Ann. Zool. Fennici 27:29–47
Helsinki 4 September 1990

ISSN 0003-455X

Morphological variation in *Aradus cinnamomeus* (Heteroptera, Aradidae): discrimination between parapatric alternate-year populations

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Received 21 July 1989, revised 4 May 1990

Morphological variation in the pine bark bug *Aradus cinnamomeus* Panzer was studied by making 43 metric measurements of the head, thorax and abdomen of adult males and 40 of the females. The differences between parapatric alternate-year populations (cohorts) and between the sexes were analysed using discriminant function analysis. Classification functions determined for the parapatric local majority cohorts — the cohorts reproducing in even years in eastern Finland and in odd years in western Finland — were used to identify the temporally isolated local minority cohorts from Harjavalta (western even-year) and Valkeala (eastern odd-year). The temporal variation was investigated by re-sampling three populations and classifying the individuals on the basis of the same functions.

More than 80% of the individuals belonging to the even- and odd-year majority populations could be identified on the basis of multivariate morphometrics. According to the discrimination functions determined for the two majority cohorts, the two minority cohorts should be classified together with the allopatric synchronic populations rather than with the sympatric but allochronic majority populations. Variables related to snout length and head size discriminated most effectively between parapatric majority cohorts.

Classification functions based on a one-year sample did not succeed in identifying the samples from another year, which differed distinctly from both the odd- and even-year cohorts previously analysed. Consequently, the identification of museum specimens seems difficult. The results show that the temporal composition of samples in morphological studies should not be ignored.

1. Introduction

The degree of geographical and temporal isolation affects the morphological features of insect populations. Variation in populations partly reflects their historical background, e.g. different dispersal routes. Although the environment, both abiotic and biotic, influences the individual variation, the environmental component is often difficult to separate from the variation caused by heredity (Gould & Johnston 1972, Atchley et al. 1981, Pankakoski & Nurmi 1986). In certain cases in which an insect species has sympatric but allochronic broods or cohorts, it seems reasonable to assume that the effect of the environment will be almost the same for the two cohorts. This can make it easier to evaluate the proportion of variation which is due to the common historical background and the proportion which is due to the local ecological circumstances. However, the picture may be obscured by temporal variation and the ecological interactions of the sympatric cohorts themselves.

Here, we will examine the morphological variation in the pine bark bug *Aradus cinnamomeus* Panzer (Heteroptera, Aradidae) in Finland. Both the larvae and adult bug live under the bark of young Scots pines (*Pinus sylvestris* L.), sucking sap from xylem, phloem and cambium (Heliövaara & Laurema 1988). The bug is a biennial insect, having sympatric but allochronic and synchronic but allopatric cohorts or groups of populations. The aim of the present article is to study the variation between the allopatric (parapatric) alternate-year populations of the bug in the southern and central part of the country, where the life-cycle of the species takes two years.

In the east the cohort reproducing in even years almost exclusively predominates over the odd-year cohort, while in the west the odd-year cohort predominates over the even-year cohort. This results in a kind of parapatry of these alternate-year cohorts (Heliövaara & Väisänen 1984a). Key (1981) has defined parapatry as a distributional relationship in which two populations occupy contiguous territories that overlap only very narrowly in relation to both the length of the zone and the vagility of the individuals. In the case of the pine bark bug the parapatry is apparent in the field due to the extremely distinct preponderance relationships of the alternate-year cohorts, in spite of the fact that there always seem to be two sympatric allochronic bug cohorts. Furthermore, the distributional relationship between the allochronic bug cohorts represents ecological parapatry (vs. hybridization parapatry; see Key 1981), although there is no sharp ecological interface between the habitats of the two bug cohorts which could lead to restriction of interpenetration. In this case it is suggested that the parapatry is maintained by intraspecific competition and/or predators (Heliövaara & Väisänen 1984b, 1986b).

Heritable morphological differences may have accumulated within each allochronic cohort, in spite of similar selection pressures (parapatry, sympatry). We use discriminant function analysis in order to determine whether there are any differences between the two parapatric allochronic local majority cohorts, i.e. the eastern even-year and the western odd-year populations. In addition, the discriminant functions are used to identify rare individuals from the local minority populations, which are geographically separated from the synchronic majority cohort and temporally separated from the sympatric majority cohort.

Since temperature, humidity, the physiological condition of host trees, etc. vary from year to year, potentially affecting insect development, annual variation in the environmental conditions may explain some of the possible morphological differences between allochronic cohorts. Thus, a few local populations were re-sampled and classified using the previously calculated discriminant functions.

The natural history and biogeography of the pine bark bug have recently been examined in several papers (Brammanis 1975, Heliövaara & Väisänen 1983, 1984a, b, 1986a, b, 1987, 1988). This study belongs to the series dealing with the morphological variation of the pine bark bug in Finland (Väisänen & Heliövaara 1989, 1990), and is a continuation of a genetic study on the differences between alternate-year populations (Heliövaara et al. 1988). The recent papers dealing with traditional taxonomic aspects of the morphology of *Aradus cinnamomeus* and related species include Heiss (1980) and Vásárhelyi (1985).

2. Material and methods

2.1. Bug material

The basic data set of 1905 adult individuals, 921 males and 984 females, was collected from 27 populations at 25 localities in southern and central Finland in 1984 (Table 1, Fig. 1). The even-year cohort, reproducing in the same year, was sampled in spring and the odd-year cohort, reproducing in the next year, in autumn. Thus, the larval period of the even-year cohort was 1982–1983 and that of the odd-year cohort 1983–1984.

The same localities have been included in the genetic study on the enzymatic variation in the pine bark bug (Heliövaara et al. 1988). The proportion of the local minority cohort sampled was 0.06% at Harjavalta (*n* = 54000) and 0.07% at Valkeala (*n* = 36000). The collection methods have been described, for instance, by Heliövaara & Väisänen (1987). Each sample comprised bugs from at least ten pines.

Additional even-year bug material, 199 males and 213 females, was collected from Pernaja, Pyhtää and Vehkalahti in October 1989. These were exactly the same localities as five years

Table 1. The Finnish material of *Aradus cinnamomeus*. Sample codes, sampling sites with their coordinates according to the Finnish uniform 10 km-grid (27°E) system, sampling dates, and number of individuals measured. Additional samples from Pernaja, Pyhtää and Vehkalahti were collected in 1989.

Generation	Code	Locality	Grid	Date	Females	Males
Western odd-year majority	VAA1	Vaasa	700:23	17.VIII.1984	40	40
	ÖVE1	Övermark	695:21	17.VIII.1984	40	40
	KRI1	Kristiinankaupunki	692:20	17.VIII.1984	40	40
	MER1	Merikarvia	687:21	17.VIII.1984	40	40
	LUV1	Luvia	681:21	17.VIII.1984	40	40
	HAR1	Harjavalta	680:24	4.IX.1984	40	40
	LAI1	Laitila	676:21	17.VIII.1984	40	40
	HUM1	Humppila	676:30	4.IX.1984	40	40
	RAI1	Raisio	672:23	15.VIII.1984	40	30
	SAL1	Salo	670:28	4.IX.1984	40	40
	NUM1	Nummi-Pusula	673:32	4.IX.1984	40	40
Eastern even-year majority	NUM2	Nummi-Pusula	673:32	28.V.1984	40	40
	KAR2	Karkkila	671:34	28.V.1984	20	8
	HAN2	Hanko	664:28	12.VI.1984	40	40
	TUU2	Tuusula	669:38	17.VI.1984	40	32
	KER2	Kerava	670:39	6.VI.1984	40	40
	PER2	Pernaja	670:44	5.VI.1984	40	40
	PYH2	Pyhtää	670:47	5.VI.1984	40	33
	VEH2	Vehkalahti	671:51	5.VI.1984	40	40
	YLÄ2	Ylämaa	674:55	5.VI.1984	40	40
	LAP2	Lappeenranta	677:56	5.VI.1984	40	30
	IMA2	Imatra	678:59	5.VI.1984	30	23
	MIK2	Mikkeli	684:51	6.VI.1984	40	40
	PUN2	Punkaharju	685:62	5.VI.1984	38	40
	JUV2	Juva	686:54	6.VI.1984	40	40
Western even-year minority	HAR2	Harjavalta	680:24	29.V.1984	3	3
Eastern odd-year minority	VAL1	Valkeala	675:48	20.IX.1984	13	2

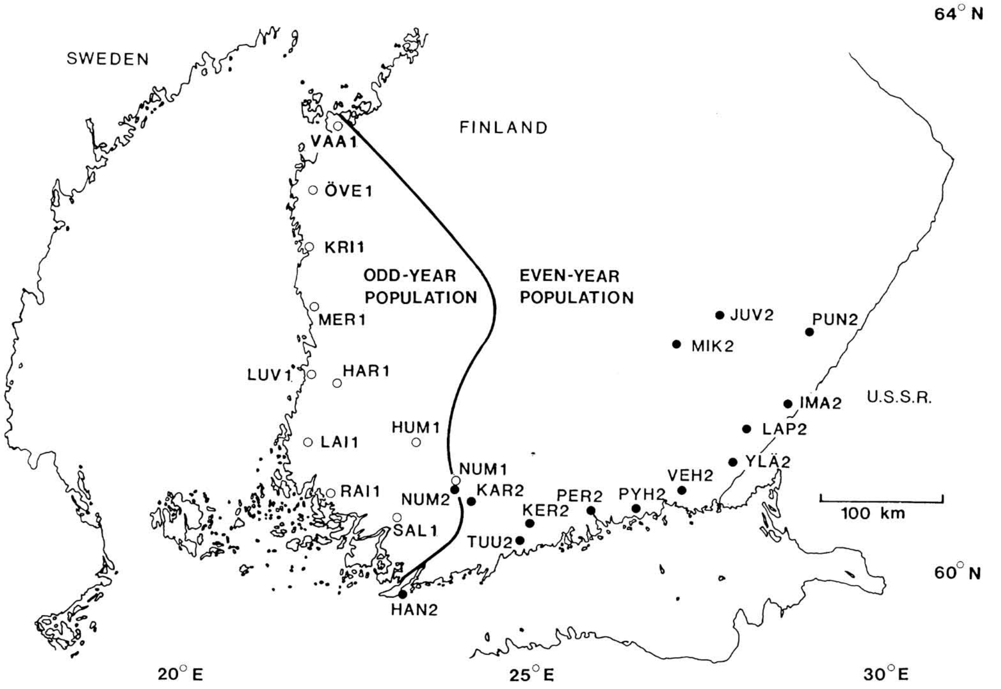

Fig. 1. Map showing the distribution of the alternate-year pine bark bugs *Aradus cinnamomeus* in Finland and the sampling localities. For the sample codes, see Table 1.

earlier (PER2, PYH2, VEH2). However, the habitats had undergone changes due to moderate silvicultural activity.

2.2. Preparation procedures

The bugs, collected in 75% ethanol, were transferred to 20% KOH solution, left to stand for one night, and then washed in water for two minutes the next morning. They were then placed in 5% acetic acid for half an hour, washed in water for another 30 minutes, and transferred to 75% ethanol for a further 30 minutes. After this the bugs were submerged in clove oil for two hours, and then in absolute ethanol overnight. Similar methods have been used to make other strongly sclerotized insects, such as fleas, transparent for study.

The bugs were set in Permount between the covers of film slide frames. Air bubbles were removed from these permanent film slide preparations by warming. Since the bugs are very flat (maximum thickness 0.75 mm) and strongly sclerotized, the procedure did not affect their dimensions (cf. e.g. Lee 1982). Each film slide usually contained ten bugs of one sex from one locality. The slides were numbered, each bug being numbered individually.

2.3. Measurements

For the measurements, the film slides were projected at right angles on to a smooth white wall. The distance between the film slide plane and the wall was 4609 mm, and the distance between the film slide plane and the outer surface of the objective 144 mm. A 120-mm lens (4.75″, f=3.5) was used. The measurement were made to an accuracy of 0.01 mm, i.e. an accuracy of 1 mm on the wall (coefficient of magnification 65.35). The optical distortion of the lens was tested by placing

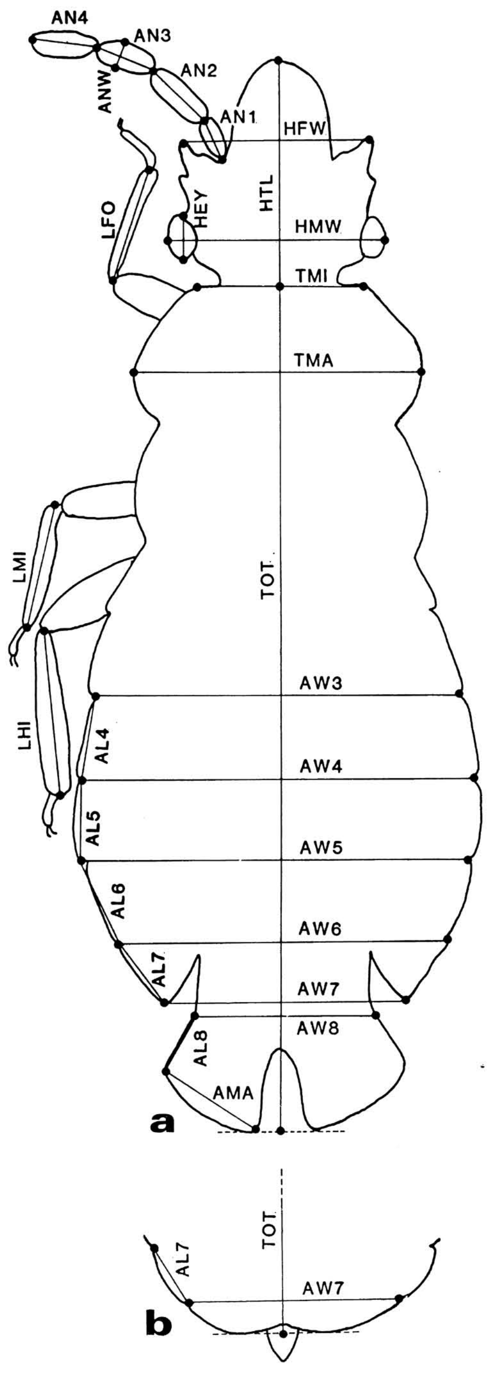

Fig. 2. The 27 "traditional" measurements made of *Aradus cinnamomeus*. — a. Male (measurements *AW8*, *AL8*, *AMA* for males only). — b. Apex of female abdomen. For the abbreviations, see Table 2.

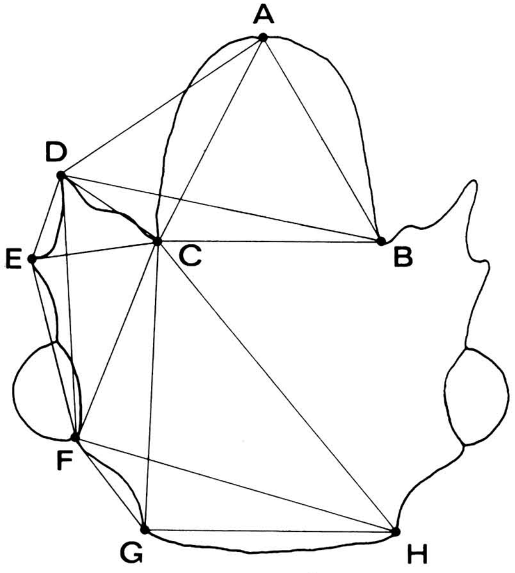

Fig. 3. The 16 measurements made on the head truss network of *Aradus cinnamomeus*. Abbreviations: *HAB* = head, distance between points A and B, *HAC* = head, distance between A and C, etc.

a Formatt No. 7022 screen sheet between the film slide covers. No differences could be detected in the size of the image of small circles reflected on the wall. In any case, the bugs were placed in the middle of the film slides, where any distortion should be minimal. All measurements on the 1984 material were carried out by one and the same person (M. P.).

Altogether 43 measurements were made on each male and 40 on each female. The parameters are listed in Figs. 2–3 and Table 2. They include 25 measurements of the head, 5 of the thorax and 13 of the male and 10 of the female abdomen. A truss network method was used for 16 measurements on the head (Fig. 3; Strauss & Bookstein 1982). Re-measurements of 10 female heads revealed no statistically significant differences between original and replicated data sets (one-sample $t = -0.97$, $P = 0.333$, $df = 159$).

Head truss networks of altogether 213 females and 199 males from the three populations resampled in 1989 were measured by another person (A. I.) and with other equipment (90 mm lens, f=2.8). Altogether 60 females from three western odd-year (KRI1, MER1, SAL1) and 60 from three eastern even-year populations (PER2, PYH2, VEH2) were re-measured by the same system.

2.4. Statistical analyses

Discriminant function analysis (DFA; stepwise discriminant analysis computer program, Jennrich & Sampson, Univ. California, BMDP7M) was used to determine the degree to which the allochronic samples can be maximally distinguished. Linear correlation analysis was used to correlate the canonical variates with the measured variables. Males and females were analysed both separately and together using both all the measurements and a subset of measurements comprising only the "head truss". To avoid the possibility of circular reasoning concerning the morphological differentiation between the parapatric majority cohorts, half of the individuals were used to calculate the discriminant function for the majority cohorts and the other half then classified using this function. The material was first halved using a random set of individuals from both of the cohorts, and then using a random set of population samples from both of the cohorts. The halved materials were analysed using all the variables, "head truss" and traditional "non-truss" variables. The discriminant functions determined for the two majority cohorts (all individuals) were used to classify the minority cohorts. The customary multinormality assumption has been made for the variables used in this study. Although this assumption may not necessarily be very realistic, discriminant function analysis can produce useful results.

Canonical discriminant analysis program (CANDISC, SAS multivariate procedures, Cary, N. C.) was used in relating the female bugs collected in 1989 to the different bug populations collected in 1984. This was first done using the whole material and relative values of the head truss network, to exclude the effects of allometric size-scaling variation. The relative values were calculated using *HFW* as a size variable according to the formula:

$$\text{relative value} = \ln x_i - \ln HFW,$$

where x_i = absolute values (Mosimann & James 1979, Pankakoski & Nurmi 1986; see also LaBarbera 1989). Secondly, we used absolute values obtained from re-measurements from six populations collected in 1984 and measurements of the bugs collected in 1989.

Table 2. Abbreviations of the "traditional" measurements of *Aradus cinnamomeus.* Note the difference between male and female in *TOT* (Fig. 2a and b).

HTL	total length of head
HFW	"frontal" width of head
HMW	maximal width of head
HEY	length of eye
ANW	width of antennal segement III
AN4	length of antennal segment IV
AN3	length of antennal segment III
AN2	length of antennal segment II
AN1	length of antennal segment I
TMI	minimal (anterior) width of thorax
TMA	maximal width of thorax
LFO	length of fore tibia
LMI	length of mid tibia
LHI	length of hind tibia
AL7	lateral length of abdominal segment VII
AL6	lateral length of abdominal segment VI
AL5	lateral length of abdominal segment V
AL4	lateral length of abdominal segment IV
AW3	posterior width of abdominal segment III
AW4	posterior width of abdominal segment IV
AW5	posterior width of abdominal segment V
AW6	posterior width of abdominal segment VI
AW7	posterior width of abdominal segment VII
AW8	minimal width of abdominal segment VIII (male)
AL8	lateral length of abdominal segment VIII (male)
AMA	apical measurement of abdomen (male)
TOT	total length of thorax and abdomen

3. Results

3.1. Discrimination between the majority cohorts using different data sets

The first step in the discriminant function analysis, the multivariate analysis of variance (MANOVA), showed that the parapatric alternate-year majority cohorts, i.e. the eastern even-year cohort and the western odd-year cohort, differed from each other in 1984 to a statistically highly significant degree. The relationship between the actual cohorts and the grouping given by discriminant function analysis (DFA) is presented in Table 3.

Table 3. Classification matrix of eastern even-year and western odd-year majority cohorts of *Aradus cinnamomeus* sampled in 1984 based on discriminant analyses. The rows are actual groups and columns predicted groups. The sexes are analysed separately. The Roman numeral I following the name of an actual cohort indicates the half of the material used in determining the discriminant function, while II indicates the other half, which has only been classified using this previously determined function.

Groups: Actual			DFA even	DFA odd	Total	Hit %
All individuals and variables	Males	even-year	365	55	420	86.9
		odd-year	47	320	367	87.2
	Females	even-year	403	76	479	84.1
		odd-year	51	329	380	86.6
All individuals but only variables of the head truss network	Males	even-year	393	92	485	81.0
		odd-year	68	360	428	84.1
	Females	even-year	420	104	524	80.2
		odd-year	82	351	433	81.1
Halved material (a random set of individuals), all variables	Males	even-year I	166	19	185	89.7
		odd-year I	16	153	179	90.5
		even-year II	191	44	235	81.3
		odd-year II	30	168	198	84.9
	Females	even-year I	218	48	266	82.0
		odd-year I	22	158	179	87.8
		even-year II	181	32	213	85.0
		odd-year II	32	168	200	84.0
As previous but only variables of the head truss network	Males	even-year I	183	30	213	85.9
		odd-year I	33	168	201	83.6
		even-year II	215	57	272	79.0
		odd-year II	43	184	227	81.1
	Females	even-year I	230	62	292	78.8
		odd-year I	44	164	208	78.8
		even-year II	189	43	232	81.5
		odd-year II	42	183	225	83.2
As previous but only non-truss variables	Males	even-year I	149	38	187	79.7
		odd-year I	30	139	169	82.2
		even-year II	174	62	236	73.7
		odd-year II	44	154	198	77.8
Halved material (a random set of population samples), all variables	Males	even-year I	130	24	154	84.4
		odd-year I	22	166	188	88.3
		even-year II	196	69	265	74.0
		odd-year II	23	156	179	87.2
	Females	even-year I	149	30	179	83.2
		odd-year I	32	169	201	84.1
		even-year II	233	67	301	77.7
		odd-year II	36	143	179	79.9
As previous but only variables of the head truss network	Males	even-year I	145	31	176	82.4
		odd-year I	39	189	228	82.9
		even-year II	226	83	309	73.1
		odd-year II	22	178	200	89.0
	Females	even-year I	152	44	196	77.6
		odd-year I	38	196	234	83.8
		even-year II	251	77	328	76.5
		odd-year II	33	166	199	83.4
As previous but only non-truss variables	Males	even-year I	114	41	155	73.5
		odd-year I	38	150	188	79.8
		even-year II	165	103	268	61.6
		odd-year II	55	124	179	69.3

The discriminant function determined for the two majority cohorts using halved material with a random set of individuals from both cohorts classified 81–85% of the independent male material correctly, i.e. assigned them to the cohorts to which they actually belong. Of the independent females, 84–85% were correctly classified. The hit percentage was also high when a halved material with a random set of population samples from both of the majority cohorts and/or a subset of variables was used in the analyses. Only in the case of "non-truss" variables and halved material with a random set of population samples was the hit percentage of the independent material less than 70.

In the preliminary analysis using the hit percentage, no distinct geographical trends could be detected among samples from different localities (Table 4).

Table 4. *Aradus cinnamomeus.* Relationship between actual grouping into eastern even-year and western odd-year majority populations and the grouping given by the discriminant function analysis in different localities. Sexes analysed separately using all variables and all individuals of the majority cohorts sampled in 1984.

		Females				Males			
		DFA grouping		Total	Hit	DFA grouping		Total	Hit
Actual group	Locality	even	odd	ind.	%	even	odd	ind.	%
Western odd-year	VAA1	13	21	34	62	10	25	35	71
	ÖVE1	6	25	31	81	7	27	34	79
	KRI1	2	38	40	95	3	35	38	92
	MER1	7	30	37	81	7	28	35	80
	LUV1	6	28	34	82	9	26	35	74
	HAR1	3	33	36	92	1	32	33	97
	LAI1	2	29	31	94	3	31	34	91
	HUM1	5	27	32	84	0	34	34	100
	RAI1	3	32	35	91	0	14	14	100
	SAL1	4	33	37	89	1	38	39	97
	NUM1	0	33	33	100	6	30	36	83
Eastern even-year	NUM2	5	3	8	63	2	2	4	50
	KAR2	30	5	35	86	29	8	37	78
	HAN2	35	1	36	97	32	2	34	78
	TUU2	36	0	36	100	25	1	26	96
	KER2	33	5	38	87	30	7	37	81
	PER2	30	5	35	86	31	4	35	89
	PYH2	25	12	37	68	24	6	30	80
	VEH2	28	9	37	76	28	3	31	90
	YLÄ2	31	3	34	84	30	3	33	91
	LAP2	31	6	37	84	20	4	24	83
	IMA2	26	14	40	65	26	5	31	84
	MIK2	33	0	33	100	28	2	30	93
	PUN2	27	6	33	82	32	2	34	94
	JUV2	32	7	39	82	28	6	34	82
Eastern odd-year	VAL1	2	7	9		0	0	0	
Western even-year	HAR2	2	0	2		2	0	2	

3.2. Classification of the minority cohorts

Classification functions can be used to classify new cases: the case is assigned to the group for which the classification function has the largest value. All the majority individuals were used to determine the discriminant functions employed in classifying individuals belonging to the two minority cohorts. Canonical discriminant scores for males and females are given separately in Fig. 4. The western even-year males from Harjavalta (HAR2) were classified together with the eastern even-year bugs. Correspondingly, the western even-year females (HAR2) were classified together with the eastern even-year bugs, and 7 of the 9 eastern odd-year females from Valkeala (VAL1) together with the western odd-year females.

When both sexes and all the majority individuals were analysed together using all the measurements, the discriminant functions classified 11 of the 13 individuals belonging to the local minority cohorts (HAR2, VAL1) together with the allopatric but synchronic majority cohort, but only 2 together with the sympatric but allochronic cohort. The eastern odd-year females representing the local minority cohort differed from the eastern even-year majority cohort (F computed from the Mahalanobis D^2 statistics = 3.09^{***}, $df_1 = 22$, $df_2 = 1836$).

3.3. Canonical functions

The first canonical function for the whole 1984 material explained 82% of the total discrimination, and the second a further 3% of the total discrimination. The first canonical function reflected sexual differences and correlates best with the abdominal segment measurements (Table 5). The size difference between sexes was in favour of the females (Table 6). In the present set of measurements, which did not include the distinctly sexually dimorphic wing characteristics, sexual dimorphism was greatest (more than 40%) in *AL4*, *AL5*, *AL7*, *AW3* and *AL6*. Similar tendencies in sexual dimorphism were observed both in the eastern even-year cohort and in the western odd-year cohort. The second canonical function reflected the differences between the allochronic bug cohorts and was best correlated with the head measurements *HAB*, *HCE* and *HCD* (Table 5).

Similar results concerning the classification of the minority cohorts were obtained when only the variables of the head truss network were used. The first canonical function explained 70.1% of the total discrimination, and the second a further 9.4%. The first canonical function reflected the width (and size) of the head, and was best correlated with *HFH*, *HCH* and *HBC*. On the other hand, the second canonical function reflected the shape of the appendages, and was best correlated with *HAB* (and *HAC*) and *HCD*. The centroids and standard deviation ellipses of the alternate-year majority and minority cohorts are given for both males and females in Fig. 5.

Table 5. *Aradus cinnamomeus*. Correlation coefficients of the measurements with the first, second and third canonical functions discriminating between the sexes and allochronic cohorts. The most effectively discriminating variables (all measurements and all individuals of the majority cohorts sampled in 1984) were used in calculating the discriminant function.

	1st	2nd	3rd
AL5	0.99	−0.01	−0.02
AL7	0.98	0.02	0.03
AW3	0.97	−0.01	−0.04
TOT	0.86	−0.10	−0.05
HTL	0.86	0.16	−0.24
TMA	0.91	0.10	−0.05
AW7	0.38	−0.13	−0.26
LFO	0.80	−0.11	−0.26
AL6	0.97	−0.01	0.04
AN4	0.32	−0.03	0.16
ANW	0.49	0.10	−0.04
TMI	0.84	−0.12	−0.08
AL4	0.93	−0.00	−0.01
LHI	0.83	−0.13	−0.06
HMW	0.89	0.01	−0.07
HEY	0.47	0.08	−0.21
AN1	0.48	−0.14	−0.10
HAB	0.77	0.37	−0.26
HCH	0.86	−0.22	−0.15
HCE	0.58	−0.31	−0.23
HCD	0.38	0.31	−0.17
HAD	0.67	−0.16	−0.20
HGH	0.83	−0.15	−0.06
HDF	0.73	0.02	−0.31
HFG	0.34	0.27	−0.10
HBC	0.85	−0.15	−0.23
HFH	0.88	−0.15	−0.07

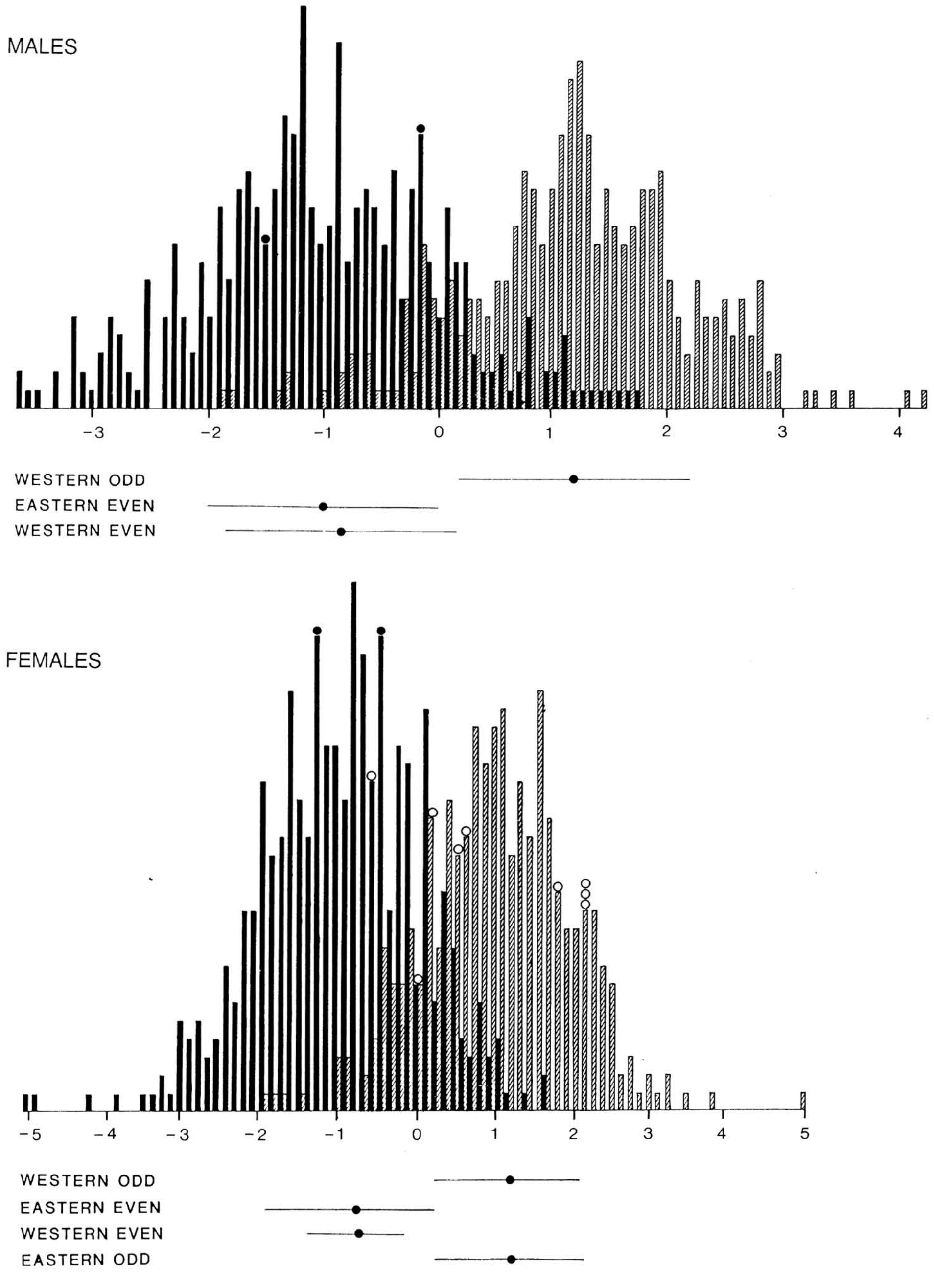

Fig. 4. *Aradus cinnamomeus.* Histogram of canonical discriminant scores for eastern even-year (black) and western odd-year (hatched) majority cohorts (all variables and all individuals of the majority cohorts sampled in 1984 were used to determine the discriminant function). Western even-year minority cohorts are marked with black dots and eastern odd-year cohorts with circles. Means and standard deviations are given below for each group.

Table 6. *Aradus cinnamomeus* cohorts. Sexual dimorphism (%) in measurements (in mm; mean±*SD*, *n*). The variables are arranged in decreasing order of female dominance in absolute size. The differences are in all cases statistically highly significant.

Variable	Males		Females		Dimorph.	Variable	Males		Females		Dimorph.
Western odd-year						Eastern even-year					
AL4	0.32±0.01	425	0.47±0.05	433	46.9	*AL4*	0.32±0.01	488	0.46±0.05	524	44.6
AL5	0.32±0.01	425	0.47±0.02	434	45.7	*AL5*	0.32±0.02	488	0.46±0.02	525	44.2
AL7	0.32±0.01	425	0.47±0.02	434	44.7	*AW3*	1.45±0.11	489	2.08±0.10	526	43.8
AW3	1.47±0.07	422	2.13±0.12	436	44.4	*AL7*	0.32±0.02	489	0.45±0.02	525	41.9
AL6	0.32±0.01	425	0.47±0.02	434	43.6	*AL6*	0.32±0.02	489	0.45±0.03	526	40.7
AW4	1.61±0.06	421	2.18±0.15	435	35.6	*AW4*	1.58±0.06	489	2.11±0.09	526	33.9
AW5	1.58±0.08	422	1.98±0.11	435	25.3	*AW5*	1.54±0.06	489	1.95±0.09	526	26.1
TMA	1.24±0.05	426	1.50±0.08	433	20.9	*AW6*	1.29±0.13	488	1.57±0.08	526	21.3
AW6	1.33±0.06	421	1.60±0.14	436	19.8	*HBC*	0.37±0.02	489	0.45±0.03	528	21.3
HCF	0.34±0.02	428	0.41±0.03	434	19.2	*TMA*	1.19±0.05	487	1.44±0.07	525	21.0
HBC	0.38±0.02	429	0.45±0.03	434	18.5	*HCF*	0.34±0.03	487	0.41±0.03	527	20.2
HGH	0.41±0.02	429	0.48±0.03	434	18.3	*HCH*	0.60±0.03	489	0.72±0.04	526	19.4
TOT	3.20±0.17	413	3.78±0.21	434	18.2	*HGH*	0.41±0.02	487	0.49±0.03	525	18.9
HCH	0.61±0.03	429	0.71±0.04	434	17.9	*HBD*	0.54±0.03	488	0.64±0.04	529	18.6
HBD	0.54±0.03	428	0.65±0.03	434	17.7	*TOT*	3.15±0.18	472	3.73±0.18	523	18.4
HFH	0.55±0.02	429	0.65±0.03	434	17.2	*HFH*	0.55±0.02	487	0.64±0.03	525	17.9
TMI	0.79±0.04	426	0.92±0.05	431	16.7	*HCG*	0.46±0.03	488	0.54±0.04	526	17.8
HCG	0.47±0.02	429	0.55±0.04	434	16.6	*HEF*	0.29±0.02	488	0.35±0.03	527	17.6
LHI	0.68±0.03	426	0.79±0.04	431	16.5	*TMI*	0.77±0.04	489	0.91±0.05	524	17.5
HFW	0.74±0.04	428	0.84±0.05	434	15.8	*LFO*	0.43±0.03	473	0.50±0.03	513	17.4
LFO	0.44±0.02	423	0.50±0.03	423	15.0	*LMI*	0.44±0.03	479	0.52±0.03	524	16.9
LMI	0.45±0.02	425	0.52±0.03	433	14.7	*HFW*	0.70±0.05	488	0.82±0.04	528	16.8
AN2	0.28±0.02	414	0.32±0.02	416	14.7	*LHI*	0.67±0.04	479	0.78±0.05	512	16.5
HAD	0.46±0.04	428	0.52±0.03	434	13.8	*HAD*	0.45±0.02	489	0.52±0.05	528	16.2
HMW	0.90±0.03	428	1.02±0.05	435	13.6	*HCE*	0.17±0.01	488	0.20±0.02	529	15.1
HEF	0.31±0.02	428	0.35±0.03	434	13.4	*HTL*	0.86±0.03	490	1.00±0.05	526	15.6
HTL	0.91±0.04	428	1.03±0.05	434	13.1	*AN2*	0.28±0.02	488	0.32±0.05	528	15.2
HCE	0.17±0.01	428	0.19±0.02	434	11.6	*HMW*	0.87±0.03	490	1.00±0.04	527	14.1
HDF	0.46±0.02	428	0.51±0.03	434	11.6	*HAB*	0.42±0.02	489	0.48±0.02	527	13.3
HAB	0.46±0.02	429	0.51±0.03	434	11.5	*HAC*	0.43±0.02	489	0.48±0.03	528	13.6
HAC	0.46±0.02	429	0.51±0.02	434	11.3	*HFG*	0.18±0.02	489	0.20±0.02	526	12.3
ANW	0.13±0.01	403	0.15±0.02	407	11.0	*ANW*	0.13±0.01	487	0.14±0.01	527	11.0
AN3	0.22±0.01	409	0.24±0.01	409	10.6	*AN3*	0.22±0.01	486	0.24±0.02	527	10.3
HFG	0.20±0.02	429	0.22±0.05	434	10.3	*HEY*	0.14±0.01	490	0.15±0.01	527	10.2
ANI	0.15±0.01	424	0.16±0.01	428	7.7	*ANI*	0.14±0.01	488	0.16±0.01	528	9.1
HEY	0.15±0.01	428	0.16±0.01	433	7.7	*HCD*	0.19±0.02	489	0.20±0.02	529	9.0
HCD	0.21±0.02	428	0.22±0.02	434	7.3	*HDE*	0.14±0.01	488	0.15±0.01	529	8.0
AN4	0.26±0.02	403	0.27±0.02	405	5.7	*HDF*	0.43±0.03	488	0.54±0.04	527	5.7
HDE	0.15±0.01	428	0.16±0.01	434	5.6	*AN4*	0.25±0.02	482	0.26±0.02	526	4.8
AW7	0.93±0.04	419	0.96±0.03	436	2.7	*AW7*	0.90±0.04	484	0.94±0.05	524	4.4
AW8	0.70±0.05	421				*AW8*	0.68±0.05	484			
AL8	0.21±0.02	421				*AL8*	0.20±0.02	484			
AMA	0.39±0.02	421				*AMA*	0.37±0.02	484			

In the case of males analysed separately using all measurements, the discriminant function was best correlated with *HAB*, *HFG* and *HTL*, and reflected the length of the snout and head, and in the case of the females, it was negatively correlated with *HCH* and *HCE*, reflecting the width of the head, and positively with *HAB* (Table 7). Classification functions obtained using all variables and the halved 1984 material (a random set of population samples) for males and females of the different cohorts are given in Table 8. The use of the whole material and the halved material of randomly taken individuals gave similar results.

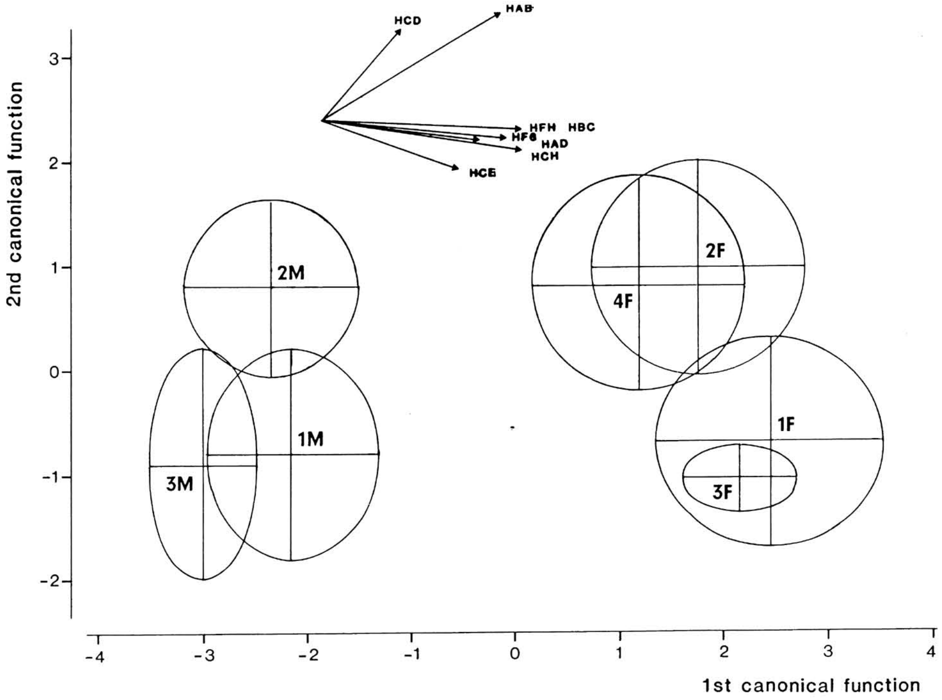

Fig. 5. *Aradus cinnamomeus*. Diagram showing the discrimination of eastern even-year (1) and western odd-year (2) majority cohorts and sexes (M = males, F = females) according to the head truss neatwork measurements (all individuals of the majority cohorts sampled in 1984 were used to determine the discriminant function). The positions of the western even-year minority cohort (3) and eastern odd-year minority cohort (4) are also shown. Solid lines indicate areas of mean and one standard deviation. Arrows indicate the effect of each variable in the discriminatory space.

3.4. Classification of re-sampled populations

To study temporal variation in the bug, three populations were sampled in both 1984 and 1989. Firstly, all the majority individuals collected in 1984, males and females separately, were used to determine the discriminant functions employed in the classification of the bugs collected in 1989. The use of absolute (standardized) values of measurements of the head truss network gave correct allocation to the eastern cohort of only 3 females out of 213, and 34 males out of 199. Secondly, the use of relative values gave similar results (3 out of 211 and 39 out of 198, respectively). Thirdly, when the smaller re-measured material (KRI1, MER1, SAL1, PER2, PYH2, VEH2) was used in calculating the discriminant function, 93 out of 198 new females were classified correctly in the eastern cohort.

The canonical discriminant analysis (CV3 vs. CV2) plotted the females sampled in 1989 together with the eastern even-year female swarm of points, but far away from the previous samples from the same sites (Fig. 6). CV1 is mostly related to size and consequently sensitive to errors caused by different measurers and equipment. When only the smaller material, measured by one and the same person using the same equipment, was used, a similar pattern still emerged (Figs. 7–8). The 1989 bugs really differ distinctly from the 1984 bugs collected from the same sites, but also considerably from the western odd-year bugs.

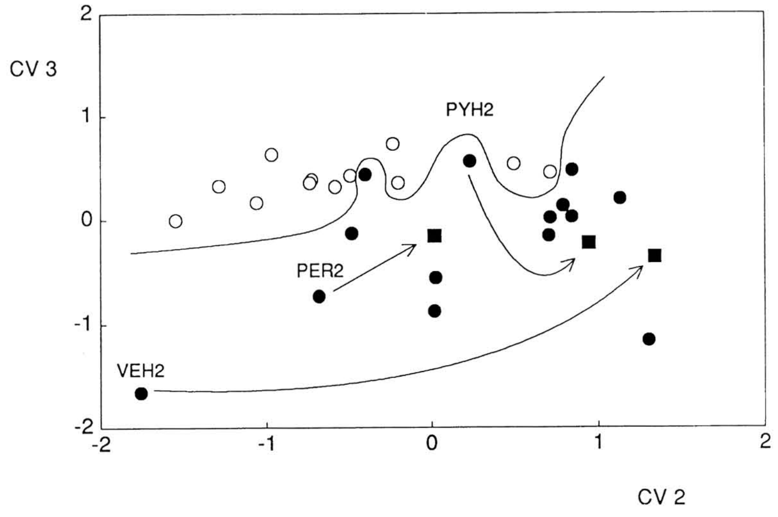

Fig. 6. *Aradus cinnamomeus*. Population scores for the second and third canonical variables for female pine bark bugs collected in 1984 (white circles — odd-year populations, black dots — even-year populations) and in 1989 (black squares). Arrows indicate the change within a single sample locality.

Table 7. *Aradus cinnamomeus*. Correlation coefficients of the measurements made on males and females with the canonical function discriminating between eastern even-year and western odd-year cohorts (sexes analysed separately, all measurements, all individuals of majority cohorts sampled in 1984).

Males Variable	*r*	Females Variable	*r*
HAB	0.63	*HCH*	–0.47
HFG	0.43	*HAB*	0.43
HTL	0.42	*HCE*	–0.43
HCF	–0.38	*HBC*	–0.37
AL6	–0.31	*HGH*	–0.35
HFH	–0.30	*HCF*	–0.34
HCE	–0.28	*HFH*	–0.32
LHI	–0.25	*LFO*	–0.29
AMA	0.23	*HCD*	0.28
AW4	–0.22	*HAD*	–0.28
HDF	0.21	*TMI*	–0.26
HBD	–0.20	*LHI*	–0.24
TMI	–0.20	*HEF*	–0.23
AW8	–0.19	*AW7*	–0.22
HCG	–0.19	*HFG*	0.21
HEY	0.18	*AN1*	–0.20
TMA	0.18	*TMA*	0.16
AN2	–0.17	*HTL*	0.13
AW6	–0.01	*ANW*	0.09
		AL7	0.07
		HMW	–0.04
		HEY	0.02

Table 8. Classification functions for the cohorts of *Aradus cinnamomeus* based on all variables and the halved material (a random set of population samples) collected in 1984.

Variable	Eastern even-year	Western odd-year
Males		
HAB	10.943	12.035
HAD	5.178	4.416
HDF	2.588	2.997
HCG	0.464	0.115
HFG	2.954	3.547
HCH	–1.464	–1.831
HFH	5.452	5.067
HTL	3.510	4.026
LMI	6.200	6.540
AL6	12.380	11.864
AW8	6.945	6.432
AMA	8.414	9.215
Constant	–932.934	–946.871
Females		
HAB	7.542	8.404
HBC	0.554	0.077
HAD	1.014	0.859
HBD	–0.142	–0.415
HCD	1.520	1.931
HCE	–2.509	–3.254
HCF	1.539	1.897
HFG	3.785	4.444
HCH	2.417	2.140
ANW	3.120	3.498
TMA	2.306	2.494
LFO	4.157	3.872
Constant	–428.785	–439.800

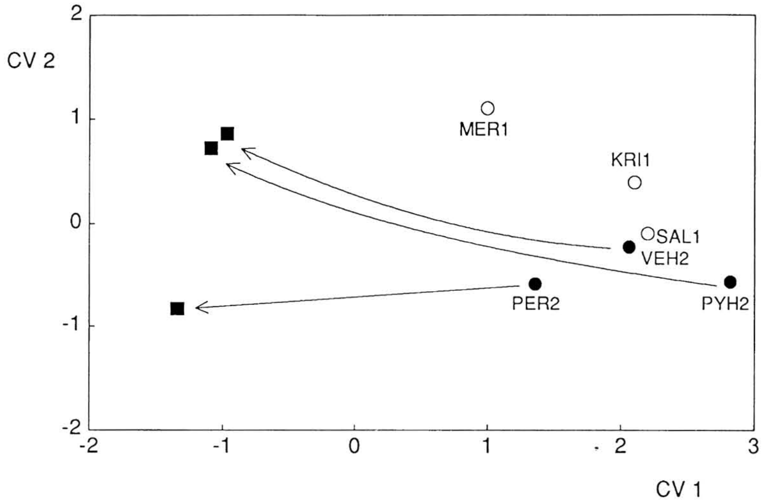

Fig. 7. Population scores for the first and second canonical variables for female *Aradus cinnamomeus* re-measured. Symbols as in Fig. 6. The eigenvalues for CV1, CV2 and CV3 are 2.48, 0.56 and 0.26, and the proportions of the variance explained 0.68, 0.15 and 0.07, respectively.

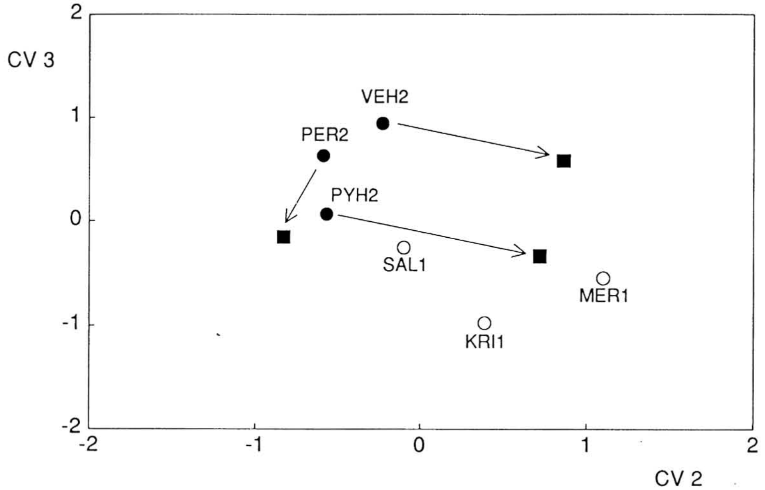

Fig. 8. Population scores for the second and third canonical variables for female *Aradus cinnamomeus* re-measured. Symbols as in Fig. 6. See also Fig. 7.

4. Discussion

4.1. Between-cohort variation

Morphometric techniques have been applied successfully to a wide variety of taxa, including several groups of insects and other arthropods (e.g. Moss et al. 1977, Busvine 1978, Simon 1983, Butlin & Hewitt 1985, Daly 1985, Rochette 1985, Pungerl 1986, Wetton 1987). These studies have often dealt with problems which are very difficult to solve using traditional qualitative morphological analysis. Such cases include enigmatic species pairs, sibling species or various kinds of intraspecific groups of individuals.

We have also several well-defined problems concerning the variation in *Aradus cinnamomeus* which are troublesome to resolve using traditional techniques of a univariate or bivariate nature. For instance, although some other aspects of morphological variation in the pine bark bug have been investigated (Väisänen & Heliövaara 1989, 1990), the magnitude of the morphological differences between allochronic cohorts of the bug has not so far been evaluated. The biological background of these cohorts and their taxonomic status have remained obscure, although this species is a widely distributed and well-known pest of considerable significance for practical forestry (Brammanis 1975, Hokkanen et al. 1987). In fact, evidence was only recently obtained in a genetic study that the cohorts really are conspecific (Heliövaara et al. 1988).

The division of the bugs into two allochronic cohorts (for the origin of these cohorts, see Heliövaara & Väisänen 1987) has led to morphological differentiation between the cohorts, at least when a snap-shot picture from one year is constructed. The difference is most distinct in character variables related to snout length and head size.

The present results indicate that a high proportion of both the males and females collected in the same year belonging to the parapatric alternate-year majority cohorts could be correctly identified using morphometric criteria, although the two cohorts have traditionally been considered morphologically identical. Furthermore, on the basis of the 1984 material it seems that the minority cohorts should preferably be classified together with the allopatric but synchronic cohorts rather than with the sympatric but allochronic majorities. The same pattern appears in males and females. This similarity between synchronic allopatric bugs may be due to the fact that they are not reproductively isolated from each other, the minor differences being mainly caused by environmental conditions. The biogeographic evidence (Heliövaara & Väisänen 1987) supports this view: the minority cohort seems always to be present, so that the synchronic bugs form a geographical continuum, although there are great regional differences in the densities of synchronic bugs, depending on the habitats and the preponderance relationships of the alternate-year cohorts.

The sexual dimorphism of the pine bark bug is distinct, especially in the abdominal measurements, and a similar pattern of sexual dimorphism exists in the two majority cohorts. This dimorphism is not self-evident, e.g. in the head dimensions, although the general sexual differences have been well documented (Strawinski 1925, Brammanis 1975).

4.2. Temporal variation

The distinct pattern revealed by one-year samples is greatly obscured by between-year variation. The morphological differences between the allochronic bug cohorts may reflect annual differences in the environmental conditions during the developmental periods 1982–1983 and 1983–1984 (note, however, the overlap in the developmental period of the allochronic cohorts). The bug material originated from a relatively large geographical area, stretching from the southern coast to the inland areas of central Finland. Thus, in addition to the considerable differences between the sample localities, there must be differences due to local ecological conditions and microclimates.

The fact that allopatric minority cohorts were morphologically similar to synchronic but allopatric majority cohorts suggests that the morphology of bug populations is relatively little affected by local environmental conditions. The fact that they retain similarity to other populations of their respective cohorts is very likely the result of a common evolutionary history. The annual variation between years remains an alternative or supplementary explanation for the similarity of synchronic bugs.

The re-sampling and analysis of three eastern even-year populations uncontestably showed the considerable importance of temporal variation in the pine bark bug. Classification functions based on a one-year sample did not succeed in identifying the samples collected in another year. The re-sampled bug populations differed distinctly from both the alternate-year cohorts previously used in calculating the discriminant functions. The differences in the meteorological conditions between 1984 and 1989 may be associated with the deviation of the re-sampled material. Summer 1987 was cold and rainy, affecting the pine growth and needle biomass, and presumably also the population dynamics of the pine bark bug. The biennial variation in a single bug population deserves further investigation, although it would not necessarily be possible to solve the problems involved in identifying the contributions of the temporal and spatial environment and heredity to the morphological variation (see e.g. Atchley et al. 1981, Pankakoski & Nurmi 1986).

4.3. Other sources of variation

Several factors complicate the interpretation of morphometric studies on insects. In addition to the between-cohort variation, the variation between the offspring of individual females may affect the results, although in the present case this pitfall was avoided by collecting the material from several pines. The bugs are relatively immobile and stay in the trees where they have hatched (Brammanis 1975).

In addition to geographical variation (Väisänen & Heliövaara 1989), the between-tree variation within a single sample plot may affect the morphology of bugs. Although the host trees did not differ markedly in their height, their physiological condition may have affected the bugs. There is at least a numerical response in pine bark bugs to the distance of host trees from pollutant sources (Heliövaara & Väisänen 1986a), which suggests a relation between the physiological condition of the tree and the bug performance. Differences in the undergrowth and the pine stand density may affect the bugs as well, e.g. through selective winter mortality (see Hokkanen et al. 1987).

The sampling procedure itself is a possible source of variation between the samples taken from the same locality in different years. This may be due to changes in the tree condition or in the bug population itself. The timing of sampling may affect the results, depending on the weather conditions and the season. The weather may affect the bug behaviour selectively, while the sampling season may cause variation due to selective seasonal mortality.

4.4. Comparison with enzymatic studies

In a previous study on the enzymatic variation in the pine bark bug in Finland, the sympatric allochronic cohorts were shown to differ distinctly from each other (Heliövaara et al. 1988). The most interesting point, however, was that the parapatric alternate-year majority cohorts did not differ markedly from each other in the enzyme systems studied. When one of the alternate-year cohorts predominates over the other in large geographical areas, the minority cohorts may differentiate genetically from the sympatric majority cohorts. This may be due to intraspecific competition between allochronic cohorts and/or decreased gene flow (genetic drift) among the synchronic minority bugs. In *Erebia embla* (Thuneberg) (Lepidoptera, Satyridae), another insect species with alternate-year cohorts, the enzymatic difference between the odd- and even-year populations were no larger than the differences among the even-year populations (Douwes & Stille 1988).

The present multivariate morphometric analysis of the bug and the enzyme electrophoresis gave some contradictory results. This is not, in itself, very surprising (e.g. Thorpe 1983), since the study of different character sets often results in different classification.

Judging by the morphological data, there appear to be considerable differences between the alternate-year cohorts, although the picture may be slightly obscured by temporal variation. Studies on the North American periodical cicadas (Homoptera: *Magicicada*) have given similar results (Simon 1983). The allochronic broods or year-classes of cicadas differ distinctly from each other in morphological terms (and in allozymes as well; Simon 1979), while most characteristics showed low levels of variation among the populations within broods.

4.5. Taxonomic status of cohorts

The morphological difference between the even- and odd-year cohorts, which is so evident in both males and females sampled in 1984 raises the question of the taxonomic status of such intraspecific groups. Traditionally, it has often been considered useful to recognize morphologically distinguishable and reproductively more or less isolated intraspecific units as subspecies (or in the present case more exactly as temporal subspecies; e.g. Edwards 1954). Subspecies are to be named only if they differ taxonomically, that is on the basis of diagnostic characters (Mayr 1975). Thus, there always remains the question of how great this taxonomic difference ought to be. However, it should be borne in mind that, in contrast to many named subspecies which appear to be artifacts rather than units of evolution, we are here apparently dealing with real evolutionary units. This is not to be understood as a criticism of formally named subspecies in general. We take it for granted that the subspecies is a useful taxonomic category (see e.g. Amadon & Short 1976).

As shown by previous studies on the life-history characteristics of the pine bark bug, the allochronic two-year bug cohorts are in general reproductively isolated. However, the isolation is not absolute. It has been suggested that gene exchange between allochronic alternate-year cohorts takes place via contact between the bugs with a three-year life-cycle in northern areas and in the Åland archipelago (for details, see Heliövaara & Väisänen 1987). There are also other possible mechanisms for gene exchange between the alternate-year cohorts, although there is no evidence of these from the field. Occasionally individuals with a two-year life-cycle can lengthen their developmental time to three years, whereas developmental acceleration by one year seems highly improbable. In many insects variation in the rate of development occurs among individuals in a given population (Tauber & Tauber 1981, Taylor & Karban 1986). For instance, in periodical cicadas stragglers are commonly sighted one year before, one year after, and four years before particularly dense emergences of 17-year cicadas (Simon 1988, Martin & Simon 1990).

In the genetic study, the allopatric allochronic majority cohorts showed a greater degree of similarity with each other than did the minority cohorts with the synchronic allopatric or sympatric allochronic majorities (Heliövaara et al. 1988). This would suggest that as many as four intraspecific groups of populations could be distinguished. Furthermore, if the analogous situation of two allochronic parapatric cohorts in Scandinavia (Heliövaara & Väisänen 1988) and possibly elsewhere (Heliövaara & Väisänen 1984a, and references therein), and the complex mosaic-like preponderance pattern of three-year cohorts (Heliövaara & Väisänen 1987) were taken into account, the decision to distinguish any of these cohorts or synchronic groups of populations as subspecies would result in complete chaos. Thus, we consider it highly inconvenient to give them any formal scientific names, irrespective of whether their diagnostic differences are great enough. The considerable temporal variation makes such descriptions still more unpractical. In addition, it seems difficult to classify the old museum specimens correctly using morphometric data of this kind.

It remains to be studied how similar the eastern Finnish even-year bugs are to the synchronic eastern Swedish even-year bugs, and the western Finnish odd-year bugs to the synchronic western Swedish odd-year bugs. This kind of comparison of the local majority populations could throw new light on the role of temporal versus geographical factors and on the taxonomic questions as well.

4.6. Problems caused by temporal composition of the sample

Very often the temporal composition of data used in morphological analyses has been ignored. Many papers do not even mention the period during which the material was sampled, not to speak of the distribution of the material among different years. This aspect surely deserves examination and discussion. In the comparison of allochronic units, the discrimination is always susceptible to temporal bias in the data. However, repeated sampling over a longer period can measure the temporal variation in relation to the variation due to other underlying groupings.

We consider the temporal variation in the structure of the material to be a major pitfall in traditional discriminating studies on insect morphology. It may be an important source of error in other organisms as well. On the other hand, temporal variation provides suitable testing opportunities: the discriminant functions calculated on the basis of one-year (or one-period) data can be tested on several comparable occasions and the functions can be compared in variable annual conditions. This can throw light on the microevolution of closely related taxa. Such an opportunity should not be missed by lumping material and ignoring its structure. This should also be taken into account when planning the sampling procedure.

Acknowledgements. We wish to thank Mr. Markku Pulkkinen and Miss Auli Immonen for their help in carrying out the measurements, Mr. Ari Nikula, Mr. Eero Kemppi and Mr. Veli Pekka Salmi for their help in computing. Dr. Chris Simon, Dr. Risto A. Väisänen and Dr. Mark Wetton are thanked for their valuable comments on the manuscript. The names of the authors appear in reversed alphabetical order for a change, the order, as usual, having no significance in our joint projects.

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