE

The Mahalanobis Generalized Distance takes into account the discriminatory information which is unique to each character, having eliminated that variation due to correlation with other characters (Atchley et al. 1982). When compared to the previous analyses where the specimens were projected onto the first two discriminant axes, the phenogram showed a similar structure, which confirmed the impression that most of the important taxonomic information is present on the first few discriminant axes.

The samples of C. contortae and C. medispinosa and C. murrayanae remained clustered together. The most apparent difference was the position of C. parvicornis; it was placed completely away from the other species, holding as unique a position as that of C. pergandei.

In order to quantify the ability of the set of 32 variables to discriminate among the species of Cinara, separate identity functions were calculated for each of the 12 samples. These functions were used to assign the individual specimens to the group with which they shared the highest probability of membership. The results were summarized in an identification table (Table XXVIX) showing the correct and incorrect placements of the individual specimens. Over 94% of the specimens were correctly allocated into the sample they originated from. If the samples of C. contortae and the samples of C. murrayanae are grouped, the rate of correct allocations is over 98%.

Table XXIX. Identification table for 12 samples of 9 species of Cinara. Identification functions based on 32 morphological variables. See Table XII for collection data. The numbers of correct identifications are shown in the diagonal positions, incorrect identifications are in the off-diagonal positions.

Cinara Species		Sample No.											
		1	2	3	4	5	6	7	8	9	10	11	12
nigra	1	25											
pergandei	2		25										
brevispinosa	3			24		1							
parvicornis	4				15								
contortae	5					22	3						
contortae	6						24	1					
contortae	7					2		23					
medispinosa	8								23		2		
murrayanae	9							3		20	2		
murrayanae	10									1	18	1	
ponderosae	11											25	
kuchea	12												25

In order to check for the amount of upward bias in this procedure (see Chapter 3), each of the 12 samples was reduced by 5 specimens each; one specimen chosen at random from each subsample. These 5 specimens from each sample were "unknowns" which were allocated using identity functions calculated from the reduced sample size. The result was that 86.7% of the "unknown" specimens were correctly allocated into the sample they originated from. If the samples of C. contortae and C. murrayanae are grouped, the rate of correct allocation to species is 95%. This compares with 98% from the previous analysis, indicating that the degree of bias in this case is negligible.

5.5 Discussion

The principal component analysis of the samples of the Cinara species demonstrated that each species of Cinara has its own characteristic pattern of morphometric variation. The functional groups of characters responded in different ways along the major components of variation. This heterogeneity of morphometric trends was also evident at the sub-sample level. Within some species, such as C. medispinosa and C. pergandei, individual sub-samples responded differently along the major components of variation, as was demonstrated when the specimens were projected onto the principal axes. In species such as these, the potential for the demonstration of geographic variation is present. It would be possible to

determine those characters that are the least influenced by size variation and which may prove useful in the study of geographic variation. This information would shed light on the interpretation of the adaptive significance of variation in the functional groups of characters, such as the tarsal segments. For example, it is believed that differences in the shape of the tarsal segments have direct bearing on the ability of an aphid to attach to and therefore exploit certain host plants (Kennedy 1986).

The pattern of morphometric variation as observed in C. nigra was evident also in other species, particularly C. kuchea and C. ponderosae. That is, some species are influenced by relatively local factors which affect size; this in turn influences most or all of the variables that were measured. Further work on these and related species may require the evaluation of additional characters.

From the point of view of character selection, the results of this study have shown the importance of measuring the individual segments of such structures as the antenna and the rostrum. That is, the relationships among the segments of these structures vary also, geographically within species, and between species. Unique discriminatory information is lost by lumping the segments of these structures.

The analyses using discriminant function analysis and the Mahalanobis Generalized Distance showed that the range of characters that was selected was important to the successful establishment of the boundaries between the species that were studied. Confirmation

of this was achieved through the use of the allocation procedures. The discriminant function analysis also emphasized the polythetic nature (Sneath and Sokal 1973) of the Cinara species. In all of the analyses, no single character served to completely discriminate among the OTU's. Often, for any one analysis, it was found that as many as one half of the 32 characters that were measured were shown to be strong contributors to discrimination. The importance of a polythetic form of systematic analysis in aphid taxonomy, at all levels of the taxonomic hierarchy, is discussed in Chapter 7.

6. DESCRIPTIONS AND DISTRIBUTIONS OF THE SPECIES OF *CINARA* FOUND ON *PINUS CONTORTA*.

6.1 Introduction

As was mentioned previously, the original and subsequent descriptive material on the species of *Cinara* in North America has been incomplete; for many species, the only descriptive literature is the original description which was often brief and of limited use. As extensive geographic sampling was carried out during the course of this study, it presented an opportunity to describe more completely the morphology of the species.

Descriptions of the apterous viviparous morph of the *Cinara* species feeding on *P. contorta* that were studied are provided below along with information on synonymy, type material, distribution, and the taxonomic relationships among the species. All diagrams were drawn at the same scale. All collections are from *P. contorta* and were collected by R. Foottit unless indicated otherwise. The following abbreviations are used in the text: BM (British Museum, Natural History, London), CAES (Colorado Agicultural Experiment Station, Fort Collins), CNC (Canadian National Collection of Insects, Ottawa), FEM (Frost Entomological Museum, Pennsylvania State University, University Park), FSCA (Florida State Collection of Arthropods, Gainsville), UMC (University of Minnesota Collection,

St. Paul), UCB (University of California, Berkeley), USNM (U. S. National Museum of Natural History, Washington, D. C.). The mean ± one standard deviation, followed by the range, is given for some morphological features. All continuous measurements are in millimeters. The biometric data provided are based on the following sample sizes: n = 25 for C. brevispinosa, C. medispinosa, and C. pergandei; n = 380 for C. nigra; n = 16 for C. parvicornis; n = 75 for C. contortae and n = 45 for C. murrayanae. C. oregonensis is included for completeness as it was present in the area of study.

6.2 Cinara brevispinosa (Gillette and Palmer, 1924)

Lachnus brevispinosus Gillette and Palmer, 1924: 27-30. Holotype: No. 41962, USNM; paratypes, CAES, USNM.

Cinara brevispinosus, Knowlton, 1930: 154.

Cinara brevispinosa, Gillette and Palmer, 1931: 848-849. Palmer, 1952: 25-26; Bradley, 1961: 55-56; Eastop and Hille Ris Lambers, 1976: 148; Smith and Parron, 1978: 88.

Cinara sclerosa, Richards, 1956: 203-204 (vide Eastop and Hille Ris Lambers 1976: 148). Holotype: No. 6372, CNC; paratypes: BM, CNC.

Apterous Viviparous Female (Figures 29, 30)

Colour, when alive, dark reddish brown. Colour of cleared specimens: head, thorax and antennae brown; legs dark brown except

Figure 29. Photographs of the ventral view of slide-mounted specimens of Cinara brevispinosa (top) and Cinara contortae (bottom).

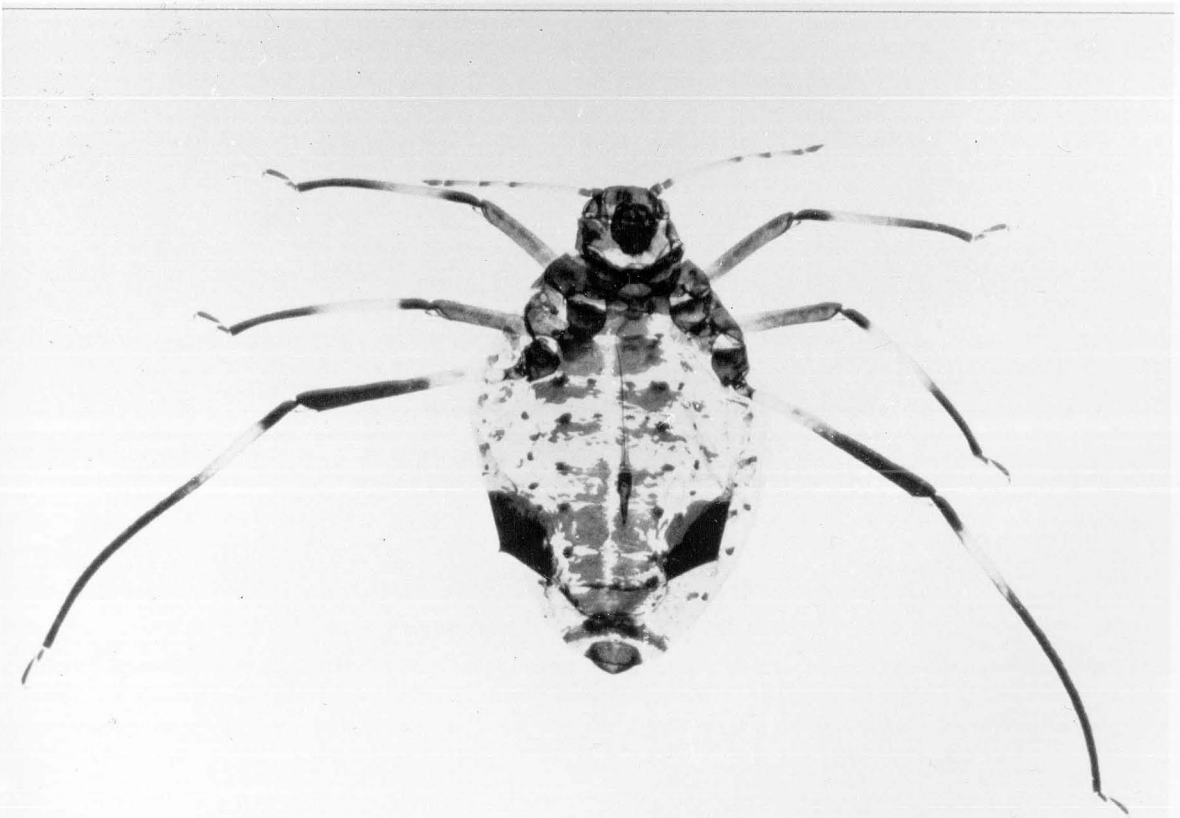
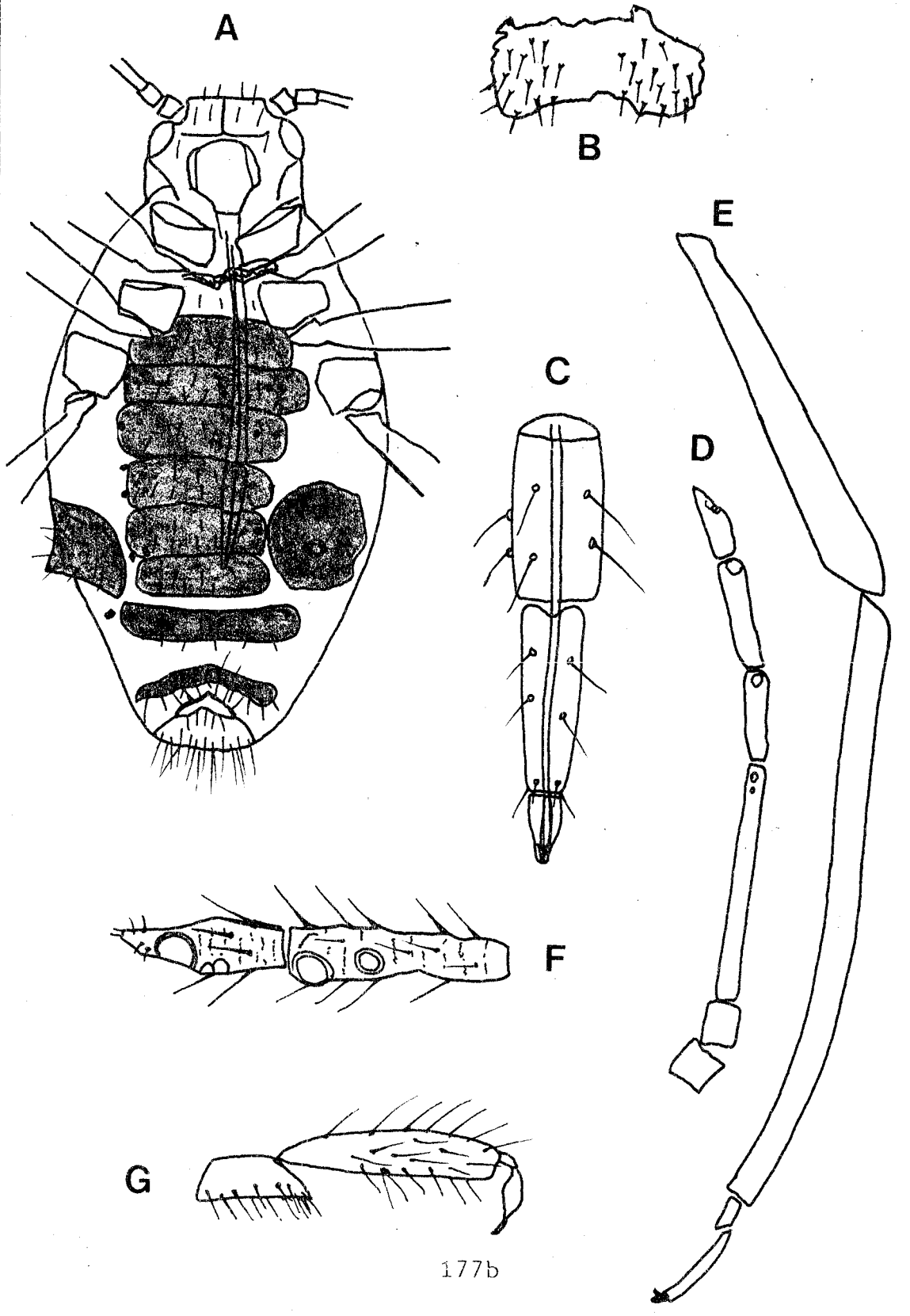


Figure 30. Morphological features of Cinara brevispinosa. A, ventral projection of body; B, genital plate; C, rostrum, segments III, IV and V; D, antenna; E, hind leg; F, antennal segments V and VI; G, hind leg, tarsal segments I and II.


A
B
C
D
E
F
G

proximal one third of femur light brown and light patch present near proximal end of tibia; abdominal sclerites, cornicles, and genital plate light brown.

Body length, 2.99 ± 0.30, 2.62 - 3.56. Head with few, short, spine-like setae. Frons width, .340 ± .024, .301 - .379. Length of antennal segments; II, .108 ± .007, .097 - .122; III, .481 ± .040, .411 - .563; IV, .226 ± .028, .168 - .268; V, .257 ± .027, .197 - .303; VI - base length, .132 ± .008, .114 - .147; VI - base width, .056 ± .003, .049 - .062; VI - processus terminalis, .045 ± .009, .026 - .059. Secondary sensillae on antennal segments III, IV and V. Length of antennal setae slightly less than the base of segments III, IV, and V. Length of setae on antennal segment III, .043 ± .003, .035 - .048. Number of setae on antennal segments; II, 7.7 ± 1.1, 6.0 - 11.0; V, 21.9 ± 3.70, 14.0 - 30.0; VI - base, 8.3 ± 1.4, 6.0 - 13.0; VI - processus terminalis, 4.1 ± 0.5, 3.0 - 5.0. Rostrum extends to middle of abdomen. Length of rostrum segments; V, .088 ± .006, .076 - .103; IV, .206 ± .010, .180 - .228; III, .202 ± .010, .184 - .225; II, .090 ± .012, .067 - 1.33. Number of accessory setae, rostrum IV, 4.8 ± 1.1, 3.0 - 7.0.

Mesosternal tubercle present. Legs with spine-like setae, set at an angle of approximately 45 degrees; those on tibia less than one half the width of the tibia, length, .050 ± .002, .046 - .057. Setae on hind tibia moderately dense; number on .2 mm of mid-section of hind tibia, 41.1 ± 5.1, 29.0 - 52.0. Tarsal setae fine; length of those on tarsal segment II slightly less than width of segment.

A single, ventral, apical, blunt seta, shorter than others, present on tarsal segment I. Hind leg dimensions; femur length, 1.42 ± 0.14, 1.19 - 1.68; femur width, .189 ± .014, .166 - .210; tibia length, 2.21 ± 0.22, 1.89 - 2.66; tarsus I - ventral length, .131 ± .009, .118 - .153; tarsus II - length, .298 ± .017, .267 - .328.

A large, rectangular, heavily pigmented sclerite present on the dorsum of each abdominal segment. Those of abdominal sclerites I, II, and III may be divided along mid-dorsal line. Dorsal abdominal setae short, straight, few, distributed in two irregular rows on abdominal segments I to VII and in a single row along the posterior margin of the transverse sclerite of abdominal segment VIII. Setae on abdominal sclerite V; length, .038 ± .005, .030 - .048; number, 14.5 ± 4.7, 8.0 - 27.0. Number of setae on abdominal sclerite VIII, 10.7 ± 1.1, 9.0 - 13.0. Ventral setae fine, more numerous, variable in length, but greater than two times the length of dorsal setae. Setae on genital plate; length, .077 ± .008, .065 - .093, number, 36.6 ± 6.5, 27.0 - 47.0. Cornicles of moderate size with irregular edges. Setae on cornicles few to moderately dense, of two types, short, spine-like and others approximately two times as long; number of setae on cornicle, 28.9 ± 5.5, 20.0 - 42.0.

Integument of body smooth except for spiculose imbrications on abdominal segments VII and VIII, cauda, and genital plate. Integument of antennal segments smooth except for spiculose imbrications on antennal segments V and VI and apices of II and IV.

Additional Descriptive Material. Fundatrix, Gillette and Palmer 1924, Palmer 1952; apterous viviparous female, Gillette and Palmer 1924, 1931, Palmer 1952, Voegtlin 1976; alate viviparous female, Gillette and Palmer 1924, 1931, Palmer 1952; ovipara, Gillette and Palmer 1924, Palmer 1952; alate male, Gillette and Palmer 1924, Palmer 1952.

Material Examined. (a). Type Material: Four slides, all labelled "Holotype, No. 41962.", as follows: oviparous female and one paratype, on Pinus contorta, 2 X 1921, Stove Prairie Hill, Bellvue, Colorado, M. A. Palmer. Fundatrix and one paratype, on Pinus contorta, 23. V. 1922, reared in insectary, Bellvue, Colorado, M. A. Palmer. Alate viviparous female and apterous viviparous female and one paratype (alate viviparous female), on Pinus contorta, 17. VI. 1922, Stove Prairie Hill, Bellvue, Colorado, M. A. Palmer. Alate male and two metatypes (apterous viviparous female), on Pinus contorta , 21, VIII, 1922, Stove Prairie Hill, Bellvue, Colorado, M. A. Palmer.

Two slides, labelled: Colorado Agricultural Experiment Station. No. 2126. Paratype, three apterous viviparous females, on Pinus contorta, 17. VI. 1922, Stove Prairie Hill, Bellvue, Colorado, M. A. Palmer; No. 3427. Metatypes, three apterous viviparous females, on Pinus contorta, 24. VII. 1923, Estes Park, Colorado, M. A. Palmer.

Cinara sclerosa Richards, Holotype, No. 6272, CNC. Two

apterous, viviparous females, on Pinus contorta, Fawn P. O., British Columbia, 23. VI. 1952, D. A. Ross. Four paratypes, same data as holotype.

(b). Material Collected: CANADA: British Columbia, 26 km N Westbridge, Hwy 33, 27. VII. 1977; Long Beach, Vancouver Island, 13. V. 1979; Mt. Robson Provincial Park, 5. VIII. 1977; Beaverdell, 19. VII. 1979; 26 km NE Princeton, 17. VI. 1980; Christian Valley, 21. VI. 1980; 70 km N Westbridge, 21. VI. 1980; 22 km N Westbridge, 21. VI. 1980; 12 km N Nakusp, Hwy 23, 22. VI. 1980; 10 km E. Hefley Creek, 26. VI. 1980; 83 Mile House, Hwy 97, 29. VII. 1980; Lac La Hache, 29. VII. 1980; 7 km S Hixon, Hwy 97, 31. VII. 1980; 19 km W Prince George, Hwy 16, 31. VII. 1980; 38 km W Burns Lake, Hwy 16, 1. VIII. 1980; Terrace, 3. VIII. 1980; Houston, 4. VIII. 1980; 10 km E. Houston, Hwy 16, 4. VIII. 1980; 31 km N Prince George, Hwy 97, 5. VIII. 1980; McLeod Lake, 5. VIII. 1980; Mackenzie, 6. VIII. 1980; 2 km E Mt. Robson Provincial Park, Hwy 16, 12. VIII. 1980; Mt Robson Provincial Park, 12. VIII. 1980; Pitt Meadows, 27. VI. 1981; 18 km NE Princeton, 1. VII. 1981; 25 km NE Princeton, 1. VII. 1981; 2 km N Nanaimo, Hwy 19, 7. VII. 1981; 3 km N Bowser, Hwy 19, 7. VII. 1981; 10 km S Sayward, Hwy 19, 8. VII. 1981; Parksville, 7. VII. 1981; Sparwood, 9. VII. 1982; 5 km E Moyie Lake, Hwy 95, 10. VII. 1982; Yahk, 10. VII. 1982; 11 km E Stagleap Provincial Park, Hwy 3, 10. VII. 1982; 1.5 km N Salmo, Hwy 6, 10. VII. 1982; 29 km E Castlegar, Hwy 3, 10. VI. 1982; 40 km W Creston, Hwy 3, 10. VII. 1982; Allison

Pass, Hwy 3, 11. VII. 1982; Alberta, Lake Louise, 2. VIII. 1977. U. S. A.: Washington, 3 km S Newport, 29. VI. 1982; Idaho, Priest Lake, 29. VI. 1982; 13 km S Priest Lake, Hwy 57, 29. VI. 1982; 8 km S Cascade, Hwy 55, 30. VI. 1982; 11 km S Island Park, Hwy 20, 4. VII. 1982; Montana, 10 km W West Yellowstone, Hwy 20, 6. VII. 1982; 29 km N West Yellowstone, Hwy 191, 6. VII. 1982; 8 km N Big Sky, Hwy 191, 6. VII. 1982; MacDonald Pass, 32 km W Helena, Hwy 12, 7. VII. 1982; Seeley Lake, 7. VII. 1982; 16 km N Seeley Lake, Hwy 83, 8. VII. 1982; 47 km N Seeley Lake, Hwy 83, 8. VII. 1982; 6 km S West Glacier, Hwy 2, 8. VII. 1982; Wyoming, Madison Junction, 5. VII. 1982. Oregon, Cascadia, 5. VII. 1975; Nehalem, 20. VI. 1979.

(c). Additional Material Examined: CANADA: British Columbia, New Hazelton, 22 V. 1941; Cedarvale, 28. VI. 1941; Campbell River, 26. IX. 1941; Lake Cowichan, 25. V. 1956, 1. VI. 1956, G. A. Bradley; Vernon, 16. VI. 1956, G. A. Bradley; Cascade, 28. V. 1957, G. A. Bradley; Nanaimo, 28. V. 1958, G. A. Bradley; Nechak, 4. VI. 1959, D. A. Ross; Shuswap Lake, 11. VI. 1959, G. A. Bradley; Tofino, 26. V. 1962, G. A. Bradley; Alberta, Pyramid Lake, 25. VIII. 1955, J. D. Stanger; Banff, 30. VIII. 1955, G. A. Bradley; Hinton, 30. VI. 1956, G. A. Bradley; Seebe, 13. VII. 1959, G. A. Bradley; Elkwater, 5. VI. 1962, G. A. Bradley; Lake Louise, 27. VI. 1962, G. A. Bradley; Coleman, 11. VII. 1962, G. A. Bradley; U. S. A.: California, Tioga Pass, 17. VII. 1973, D. Voegtlin; Edson Crk., Siskyou Co., 3. VII. 1977, D. Voegtlin; Colorado, Cameron Pass, 9.

VIII. 1965, G. F. Knowlton; Gould, 9. VIII. 1965, G. F. Knowlton; Linland, 10. VIII. 1965, G. F. Knowlton; Teller City, 10. VIII. 1965, G. F. Knowlton; Rand, 10. VIII. 1965, G. F. Knowlton; Oregon, Malheur Nat. For., Grant Co., 21. VII. 1979, D. Voegtlin; Utah, Unitah Mtns. (Little Bush Crk.), 22. VII. 1966, G. F. Knowlton.

Distribution: CANADA: Alberta, British Columbia. U. S. A.: Colorado, Idaho, Oregon, Montana, Utah, Washington, Wyoming.

Host Range: Pinus contorta

Feeding Site: New growth shoots, needle fascicles, and small branches; small to large (over 100 individuals), dense colonies.

Comments. This species is easily distinguished from the other species of Cinara feeding on P. contorta by the presence of the transverse abdominal bands and the relatively short setae on all appendages. The alate virginopara is more difficult to separate, particularly from C. medispinosa and C. murrayanae, but C. brevispinosa can usually be separated from these by the presence of the relatively short setae on the hind tibia of this morph.

Richards (1956) erected C. sclerosa as a new species on the basis of the extremely dark and heavily sclerotized transverse bands

and the presence of two setal types on the cornicles of the specimens which he examined. He noted the presence of fine setae clustered around the orifice of the cornicle and of spine-like setae closer to the margin of the base of the cornicle. However, examination of material of C. brevispinosa collected during this study showed this pattern of cornicle setation to be consistently present in all samples.

This is a geographically variable species, exhibiting a wide range of size variation.

6.3 Cinara contortae Hottes, 1958.

Cinara contortae Hottes, 1958: 75-76. Holotype: UCB; paratypes, USNM.

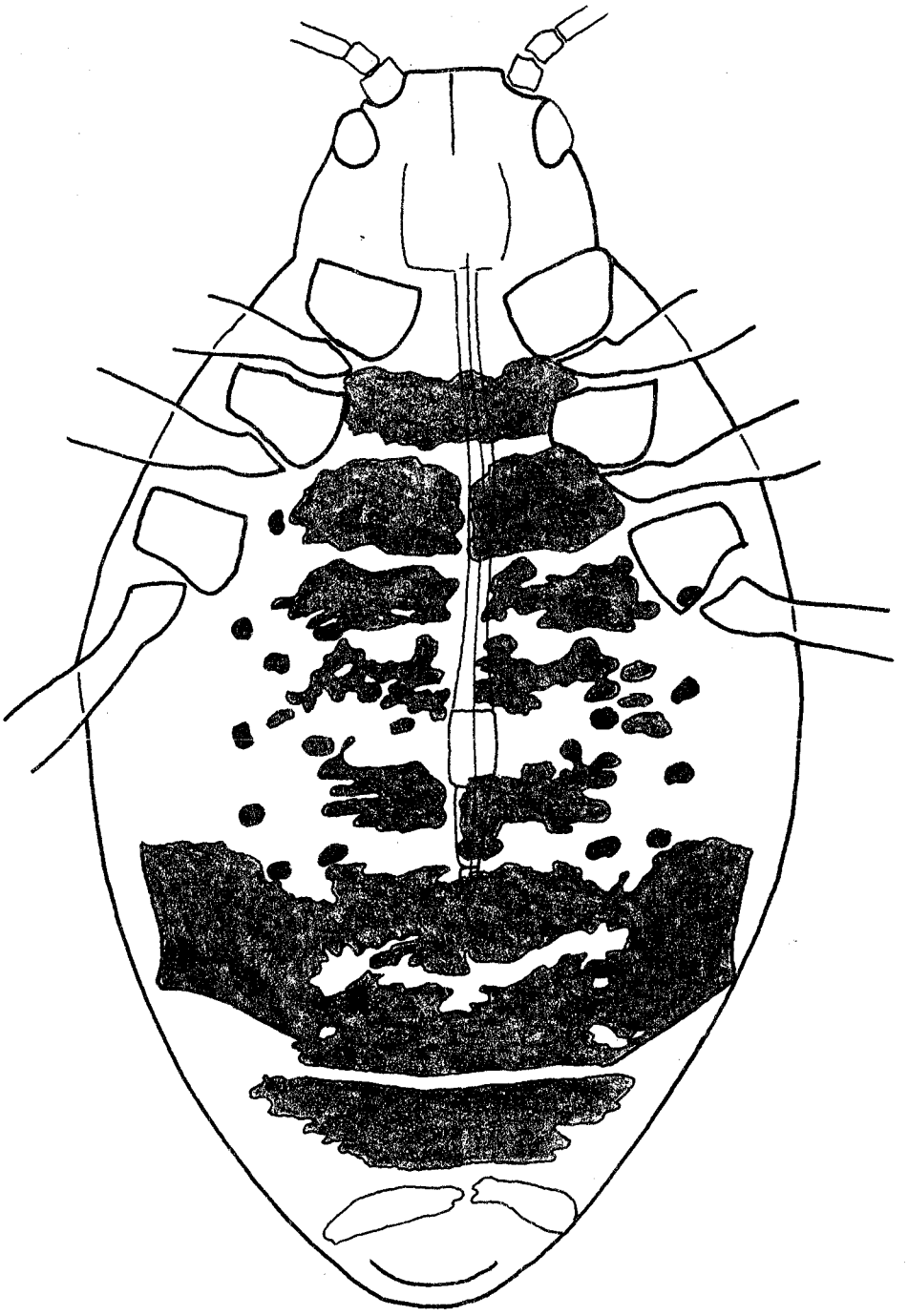
Cinara contortae, Eastop and Hille Ris Lambers, 1976: 149; Smith and Parron, 1978: 89.

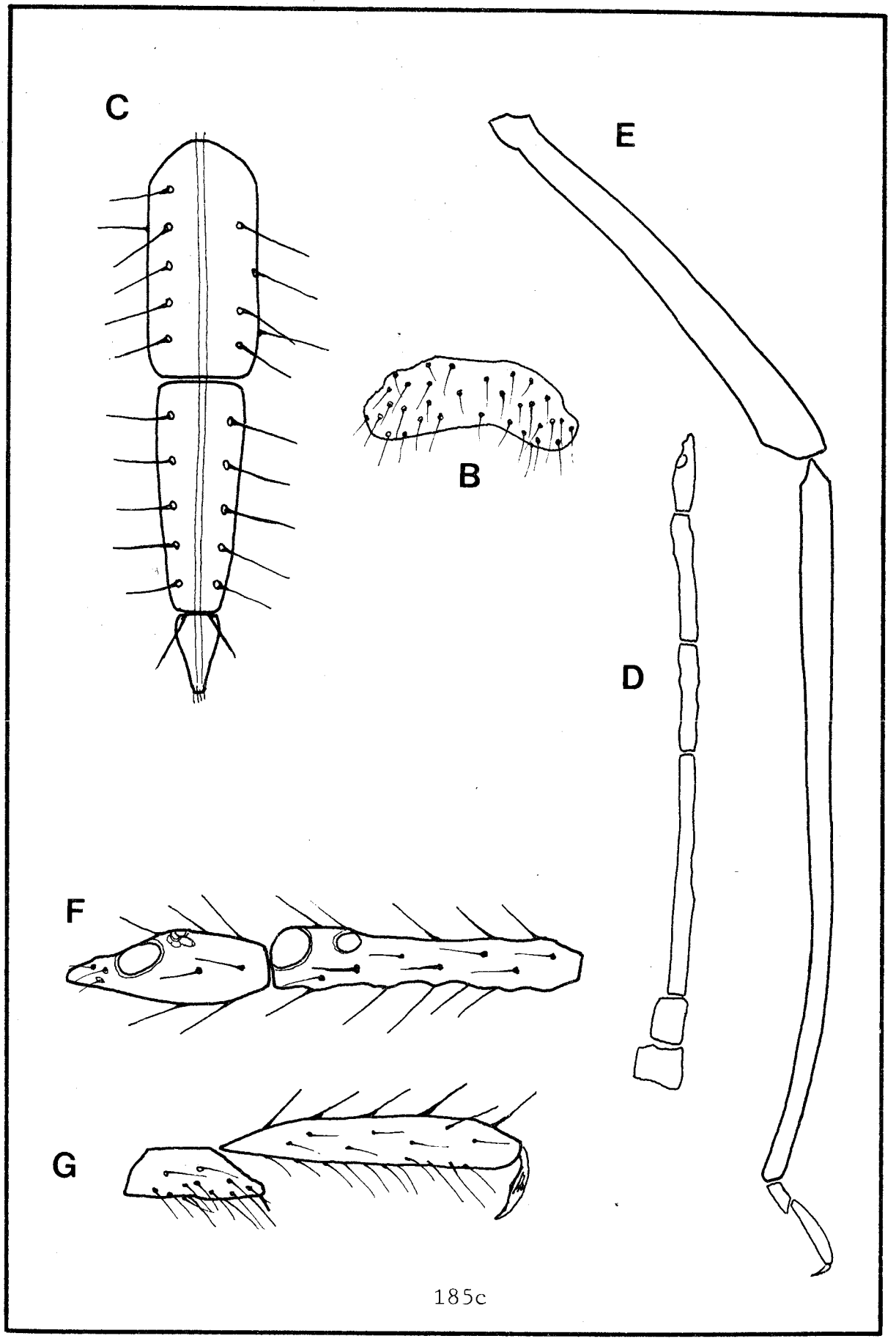
Apterous Viviparous Female (Figures 29, 31)

Colour, when alive, reddish brown. Colour of cleared specimens: head, thorax, and antennae light brown; distal ends of antennal segments III, IV, and V darker, segment VI dark; legs dark except proximal one half of tibia light, proximal tip of tibia dark brown; femur lighter proximally; abdominal sclerites, cornicles, and genital plate light brown.

Figure 31. Morphological features of Cinara contortae. A, ventral projection of body; B, genital plate; C, rostrum, segments III, IV and V; D, antenna; E, hind leg; F, antennal segments V and VI; G, hind leg, tarsal segments I and II.

A




C
E
B
D
F
G

Body length, 3.16 ± 0.40, 2.32 - 4.08. Head with few, short, spine-like setae. Frons width, .331 ± .021, .288 - .384. Lengths of antennal segments; II, .101 ± .009, .084 - .126; III, .521 ± .060, .378 - .667; IV, .218 ± .025, .158 - .268; V, .250 ± .032, .188 - .324; VI - base length, .134 ± .010, .113 - .154; VI - base width, .055 ± .004, .046 - .067; VI - processus terminalis, .046 ± .007, .033 - .062. Secondary sensilla on antennal segments III, IV, and V. Length of antennal setae appoximately longer than the base of segment III. Length of setae on antennal segment III, .040 ± .007, .024 - .055. Number of setae on antennal segments; II, 7.2 ± 1.1, 5.0 - 11.0; V, 26.2 ± 4.5, 12.0 - 35.0; VI - base, 14.2 ± 2.7, 9.0 - 20.0; VI - processus terminalis, 3.9 ± 0.4, 1.0 - 4.0. Rostrum extends to cornicles. Length of rostrum segments; V, .077 ± .007, .061 - .115; IV, .196 ± .017, .167 - .238; III, .217 ± .019, .189 - .264; II, 1.19 ± .012, .089 - 1.55. Number of accessory setae, rostrum IV, 8.2 ± 1.1, 6.0 - 11.0.

Mesosternal tubercle present. Legs with setae, set at an angle of approximately 45 degrees; those on tibia greater than one half the width of the tibia; length, 0.56 ± .007, .033 - .073. Setae on hind tibiae moderately dense; number on 0.2 mm of mid-section of hind tibia, 36.4 ± 5.0, 27.0 - 48.0. Tarsal setae fine; length of those on tarsal segment II slightly greater than width of the segment. A single, ventral, apical, blunt seta, shorter than others, present on tarsal segment I. Hind leg dimensions; femur length, 1.50 ± 0.22, 1.05 - 1.91; femur width, .166 ± .028, .118 -

.271; tibia length, 2.29 ± .033, 1.55 - 2.89; tarsus I - ventral length, .122 ± .013, .087 - .149; tarsus II - length, .263 ± .022, .224 - .320.

Abdominal sclerites I, II, and III covered by heavily pigmented areas; abdominal sclerites IV and V with smaller, irregular, pigmented patches. Dorsal abdominal setae short, straight, few, distributed in two irregular rows on abdominal segments I to VII and in a single row along the posterior margin of the transverse sclerite of abdominal segment VIII. Setae on abdominal sclerite V: length, .023 ± .007, .010 - .037; number, 26.2 ± 4.5, 12.0 - 35.0. Number of setae on abdominal sclerite VIII, 15.2 ± 3.1, 11.0 - 26.0. Ventral setae variable in length, fine, more numerous than dorsal setae, greater than three times the length of the dorsal setae. Setae on genital plate; length, .082 ± .012, .051 - .114; number, 27.4 ± 6.5, 16.0 - 47.0. Cornicles of moderate size with irregular edges. Setae on cornicles moderately dense, of two types, short, spine-like and others approximately three times as long; number of setae on cornicle, 39.3 ± 9.7, 21.0 - 73.0.

Integument of body smooth except for spiculose imbrications on abdominal segments VII and VIII, cauda, and genital plate. Integument of antennal segments smooth except for spiculose imbrications on antennal segments V and VI.

Additional Descriptive Material: Apterous viviparous female, Hottes 1958, Voegtlin 1976.

Material Examined. (a). Type Material: Paratypes, USNM, two slides, apterous viviparous female, on Pinus contorta murrayana, Upper Echo Lake, California, 6. VIII. 1937, E. O. Essig. (b). Material collected: CANADA: British Columbia, 5 km E Westbridge, 23. VII. 1979; 2 km E Princeton, 17. VI. 1980; Westbridge, 21. VI. 1980; Christian Valley, 21. VI. 1980; McLeese Lake, 29. VII. 1980; 15 km E Quesnel, Hwy 26, 30. VII. 1980; 10 km N Quesnel, Hwy 97, 31. VII. 1980; Fraser Lake, I. VIII. 1980; Terrace, 3. VIII. 1980; 11 km N Moricetown, Hwy 16, 3. VIII. 1980; 10 km SW S. Hazelton, Hwy 16, 3. VIII. 1980; Houston, 4. VIII. 1980; 18 km E Burns Lake, Hwy 16, 4. VIII. 1980; 6 km N Summit Lake, Hwy 97, 5. VIII. 1980; Mackenzie, 6. VIII. 1980; Pitt Meadows, 27. VI. 1981; 7. VIII. 1981; 18. IX. 1981; 25 km E Princeton, 1. VII. 1981; Nanaimo, 7. VII. 1981; Bowser, 7. VII. 1981; Burns Bog, Delta, 6. VIII. 1981, 2. X. 1981; 29. VII. 1982; 8 km E Jaffray, Hwy 3, 9. VII. 1982; 5 km E Moyie Lake, Hwy 95, 10. VII. 1982; 29 km E. Castlegar, Hwy 3, 10. VII. 1982; Port Coquitlam, 9. IX. 1982, 11. X. 1982. U. S. A.: California, Crescent City, 22. VI. 1979; Idaho, Priest Lake, 29. VI. 1982; 37 km N Plummer, Hwy 95, 30. VI. 1982; 5 km S Cascade, Hwy 55, 2. VII. 1982; 90 km N Boise, Hwy 55, 2. VII. 1982; 11 km S Island Park, Hwy 20, 5. VII. 1982; 18 km SW West Yellowstone, Hwy 20, 5. VII. 1982; Montana, 29 km N West Yellowstone, Hwy 191, 6. VII. 1982; Helena, 7. VII. 1982; MacDonald Pass, 32 km W Helena, Hwy 12, 7. VII. 1982; Seeley Lake, 7. VII. 1982; 16 km N Seeley Lake, Hwy 83,

8. VII. 1982; 6 km S West Glacier, Hwy 2, 8. VII. 1982; Oregon, Bandit Springs, 3. VIII. 1975; Nehalem State Park, 20. VI. 1979; Washington, Westport, 19. VI. 1979; 3 km S Newport, Hwy 2, 29. 6. 1982.

(c). Additional Material Examined: CANADA: British Columbia, Lumby, 12. VI. 1959, G. A. Bradley; Mt. Silver Star, 16. VI. 1959, G. A. Bradley; Christina Lake, 29. VII. 1959, G. A. Bradley; Alberta, Hinton, 30. VI. 1956, G. A. Bradley. U. S. A.: Oregon, McKenzie Pass, Lane Co., 17. VII. 1977, D. Voegtlin.

Distribution: CANADA: Alberta, British Columbia. U. S. A.: California, Idaho, Montana, Oregon, Washington.

Host Range: Pinus contorta.

Feeding Site: New growth shoots, small branches, main stems, and cankers; small to large colonies.

Comments. C. contortae is similar to C. brevispinosa in that it has short, dorsal, abdominal setae and relatively short setae on most appendages. It differs from the latter species in that it lacks the transverse, pigmented bands on the abdomen. C. contortae is a geographically variable species exhibiting a wide range of size variation.

6.4 Cinara medispinosa (Gillette and Palmer, 1929)

Lachnus medispinosus nov. nom. Gillette and Palmer, 1929: 30.
Holotype, No. 41961, USNM; paratypes, CAES, USNM.

Lachnus similis, Gillette and Palmer, nec van der Goot, 1917, Gillette and Palmer, 1924: 23-26. (preoccupied)

Lachnus medispinosus, Knowlton, 1930: 153-154.

Cinara medispinosa, Gillette and Palmer, 1931: 859; Palmer, 1952: 75; Bradley, 1961: 75; Eastop and Hille Ris Lambers, 1976: 152; Smith and Parron, 1978: 97.

Apterous Viviparous Female (Figures 32, 33)

Colour, when alive, reddish brown. Colour of cleared specimens: head, thorax and antennae brown; antennal segment VI darker, distal ends of segments III, IV, and V darker than rest of segment; legs dark except proximal one third of tibia light, proximal tip of tibia dark brown, femur lighter proximally; abdominal sclerites, cornicles, and genital plate light brown.

Body length, 3.41 ± 0.31, 2.80 - 4.00. Head with few, long, fine setae. Frons width, .345 ± .019, .309 - .376. Lengths of antennal segments; II, .111 ± .007, .101 - .127; III, .571 ± .034, .493 - .632; IV, .240 ± .022, .199 - .283; V, .282 ± .027, .234 - .331; VI - base length, .144 ± .013, .123 - .165; VI - base width, .057 ± .002, .052 - .061; VI - processus terminalis, .043 ± .006,

Figure 32. Photographs of the ventral view of slide-mounted specimens of Cinara medispinosa (top) and Cinara murrayanae (bottom).

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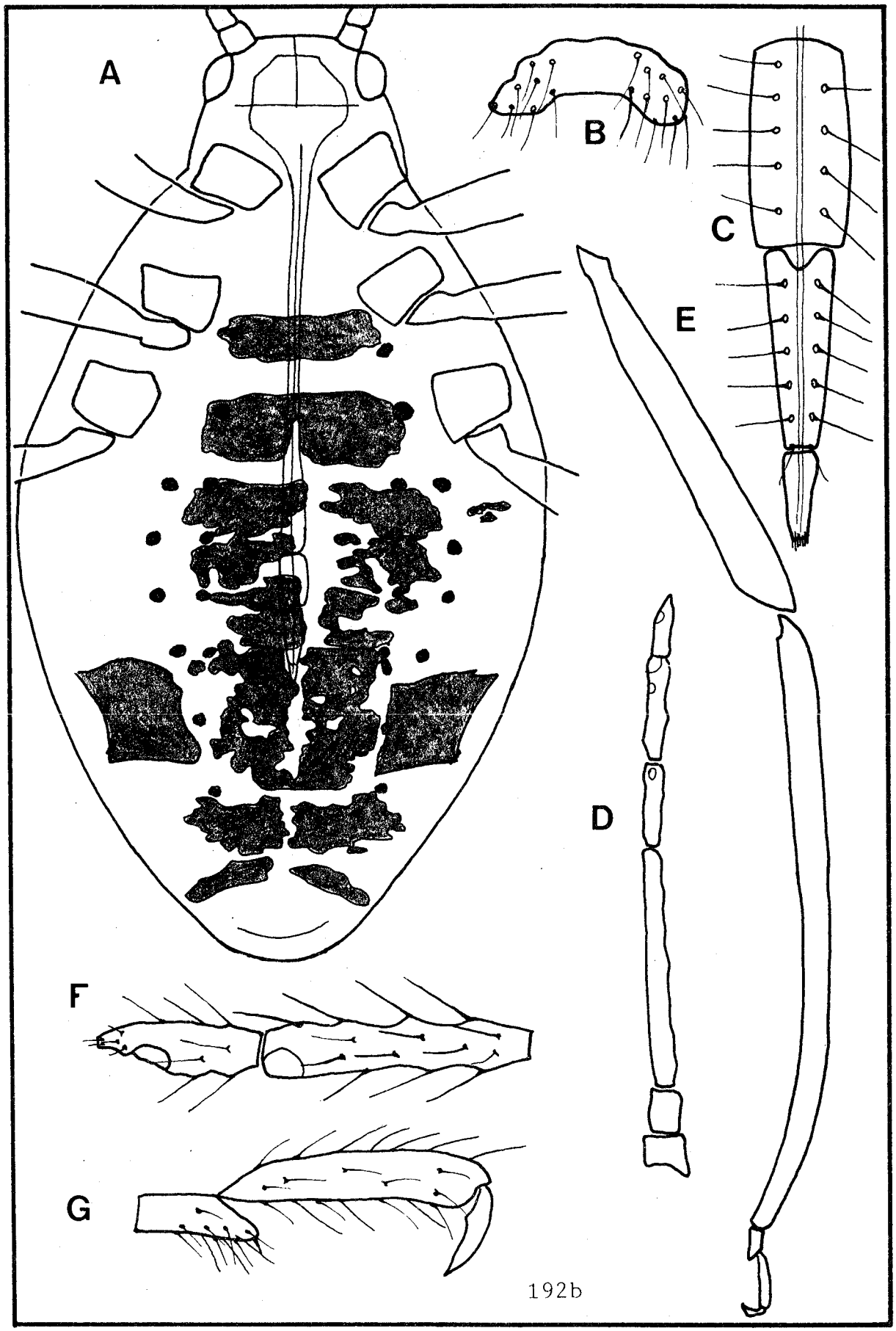
Figure 33. Morphological features of Cinara medispinosa. A, ventral projection of body; B, genital plate; C, rostrum, segments III, IV and V; D, antenna; E, hind leg; F, antennal segments V and VI; G, hind leg, tarsal segments I and II.



192b

.034 - .054. Secondary sensillae on antennal segments III, IV, and V. Length of antennal setae slightly less than two times the base of segment III. Length of setae on antennal segment III, .072 ± .010, .056 - .102. Number of setae on antennal segments; II, 8.4 ± 1.3, 6.0 - 12.0; V, 31.2 ± 7.1, 19.0 - 44.0; VI - base, 15.5 ± 4.3, 10.0 - 24.0; VI - processus terminalis, 4.0 ± 0.2, 3.0 - 4.0; Rostrum extends to cornicles. Length of rostrum segments; V, .083 ± .005, .071 - .092; IV, .212 ± .020, .184 - .248; III, .227 ± .011, .202 - .248; II, 1.23 ± .011, .101 - 1.33. Number of accessory setae, rostrum IV, 8.8 ± 1.1, 7.0 - 11.0.

Mesosternal tubercle present. Legs with setae set at an angle of approximately 45 degrees; those on tibia greater than one half the width of tibia, length, 0.74 ± .007, .064 - .087. Setae on hind tibia moderately dense; number on 0.2 mm of mid-section of hind tibia, 41.0 ± 6.7, 24.0 - 54.0. Tarsal setae moderately fine; length of those on tarsal segment II slightly greater than width of segment. A single, ventral, apical, blunt seta, shorter than others, present on tarsal segment I. Hind leg dimensions; femur length, 1.59 ± 0.12, 1.36 - 1.90; femur width, .181 ± .016, .152 - .212; tibia length, 2.38 ± 0.19, 2.00 - 2.89; tarsus I - ventral length, .130 ± .009, .116 - .149; tarsus II - length, .281 ± .013, .244 - .302.

Abdominal sclerites I, II, and VIII covered by heavily pigmented areas; abdominal sclerites III to VII with small, irregular pigmented patches. Dorsal abdominal setae long, slightly curved,

numerous, in two irregular rows on segments I to VII and in a single row along the posterior margin of the transverse sclerite of abdominal segment VIII. Setae on abdominal sclerite V; length, .098 ± .008, .084 - .125; number, 22.4 ± 6.4, 9.0 - 35.0. Number of setae on abdominal sclerite VIII, 16.5 ± 3.6, 12.0 - 26.0. Ventral setae fine, more numerous than, as long as dorsal setae. Setae on genital plate; length, .103 ± .011, .078 - .121; number, 26.9 ± 6.1, 15.0 - 39.0. Cornicles of moderate size with irregular edges. Setae on cornicles dense, all long, fine; number, 71.9 ± 19.9, 38.0 - 115.0.

Integument of body smooth except spiculose imbrications on abdominal segments VII and VIII, cauda, genital plate, and antennal segment VI.

Additional Descriptive Material: Fundatrix, Gillette and Palmer 1924, Knowlton 1930, Palmer 1952; apterous viviparous female, Gillette and Palmer 1924, 1931, Knowlton 1930, Palmer 1952, Voegtlin 1976; alate viviparous female, Gillette and Palmer 1924, 1931, Knowlton 1930, Palmer 1952; ovipara, Gillette and Palmer 1924, Palmer 1952; alate male, Gillette and Palmer 1924, Palmer 1952.

Material Examined. (a). Type Material: Holotype, No. 41961, USNM, fundatrix, on Pinus contorta murrayana, 8. VI. 1922, Stove Prairie Hill, Bellvue, Colorado, M. A. Palmer. Paratypes, one alate viviparous female, 5 apterous viviparous females, on Pinus contorta

murrayana, 31. V. 1922, Stove Prairie Hill, Bellvue, Colorado, J. L. Hoerner.

(b). Material Collected: CANADA: British Columbia, 26 km N Westbridge, Hwy 33, 27. VII. 1977; Hefley Creek, 26. VI. 1980; McLeese Lake, 29. VII. 1980; 15 km E Quesnel, Hwy 26, 30. VII. 1980; 10 km N Quesnel, Hwy 97, 31. VII. 1980; 12 km N Hixon, 31. VII. 1980; 74 km N Terrace, Hwy 16, 3. VIII. 1980; Houston, 4. VIII. 1980; 20 km E Chetwynd, Hwy 97, 6. VIII. 1980; ;18 km S Taylor, 7. VIII. 1980; Mt. Robson, Hwy 16, 12. VIII. 1980; Blue River, 13. VIII. 1980; 18 km E Princeton, 17. VI. 1980, 3. VII. 1981; 24 km E Princeton, 1. VII. 1981; Bowser, 7. VII. 1981; 10 km E Duncan, 8. VII. 1981; Crowsnest Pass, 9. VII. 1982; 8 km E Jaffray, Hwy 3, 9. VII. 1982; 5 km E Moyie Lake, Hwy 95, 10. VII. 1982; 5 km E Stagleap Prov. Park, Hwy 3, 10. VII. 1982; Alberta, 5 km W Edson, 11. VIII. 1980; 30 km N Hinton, 11. VIII. 1980; 2 km W Jasper, 12. VIII. 1980. U. S. A.: Idaho, 13 km S Priest Lake, 29. VI. 1982; 90 km N Boise, Hwy 55, 2. VII. 1982; 11 km S Island Park, Hwy 20, 5. VII. 1982; 18 km SW West Yellowstone, Hwy 20, 5. VII. 1982; Montana, 10 km W West Yellowstone, Hwy 20, 6. VII. 1982; Washington, 3 km S Newport, Hwy 2, 29. VI. 1982.

(c). Additional Material Examined: CANADA: British Columbia, Topley, 3. VII. 1941; Cascade, 29. VII. 1954, 23. V. 1957, G. A. Bradley; Vernon, 16. VI. 1956, G. A. Bradley; Trinity Valley, 14. V. 1959, G. A. Bradley; Grand Forks, 28. V. 1959, G. A. Bradley; Rossland, 29. V. 1959, G. A. Bradley; Greenwood, 3. VI. 1959, G. A.

Bradley; Squilax, 11. VI. 1959, G. A. Bradley; Lumby, 12. VI. 1959, 16. VI. 1962, G. A. Bradley; Christina Lake, 29. VII. 1959, G. A. Bradley; Shushwap Falls, 10. VI. 1959, G. A. Bradley; Nanoose, 25. V. 1962, G. A. Bradley; Qualicum, 25. V. 1962, G. A. Bradley; Chemainus, 24. V. 1962, G. A. Bradley; Tofino, 26. V. 1962, G. A. Bradley; Alberta, Hardisty, 11. VIII. 1950, G. A. Bradley; Nordegg, VII. 1952; Entrance, 21. VII. 1954, G. A. Bradley; Miette Hot Springs, 16. VIII. 1955, J. D. Stanger; Jonas Creek, 20. VIII. 1955, J. D. Stanger; Pyramid Lake, 25. VIII. 1955, J. D. Stanger; Banff, 30. VIII. 1955, J. D. Stanger; Rock Lake, 28. VI. 1956, G. A. Bradley; Mt. Eisenhower, 18. VII. 1959, G. A. Bradley; Seebe, 11. VIII. 1959, 4. IX. 1968, G. A. Bradley; Barrier Lake, 20. VIII. 1965, J. M. Powell; Saskatchewan, Indian Head, 30. VI. 1955, G. A. Bradley, Cypress Hills, 23. VI. 1959, G. A. Bradley; Yukon, Mayo Rd., 4. VII. 1964, R. Wood; U. S. A.: California, Blodgett Exp. Forest, Eldorado Co., 1. VI. 1975, D. Voegtlin; Loon Lk., Eldorado Co., 23. VI. 1975, D. Voegtlin; Idaho, Hillyard Canyon, 5. VII. 1968, G. F. Knowlton; Oregon, Portland, 7. IV. 1971, F. P. Larson; Sutton Camp Ground, Lane Co., 7. V. 1978, D. Voegtlin; Utah, East McKee, Unitah Mtns., 22. VII. 1966, G. F. Knowlton.

Distribution: CANADA: Alberta, British Columbia, Saskatchewan, Yukon. U. S. A.: California, Colorado, Idaho, Oregon, Utah.

Host Range: Pinus contorta

Feeding Site: New growth shoots, small to large branches, scar tissue on trunk, cankers; large dense colonies.

Comments. The dorsal pigmentation pattern of this species resembles somewhat that of C. brevispinosa. However, it can be distinguished from this species by its larger setae and longer rostrum. C. medispinosa is intermediate between C. brevispinosa and C. murrayanae with respect to the length of setae.

6.5 Cinara murrayanae (Gillette and Palmer, 1924)

Lachnus murrayanae Gillette and Palmer, 1924: 26-27. Holotype, No. 41960, USNM; paratypes: BM, USNM.

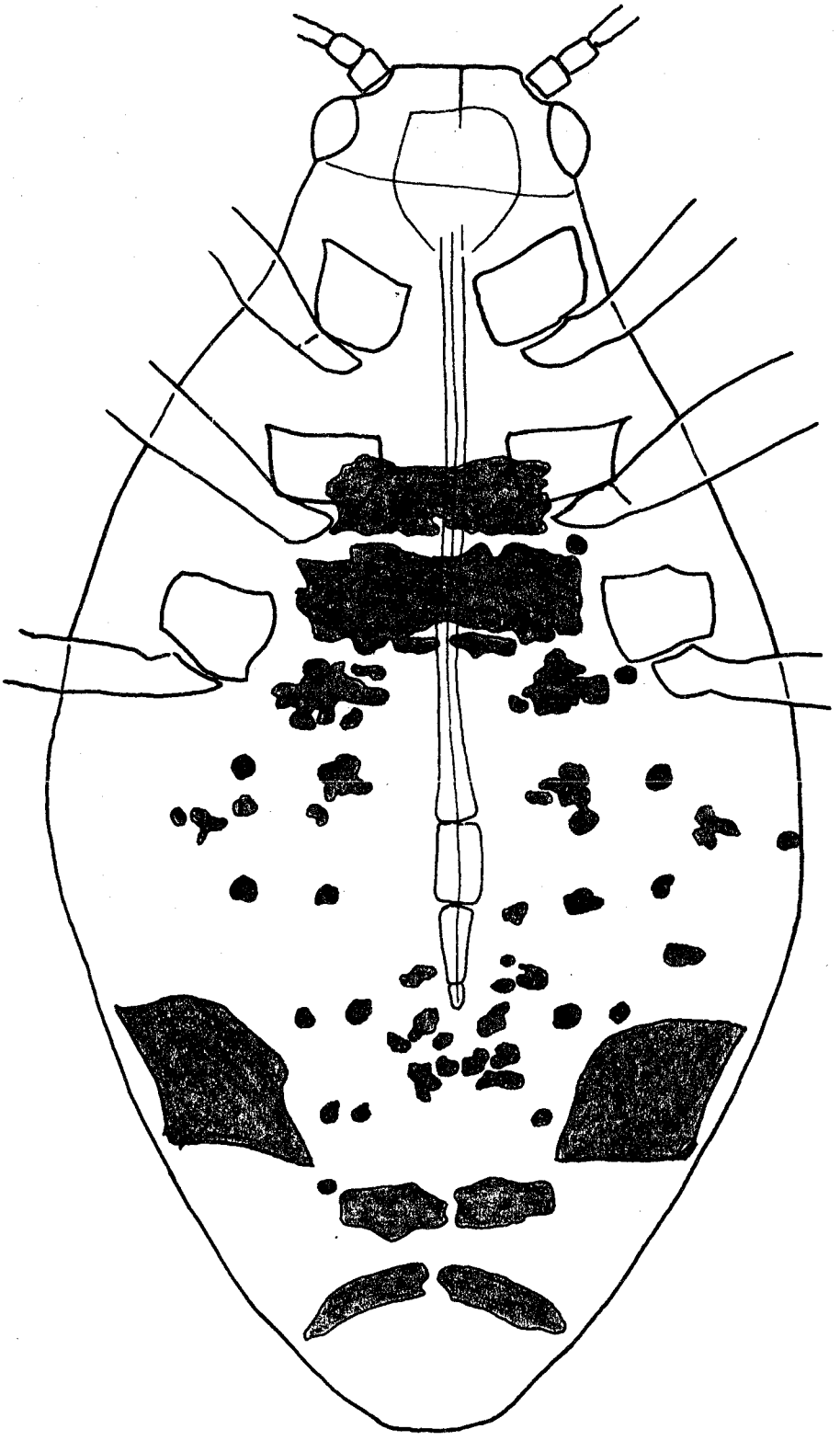
Cinara murrayanae, Gillette and Palmer, 1931: 860-861; Palmer, 1952: 35-36; Bradley, 1961: 64-65; Eastop and Hille Ris Lambers, 1976: 152; Smith and Parron, 1978: 98.

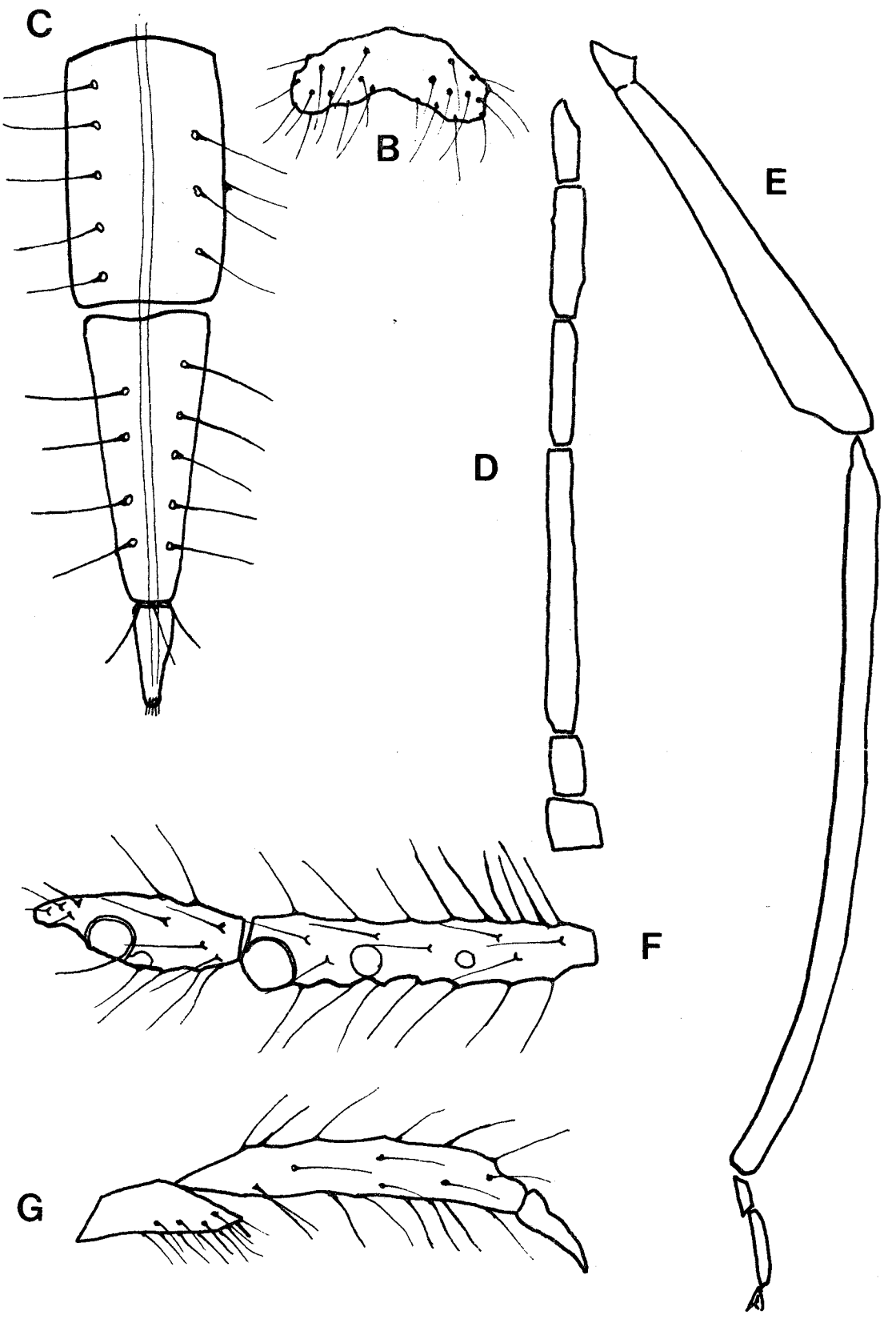
Apterous Viviparous Female (Figures 32, 34)

Colour when alive, reddish brown. Colour of cleared specimens: head, thorax, and antenna dark brown; antennal segments I, II, and VI dark brown, distal ends of segments III, IV, and V darker than rest of segments. Legs dark except proximal one fifth of tibia light, proximal tip of tibia dark, femur lighter proximally;

Figure 34. Morphological features of Cinara murrayanae. A, ventral projection of body; B, genital plate; C, rostrum, segments III, IV and V; D, antenna; E, hind leg; F, antennal segments V and VI; G, hind leg, tarsal segments I and II.

A

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abdominal sclerites and genital plate brown, cornicles dark brown.

Body length, 3.68 ± 0.35, 2.96 - 4.24. Head with many, fine setae. Frons width, .374 ± .025, .310 - .438. Lengths of antennal segments; II, .120 ± .009, .104 - .140; III, .572 ± .071, .446 - .707; IV, .259 ± .032, .201 - .328; V, .309 ± .036, .248 - .410; VI - base length, .150 ± .011, .130 - .175; VI - base width, .064 ± .005, .053 - .072; VI - processus terminalis, .045 ± .005, .034 - .055. Secondary sensilla on antennal segments III, IV, and V. Length of antennal setae greater than two times the base of segment III. Length of setae on antennal segment III, .082 ± .010, .083 - .114. Number of setae on antennal segments; II, 10.4 ± 1.9, 7.0 - 14.0; V, 37.6 ± 4.6, 27.0 - 48.0; VI - base, 19.4 ± 2.8, 13.0 - 24.0; VI - processus terminalis, 3.9 ± 0.3, 3.0 - 4.0; Rostrum extends to cornicles. Length of rostrum segments; V, .088 ± .006, .074 - .099; IV, .230 ± .018, .187 - .261; III, .244 ± .018, .200 - .280; II, 1.39 ± .014, 1.11 - 1.66. Number of accessory setae, rostrum IV, 10.3 ± 1.4, 8.0 - 14.0.

Mesosternal tubercle present. Legs with setae set at an angle of approximately 45 degrees; those on tibia almost as long as width of tibia; length, .087 ± .014, .064 - .116. Setae on hind tibia dense; number on 0.2 mm of mid-section of hind tibia, 45.5 ± 5.3, 35.0 - 58.0. Tarsal setae on hind tibia moderately fine; length of those on tarsal segment II greater than width of segment. A single, ventral, apical, blunt seta, shorter than others, present on tarsal segment I. Hind leg dimensions; femur length, 1.63 ± 0.19, 1.39 -

2.03; femur width, .188 ± .022, .148 - .237; tibia length, 2.45 ± 0.34, 2.00 - 3.11; tarsus I - ventral length, .136 ± .011, .115 - .160; tarsus II - length, .295 ± .021, .252 - .339.

Abdominal sclerites I, II, and VIII covered by heavily pigmented areas; abdominal sclerites III to VII with small, irregular pigmented patches. Dorsal abdominal setae long, slightly curved, numerous, in two irregular rows on each sclerite. Setae on abdominal sclerite V; length, .114 ± .016, .085 - .152; number, 37.5 ± 13.6, 12.0 - 64.0. Number of setae on abdominal sclerite VIII, 18.1 ± 4.0, 12.0 - 29.0. Ventral setae fine, more numerous than, as long as, dorsal setae. Setae on genital plate; length, .113 ± .013, .088 - .154; number, 32.4 ± 5.0, 24.0 - 45.0. Cornicles of moderate size, with irregular edges. Setae on cornicle dense, all long, fine; number of setae on cornicle, 87.7 ± 15.9, 61.0 - 135.0.

Integument of body smooth except spiculose imbrications on abdominal segments VII and VIII, cauda, genital plate and antennal segment VI.

Additional Descriptive Material: Apterous viviparous female, alate viviparous female, ovipara, alate male, Palmer 1952.

Material Examined. (a). Type Material: Holotype, No. 41960, USNM, 1 slide, apterous viviparous female, on Pinus contorta var. murrayana, Stove Prairie Hill, Bellvue, Colorado, 3. VI. 1922, J. L. Hoerner. Paratypes, 1 slide, fundatrix, same data as holotype,

except collected 20. V. 1922; 1 slide, alate viviparous female, same data as holotype.

(b). Material Collected: CANADA: British Columbia, Pitt Meadows, 29. V. 1979, 27. VI. 1981, 7. VIII. 1981, 18. IX. 1981, 4. X. 1981; Naramata, 17. VI. 1979; Christian Valley, 21. VI. 1980; Williams Lake, 29. VII. 1980; 12 km N Hixon, Hwy 97, 31. VII. 1980; Mackenzie, 6. VIII. 1980; Mt. Robson, Hwy 16, 12. VIII. 1980; 26 km S Valemount, Hwy 5, 13. VIII. 1980; Burns Bog, Delta, 6. VIII. 1981, 2. X. 1981, 29. VII. 1982; Sparwood, 9. VII. 1982; 8.0 km E Jaffray, Hwy 3, 9. VII. 1982; 5 km E Moyie Lake, Hwy 95, 10. VII. 1982; 29 km E Castlegar, Hwy 3, 10. VII. 1982; Alberta, 7 km S Swan Hills, 10. VIII. 1980; 20 km W Edson, 11. VIII. 1980; U. S. A.: California, Crescent City, 22. VI. 1979; Idaho, 5 km S Cascade, Hwy 55, 2. VII. 1982; 18 km SW West Yellowstone, Hwy 20, 5. VII. 1982; Montana, Seeley Lake, 8. VII. 1982; Oregon, Nehalem State Park, 20. VI. 1979.

(c). Additional Material Examined: CANADA: British Columbia, Salmon Arm, 14. VI. 1955, G. A. Bradley; Englishman River Falls, 20. V. 1962, G. A. Bradley; Chemainus, 24. V. 1962, G. A. Bradley; Qualicum, 25. V. 1962, G. A. Bradley; Grand Forks, 28. V. 1962, G. A. Bradley; Alberta, Barrier Lake, 20. VIII, 1965, J. N. Powell.

Distribution: CANADA: Alberta, British Columbia. U. S. A.: California, Idaho, Montana, Oregon.

Host Range: Pinus contorta

Feeding Site: Small branches, main stem, cankers; large, dense colonies.

Comments. In the apterous morph of this species, the setae on the hind tibia are nearly as long as the width of the tibia; in the alate morph they are nearly twice as long as the width of the tibia. This characteristic, and the fact that the setae are heavier and more erect, distinguish this species from other species of Cinara on P. contorta.

6.6 Cinara nigra (Wilson, 1919)

Lachniella nigra Wilson, 1919: 41-432. Lectotype, UMN; paralectotypes, FEM, USNM.

Cinara kocheta, Hottes, 1958: 81-83. (vide Pepper and Tissot, 1973: 67-74). Holotype, paratypes, USNM.

Cinara nigra, Pepper and Tissot, 1973: 67-74; Eastop and Hille Ris Lambers, 1976: 152; Smith and Parron, 1978: 98.

Apterous Viviparous Female (Figures 35, 36)

Colour when alive, shiny, dark reddish brown. Colour of cleared specimens: head and thorax brown; antennae lighter brown, distal ends of segments darker than rest of segment; legs brown except

Figure 35. Photographs of the ventral view of slide-mounted specimens of Cinara nigra (top) and Cinara oregonensis (bottom).

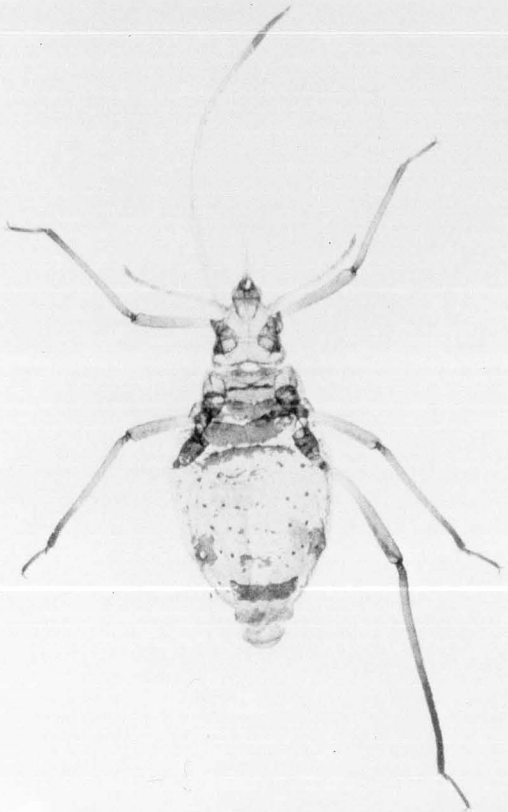

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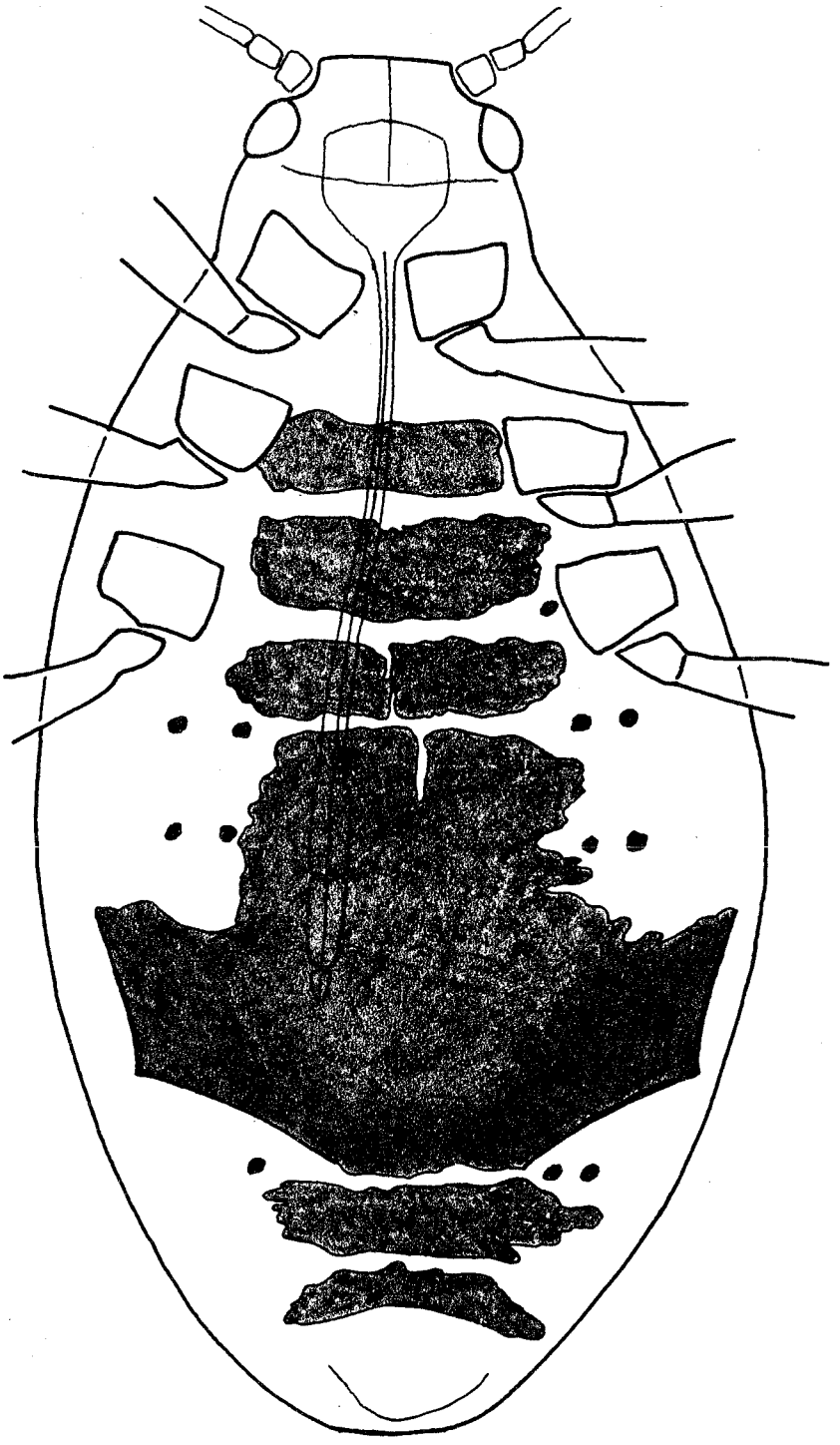
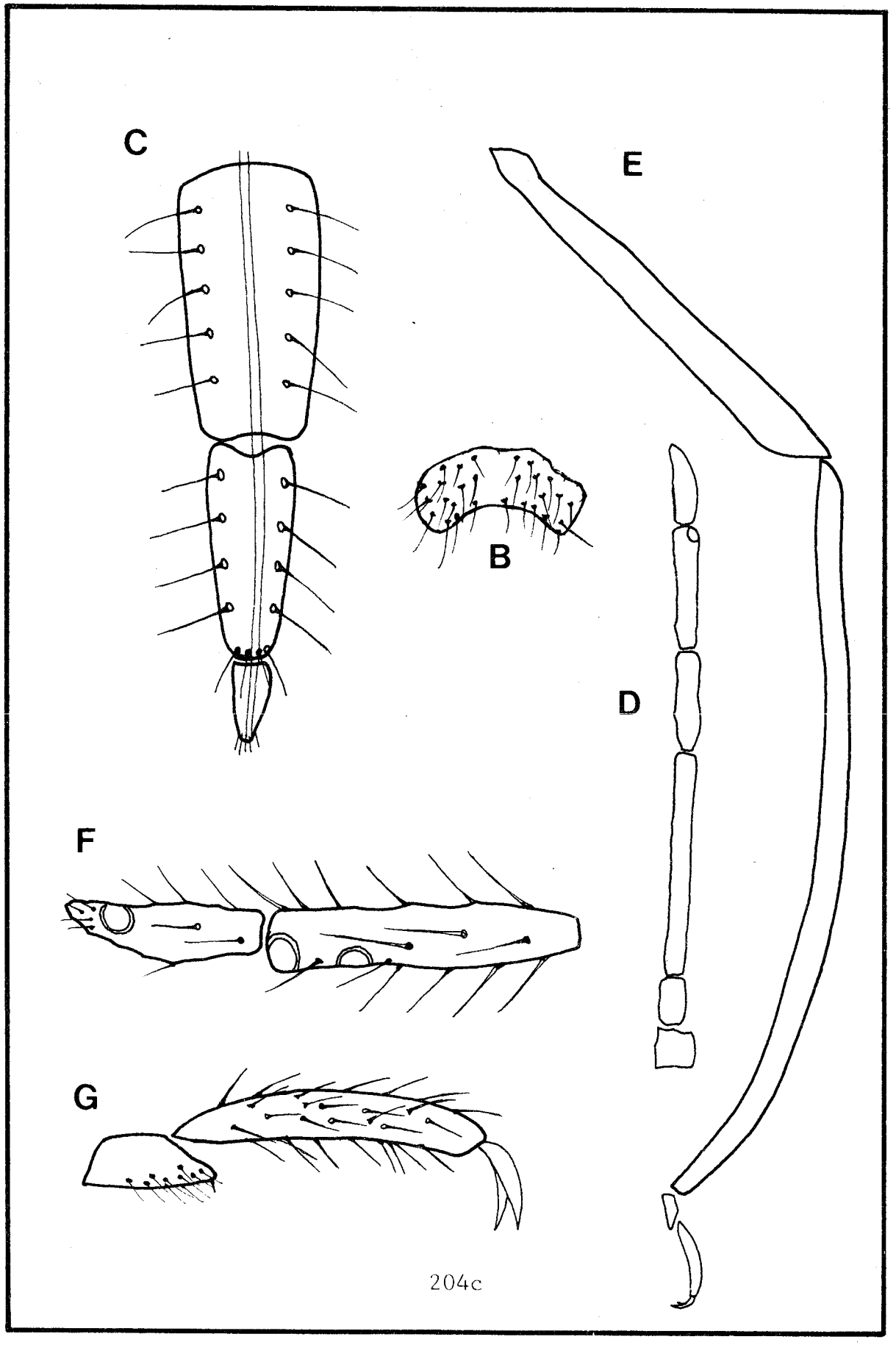
Figure 36. Morphological features of Cinara nigra. A, ventral projection of body; B, genital plate; C, rostrum, segments III, IV and V; D, antenna; E, hind leg; F, antennal segments V and VI; G, hind leg, tarsal segments I and II.

A




C
E
B
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G

proximal one fifth of tibia light, proximal tip of tibia dark brown, femur lighter proximal one half; abdominal sclerites and genital plate brown, cornicles darker brown.

Body length, 3.51 ± 0.31, 2.78 - 4.32. Head with numerous, long, fine setae; length of setae greater than distance between setae. Frons width, .355 ± .019, .304 - .440. Lengths of antennal segments; II, .114 ± .006, .098 - .134; III, .545 ± .035, .400 - .651; IV, .241 ± .019, .184 - .299; V, .290 ± .017, .248 - .345; VI - base length, .140 ± .006, .116 - .158; VI - base width, .056 ± .003, .046 - .066; VI - processus terminalis, .048 ± .004, .036 - .062. Secondary sensillae on antennal segments III, IV, and V. Length of antennal setae slightly longer than base of III. Length of setae on antennal segment III, .059 ± .005, .043 - .080. Number of setae on antennal segments; II, 9.1 ± 1.1. 6.0 - 13.0; V, 35.9 ± 3.5, 27.0 - 48.0; VI - base, 12.7 ± 1.5, 9.0 - 17.0; VI - processus terminalis, 5.1 ± .05, 4.0 - 7.0. Rostrum extends to cornicles. Length of rostrum segments; V, .082 ± .003, .077 - .088; IV, .209 ± .016, .184 - .230; III, .271 ± .015, .234 - .294; II, 1.41 ± .114, 1.11 - 1.60. Number of accessory setae, rostrum IV, 8.8 ± 0.9, 8.0 - 11.0.

Mesosternal tubercle present, prominent. Legs with setae set at an angle of approximately 45 degrees; those on tibia greater than one half the width of the tibia, length, .075 ± .006, .055 - .094. Setae on hind tibiae moderately dense; number on 0.2 mm of mid-section of hind tibia, 42.3 ± 4.9, 25.0 - 58.0. Tarsal setae

fine; length of those on tarsal segment II equal to width of segment. A single, ventral, apical, blunt seta, shorter than others, present on tarsal segment I. Hind leg dimensions; femur length, 1.62 ± 0.14, 1.28 - 1.97; femur width, .177 ± .018, .128 - .224; tibia length, 2.55 ± 0.21, 1.99 - 3.22; tarsus I - ventral length, .129 ± .006, .108 - .146; tarsus II - length, .309 ± .015, .269 - .357.

Dorsum of abdomen with large, continuous sclerotized area. Dorsal abdominal setae short, straight; those within sclerotized patch appear as small, clear dots; distributed in single rows on each segment. Setae on abdominal sclerite V; length, .011 ± .002, .003 - .018; number, 6.9 ± 1.0, 4.0 - 10.0. Number of setae on abdominal sclerite VIII, 12.9 ± 1.3, 9.0 - 16.0. Ventral setae fine, variable in length, more numerous than, greater than ten times the length of dorsal setae. Setae on genital plate; length, .083 ± .009, .054 - .104; number, 32.9 ± 5.0, 19.0 - 48.0. Cornicles large, sclerotized, fused with large dorsal patch. Setae on cornicles moderately dense, as long as ventral setae; number of setae on cornicle, 41.9 ± 6.8, 24.0 - 62.0.

Integument of body smooth except for spiculose imbrications on abdominal segments VII and VIII, cauda, and genital plate. Integument of antennal segments smooth except for spiculose imbrications on antennal segments VI.

Additional Descriptive Material. Apterous viviparous female, Pepper and Tissot 1973, Wilson 1919; alate viviparous female, Hottes 1958, Pepper and Tissot 1973, Wilson 1919; ovipara, apterous male, Pepper and Tissot 1973.

Material Examined. (a). Type Material: Lectotype, USNM, designated by Pepper and Tissot (1973), apterous viviparous female, on Pinus sylvestris, Kilburn, Wisconsin, 18. VIII. 1917, H. F. Wilson. Morphotype, FEM, designated by Pepper and Tissot (1973), ovipara, on Pinus banksiana, Sanford, Michigan, 30. IX. 1964, T., P & B. coll.

(b). Material Collected: CANADA: British Columbia, Hefley Creek, 26. VI. 1980; 83 Mile House, 29. VII. 1980; 15 km E Quesnel, Hwy 26, 30. VII. 1980; 10 km N Quesnel, Hwy 97, 31. VII. 1980; 12 km N Hixon, Hwy 97, 31. VIII. 1980; 5 km W Prince George, Hwy 16, 31. VII. 1980; 30 km W Prince George, Hwy 16, 31. VII. 1980; 46 km NW Smithers, Hwy 16, 3. VIII. 1980; Lakelse Lake, 3. VIII. 1980; 31 km N Prince George, Hwy 97, 5. VIII. 1980; Mackenzie, 6. VIII. 1980; 45 km SE Chetwynd, Hwy 97, 6. VIII. 1980; 18 km S Taylor, Hwy 97, 7. VIII. 1980; 105 km NW Fort St. John, Alaska Hwy., 8. VIII. 1980; 2 km S Fort St. John, 8. VIII. 1980; 2 km E Mt. Robson Prov. Park, Hwy 16, 12. VIII. 1980; Tête Jaune, 12. VIII. 1980; Valemount, 13. VIII. 1980; 26 km S Valemount, Hwy 5, 13. VIII. 1980; Sparwood, 9. VII. 1982; Alberta, 5 km N Swan Hills, Hwy 33, 9. VIII. 1980; 7 km S Swan

Hills, 10. VIII. 1980; 5. km W Edson, Hwy 16, 11. VIII. 1980; 20 km W Edson, Hwy 16, 11. VIII. 1980.

(c). Additional Material Examined: CANADA: Alberta, Grande Prairie, 21. VI. 1956, G. A. Bradley; Kananaskis, 24. VI. 1956, J. D. Stanger; Mt. Eisenhower, 20. VI. 1959, G. A. Bradley; Ricinus, 5. VII. 1963; Spirit River, 6. VII. 1962, G. J. Smith; Manitoba, Eganoff Lake, 13. VIII. 1964, G. A. Bradley, Pinus banksiana; Sandilands For. Res., 30. VI. 1966, G. A. Bradley, Pinus banksiana; Ontario, Cedar Lake, 15. VIII. 1960, G. A. Bradley, Pinus banksiana; Kormack, 2. VIII. 1962, F. Livesay, Pinus banksiana; Caramat, 13. VII. 1964, U. Jansons, Pinus banksiana; Northwest Territories, Yellowknife, 16. VII. 1962, Pinus banksiana;

Distribution: CANADA: Alberta, British Columbia, Manitoba, Northwest Territories, Ontario; U. S. A.: Michigan, Wisconsin.

Host Range: Pinus banksiana, Pinus contorta.

Feeding Site: Main stem, branches; large, dense colonies.

Comments. The distribution of this species, and its morphological relationships with the other Cinara species having a dark, dorsal, abdominal patch, are discussed in Chapter 4 and in section 6.11. Pepper and Tissot (1973) described in detail the morphology of this species and discussed the type material.

6.7 Cinara oregonensis (Wilson, 1915)

Lachnus oregonensis Wilson, 1915: 103. Holotype: UMN.

Lachnus oregonensis, Palmer, 1926: 311-314.

Cinara oregonensis, Gillette and Palmer 1931: 862; Palmer, 1952: 37; Bradley, 1961: 53-54; Eastop and Hille Ris Lambers, 1976: 152; Smith and Parron, 1978: 100.

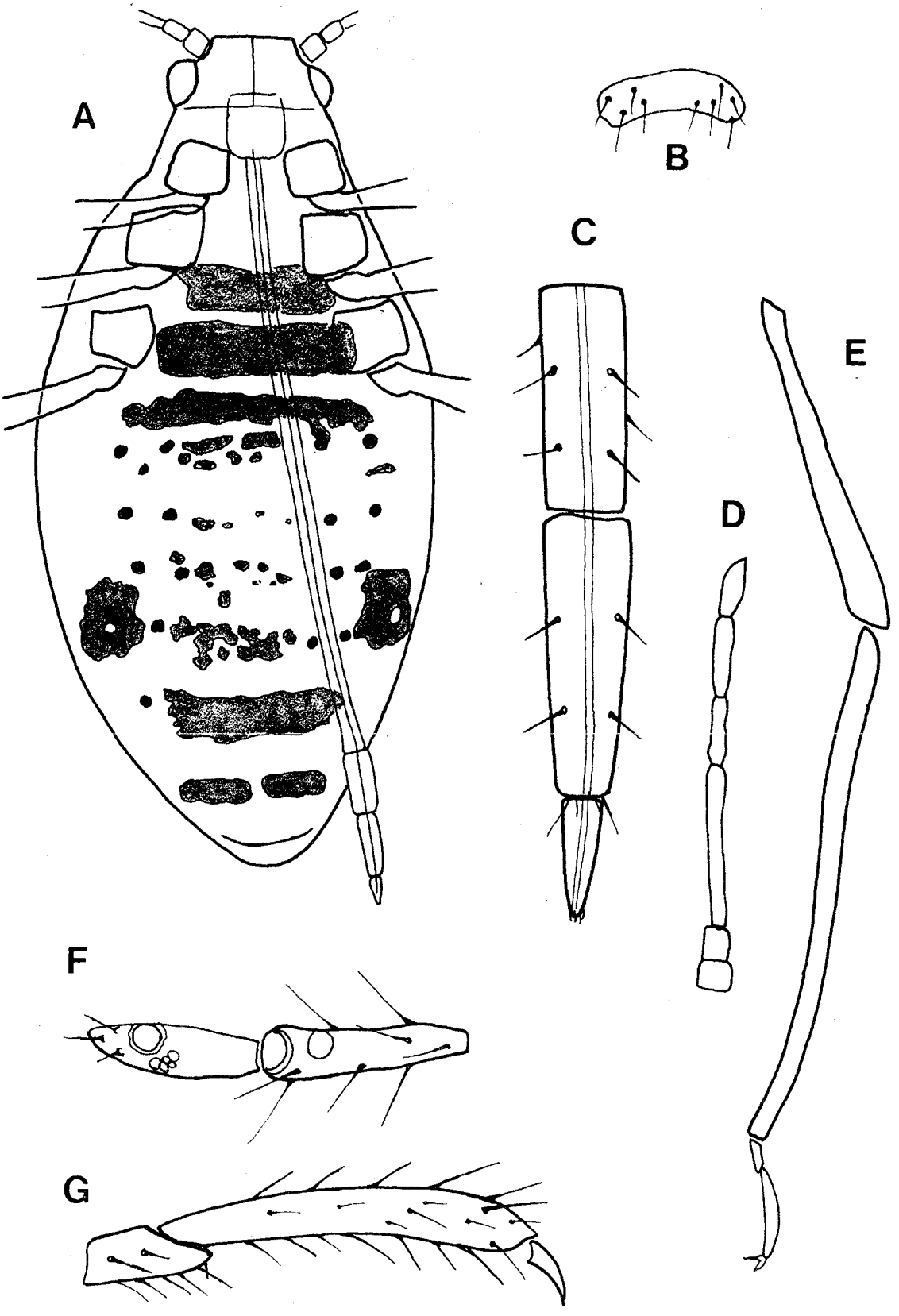
Apterous Viviparous Female (Figures 35, 37)

Colour, when alive, reddish brown (Palmer 1952). Colour of cleared specimens: head and thorax light brown, antennae light except distal ends of III, IV, and V darker than rest of segment, I, II, and VI darker; legs light brown, femur and tibia darker distally; abdominal sclerites, cornicles and genital plate light brown.

Body length, 2.5 - 3.0 (Palmer 1952). Head with few, short, spine-like setae. Secondary sensillae on antennal segments III, IV, and V. Length of antennal setae slightly greater than two times the base of segment III. Rostrum extends past cauda.

Mesosternal tubercles present. Legs with fine, erect setae; those on tibia slightly less than width of tibia. Setae on hind tibia moderately dense. Tarsal setae fine, length of those on tarsal segment II slightly longer than width of segment. A single,

Figure 37. Morphological features of Cinara oregonensis. A, ventral projection of body; B, genital plate; C, rostrum, segments III, IV and V; D, antenna; E, hind leg; F, antennal segments V and VI; G, hind leg, tarsal segments I and II.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G

ventral, apical, blunt seta, shorter than others, present on tarsal segment I. Hind tibia, length, 1.6 - 2.0 (Palmer 1952).

Small, irregularly-shaped, pigmented areas on dorsum of abdomen; one single, large patch on abdominal segment VIII. Dorsal, abdominal setae long, fine, moderately dense. Ventral setae more numerous than, slightly shorter than, dorsal setae. Cornicles small with irregular edges. Setae on cornicles few, similar to other dorsal setae.

Integument of body smooth except for spiculose imbrications on abdominal segment VIII, cauda, and genital plate. Integument of antennal segments smooth except for spiculose imbrications on antennal segment VI.

Additional Descriptive Material. Fundatrix, Palmer 1926, 1952; apterous viviparous female, Gillette and Palmer 1931, Palmer 1926, 1952, Wilson 1915; alate viviparous female, Gillette and Palmer 1931, Palmer 1926, 1952, Wilson 1915; ovipara, Palmer 1926, 1952; apterous male, Palmer 1926, 1952.

Material Examined. (a). Type Material: UMC, 2 slides, labelled: "Type", Pinus, Fort Kamath, Oregon, 6. VI. 1914, H. F. W.

(b). Material Collected: None.

(c). Additional Material Examined: CANADA: Alberta, Kananaskis, 24. VI. 1956, G. A. Bradley.

Distribution: CANADA: Alberta, Saskatchewan; U. S. A.: Colorado, Idaho, Oregon, Utah (Palmer 1952).

Host Range: Pinus contorta, Pinus ponderosa.

Feeding Site: Green cones; large, dense colonies (Bradley 1961).

Comments. The unusually long rostrum is a unique characteristic among species of Cinara on P. contorta. Palmer (1926) described the life history of this species; she found it to be specific to the young cones of P. contorta and to a lesser extent P. ponderosa. It is apparently rare, but where it occurs it is abundant (Palmer 1952).

6.8 Cinara parvicornis Hottes, 1958

Cinara parvicornis Hottes, 1958: 76-79. Holotype: USNM; paratypes, USNM

Cinara parvicornis, Eastop and Hille Ris Lambers, 1976: 153; Smith and Parron, 1978: 101.

Cinara ontarioensis, Bradley, 1962: 1178-1181. (new synonymy). Holotype: CNC; paratypes, CNC.

Apterous Viviparous Female (Figures 38, 39)

Colour, when alive, reddish brown. Colour of cleared specimens:

Figure 38. Photographs of the ventral view of slide-mounted specimens of Cinara parvicornis (top) and Cinara pergandei (bottom).

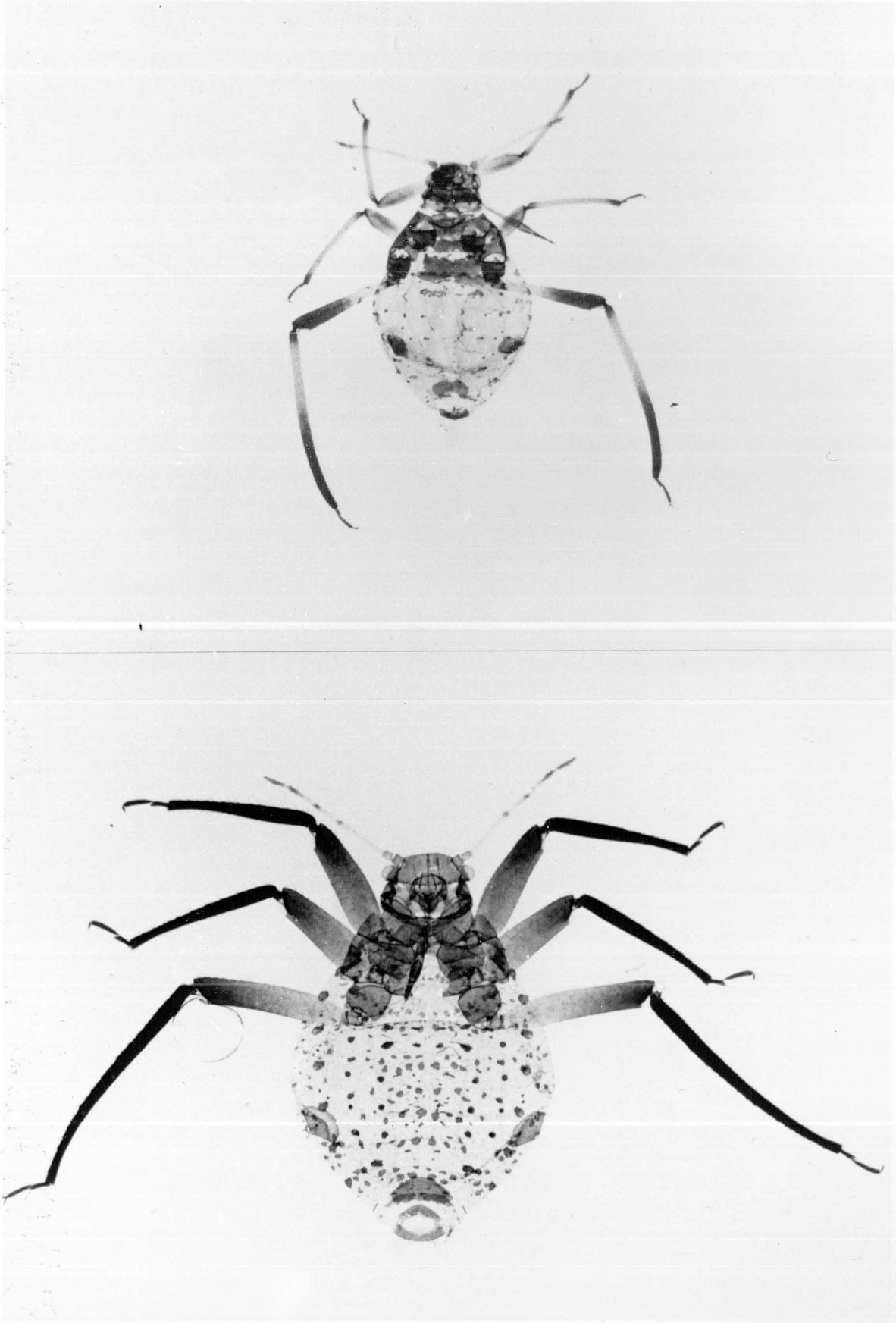

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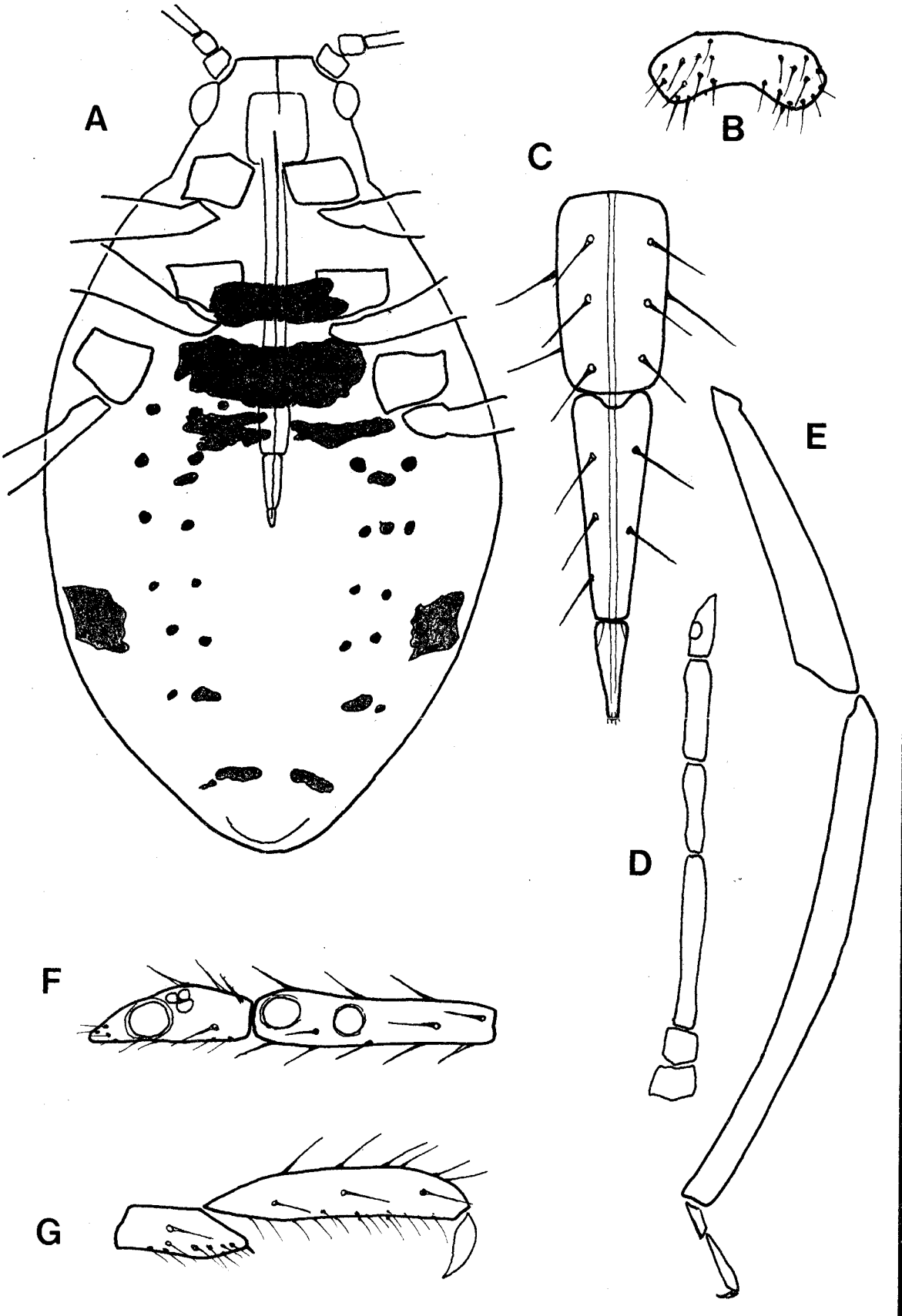
Figure 39. Morphological features of Cinara parvicornis. A, ventral projection of body; B, genital plate; C, rostrum, segments III, IV and V; D, antenna; E, hind leg; F, antennal segments V and VI; G, hind leg, tarsal segments I and II.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head, thorax, and antenna brown, except antennal segments II to IV light, distal ends only of V and VI brown; legs dark brown except proximal one half of tibia with light brown patch, femur lighter proximally. Cornicles and genital plate light brown.

Body length, 2.73 ± 0.18, 2.40 - 2.96. Head with few, short, spine-like setae. Frons width, .318 ± .009, .304 - .339. Length of antennal segments; II, .093 ± .004, .084 - .100; III, .422 ± .027, .392 - .493; IV, .215 ±.009, .202 - .232; V, .241 ± .012, .224 - .270; VI - base length, .130 ± .006, .121 - .142; VI - base width, .056 ± .003, .051 - .064; VI - processus terminalis, .036 ± .003, .030 - .045. Secondary sensillae on antennal segments III, IV, and V. Length of antennal setae approximately equal to base of segment III. Length of setae on antennal segment III, .034 ± .002, .030 - .039. Number of setae on antennal segments; II, 7.5 ± .09, 6.0 - 9.0; V, 19.8 ± 3.2, 13.0 - 25.0; VI - base, 6.7 ± 1.2, 5.0 - 9.0; VI - processus terminalis, 3.9 ± 0.3, 3.0 - 4.0; Rostrum extends past hind coxae. Length of rostrum segments; V, .092 ± .003, .085 - .098; IV, .204 ± .007, .188 - .213; III, .194 ± .008, .183 - .215; II, 0.87 ± 0.05, 0.77 - 0.89. Number of accessory setae, rostrum IV, 4.5 ± 0.6, 3.0 - 5.0.

Mesosternal tubercle present. Legs with spine-like setae, set at an angle of approximately 45 degrees; those on tibia approximately equal to one third the width of the tibia, length, .058 ± .006, .047 - .071. Setae on hind tibia moderately dense; number on 0.2 mm of mid-section of hind tibia, 53.5 ± 2.9, 48.0 -

59.0. Tarsal setae fine, length of those on tarsal segment II slightly less than width of segment. A single, ventral, apical, blunt seta, shorter than others, present on tarsal segment I. Hind leg dimensions; femur length, 1.22 ± 0.09, 0.96 - 1.32; femur width, .191 ± .010, .169 - .202; tibia length, 1.94 ± 0.09, 1.78 - 2.00; tarsus I - ventral length, .127 ± .004, .120 - .136; tarsus II - length, .253 ± .011, .237 - .271.

A single, rectangular pigmented patch on abdominal sclerites I and II. Dorsal abdominal setae straight, few, in two irregular rows on abdominal segments I to VII and in a single row along the posterior margin of the transverse sclerite of abdominal segment VIII. Setae on abdominal sclerite V; length, .035 ± .006, .024 - .045; number, 18.5 ± 2.4, 14.0 - 24.0. Number of setae on abdominal sclerite VIII, 12.6 ± 2.7, 8.0 - 17.0. Ventral setae fine, variable in length, more numerous than, less than two times , dorsal setae. Setae on genital plate; length, .076 ± .004, .068 - .079; number, 31.2 ± 3.6, 25.0 - 36.0. Cornicles small with irregular edges. Setae on cornicles few, short; number of setae on cornicle, 17.3 ± 2.9, 14.0 - 23.0.

Integument of body smooth except for spiculose imbrications on abdominal segments VII and VIII, cauda, and genital plate. Integument of antennal segments smooth except for spiculose imbrications on antennal segments V and VI.

Additional Descriptive Material. Apterous viviparous female, Bradley 1962; alate viviparous female, Bradley 1962; ovipara, Hottes 1958; alate male, Hottes 1958.

Material Examined. (a). Type Material: Cinara parvicornis; Holotype, USNM, 1 slide, ovipara, on Pinus contorta, 21. IX. 1955, Flathead, Montana, D. McComb. Allotype, 1 slide, alate male, same data as holotype. Cinara ontarioensis; Holotype, No. 8152, CNC, 1 slide, alate viviparous female, on Pinus banksiana, 8. VII. 1957, Camp Robinson, Ontario, G. A. Bradley. Paratypes; 3 slides, alate viviparous female, 3 slides, apterous viviparous female, same data as holotype; 7 slides, alate viviparous female, on Pinus banksiana, 2. VII. 1958, Cedar Lake, Ontario, G. A. Bradley; 4 slides, ovipara, on Pinus banksiana, X. 1957, Richer, Manitoba, G. A. Bradley.
(b). Material Collected: CANADA: British Columbia, 20 km N Chetwynd, 6. VIII. 1980; Mt. Robson, 12. VIII. 1980; Alberta, 58 km E Edson, Hwy 16, 10. VIII. 1980.
(c). Additional Material Examined: CANADA: Alberta, Miette Hot Springs, 23. VIII. 1955, J. D. Stanger, Pinus banksiana; Slave Lake, 18. VII. 1963, G. J. Smith, Pinus banksiana; Manitoba, Sandilands, 19. VI. 1963, 20. IX. 1966, A. G. Robinson, Pinus banksiana; Egg Lake, 3. VII. 1963, A. E. Campbell, Pinus banksiana; Ontario, Vermilion Bay, 29. V. 1963, G. A. Bradley, Pinus banksiana; Saskatchewan, Fontaine Lake, 23. VIII. 1962, L. McDowell, Pinus banksiana;

Distribution: CANADA: Alberta, British Columbia, Manitoba, Ontario, Saskatchewan; U. S. A.: Montana.

Host Range: Pinus banksiana, Pinus contorta.

Feeding Site: New growth shoots, needle fascicles; small colonies.

Comments. This species is similar to C. brevispinosa but lacks the transverse pigmented bands of that species. Bradley (1962) described the life history as C. ontarioensis. Based on an examination of the ovipara of C. ontarioensis with the holotype (ovipara) of C. parvicornis, I concluded that C. ontarioensis is a synonym of C. parvicornis. The setae on the cornicles are distinctive; they are sparse and as numerous on the raised area of the cornicle as on the margin of this structure.

6.9 Cinara pergandei (Wilson, 1919)

Lachniella pergandei Wilson, 1919: 46. Holotype: USNM; paratypes, USNM (Pepper and Tissot, 1973: 76).

Lachniella inoptis, Wilson, 1919: 18 (partim)(misidentification).

Dilachnus pergandei, Wilson, 1923: 264.

Cinara pergandei, Palmer, 1945: 451; Bradley, 1951: 334; Bradley

1961: 53-54; Pepper and Tissot, 1973: 75-83; Eastop and Hille Ris Lambers, 1976: 153; Smith and Parron, 1978: 101.

Cinara longispinosa, Tissot, 1932: 4; (vide Bradley, 1951: 334). Holotype: No. 44303, USNM; paratypes, FSCA.

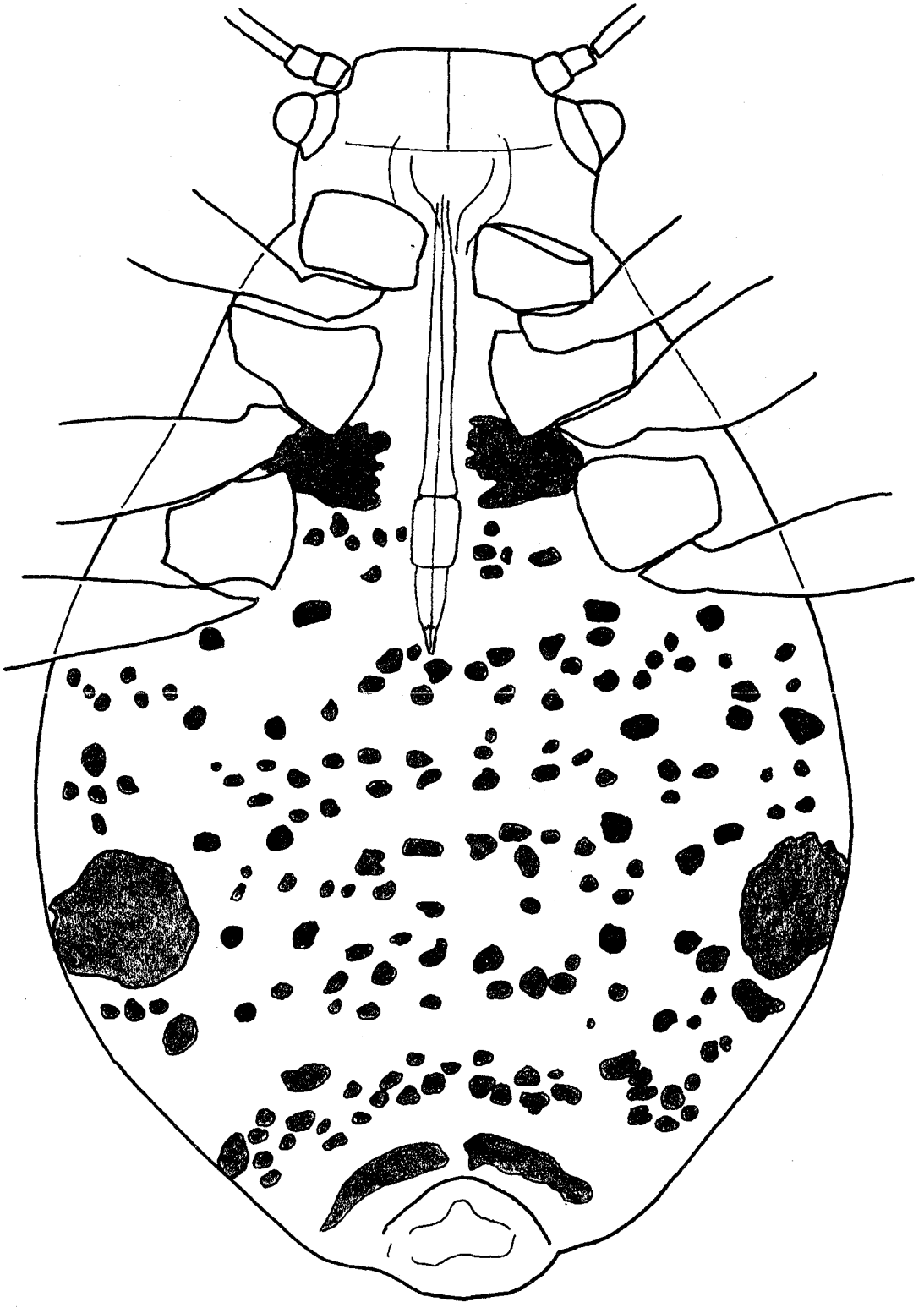
Apterous Viviparous Female (Figures 38, 40)

Colour, when alive, reddish brown, often shiny. Colour of cleared specimens: head and thorax brown, antennae lighter, except distal ends of III, IV, and V darker, VI dark. Tibia and tarsi dark brown to black, femur dark distally, lighter basally. Cornicles, cauda, genital plate and muscle attachment plates light to medium brown.

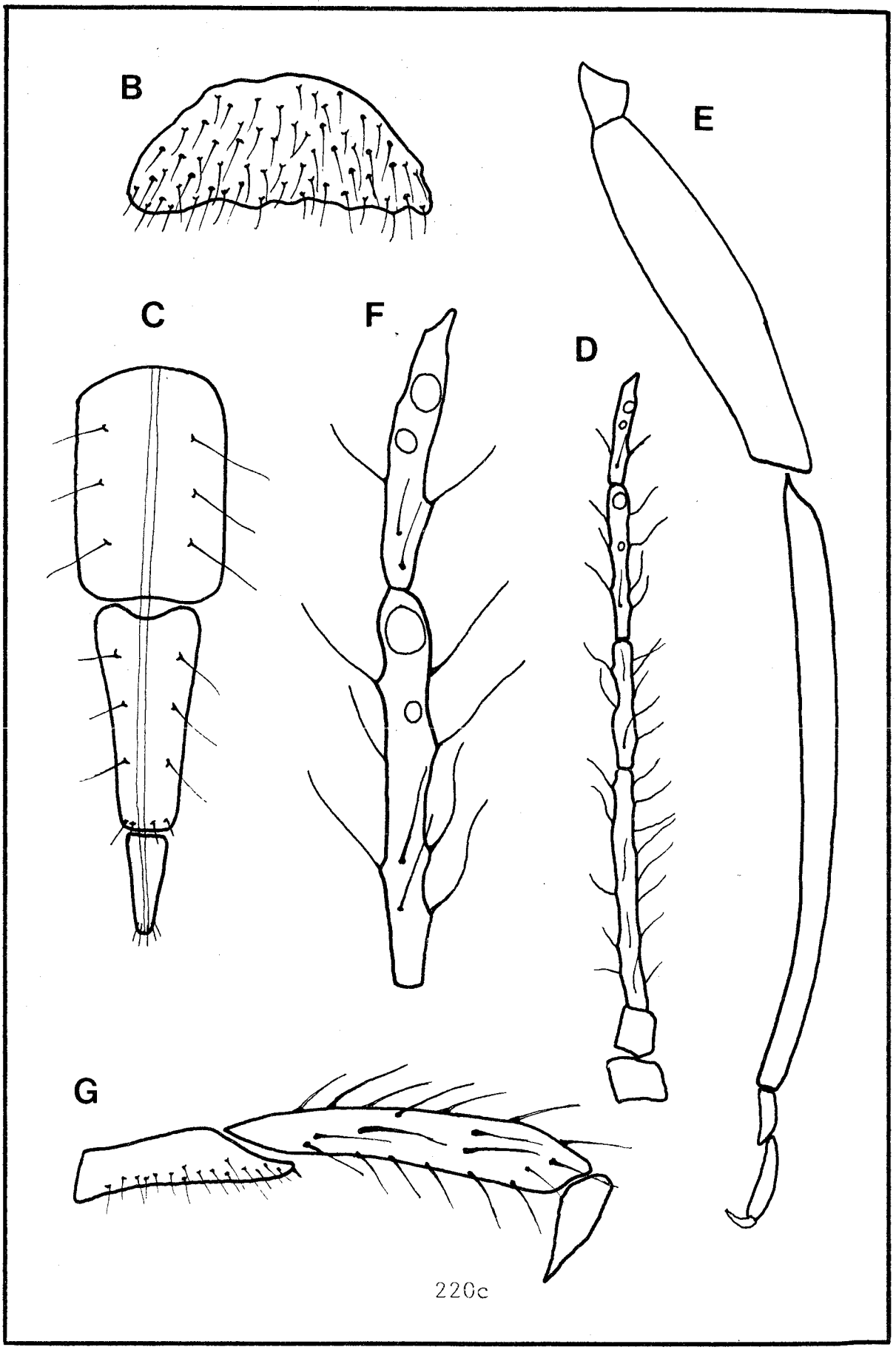
Body length, 4.10 ± 0.25, 3.76 - 4.76. Head with numerous, long, fine setae. Eyes on prominent stalks. Frons width, .566 ± .042, .498 - .674. Lengths of antennal segments; II, .126 ± .006, .118 - .145; III, .571 ± .035, .496 - .642; IV, .271 ± .023, .228 - .314; V, .335 ± .020, .302 - .377; VI - base length, .203 ± .009, .182 - .224; VI - base width, .048 ± .002, .043 - .052; VI - processus terminalis, .074 ± .007, .060 - .089. Secondary sensilla on antennal segment V. Length of longest antennal setae greater than two times the base of segment III. Length of setae on antennal segment III, .129 ± .013, .104 - .166. Number of setae on antennal segment; II, 8.4 ± 1.15, 6.0 - 11.0; V, 10.0 ± 1.5, 7.0 - 13.0; VI - base, 5.9 ± 0.7, 5.0 - 8.0; VI - processus terminalis, 3.9 ± 0.3, 3.0 - 4.0. Rostrum extends past hind coxae. Length of rostrum

Figure 40. Morphological features of Cinara pergandei. A, ventral projection of body; B, genital plate; C, rostrum, segments III, IV and V; D, antenna; E, hind leg; F, antennal segments V and VI; G, hind leg, tarsal segments I and II.

A



220b


B
E
C
F
D
G

segments; V, .093 ± .007, .077 - .106; IV, .222 ± .007, .207 - .232; III, .247 ± .011, .215 - .276; II, 0.96 ± .117, .067 - 1.11. Number of accessory setae, rostrum IV, 6.1 ± 0.3, 6.0 - 7.0.

Mesosternal tubercle absent. Legs with long, tapering setae, those on base of tibia upright, apicial tibial setae reclinate; length, .148 ± .017, .127 - .182. Setae on hind tibia not dense; number on 0.2 mm of mid-section of hind tibia, 22.9 ± 2.5, 19.0 - 33.0. Tarsal setae fine; length of those on tarsal segment II slightly less than two times width of segment. A single, ventral, apical, blunt seta, shorter than others, present on tarsal segment I. Hind leg dimensions; femur length, 1.74 ± 0.09, 1.53 - 1.90; femur width, .268 ± 0.02, .231 - .310; tibia length, 2.40 ± 0.17, 2.00 - 2.66; tarsus I - ventral length, .225 ± .009, .208 - .239; tarsus II - length, .367 ± .014, .331 - .400.

Dorsum of abdomen with numerous medium brown scleroites around bases of setae. Dorsal abdominal setae of two types; short, spine-like setae on mid-dorsal region; long, fine setae on anterior segments and lateral margins. Setae on abdominal sclerite V; length, .152 ± .014, .128 - .184; number, 133.2 ± 18.9, 95.0 - 179.0. Number of setae on abdominal sclerite VIII, 28.8 ± 4.7, 18.0 - 41.0. Ventral setae fine, as numerous as, slightly shorter than, dorsal setae. Setae on genital plate; length, .131 ± .010, .114 - .154; number, 64.4 ± 8.3, 49.0 - 84.0. Cornicles of moderate size with irregular edges.. Setae on cornicles dense, of two types;

numerous short, fine setae and few, long, fine setae; number of setae on cornicle, 170.6 ± 27.2, 85.0 - 214.0.

Integument of body smooth except for spiculose imbrications on abdominal segments VII and VIII, cauda, and genital plate. Integument of antennal segments smooth.

Additional Descriptive Material. Apterous viviparous female, Wilson 1919, Patch 1923, Tissot 1932, Palmer 1945, Pepper and Tissot 1973; alate viviparous female, Wilson 1919, Patch 1923, Tissot 1932, Palmer 1945, Pepper and Tissot 1973; ovipara, Pepper and Tissot 1973; alate male, Pepper and Tissot 1973.

Material Examined. (a). Type Material: Cinara pergandei, Cotype, USNM, 1 slide, apterous viviparous female, on Pinus inops, 9. VI. 1903, Washington, D. C., H. F. Wilson. Cinara longispinosa, Holotype, No. 44303, USNM, alate viviparous female, Pinus taeda, 3. VIII. 1929, Gainsville, Florida, Devil's Mill Hopper, A. N. T. Morphotype, 1 slide, apterous viviparous female, same data as holotype.

(b). Material Collected: CANADA: British Columbia, 24 km E Princeton, 17. VI. 1980, 1. VII. 1981; 18 km E Princeton, 17. VI. 1980, 1. VII. 1981; Christian Valley, 21, VI. 1980; 2 km N Nakusp, Hwy 21, 22. VI. 1980; 15 km E Quesnel, Hwy 26, 30. VII. 1980; 10 km N Quesnel, Hwy 97, 31. VII. 1980; Mackenzie, 6. VII. 1980; Blue River, 13. VIII. 1980; 29 km E Castlegar, Hwy 3, 10. VII. 1982;

Alberta, 20 km N Swan Hills, 9. VIII. 1980; 7 km S Swan Hills, 10. VIII. 1980; U. S. A.: Montana, 6 km S West Glacier, Hwy 2, 8. VII. 1982.

(c). Additional Material Examined: CANADA: British Columbia, Cascade, 29. VII. 1959, G. A. Bradley; Vancouver, 23. VI. 1975, C.-K. Chan; Alberta, Jasper, 25. VIII. 1955, J. D. Stanger; Peace River, 14. VIII. 1958. G. A. Bradley; Manitoba, Sandilands Prov. For., 19. VI. 1976, L.-Y. Wang, Pinus banksiana; Winnipeg, 6. VII. 1967, A. G. Robinson, Pinus banksiana; Duck Mtn. Prov. Park, 7. VIII. 1963, B. McLeod, Pinus banksiana; Richer, 18. VIII. 1964, G. A. Bradley, Pinus banksiana; Northwest Territories, Yellowknife, 13. VIII. 1978, A. G. Robinson, Pinus banksiana; Saskatchewan, Waskesiu, 5. VIII. 1955, J. D. Stanger, Pinus banksiana; Indian Head, 15. IX. 1950, J. D. Stanger, 29. VIII. 1955, G. A. Bradley, Pinus banksiana; Ontario, C. E. F., Ottawa, 13. VII. 1942, G. A. Bradley, Pinus banksiana; Sault Ste. Marie, 15. VII. 1945, J. D. Stanger, Pinus banksiana; St. Catherines, 27. X. 1955, J. D. Stanger, Pinus banksiana; Normandale, 4. VII. 1956, W. R. Richards, Pinus banksiana; Cedar Lake, 6. VIII. 1958, G. A. Bradley, Pinus banksiana; U. S. A.: Georgia, Athens, 6. VI. 1981, G. Fedde, Pinus sp.; North Carolina, Highlands, 11. VIII. 1957, W. R. Richards, Pinus sp.; Toxaway, 27. VIII. 1957, W. R. Richards, Pinus echinata.

Distribution: CANADA: Alberta, British Columbia, Manitoba, Ontario, Saskatchewan; U. S. A.: Alabama, Connecticut, Washington, D. C.,

Delaware, Florida, Georgia, Louisiana, Maine, Maryland, Michigan, Montana, North Carolina, New Jersey, New York, Ohio, Pennsylvania, South Carolina, Virginia, Vermont, Wisconsin.

Host Range: Pinus banksiana, P. clausa; P. contorta, P. echinata, P. glabra, P. mugo, P. rigida, P. taeda, P. virginiana.

Feeding Site: New growth shoots, branches; small, dispersed colonies.

Comments. The presence of lateral eye stalks and dark tibia and the general tick-like appearance and high mobility of this species distinguish it from other Cinara species on P. contorta. Bradley (1961) and Fedde (1965) gave accounts of the biology. Pepper and Tissot (1973) discussed the type material.

6.10 Key to the Species of Cinara Curtis on Pinus contorta.

(Based on the apterous viviparous morph. Decisions based on the length of setae should be based on geographically sampled material.)

1. Ocular tubercles absent.....pergandei (Wilson)
- Ocular tubercles present.....2

2.(1) Dorsal, transverse abdominal bands present.....
.....brevispinosa (Gillette and Palmer)

- Dorsal abdominal pigmentation in irregular patches.....3

3.(2) Dorsum of abdomen covered by one large, pigmented patch, not broken by mid-dorsal line.....nigra (Wilson)

- Dorsum of abdomen covered by irregular pigmented patches broken by mid-dorsal line.....4

4.(3) Rostrum extends beyond cauda.....oregonensis (Wilson)

- Rostrum extends to mid-section of abdomen, no further than cornicles.....5

5.(4) Dorsal abdominal setae short (.010 - .045 mm).....6

- Dorsal abdominal setae long (.084 - .152 mm).....7

6.(5) Dorsum of abdomen with small, irregular pigmented patches, setae on cornicles moderately dense (range, 21 - 73).....
.....contortae Hottes

- Mid-dorsal region of abdomen with few pigmented patches, setae on cornicles few (range, 14 - 23)...parvicornis Hottes

7.(5) Length of setae, mid-section of hind tibia, greater than one half width of tibia....medispinosa (Gillette and Palmer)

- Length of setae, mid-section of hind tibia, nearly equal to width of tibia.....murrayanae (Gillette and Palmer)

6.11 Feeding Sites

Bradley (1959, 1961) attached taxonomic significance to the feeding sites of species of Cinara and attempted to relate the size of the rostrum to particular feeding sites. In this study I found that some species have a single, characteristic feeding site which does not alter seasonally or geographically. For example, C. nigra was always found on the main stem or adjacent branches near the periphery of the crown and C. brevispinosa was always found on new growth foliage or needle fascicles. However, I found other species of Cinara (C. contortae, C. medispinosa, and C. murrayanae) to exhibit a range of feeding site preferences. Also, it has been shown (Fedde 1965) that there are seasonal changes in feeding site preferences among species of Cinara, likely in response to changes in the nutritive quality of parts of the tree (Dixon 1985). Therefore, feeding site characteristics are of limited value in separating some of the morphologically similar species of Cinara.

The species C. contortae, C. medispinosa, and C. murrayanae were observed to be opportunistic in their choice of a feeding site. The comparatively longer rostrum of these species enables them to feed on a wide range of sites on the tree. During this study, these species were found feeding on new growth tips, branches, main stems, and on cankers (Section 2.2.2). At sample locations where cankers were present, these species would usually be found feeding

exclusively at these sites; a thorough search of the surrounding trees did not show them to be feeding elsewhere, although other species such as C. brevispinosa were present, confined to their characteristic sites.

It has been shown that the lesions and cankers produced by pine rusts provide a suitable habitat for the development of a wide range of insect species (Coulson and Franklin 1970, Powell 1971). The association of Cinara with rust fungus cankers and lesions may be analogous to situations where aphids produce galls on their host plants by injecting salivary secretions into the plant tissue (Blackman 1974). Galled tissue and rust blisters act as nutrient sinks where the translocation of plant metabolic products, on which the aphids feed, to these areas is stimulated (Dixon 1985). The cankers also offer an optimal feeding site due to other characteristics. They have a thin layer of bark through which the aphid must insert its stylets. There is some measure of protection against other insects and weather provided by the scales of bark and crevices on the surface of the canker.

6.12 Host Plant Ranges and General Distribution Patterns

P. contorta is grouped taxonomically with P. banksiana Lamb., P. clausa (Engelm.) Sarg., and P. virginiana Mill. in subsection Contortae of the section Pinus (Little and Critchfield 1969). Based on genetic distance values calculated from isoenzyme data, Wheeler

et al. (1983) suggested that P. contorta most closely resembles the ancestral taxon from which the other species in the subsection are derived. They also suggest that P. clausa and P. virginiana should be considered as subspecies of the same species. In addition, Rudolph and Yeatman (1982) have proposed that P. contorta was more widely distributed in early postglacial time than at present. Recent work (MacDonald and Cwynar 1985), based on fossil pollen, has shown a clear path of remigration of lodgepole pine into what is now the northern part of its distribution.

Given the information outlined above, some of the distributions of the Cinara species that were studied can be placed in context. The Cinara species that were studied are closely tied to the biogeographic and systematic relationships of their hostplants. C. nigra is a widespread species, although it has a limited distribution (Figure 8) on P. contorta. Species of Cinara that are morphologically similar to C. nigra, mentioned in Chapter 4, are found exclusively on related pine species in the subsection Contortae in eastern North America; they are not found on pine species in the western region. C. parvicornis is widely distributed on P. banksiana, but it is confined to a limited portion of the range of P. contorta, particularly those areas where P. contorta and P. banksiana are known to hybridize. C. pergandei feeds on all pine species in subsection Contortae and on some of the species of the southern yellow pines (subsection Australes) (Little and Critchfield 1969) in eastern North America, but it does not feed on other western North American pines.

The appearance of C. nigra on P. contorta in British Columbia and Alberta is noteworthy since all other populations of this species have previously been found only in a relatively restricted area of the eastern United States, namely, Minnesota and Wisconsin (Pepper and Tissot 1973). The most important characters for the separation of C. nigra from C. canatra are the numbers and lengths of setae on the head and cornicles. Examination of material of C. nigra and C. canatra which has been deposited in the CNC revealed that all material collected from British Columbia and Alberta on P. contorta was C. nigra. This Cinara species was also found on P. banksiana from Alberta to Ontario. C. canatra was collected only on P. banksiana from Alberta to Ontario.

Based on the sampling program carried out in this study, on material deposited in the CNC, and on published records, the species C. brevispinosa, C. contortae, C. medispinosa, and C. murrayanae were shown to be confined to P. contorta. No species of Cinara known from P. monticola and P. ponderosae was identified among the 308 samples collected on P. contorta. Among the 105 samples of Cinara collected from P. monticola and P. ponderosae were 5 samples of C. brevispinosa and 2 samples of C. contortae. However, all of these 7 samples consisted of newly founded colonies on new growth tips, that is, single alate female aphids and some nymphs. No advanced colonies were found which indicates that these species of Cinara may test new foliage of other pine species but they do not survive on it.

In summary, the biogeographic and taxonomic relationships of the North American pines are reflected in the systematic patterns of the Cinara species that were studied. P. contorta has some unique species of Cinara associated with it while other species of Cinara are shared with the three related pine species in the subsection Contortae. In addition, the previously mentioned observation (Chapter 1) that the eastern pine Cinara species are more polyphagous than the western pine Cinara species can be interpreted in the context of their hostplant relations. The majority of the eastern pines, other than those of subsection Contortae, are relatively closely related members of one subsection, Australes (Mirov 1967); many Cinara species, with the exception of those on species of subsection Contortae, are able to feed on this range of hostplant species (Pepper and Tissot, 1973).

7. GENERAL SUMMARY AND CONCLUSIONS

7.1 General Summary

The first stage of this study was concerned with the univariate and multivariate analysis of morphological variation within a single species of Cinara (C. nigra). Morphological variation within a single sample of this species was examined by correlation analysis and principal component analysis in order to determine the relationships among a preliminary set of 52 characters. A number of components of variation were identified in addition to a strong size component.

Most of the variables (49) were retained at this stage. These were then measured on specimens from 19 population samples of C. nigra in order to examine morphological variation within and between samples on a geographic basis, using discriminant function analysis. Little geographic pattern was observed; most variation among samples was due to overall size differences. However, a number of characters, particularly the counts of setae, were shown to be independent of size, and of potential taxonomic use.

This study provided new information on the components of morphological variation in an aphid and on the covariation among characters. This information allowed for the reduction of the character set from 49 to 32 characters, for the subsequent analysis

of variation among species of Cinara. Reduction in the number of variables resulted in relatively little loss of information content, as demonstrated by the allocation procedures.

Samples of 9 species of Cinara were measured for the reduced character set. These samples were then analyzed using correlation analysis and principal component analysis in order to determine what patterns of variation these species had in common. Morphometric variation within and among these species was shown to be relatively complex. Other than a common size component, each species showed unique patterns of variation. Some species were observed to be geographically variable while the morphometric patterns in other species were largely influenced by size variation.

The discriminatory ability of the characters chosen was tested using discriminant function analysis and cluster analysis of Mahalanobis Generalized Distances. On the basis of this study, it is evident that a wide range of morphological characters from all areas of the aphid body is necessary in order to establish species boundaries. In addition, geographic sampling is necessary in order to include the spatial variation inherent in these insects.

In Chapter 6, the apterous viviparous morph of each of the species that was studied was described using biometric data resulting from the morphometric analysis. Information on synonymy, distributions, and hostplant ranges, and a morphological key to the species, was supplied. Extensive geographic sampling carried out during the course of this study,and comparisons with material from

other parts of the North American continent, allowed for some distributional patterns to be recognized, including the extension of the geographical and the hostplant ranges of some species. This work showed the need for more extensive studies of species relationships within this group, that is, on a continent wide basis, rather than on a regional basis.

7.2 Application of Morphometrics to the Phylogenetic Analysis of the Tribe Cinarini Börner.

The aphid family Lachnidae is a useful test for the application of morphometric analysis to the solution of taxonomic problems because there has been considerable difference of opinion among aphidologists about not only the discrimination of taxa at the subspecies, species, subgenus, and genus levels but also of the phylogenetic placement of the Lachnidae as a whole within the Aphidoidea. Evolutionary trends in the Aphidoidea are difficult to determine because of uncertainties about what are the plesiomorphic and what are the apomorphic states of characters. Some morphological features may in fact be primitive but it is apparent that some morphological features have re-occurred during the evolution of aphids. Eastop (1973) has suggested that aphids, with a succession of morphologically distinct, parthenogenetic generations, likely possess genetic mechanisms that result in the appearance of characteristics that may have been evolutionarily

dormant for a period of time. It is evident that some aphid groups show a trend towards progressive neoteny so that relatively young aphid groups have lost some advanced adult characteristics (Richards 1965). Many examples of convergent evolution are evident (Heie 1967) and parallel evolution may have resulted in a mosaic distribution of apomorphic characters (Heie 1980). These processes could explain some of the notorious difficulties involved in studying aphid taxonomy and in interpreting systematic patterns.

A number of European aphid taxonomists, particularly C. Börner (1939, 1949, 1952, 1957) have erected new genera and subgenera within the tribe Cinarini Börner or have adopted these taxonomic subdivisions. The most extensive classification of this group, Börner's, is shown in Appendix 4. North American aphidologists have been slow to accept these generic and subgeneric categories. Hottes (1960) was of the opinion that it would be useful if Börner's generic subdivisions were considered at the subgeneric level within Cinara. However, Hottes did not adopt Börner's system or his proposed modification of it in his subsequent papers, retaining the single genus Cinara. Bradley (1965) maintained that application of the European system to North American species would result in their being divided into more manageable groups. The survey of the world's aphids by Eastop and Hille Ris Lambers (1976) placed all of the genera and subgenera of Börner and others into synonymy with Cinara Curtis, 1835.

There are some obvious morphological differences between the

genera in Börner's classification. For example, Lachniella is characterized by heavily pigmented wings and a long apical rostral segment and Cinaropsis by the presence of a caudal wax ring. Species of Cupressobium are usually of relatively large size with a relatively flat dorsum and random setal pattern.

Consistent differences between Börner's subgeneric categories are more difficult to determine, particularly those of the genus Cinaropsis, which are based on differences in setal lengths, rostrum lengths, and hind leg dimensions (Börner 1949, Eastop 1972). The present study has shown these characters to be variable in some species of Cinara. The subgenera within the genus Cinara have some distinctive characters, particularly the subgenus Cinarellia which is characterized by the absence of a mesosternal tubercle and the presence of stalked eyes in the apterae.

The hostplant relationships of the genera and subgenera are generally consistent; Cinara and Cinaria are found on species of Pinus, Todolachnus on species of Abies, Cupressobium on species of Cupressaceae, Lachniella on species of Picea, Buchneria on species of Abies, and Laricaria on species of Larix. The only exceptions are in the genus Cinaropsis where most species feed on Picea but some species are found on Larix and Abies. Eastop (1972) has suggested that this may represent relatively recent hostplant shifts as the fundatrices of one species that feeds on Abies are very

similar morphologically to the summer apterae.

I believe that there is enough morphological and ecological evidence to warrant a "second look" at Börner's system; perhaps modification of the species groups which he originally delineated and the levels in the Linnaean hierarchy at which he set them should be attempted. Many of the problems in applying Börner's system occur when one attempts to rely on univariate differences between the taxa. Analysis of the species groups within the Cinarini by methods of multivariate morphometrics, as employed in this study, would enable the determination of the internal variability of taxonomic characters within the genera and subgenera, assessment of the discriminatory ability of these characters, and allow for the detection of patterns of variation and gaps in this variation which would enable the objective construction of a balanced taxonomic hierarchy. Knowledge of the variability of characters within and between taxa at all levels in the hierarchy would facilitate the development of a sound phylogenetic scheme for the Cinarini. These methods would provide a more objective approach to the determination of character polarity in the phylogenetic reconstruction of the group.

7.3 Application of Morphometrics to Other Aphid Groups

Many of the species of Cinara are comparatively similar morphologically, and they appear to be relatively monophagous,

although this conception may be the result of inadequate taxonomy. Heie (1967) proposed that originally the cinarans consisted of one or a few polyphagous species consisting of hostplant races and that relatively recently they have evolved into many distinct species. A parallel situation is believed to be that of the genus Aphis in the Aphididae. This genus is also rich in species, which are difficult to distinguish morphologically. Most species are apparently monophagous, but there are a number of polyphagous species complexes (Heie 1986, Stroyan 1984). These interpretations can only be clarified with the advent of a more stable classification of the group.

The genus Aphis consists of over 400 described species. It is included in the subfamily Aphidinae which is characterized by a mosaic of interrelated and morphologically overlapping genera and species (Stroyan 1984). For example, the precise limits of the genera Rhopalosiphum, Melanaphis, and Schizaphis are unclear (Blackman and Eastop 1984). Within the genus Aphis there are evident species groups but no pattern of morphology and host association has been determined (Blackman and Eastop 1984). Börner (1952) attempted to subdivide Aphis into a number of genera but currently only 5 subgenera are recognized (Eastop and Hille Ris Lambers 1976). The taxonomic status of the economically important polyphagous species complexes such as the A. frangulae complex and A. fabae complex is confused, which makes it difficult to interpret biological information. At present there are no stable taxonomic

accounts of the genus even on a regional basis (Stroyan 1984).

Techniques of morphometric analysis should be applied at different systematic levels within the Aphidinae in order to determine the value of taxonomic characters. Börner (1952) relied on the chaetotaxy of the first instar for many of his generic placements. Morphometric techniques would allow for the quantitative assessment of the discriminatory ability of these characters and for testing of the congruency of characters from different stages and morphs.

Finally, another group in need of a quantitative approach to its taxonomic analysis are the Adelgidae, or conifer woolly aphids. Within this family, the status of the genera remains uncertain. European workers recognize six genera on the basis of morphology and host plant groups (Börner 1952) while British and North American workers recognize only two genera (Annand 1928, Varty 1956). At the species level, there is considerable morphological variability making the determination of the limits of most taxa difficult (Foottit and Mackauer 1980). This variation can only be ordered using techniques of multivariate analysis.

The taxonomist's judgement is still an integral part of the process of classification. However, methods of multivariate morphometrics are useful in simply sorting the large amounts of taxonomic information inherent in studies of species and generic relationships into manageable patterns. This study has shown that the individual character loadings as calculated in the principal

component analyses and discriminant function analyses are species-specific. This information will determine the potential use and interpretation of these characters in the phylogenetic reconstruction of aphid taxa. As aphids are notorious for their variability it stands to reason that the use of this variability as a taxonomic character will prove worthwhile, particularly since the recognition of the degree of internal variation and the extent of the gaps in this character variability is the essence of the process of establishing taxa.

APPENDIX I

Cinara species recorded on *Pinus* in western North America. From Mirov (1967) and Smith and Parron (1978).

PINE SPECIES (Subgenus Haploxylon)

CINARA SPECIES	albicaulis	aristata	balfouriana	edulis	flexilis	lambertiana	monophylla	monticola	quadrifolia
anzai Hottes & Essig	X								
apacheca Hottes & Butler				X					
apini (Gillette & Palmer)					X				
atra (Gillette & Palmer)				X					
caliente Hottes				X					
edulis (Wilson)				X			X		
ferrisi (Swain)	X							X	
flexilis (Gillette & Palmer)					X				
hirsuta Hottes & Essig								X	
hirticula Hottes						X			
inscripta Hottes & Essig	X								
kuchea Hottes								X	
metalica Hottes				X					
moketa Hottes						X			
nitidula Hottes				X					
oregoni Hottes & Essig	X								
pinata Hottes				X					
pinona Hottes				X					
poketa Hottes				X					
puerca Hottes				X					
rustica Hottes				X					
saccharinipini Hottes						X			
tanneri (Knowlton)				X				X	
terminalis (Gillette & Palmer)				X					
villosa (Gillette & Palmer)					X				
wahtolca Hottes				X				X	

PINE SPECIES (Subgenus Diploxylon)

CINARA SPECIES	attenuata	contorta	coulteri	jeffreyi	muricata	ponderosa	radiata	sabiniana	torreyana	washoensis
arizonica (Wilson)			X	X		X		X		
brevispinosa (Gillette & Palmer)		X								
contortae Hottes		X								
diabola Hottes			X							
essigi Hottes	X									
glabra (Gillette & Palmer)						X				
medispinosa (Gillette & Palmer)		X								
montanesa Hottes			X							
murrayanae (Gillette & Palmer)		X								
nigrita Hottes & Essig						X				
oregonensis (Wilson)		X				X				
parvicornis Hottes		X								
pergandei (Wilson)		X								
ponderosae (Williams)				X		X				
pseudoschwarzii Palmer						X				
schwarzii (Wilson)						X				
sclerosa Richards		X								
solitaria (Gillette & Palmer)						X				
thatcheri Knowlton & Smith						X				
vagabunda Hottes & Essig						X				

APPENDIX 2

Measurement data (mean ± standard error and coefficient of variation) for 19 population samples of the adult apterous morph of *Cinara nigra*. The sample numbers are as indicated in Table IV. All measurements are in mm. The decimal point for the mean and standard error is indicated below the variable name. All coefficients of variation are given as 1×10^{-1}.

Appendix 2

Sample Number	Variable								
	Body length			Distance between eyes			Distance between hind coxae			Frons width		
	BL			DE			DHC			FRW		
	($\times 10^{-2}$)			($\times 10^{-3}$)			($\times 10^{-2}$)			($\times 10^{-3}$)		
1	404	3	34	538	3	25	110	2	68	399	5	55
2	359	5	68	508	5	44	97	2	83	358	3	42
3	327	4	50	477	3	33	84	1	75	341	2	29
4	331	5	66	492	5	42	82	2	92	346	3	40
5	338	3	40	476	3	27	91	1	72	343	3	34
6	353	4	51	503	4	33	97	2	75	353	2	28
7	369	3	35	513	3	26	91	1	53	365	2	26
8	373	3	41	523	4	35	90	2	87	366	2	26
9	367	2	30	506	3	30	94	1	47	352	2	29
10	373	4	43	506	3	28	93	1	64	356	2	30
11	357	4	56	495	4	40	97	2	76	356	4	46
12	356	3	31	533	3	25	104	1	49	374	3	35
13	364	4	50	497	4	32	98	2	77	361	3	31
14	329	3	41	480	5	48	85	2	73	347	2	28
15	326	3	43	473	5	43	82	2	89	344	2	22
16	333	4	50	475	5	48	88	2	84	353	4	50
17	304	3	37	472	6	53	84	1	72	338	2	29
18	351	4	45	492	3	30	93	1	60	355	4	56
19	312	3	48	473	6	57	82	2	92	336	4	55

Appendix 2

Sample Number	Variable											
	Head length			Antennal segment II, length			Antennal segment II, width			Antennnal segment III, length		
	HL			A2L			A2W			A3L		
	($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)		
1	418	5	57	126	1	38	79	1	38	604	7	49
2	349	7	85	119	1	40	76	1	37	564	5	43
3	344	3	43	109	1	30	71	1	66	529	6	47
4	364	4	44	112	1	32	72	1	49	532	7	62
5	341	4	55	111	1	38	72	1	44	532	4	33
6	384	6	68	115	1	43	72	1	41	552	4	34
7	391	5	55	117	1	24	76	1	66	571	4	33
8	364	5	56	118	1	35	78	1	51	575	5	38
9	360	4	52	115	1	41	73	1	49	547	5	38
10	359	5	60	116	1	42	72	1	34	555	5	43
11	362	8	93	115	1	54	72	1	42	560	7	59
12	384	4	49	119	1	48	75	1	32	566	6	47
13	395	6	64	115	1	50	71	1	34	539	5	42
14	350	3	44	109	1	36	71	1	65	513	4	39
15	363	6	72	111	1	30	68	1	36	518	3	23
16	362	6	77	111	1	38	68	1	37	514	5	44
17	317	6	88	110	1	56	68	1	35	498	8	68
18	355	4	48	112	1	53	71	1	32	530	6	51
19	330	6	82	113	1	53	71	1	53	550	7	57

Appendix 2

Sample Number	Variable											
	Antennal segment III, width			Antennal segment IV, length			Antennal segment IV, width			Antennal segment V, length		
	A3W			A4L			A4W			A5L		
	($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)		
1	54	1	43	268	4	62	56	1	51	312	3	47
2	51	0	42	253	3	55	54	1	67	304	2	26
3	45	0	42	230	3	54	48	1	43	278	2	40
4	47	1	66	239	3	59	49	1	75	287	4	57
5	47	0	43	232	3	53	49	1	65	282	1	23
6	47	1	49	241	4	66	50	1	50	289	4	55
7	50	1	50	257	2	40	53	1	73	302	3	38
8	51	1	47	253	4	74	53	1	51	294	3	43
9	48	1	53	244	3	57	51	0	43	300	3	43
10	47	0	46	253	3	55	50	0	40	298	3	43
11	49	1	65	243	4	68	51	1	89	296	3	46
12	51	0	30	257	3	55	53	0	27	304	2	34
13	48	1	49	242	3	60	50	1	49	289	3	47
14	46	1	53	230	3	63	49	1	49	277	2	36
15	45	0	35	229	3	55	48	1	53	281	2	36
16	45	1	56	221	3	57	48	0	31	271	2	40
17	44	1	56	222	4	77	47	0	43	280	4	60
18	48	1	58	235	4	84	49	1	75	287	3	50
19	46	0	48	227	4	75	49	1	64	280	4	61

Appendix 2

Sample Number	Variable											
	Antennal segment V, width			Antennal segment VI, base length			Antennal segment VI, base width			Antennal segment VI, processus terminalis, length		
	A5W			A6BL			A6BW			A6PTL		
	($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)		
1	64	1	46	145	2	68	59	1	54	46	1	99
2	63	1	36	141	2	55	58	1	41	51	1	65
3	60	1	53	137	1	36	55	0	25	46	1	88
4	60	1	76	141	1	35	55	1	47	46	1	67
5	59	1	39	135	1	30	54	0	38	46	1	61
6	60	0	30	138	1	38	55	0	40	46	1	87
7	61	0	36	143	1	35	57	0	39	50	1	105
8	61	1	43	142	1	45	57	1	43	49	1	76
9	59	0	38	142	1	36	56	0	30	48	1	77
10	59	0	35	141	1	42	56	0	39	48	1	66
11	60	1	42	142	2	50	56	1	56	51	1	75
12	60	0	34	139	1	33	57	1	57	50	1	96
13	61	1	39	142	1	39	57	1	46	48	1	64
14	60	1	57	139	1	38	56	1	58	48	1	68
15	59	1	53	139	1	29	55	1	42	47	1	86
16	56	0	40	139	1	44	54	0	28	48	1	82
17	56	0	34	140	1	46	54	0	33	48	1	91
18	58	1	48	139	1	38	57	0	35	48	1	88
19	58	1	47	135	1	32	55	0	32	49	1	77

Appendix 2

Sample Number	Variable											
	Rostrum segment V, length			Rostrum segment IV, length			Rostrum segment III, length			Rostrum segment II, length		
	R5L			R4L			R3L			R2L		
	($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-2}$)		
1	83	1	30	222	2	36	279	2	38	152	2	53
2	86	1	36	215	1	20	280	1	23	148	3	81
3	81	1	40	204	2	40	267	3	43	136	2	63
4	82	1	28	207	2	42	270	2	34	138	2	51
5	82	1	49	200	2	38	266	2	36	131	1	42
6	82	1	44	205	1	28	271	2	26	134	2	34
7	84	1	39	212	1	20	279	2	32	139	2	53
8	81	1	34	213	2	33	270	2	36	144	2	58
9	83	1	31	211	1	32	277	2	25	145	2	58
10	82	1	72	213	2	33	278	2	25	148	2	56
11	83	1	36	214	1	31	275	2	37	137	2	53
12	86	0	23	213	1	30	279	2	32	139	2	65
13	83	0	26	211	2	43	273	2	39	143	2	62
14	81	1	31	206	2	35	270	2	35	138	2	57
15	82	1	32	203	1	29	274	3	44	135	1	42
16	82	1	45	200	3	58	267	2	33	134	1	29
17	80	1	38	194	2	53	264	1	24	134	2	71
18	78	2	114	210	1	28	267	2	36	136	2	55
19	79	1	50	195	2	34	259	3	45	135	3	99

Appendix 2

Sample Number	Variable											
	Hind leg, coxa, length			Hind leg, femur, length			Hind leg, femur, width			Hind leg, tibia, length		
	CL			FL			FW			TL		
	($\times 10^{-3}$)			($\times 10^{-2}$)			($\times 10^{-3}$)			($\times 10^{-2}$)		
1	300	2	31	187	1	31	192	2	50	292	3	49
2	275	3	43	173	2	52	178	3	73	276	3	45
3	246	3	52	152	2	54	172	3	66	242	4	70
4	258	4	71	158	3	73	184	3	73	251	4	72
5	251	2	31	149	1	37	172	3	68	234	3	49
6	266	3	44	159	1	35	182	2	54	247	2	40
7	275	2	39	172	1	34	194	3	60	268	2	39
8	278	2	39	173	2	51	199	2	48	264	2	36
9	267	2	37	163	1	39	184	3	65	259	3	50
10	273	2	34	169	2	49	178	4	92	270	3	51
11	272	3	56	170	2	60	181	3	80	266	4	71
12	287	2	31	178	2	39	196	3	74	275	3	55
13	261	3	44	161	2	44	170	3	66	255	2	36
14	243	2	45	151	2	52	177	3	64	232	3	57
15	241	2	38	149	1	32	164	2	54	237	2	40
16	243	3	49	150	2	48	165	3	84	237	2	42
17	232	2	44	146	2	52	142	2	73	232	3	50
18	254	3	51	156	2	58	175	2	61	249	3	53
19	243	4	69	161	2	52	162	3	90	262	3	48

Appendix 2

Sample Number	Variable											
	Hind leg, tibia, width			Hind leg, tarsus I, width			Hind leg, tarsus I, ventral, length			Hind leg, tarsus I, dorsal length		
	TW			TS1W			TS1VL			TS1DL		
	($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)		
1	122	2	83	58	0	34	136	1	25	65	1	60
2	114	3	112	56	0	35	136	1	37	65	1	57
3	97	2	106	51	1	65	122	1	36	60	1	66
4	107	2	100	53	1	69	128	2	58	62	1	70
5	94	2	106	52	1	64	123	1	20	60	1	54
6	107	2	103	54	1	51	126	1	22	60	1	53
7	118	3	108	55	1	59	135	1	31	64	1	80
8	119	3	100	55	1	48	132	1	34	64	1	61
9	107	3	137	53	1	48	131	1	37	64	1	47
10	105	2	106	54	0	29	131	1	40	64	1	54
11	106	2	93	52	1	58	129	1	34	66	1	52
12	115	2	76	55	0	38	135	1	25	66	1	40
13	96	2	88	51	0	39	130	1	32	61	1	54
14	99	2	109	51	1	68	125	1	44	61	1	45
15	90	2	81	50	0	35	124	1	30	60	1	47
16	93	2	113	50	1	60	125	1	31	60	1	56
17	82	1	75	48	0	34	121	1	34	59	1	76
18	102	4	157	52	1	44	128	1	31	62	1	54
19	96	2	104	51	0	41	127	1	45	56	1	98

Appendix 2

Sample Number	Variable											
	Hind leg, tarsus II, length			Hind leg, tarsus II, width			Setal length, head			Setal length, antennal segment III		
	TS2L			TS2W			SLH			SLA3		
	($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)		
1	329	2	32	53	1	66	78	1	72	61	1	76
2	318	1	18	52	1	69	77	2	108	59	1	88
3	292	2	36	48	1	88	80	1	72	61	1	96
4	308	3	44	50	1	90	80	2	116	59	1	92
5	295	2	29	49	1	66	85	1	65	61	1	77
6	307	2	31	50	1	57	81	1	71	60	1	55
7	327	2	27	51	1	94	85	1	74	64	1	71
8	326	3	35	52	1	73	80	1	77	60	1	58
9	310	2	32	50	1	71	86	2	83	61	1	70
10	317	2	30	49	0	35	80	1	62	62	1	62
11	305	3	44	48	1	78	67	2	133	55	1	101
12	325	2	24	52	1	62	80	2	85	65	2	106
13	306	2	31	48	0	30	77	1	61	60	1	65
14	300	2	29	50	1	93	71	2	95	56	1	87
15	296	2	23	46	0	37	72	2	95	59	1	41
16	295	2	25	47	0	31	73	1	64	58	1	91
17	297	2	32	46	0	36	74	2	112	56	1	72
18	312	3	42	48	1	46	73	1	37	57	1	74
19	306	3	37	47	0	40	65	1	97	54	1	113

Appendix 2

Sample Number	Variable											
	Setal length, hind leg, tibia			Setal length, hind leg, tarsus II			Setal length, cornicle			Setal length, cauda		
	SLT			SLTS2			SLCO			SLCA		
	($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)		
1	78	1	57	55	1	48	92	1	63	172	2	61
2	73	2	119	53	1	86	81	2	135	164	3	95
3	77	1	61	56	1	58	87	3	159	163	2	49
4	75	1	71	53	1	72	86	2	82	166	2	59
5	74	1	80	54	0	39	90	1	74	163	2	58
6	79	1	77	56	1	56	92	1	72	176	2	56
7	80	1	66	57	1	72	97	2	76	176	1	37
8	76	1	72	57	1	56	98	2	84	174	2	58
9	80	1	58	58	1	57	101	3	122	177	2	52
10	79	1	63	57	1	60	101	2	78	175	2	51
11	72	2	102	53	1	110	81	2	110	157	4	100
12	79	1	69	56	1	62	96	2	112	168	2	56
13	78	1	60	54	1	48	91	2	85	172	2	49
14	73	1	76	54	1	65	84	2	100	162	2	61
15	74	1	62	54	1	56	85	1	70	167	2	57
16	74	1	74	53	1	61	84	2	98	166	2	50
17	73	1	55	53	1	77	82	2	119	158	2	69
18	73	1	73	56	1	50	88	2	78	162	2	67
19	66	1	54	49	1	67	71	2	117	148	3	99

Appendix 2

Sample Number	Variable											
	Setal length, genital plate			Setal length, abdominal tergite VIII			Setal length abdominal tergite V			Setal Number, antennal seg. VI, proc. terminalis		
	SLGP			SLAT8			SLAT5			SNA6SA		
	($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-1}$)		
1	90	1	69	113	1	53	11	1	276	52	1	79
2	84	2	102	114	2	82	9	1	278	53	1	108
3	81	1	54	108	3	117	11	0	194	51	1	44
4	79	1	84	109	2	82	10	0	171	50	0	11
5	85	2	86	120	2	80	13	0	173	50	1	45
6	89	1	74	115	2	59	12	1	248	51	1	60
7	89	2	77	119	3	96	10	0	213	53	1	108
8	89	2	76	114	2	68	10	0	209	51	1	60
9	89	1	65	125	2	77	11	1	252	51	1	108
10	85	1	48	115	2	69	10	0	208	52	1	118
11	76	2	95	98	2	120	9	0	228	49	1	91
12	93	2	81	117	1	46	10	0	199	52	1	101
13	85	2	92	111	3	110	11	0	177	52	1	85
14	79	1	70	104	2	79	11	1	219	49	1	63
15	76	1	77	108	2	70	13	0	150	52	1	71
16	78	1	72	108	2	68	11	0	125	50	1	92
17	73	1	78	97	2	95	9	0	207	52	1	79
18	80	1	49	111	2	73	12	1	189	49	1	91
19	71	2	104	91	2	87	11	0	174	58	1	96

Appendix 2

Sample Number	Variable											
	Setal number, antennal seg. VI, base			Setal number antennal seg. V			Setal number, antennal seg. II			Setal number, rostrum seg. IV, accessory setae		
	SNA6B			SNA5			SNA2			SNR4		
	(x 10^{-1})			(x 10^{-1})			(x 10^{-1})			(x 10^{-1})		
1	136	3	104	397	8	90	90	2	108	91	2	91
2	124	4	135	379	6	68	102	3	122	92	2	119
3	122	3	109	342	6	81	94	3	135	88	2	84
4	138	3	99	358	6	69	93	2	93	86	2	94
5	127	3	120	346	6	82	89	2	81	94	3	122
6	126	2	71	366	7	84	92	2	89	84	1	70
7	131	3	108	393	7	83	91	2	98	92	1	59
8	128	3	105	352	7	87	92	2	108	91	2	84
9	134	3	101	376	9	105	95	2	94	86	2	78
10	122	3	101	358	8	104	91	2	79	90	2	95
11	126	4	157	358	6	81	88	3	133	92	2	85
12	123	3	127	370	7	79	91	2	76	86	2	88
13	129	4	123	360	7	83	91	2	76	83	2	104
14	130	4	149	331	5	72	85	3	135	89	2	120
15	126	3	102	346	6	77	88	3	131	88	2	97
16	127	3	117	328	5	71	88	1	73	86	2	103
17	127	4	128	336	9	123	98	4	169	96	2	84
18	130	3	111	354	8	100	90	3	153	87	3	135
19	121	3	117	364	7	86	92	2	119	82	2	100

Appendix 2

Sample Number	Variable											
	Setal number, genital plate			Setal number, abdominal tergite V			Setal number, abdominal tergite VIII			Setal number, cornicle		
	SNGP			SNAT5			SNAT8			SNC		
	(x 10^{-1})			(x 10^{-1})			(x 10^{-1})			(x 10^{-1})		
1	380	10	116	68	3	192	134	3	107	486	12	106
2	388	9	101	71	2	101	136	2	94	485	8	71
3	310	8	114	72	2	107	120	2	84	371	10	116
4	310	9	122	71	3	164	128	3	95	429	16	173
5	293	6	92	70	1	93	134	3	101	375	8	96
6	319	8	116	71	2	136	128	2	88	401	13	146
7	341	9	118	68	2	106	138	4	127	488	14	127
8	371	9	112	68	2	132	128	2	73	453	10	98
9	337	10	135	75	2	133	129	3	109	450	10	97
10	344	9	111	68	2	132	126	3	91	462	12	118
11	289	8	126	62	2	179	124	4	142	383	13	155
12	388	11	128	66	2	144	132	2	64	486	10	93
13	321	8	107	72	2	153	126	2	60	393	10	114
14	293	8	120	66	2	135	122	3	118	394	10	111
15	287	8	125	71	2	151	128	3	91	337	11	150
16	288	5	79	69	3	162	122	2	87	345	11	146
17	326	10	143	71	3	198	124	3	96	404	9	94
18	335	11	141	71	2	126	132	3	98	388	11	126
19	325	9	127	70	2	131	132	2	84	438	10	106

Appendix 2

Sample Number	Variable		
	Setal number, 0.2 mm of hind tibia		
	SNT		
	($\times 10^{-7}$)		
1	441	9	94
2	465	10	92
3	405	10	105
4	424	8	83
5	424	7	72
6	435	8	81
7	468	10	99
8	456	9	92
9	442	12	119
10	445	9	85
11	371	10	125
12	471	5	47
13	378	6	71
14	407	9	104
15	398	7	73
16	385	9	102
17	371	8	93
18	427	8	79
19	430	9	97

APPENDIX 3

Measurement data (mean ± standard error and coefficient of variation) for the adult apterous morph of the Cinara species studied in Chapter 5. The species numbers are as indicated in Table XII. All measurements are in mm. The decimal point for the mean and standard error is indicated below the variable name. All coefficients of variation are given as 1×10^{-1}.

Appendix 3

Sample Number	Variable											
	Body length			Frons width			Antennal segment II, length			Antennal segment III, length		
	BL			FRW			A2L			A3L		
	($\times 10^{-2}$)			($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)		
1	358	8	108	353	4	62	116	2	66	558	7	64
2	410	5	62	566	8	74	126	1	47	571	7	61
3	299	6	101	340	5	69	108	1	61	481	8	83
4	273	5	66	318	2	29	93	1	46	422	7	64
5	344	5	80	349	3	49	106	2	77	560	11	101
6	273	4	81	313	3	55	93	1	62	481	12	124
7	330	6	86	330	2	35	103	1	60	523	7	67
8	341	6	90	345	4	55	111	1	65	571	7	60
9	381	7	95	379	5	70	123	2	80	589	17	149
10	351	6	79	368	5	63	116	1	39	552	8	66
11	356	7	98	343	3	50	107	2	90	526	9	81
12	314	5	76	367	4	49	120	1	48	507	7	73

Appendix 3

Sample Number	Variable											
	Antennal segment IV, length			Antennal segment V, length			Antennal segment VI, base length			Antennal segment VI, base width		
	A4L			A5L			A6BL			A6BW		
	($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)		
1	242	4	87	294	3	59	140	1	37	56	1	46
2	271	4	84	335	4	61	203	2	45	48	0	47
3	226	6	123	257	5	107	132	2	64	56	1	48
4	215	2	41	241	3	49	130	2	47	56	1	61
5	227	5	99	258	8	156	135	2	77	56	1	50
6	204	5	124	233	5	100	128	1	57	52	1	88
7	223	5	104	260	5	93	138	2	66	56	1	72
8	240	4	93	282	5	94	144	3	93	57	0	43
9	266	8	149	317	9	136	153	2	79	64	1	63
10	250	4	69	300	5	70	147	2	68	63	1	86
11	194	4	97	251	3	67	130	1	57	56	0	43
12	212	5	113	263	4	75	141	2	66	52	1	50

Appendix 3

Sample Number	Variable											
	Antennal segment VI processus terminalis, length			Rostrum segment V, length			Rostrum segment IV, length			Rostrum segment III, length		
	A6PTL			R5L			R4L			R3L		
	($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)		
1	48	1	87	82	1	37	209	2	55	271	3	56
2	74	1	90	93	1	73	222	1	31	247	2	46
3	45	2	200	88	1	64	206	2	51	202	2	51
4	36	1	96	92	1	38	204	2	35	194	2	43
5	49	1	125	80	2	97	202	3	78	224	4	91
6	44	1	127	75	2	122	183	2	47	202	1	37
7	46	2	170	78	1	55	204	3	77	226	3	70
8	43	1	139	83	1	64	212	4	92	227	2	49
9	48	1	112	87	1	72	232	4	96	246	4	90
10	42	1	87	90	1	60	229	2	44	242	3	50
11	51	1	68	75	1	46	203	2	51	218	2	55
12	40	1	103	65	1	54	172	2	50	192	2	48

Appendix 3

Sample Number	Variable											
	Rostrum segment II, length			Hind leg, femur, length			Hind leg, femur, width			Hind leg, tibia, length		
	R2L			FL			FW			TL		
	($\times 10^{-2}$)			($\times 10^{-2}$)			($\times 10^{-3}$)			($\times 10^{-2}$)		
1	141	2	81	166	3	86	180	3	81	260	4	81
2	96	2	122	174	2	51	268	4	80	240	3	71
3	90	2	129	142	3	101	189	3	72	221	4	99
4	87	1	57	122	2	77	191	2	50	194	2	47
5	126	2	86	163	4	113	174	7	195	249	6	116
6	111	2	81	129	3	113	144	3	95	201	5	126
7	123	3	110	156	3	96	179	4	102	235	5	101
8	123	2	86	159	2	73	181	3	89	238	4	79
9	141	3	122	168	4	125	188	5	143	254	8	155
10	136	1	36	157	3	87	189	3	72	235	5	94
11	127	2	67	160	3	93	180	3	96	242	5	100
12	106	2	88	149	2	83	189	3	90	227	4	99

Appendix 3

Sample Number	Variable											
	Hind leg, tarsus I, ventral, length			Hind leg, tarsus II, length			Setal length antennal segment III			Setal Lenght hind leg, tibia		
	TS1VL			TS2L			SLA3			SLT		
	($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-3}$)		
1	130	1	55	311	3	56	59	1	102	75	1	88
2	225	2	39	367	3	38	129	3	97	149	1	116
3	131	2	70	298	3	58	43	1	72	50	0	48
4	127	1	34	253	3	42	34	1	71	58	2	110
5	128	3	106	274	5	90	41	1	143	55	1	112
6	112	3	84	248	3	59	36	1	200	52	1	144
7	127	2	70	266	3	64	43	1	143	61	1	103
8	130	2	67	281	3	47	72	2	141	74	1	89
9	139	3	94	303	4	65	81	3	186	86	3	181
10	132	2	51	286	4	66	82	3	139	88	3	137
11	127	2	75	283	4	66	45	1	97	53	1	77
12	127	1	40	284	2	41	76	2	135	80	2	94

Appendix 3

Sample Number	Variable											
	Setal length, genital plate			Setal length, abdominal tergite V			Setal number, antennal seg. VI, proc. terminalis			Setal number, antennal seg. VI, base		
	SLGP			SLAT5			SNA6SA			SNA6B		
	($\times 10^{-3}$)			($\times 10^{-3}$)			($\times 10^{-1}$)			($\times 10^{-1}$)		
1	81	2	136	11	1	261	53	1	89	126	3	116
2	131	2	76	152	3	90	39	1	85	59	1	119
3	77	2	107	38	1	121	41	1	128	83	3	169
4	76	1	50	35	2	169	39	1	66	67	3	185
5	89	2	129	23	1	264	39	1	71	141	6	202
6	71	2	129	21	2	402	38	1	97	132	5	181
7	86	2	90	25	1	247	38	1	163	153	5	162
8	103	2	107	98	2	85	40	0	51	155	9	278
9	113	3	114	114	3	127	39	1	71	201	6	142
10	112	3	127	115	4	156	39	1	57	185	6	134
11	87	2	127	18	2	470	41	1	81	123	3	121
12	89	2	110	99	4	183	39	1	71	142	4	135

Appendix 3

Sample Number	Variable											
	Setal number, antennal seg. V			Setal number, antennal seg. II			Setal number, rostrum seg. IV, accessory setae			Setal number, genital plate		
	SNA5			SNA2			SNR4			SNGP		
	($\times 10^{-1}$)			($\times 10^{-1}$)			($\times 10^{-1}$)			($\times 10^{-1}$)		
1	371	6	84	93	2	119	88	2	106	349	11	151
2	100	3	152	84	2	138	61	1	46	644	17	129
3	219	7	169	77	2	149	48	2	221	366	13	177
4	198	8	161	75	2	123	45	2	143	312	9	114
5	261	10	186	70	2	139	82	2	107	278	13	234
6	249	9	182	70	2	130	82	2	126	246	11	215
7	276	7	132	76	3	175	81	3	172	298	13	222
8	312	14	229	84	3	154	88	2	125	269	12	227
9	379	10	129	110	4	184	106	3	144	331	12	181
10	373	10	116	97	3	161	100	2	108	315	7	104
11	232	6	131	68	2	120	72	2	121	221	9	196
12	258	8	153	156	3	109	76	1	85	202	10	250

Appendix 3

Sample Number	Variable											
	Setal number, abdominal tergite V			Setal number, abdominal tergite VIII			Setal number, cornicle			Setal number, 0.2 mm of hind tibia		
	SNAT5			SNAT8			SNC			SNT		
	($\times 10^{-1}$)			($\times 10^{-1}$)			($\times 10^{-1}$)			($\times 10^{-1}$)		
1	70	3	180	129	2	86	401	15	185	433	8	91
2	1332	38	142	288	9	164	1706	54	159	229	5	108
3	145	9	325	107	2	106	288	11	189	411	10	124
4	185	6	129	126	7	212	173	8	170	535	8	55
5	122	7	272	167	8	243	443	22	252	346	10	140
6	103	3	127	136	3	122	348	14	195	360	9	122
7	103	4	202	152	5	161	390	17	218	388	10	132
8	224	13	286	165	7	217	719	40	277	410	13	163
9	377	28	368	175	7	191	929	32	171	452	12	128
10	373	30	361	188	10	244	813	30	166	459	10	101
11	78	3	215	125	4	143	359	15	210	364	9	127
12	334	14	211	261	7	128	646	18	137	594	8	71

APPENDIX 4

Börner's (1952) classification of the tribe Cinarini (Börner) (Aphidoidea, Lachnidae).

Tribe Cinarini Borner

Cinara Curtis 1835, Börner 1930

Subgenus Cinara s. str.

Cinarellia Börner 1951

Subcinara Börner 1949

Buchneria Börner 1952

Laricaria Börner 1939

Cinaria Börner 1939

Cinaropsis Börner 1939

Cinaropsis s. str.

Pityaria Börner 1950

Mecinaria Börner 1949

Todolachnus Matsumura 1917

Cupressobium Börner 1940

Lachniella del Guercio 1909

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