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# Morphometric comparison of geographically isolated populations of Arctocorisa carinata (C. Sahlberg) (Heteroptera, Corixidae)

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Individuals of *A. carinata* from Iceland, the British Isles, northern Finland, central Sweden, the Swedish west and east coasts, the Finnish south coast and the Swiss Alps were compared morphometrically by canonical variable analysis on samples of about 50 males and 50 females from each population. Separate analyses were performed on the two sexes for wing and leg measurements, and an additional set of data was analysed for male genital characters. The first analyses showed that the populations formed distinct sets corresponding to their habitats, while the additional analysis placed the populations rather according to their geographic distribution and presumed genetic closeness.

The first analyses gave as the most coherent set the rock pool populations of southern Finland and eastern and western Sweden. In certain characters, however, the western Swedish population diverged from the two others, and the male genital characters confirmed this divergence. The first analyses indicated another set comprising the northern Finnish, central Swedish and Swiss populations, but the genital characters showed that the Swiss population is distinct. The British and Icelandic populations were quite separate in the analyses for wing and leg measurements, but the genital characters indicated the closeness of the two.

A sample of eight males from the Pyrenees allowed a preliminary comparison with the other populations. Although both analyses placed the sample as a clearly separate unit, they revealed certain affinities with the Swiss, northern Finnish and British populations.

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## 1. Introduction

*A. carinata* is a species whose range includes some of the most northern localities and highest altitudes inhabited by Corixidae in Europe. The species occurs in Iceland, the Faroes and northern Britain, in Lapland and the Scandinavian Range, and in the mountain ranges of the Pyrenees and the Alps. In addition, it is found in rock pools in the archipelagoes of southern Finland, and eastern and western Sweden (cf. JANSSON 1978a, 1978b).

Although the distribution of *A. carinata* is fragmentary and the populations have apparently been isolated for long periods, little is known about geographic variation within the species. POISSON (1957) distinguished the Pyrenean population as a separate subspecies, *A. carinata pyrenaica*, and DETHIER (1975) has reported the subspecies from Switzerland. However, JANSSON (1978a) showed that the characters on which the subspecies *pyrenaica* was separated from the nominate form are invalid or fall within the variation found in all populations. On the other hand, JANSSON (1978b) has also shown that, despite the morphological similarities, the Swiss population does not produce viable offspring when experimentally crossbred with certain northern populations, and that in some combinations the progeny of crosses between the Fennoscandian, British and Icelandic populations also have clearly lower viability. Besides these genetic differences between the populations, there are also indications of differences in developmental physiology: PAJUNEN (1975) found that during larval development the Icelandic, British and Swiss populations had a poorer tolerance of high temperatures than the Swedish west-coast and Finnish south-coast populations.

In the present study, a morphometric analysis was employed to study the differences that have evolved between the populations, and to evaluate the adaptive significance of the characteristic differences between the various populations. The Pyrenean population, however, could not be included in the main analyses, and only a few comments are made on this population.

## 2. Material and methods

Individuals of *A. carinata* were collected from the following localities:

IC — 50 ♂♂ and 50 ♀♀: Iceland, Gullbringusýsla, Hafnarfjörður, 21. IX.1972: A permanent, rather large pool; altitude about 50 m above sea level; soft bottom and some aquatic vegetation. *A. carinata* is the only Corixid in Iceland, and inhabits a variety of water bodies (FRISTRUP 1945).

BR — 50 ♂♂ and 50 ♀♀: England, Westmorland, Appleby, Dufton Fell (national grid ref. 35/728275), 5.X.1973: Peat pools with some *Carex* spp. around the edges; bottom covered by thick layer of soft detritus; altitude about 700 m.

NF — 37 ♂♂ and 39 ♀♀: Finland, Le, Kalkkoaivi and Sarvisoaivi areas (grid 27°E 7635:301), 30.VIII. 1972: Large permanent ponds at an altitude of about 650 m; bottom strewn with rocks and boulders, with soft detritus in between; no aquatic vegetation. To make up the sample to 50 ♂ ♂ and 50 ♀ ♀, additional individuals were taken from nearby localities in Lapland.

CS — 46 ♂♂ and 44 ♀♀: Sweden, Härjedalen, Saxvallbygget, 30.VIII. 1973: A woodland pond cut off from the River Ljusnan; altitude about 500 m; bottom partly of soft clay, partly boulder-covered; some aquatic vegetation. During spring floods the pond apparently receives water from the river.

WS — 50 ♂♂ and 50 ♀♀: Sweden, Bohuslän, Skaftö, Kristineberg Zoological Station, Island of Långö, 28.VIII.1973: Rock pools filled with rain water, but during heavy storms spray from the sea may make the water brackish; most pools without aquatic vegetation; some soft detritus on the bottom.

ES — 43 ♂♂ and 48 ♀♀: Sweden, Södermanland, Askö, Askölaboratoriet, Island of Persö, 25.VIII.1973: Typical rock pools of the archipelago, with some soft detritus but no aquatic vegetation; water mainly originating from precipitation, but occasional spray from the Baltic may make the water slightly brackish.

SF — 50 ♂♂ and 50 ♀♀: Finland, N, Hanko, Tvärminne Zoological Station, the island Långskär (grid 27°E 6640:290), 25.IV.1965: A permanent pond with a thick layer of soft detritus and some aquatic mosses; water originating from precipitation. The pond, a typical overwintering habitat, was sampled before the spring dispersal. In early spring most individuals migrate to smaller, more or less temporary rock pools, in which the water may be slightly brackish (PAJUNEN & JANSSON 1969).

SA — 50 ♂♂ and 50 ♀♀: Switzerland, Canton Graubünden, Lenzerheide, 18.VIII. 1972: A shallow pond; altitude about 1200 m; bottom covered with soft detritus; a belt of *Carex* spp. surrounded the pond and formed an "island" in the middle.

The northern Finnish and central Swedish populations, although collected some 700 km apart, belong to one continuous distributional area which lies mainly north of the Arctic Circle, but extends to the southwest along the Scandinavian Range (JANSSON 1978b). Similarly, populations of southern Finland and eastern Sweden, collected some 300 km apart, can be considered to belong to one distributional area extending from Finland to Sweden through the Åland Islands (=Ahvenanmaa); the widest continuous stretch of open water between the two countries is only some 30 km.

For morphometry, wings, legs, and male genitalia were mounted on microscope slides, and the various dimensions were measured with a projecting microscope or under a standard microscope equipped with an eyepiece micrometer. From specimens of both sexes the following measurements were made: Total length of fore wing, distance from fore wing base to distal end of clavus, and fore wing base to nodal furrow (Fig. 1), length of each segment of each leg, and length of claws of the middle leg. The total length of each leg was also calculated. Numbers of dorsal, posterior, anteroventral and anterior pegs on the hind femora, and number of dorsal pegs on the hind tibiae were counted (for nomenclature, see JANSSON 1969), and average peg numbers were then calculated. From males, an additional set of measurements were taken as follows: Average number of palar pegs, lengths of right and left parameres, lengths of basal and distal parts of the right paramere, and lengths of distal and proximal projections of the right paramere (Fig. 1).

Selection of the variables was based on the consideration that the legs of Corixidae are functionally highly specialized. The fore legs serve as grasping organs in predation and as scrapers in stridulation, and in males also for holding the female during copulation. The middle legs are used to grasp the support when the insects are resting, and the hind legs initiate swimming movements and are also used for ventilation, and cleaning of abdomen. Thus, the form of the legs may be expected to be a sensitive indicator of adaptive changes corresponding to differences in the habitats. The structure of the genitalia, on the other hand, is probably a more conservative feature, less affected by the environment, but probably giving more information on kinship.

To eliminate the effects of sexual dimorphism and to allow comparison of two sets of data, a canonical variable analysis was carried out separately for the two sexes. HYLPS programs of the Computer Centre, University of Helsinki, were used. For assessment of the discriminatory power of the original variables and for selection of an optimal set, a stepwise procedure was employed whereby inclusion of each new variable was decided according to the overall increase it produced in the discriminatory ability of the previously selected set, and new variables were included until the information gained did not increase appreciably. Wilk's Lambda Statistics were used as test criterion. A separate analysis was carried out with the variables describing the morphology of the male genital characters and the number of palar pegs.

To check the results, the material was classified according to the discriminatory spaces of the analyses. For each individual, generalized distances were calculated to all group centroids, and classification was based on the *a posteriori* probabilities of group memberships.

After completion of the above analyses, a sample (FP) of eight males became available from France, Pyrénées Orientales, Mt. Canigou, 28.IX. 1974. The optimal set of variables for males was measured with a stereomicroscope, and although the data may be expected to be slightly biased by the different measuring method, they nevertheless allowed a preliminary comparison with the other populations.

## 3. Results

The data on general body measurements are given in Tables 1 and 2. The lists of the optimal set of variables and their relative discriminatory powers were quite similar for the two sexes. The main differences were the inclusion of the variables "hind tibia dorsal peg number", "hind femur dorsal peg number", and "fore tibia length" in the list of optimal characters for females, and the replacement of the variable "total middle leg length" in the list of male characters with "middle femur length" and "middle tarsus length" in the list of female characters. In the female list "middle femur length" was second and "middle tarsus length" eighth in importance, while in the male list "total middle leg length" was sixth. Otherwise the order of importance of the variables was the same for the two sexes. It may be concluded that the selection of the variables is repeatable to a large degree.

In both sexes the analyses disclosed clear differences between the vectors of group means, and all seven canonical variables had significant discriminatory powers. The two analyses agreed even in detail. The proportions of the variance explained by successive canonical variables were comparable, and most of the variables seemed to measure the same general characters. The group differences on canonical variables were also comparable.

The first canonical variable separated the three rock pool populations (southern Finnish, and eastern and western Swedish) from the other populations, which formed a heterogeneous group. Differences in the length of the middle leg claw mostly contributed to this separation. The second canonical variable was strongly correlated with all major dimensional measurements, and it may be regarded as a measure of general body size. As the size of adult Corixids is strongly dependent on the availability of suitable food during larval development (Jansson 1969, Pajunen 1977), the significance of size differences is difficult to assess. However, for most populations the means for this variable were close to each other, and only the Icelandic individuals were definitely smaller than the others. The third canonical variable was mainly a function of wing length and hind tibia length, and separated the Swiss population from the others. It also separated

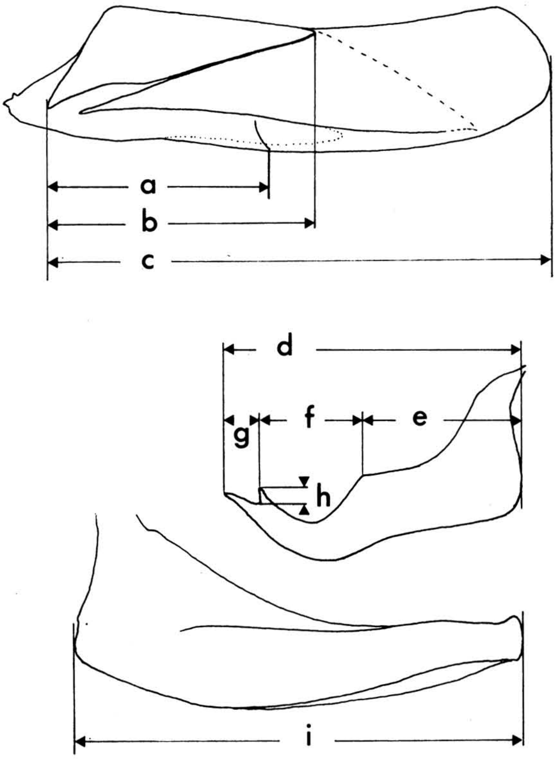

Fig. 1. Wing and genital measurements. a = nodal length, b = claval length, c = total wing length, d = total right clasper length, e = right clasper basal part, f = right clasper distal part, g = right clasper distal projection, h = right clasper proximal projection, i = left clasper total length.

Table 1. Numerical data on the most important canonical variables of wing and leg measurements of *A. carinata* males. Original variables of the optimal set, the eigenvalues ($\lambda$), their percentage contribution to the trace, and canonical correlation coefficients ($r_c$) are included. Symbols for populations: IC = Icelandic, BR = British, NF = northern Finnish, CS = central Swedish, WS = western Swedish, ES = eastern Swedish, SF = southern Finnish, and SA = Swiss.

| | Group means | | | | | | | | Canonical variable coefficients (*c*) and correlations (*r*) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | 1st | | 2nd | | 3rd | | 4th | | 5th | |
| Variables | IC | BR | NF | CS | WS | ES | SF | SA | *c* | *r* | *c* | *r* | *c* | *r* | *c* | *r* | *c* | *r* |
| Middle claw | 1.18 | 1.29 | 1.13 | 1.21 | 1.03 | 0.99 | 1.01 | 1.23 | −15.06 | −0.90 | 3.255 | −0.15 | 10.41 | 0.40 | −6.848 | −0.01 | 3.006 | 0.03 |
| Wing, total | 6.14 | 6.49 | 6.48 | 6.50 | 6.74 | 6.58 | 6.66 | 6.93 | 3.889 | 0.40 | −2.426 | −0.72 | 3.137 | 0.50 | 0.751 | 0.14 | 2.119 | −0.16 |
| Hind tarsus 1 | 2.11 | 2.37 | 2.34 | 2.39 | 2.27 | 2.24 | 2.30 | 2.38 | −7.643 | −0.23 | −13.50 | −0.84 | −14.66 | −0.01 | −8.433 | 0.05 | −5.631 | −0.39 |
| Fore tarsus | 1.00 | 1.05 | 0.99 | 1.00 | 0.99 | 0.97 | 1.01 | 1.00 | −5.618 | −0.46 | 19.85 | 0.05 | −1.654 | 0.13 | 21.74 | 0.51 | −24.23 | −0.65 |
| Hind tibia | 1.77 | 1.87 | 1.87 | 1.85 | 1.89 | 1.81 | 1.88 | 1.95 | 3.341 | 0.09 | −0.134 | −0.63 | 3.137 | 0.51 | −25.07 | −0.09 | −20.70 | −0.56 |
| Middle leg, total | 6.77 | 7.48 | 7.12 | 7.37 | 7.06 | 6.95 | 7.06 | 7.52 | −0.608 | −0.41 | −4.040 | −0.75 | −2.041 | 0.34 | 5.032 | 0.28 | 2.061 | −0.22 |
| Hind tarsus 2 | 1.00 | 1.06 | 1.07 | 1.09 | 1.01 | 1.02 | 1.05 | 1.08 | −4.603 | −0.35 | −14.41 | −0.61 | −17.09 | −0.08 | −18.75 | −0.18 | −3.741 | −0.25 |
| Hind leg, total | 6.63 | 7.13 | 7.07 | 7.12 | 7.00 | 6.86 | 7.06 | 7.30 | 1.727 | −0.12 | 6.468 | −0.80 | 7.047 | 0.27 | 6.582 | 0.03 | 3.024 | −0.44 |
| Canonical variables | | | | | | | | | | | | | | | | | | |
| 1st | | | | | | | | | | | | | | | | | | |
| Group means | −6.96 | −9.04 | −6.09 | −7.90 | −2.80 | −2.85 | −3.20 | −5.71 | $\lambda$ = 5.11 (55%) | | | | | | | | | |
| Standard deviations | 0.93 | 0.88 | 1.00 | 1.03 | 0.70 | 0.79 | 1.20 | 1.30 | $r_c$ = 0.91 | | | | | | | | | |
| 2nd | | | | | | | | | | | | | | | | | | |
| Group means | −18.84 | −22.40 | −22.71 | −23.89 | −22.10 | −22.36 | −22.21 | −24.07 | | | $\lambda$ = 2.32 (25%) | | | | | | | |
| Standard deviations | 1.03 | 1.07 | 1.03 | 0.85 | 0.81 | 1.36 | 1.01 | 0.77 | | | $r_c$ = 0.84 | | | | | | | |
| 3rd | | | | | | | | | | | | | | | | | | |
| Group means | 20.18 | 20.01 | 19.07 | 18.59 | 20.53 | 18.89 | 19.24 | 21.78 | | | | | $\lambda$ = 0.99 (11%) | | | | | |
| Standard deviations | 0.96 | 1.15 | 0.97 | 1.10 | 0.68 | 0.99 | 1.19 | 0.88 | | | | | $r_c$ = 0.71 | | | | | |
| 4th | | | | | | | | | | | | | | | | | | |
| Group means | 15.11 | 16.56 | 14.24 | 15.24 | 15.46 | 16.13 | 15.72 | 15.17 | | | | | | | $\lambda$ = 0.45 (5%) | | | |
| Standard deviations | 1.18 | 1.00 | 0.93 | 1.07 | 0.95 | 0.86 | 0.93 | 1.03 | | | | | | | $r_c$ = 0.56 | | | |
| 5th | | | | | | | | | | | | | | | | | | |
| Group means | −26.00 | −26.75 | −26.64 | −25.98 | −26.63 | −25.33 | −27.12 | −25.99 | | | | | | | | | $\lambda$ = 0.29 (3%) | |
| Standard deviations | 1.06 | 1.00 | 1.11 | 1.04 | 0.79 | 0.97 | 1.04 | 0.95 | | | | | | | | | $r_c$ = 0.47 | |
| Sample size | 50 | 50 | 50 | 46 | 50 | 43 | 50 | 50 | | | | | | | | | | |

Table 2. Numerical data on the most important canonical variables of wing and leg measurements of *A. carinata* females. Symbols for populations and explanations as in Table 1.

| | Group means | | | | | | | | Canonical variable coefficients (*c*) and correlations (*r*) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | 1st | | 2nd | | 3rd | | 4th | | 5th | |
| Variables | IC | BR | NF | CS | WS | ES | SF | SA | *c* | *r* | *c* | *r* | *c* | *r* | *c* | *r* | *c* | *r* |
| Middle claw | 1.16 | 1.28 | 1.11 | 1.24 | 1.03 | 0.98 | 1.01 | 1.21 | −12.96 | −0.92 | 3.708 | 0.00 | 4.165 | 0.27 | −1.605 | −0.01 | 6.473 | 0.22 |
| Middle femur | 3.15 | 3.51 | 3.42 | 3.50 | 3.44 | 3.34 | 3.40 | 3.60 | −1.335 | −0.27 | −7.442 | −0.78 | −0.468 | 0.31 | 0.973 | 0.18 | 0.651 | −0.01 |
| Wing, total | 6.64 | 6.96 | 6.95 | 7.08 | 7.30 | 7.01 | 7.13 | 7.45 | 3.001 | 0.16 | −0.685 | −0.63 | 1.725 | 0.51 | 0.744 | 0.20 | 2.554 | 0.17 |
| Hind tarsus 1 | 2.28 | 2.57 | 2.53 | 2.59 | 2.47 | 2.41 | 2.47 | 2.55 | −4.027 | −0.38 | −13.03 | −0.77 | −8.740 | −0.01 | −19.88 | −0.04 | −2.202 | −0.11 |
| Fore tarsus | 1.11 | 1.14 | 1.08 | 1.12 | 1.08 | 1.06 | 1.10 | 1.10 | −5.924 | −0.47 | 17.36 | 0.13 | −5.096 | 0.03 | 5.978 | 0.23 | −5.053 | −0.06 |
| Hind tibia | 1.89 | 1.99 | 2.00 | 1.98 | 2.02 | 1.93 | 2.00 | 2.10 | 3.650 | −0.08 | −1.419 | −0.59 | 15.27 | 0.60 | −28.25 | 0.02 | −9.963 | −0.14 |
| Hind tibia dorsal pegs | 7.05 | 6.32 | 7.03 | 7.10 | 7.41 | 7.30 | 7.22 | 6.71 | 0.605 | 0.53 | 0.048 | 0.04 | −0.233 | −0.19 | −0.550 | −0.28 | 0.828 | 0.32 |
| Middle tarsus | 1.15 | 1.28 | 1.20 | 1.26 | 1.22 | 1.22 | 1.23 | 1.29 | −3.000 | −0.32 | −4.253 | −0.59 | −2.815 | 0.18 | 13.78 | 0.47 | 5.103 | 0.18 |
| Hind tarsus 2 | 1.03 | 1.09 | 1.10 | 1.14 | 1.06 | 1.06 | 1.09 | 1.13 | −2.763 | −0.29 | −9.153 | −0.59 | −2.880 | 0.07 | −21.86 | −0.15 | 8.781 | 0.27 |
| Hind femur dorsal pegs | 5.60 | 4.62 | 5.12 | 5.85 | 6.01 | 6.60 | 6.44 | 5.20 | 0.226 | 0.46 | 0.079 | 0.02 | −0.202 | −0.25 | 0.003 | 0.10 | 0.396 | 0.93 |
| Fore tibia | 0.63 | 0.63 | 0.64 | 0.64 | 0.63 | 0.63 | 0.62 | 0.66 | −0.480 | −0.19 | −0.501 | −0.16 | 8.190 | 0.39 | −19.69 | −0.28 | 14.09 | 0.21 |
| Hind leg, total | 7.06 | 7.62 | 7.54 | 7.65 | 7.51 | 7.31 | 7.51 | 7.80 | −0.298 | −0.26 | 6.025 | −0.74 | −0.458 | 0.30 | 15.42 | 0.05 | −1.953 | −0.06 |
| Canonical variables | | | | | | | | | | | | | | | | | | |
| 1st | | | | | | | | | | | | | | | | | | |
| Group means | −11.33 | −14.75 | −11.22 | −13.22 | −8.34 | −8.20 | −8.72 | −11.70 | $\lambda$ = 5.05 (55%) | | | | | | | | | |
| Standard deviations | 0.79 | 0.91 | 0.88 | 0.96 | 0.95 | 1.24 | 0.92 | 1.26 | $r_c$ = 0.91 | | | | | | | | | |
| 2nd | | | | | | | | | | | | | | | | | | |
| Group means | −8.03 | −11.80 | −12.36 | −12.65 | −12.15 | −11.95 | −11.75 | −12.89 | | | $\lambda$ = 2.14 (23%) | | | | | | | |
| Standard deviations | 0.98 | 1.17 | 1.02 | 0.77 | 0.75 | 1.05 | 1.09 | 1.08 | | | $r_c$ = 0.83 | | | | | | | |
| 3rd | | | | | | | | | | | | | | | | | | |
| Group means | 11.10 | 10.35 | 10.49 | 9.81 | 11.28 | 9.83 | 10.37 | 12.65 | | | | | $\lambda$ = 0.78 (8%) | | | | | |
| Standard deviations | 0.85 | 1.05 | 1.13 | 0.86 | 0.94 | 1.04 | 0.84 | 1.21 | | | | | $r_c$ = 0.66 | | | | | |
| 4th | | | | | | | | | | | | | | | | | | |
| Group means | 0.09 | 1.48 | −1.27 | −0.17 | 0.42 | 1.00 | 0.78 | 0.55 | | | | | | | $\lambda$ = 0.63 (7%) | | | |
| Standard deviations | 1.03 | 1.21 | 0.86 | 0.81 | 0.85 | 0.79 | 1.29 | 1.01 | | | | | | | $r_c$ = 0.62 | | | |
| 5th | | | | | | | | | | | | | | | | | | |
| Group means | 15.14 | 14.24 | 14.17 | 16.05 | 14.81 | 15.32 | 14.50 | 15.26 | | | | | | | | | $\lambda$ = 0.35 (4%) | |
| Standard deviations | 1.03 | 1.04 | 0.96 | 1.07 | 0.86 | 1.02 | 0.95 | 1.06 | | | | | | | | | $r_c$ = 0.51 | |
| Sample size | 50 | 50 | 50 | 44 | 50 | 48 | 50 | 50 | | | | | | | | | | |

Table 3. Numerical data on the most important canonical variables of *A. carinata* male genital measurements and palar peg numbers. Symbols for populations and explanations as in Table 1. Abbreviation: Rc = right clasper.

| Variables | Group means | | | | | | | | Canonical variable coefficients (*c*) and correlations (*r*) | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | 1st | | 2nd | | 3rd | | 4th | |
| | IC | BR | NF | CS | WS | ES | SF | SA | *c* | *r* | *c* | *r* | *c* | *r* | *c* | *r* |
| Rc basal part | 0.388 | 0.414 | 0.410 | 0.414 | 0.428 | 0.429 | 0.435 | 0.496 | 39.04 | 0.94 | −8.341 | −0.00 | −17.53 | −0.14 | −18.83 | −0.03 |
| Rc distal part | 0.257 | 0.238 | 0.252 | 0.249 | 0.248 | 0.224 | 0.230 | 0.268 | 15.22 | 0.24 | −31.42 | −0.72 | 8.434 | 0.33 | −36.61 | −0.17 |
| Palar peg number | 33.7 | 32.6 | 35.1 | 36.7 | 37.3 | 35.5 | 37.3 | 36.6 | 0.084 | 0.43 | 0.252 | 0.41 | 0.482 | 0.78 | 0.100 | 0.12 |
| Rc proximal projection | 0.026 | 0.030 | 0.028 | 0.028 | 0.028 | 0.044 | 0.040 | 0.034 | 30.63 | 0.29 | 67.47 | 0.64 | −51.66 | −0.40 | 33.67 | 0.29 |
| Rc distal projection | 0.103 | 0.104 | 0.088 | 0.100 | 0.117 | 0.118 | 0.119 | 0.107 | 8.731 | 0.21 | 32.72 | 0.64 | −0.488 | −0.05 | −68.89 | −0.67 |
| Left clasper, total | 1.097 | 1.099 | 1.141 | 1.138 | 1.160 | 1.158 | 1.161 | 1.316 | 12.54 | 0.93 | −1.885 | −0.14 | 2.547 | 0.06 | 12.00 | 0.09 |
| Canonical variables | | | | | | | | | | | | | | | | |
| 1st | | | | | | | | | | | | | | | | |
| Group means | 37.36 | 38.11 | 38.73 | 39.00 | 40.03 | 40.04 | 40.43 | 44.99 | $\lambda$ = 4.99 (68%) | | | | | | | |
| Standard deviations | 1.06 | 0.86 | 1.12 | 0.94 | 0.93 | 0.91 | 0.87 | 1.24 | $r_c$ = 0.91 | | | | | | | |
| 2nd | | | | | | | | | | | | | | | | |
| Group means | 0.23 | 0.58 | 0.09 | 0.99 | 1.58 | 2.99 | 2.93 | −0.02 | | | $\lambda$ = 1.30 (18%) | | | | | |
| Standard deviations | 0.97 | 0.95 | 0.99 | 1.03 | 0.88 | 0.99 | 1.16 | 1.01 | | | $r_c$ = 0.75 | | | | | |
| 3rd | | | | | | | | | | | | | | | | |
| Group means | 12.95 | 11.67 | 13.25 | 13.93 | 14.02 | 12.08 | 13.15 | 12.70 | | | | | $\lambda$ = 0.59 (8%) | | | |
| Standard deviations | 0.86 | 0.78 | 1.08 | 0.84 | 0.90 | 1.27 | 1.09 | 1.11 | | | | | $r_c$ = 0.61 | | | |
| 4th | | | | | | | | | | | | | | | | |
| Group means | −6.41 | −6.20 | −4.87 | −5.50 | −6.62 | −5.49 | −5.85 | −5.96 | | | | | | | $\lambda$ = 0.29 (4%) | |
| Standard deviations | 0.97 | 0.94 | 0.98 | 0.97 | 1.08 | 0.90 | 0.88 | 1.21 | | | | | | | $r_c$ = 0.47 | |
| Sample size | 50 | 50 | 50 | 46 | 50 | 43 | 50 | 50 | | | | | | | | |

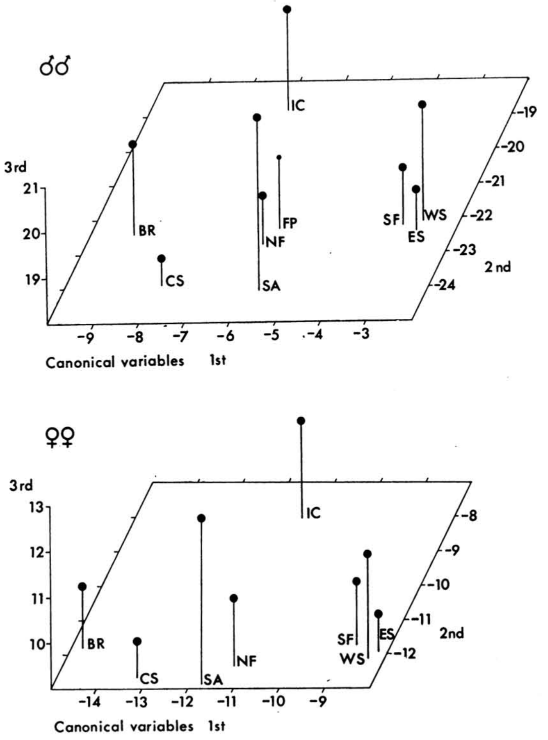

Fig. 2. Group means for the three most significant canonical variables of the *A. carinata* populations in the analyses of wing and leg measurements. Symbols for populations: IC = Icelandic, BR = British, NF = northern Finnish, CS = central Swedish, WS = western Swedish, ES = eastern Swedish, SF = southern Finnish, SA = Swiss Alpine. For males the small Pyrenean sample (FP) is also indicated.

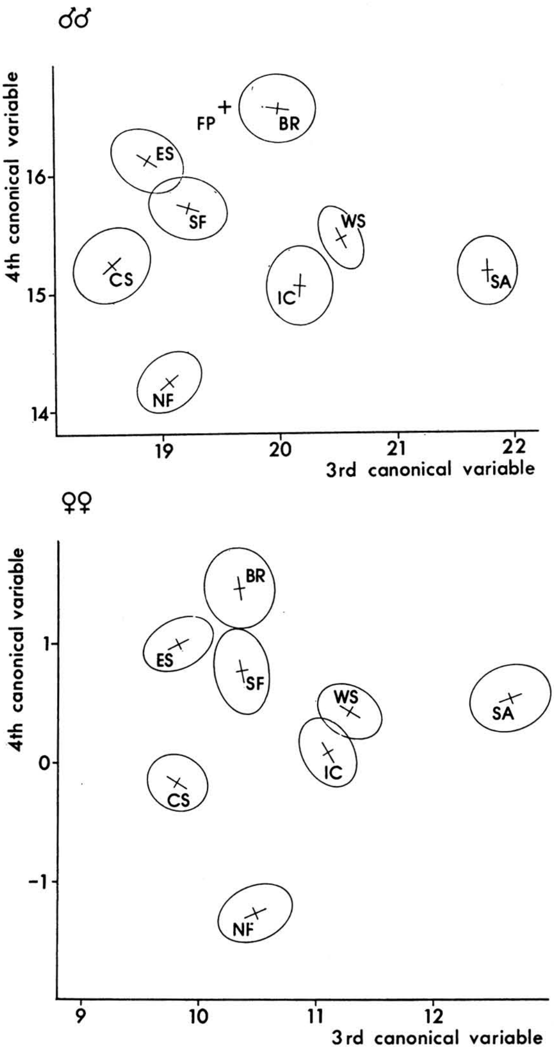

Fig. 3 (right). Group means for the third and fourth canonical variables of the *A. carinata* populations in the analyses of wing and leg measurements, with 90 % equiprobability ellipses of the mean values. Symbols for populations as in Fig. 2.

the western Swedish population from the two other rock pool populations. The fourth canonical variable described the polarity between tibia and tarsus 1 of the hind leg, and total length of the hind leg. This function separated the northern Finnish and central Swedish populations from the others, among which the British population represented an extreme type. The last canonical variables were different compound characters in the two analyses, and their discriminatory powers were small. Fig. 2 shows projections of group means on the three most significant canonical variables, and Fig. 3 the same for the third and fourth canonical variables.

Results of the analysis of the male genital characters and of palar peg number are given in Table 3, and Fig. 4 shows projections of group means on the three most significant canonical variables. Of the original variables the total length of the right paramere was not included in the optimal set. Tests of equality of the group means showed highly significant differences, and the first five canonical variables had highly significant discriminatory ability. The first canonical variable represented mainly size of genitalia (thus being comparable with the second canonical variable of the first

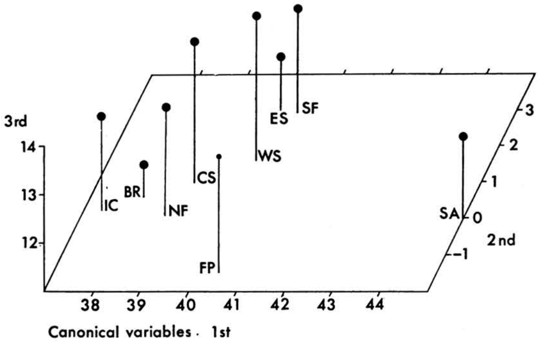

Fig. 4. Group means for the three most significant canonical variables of the *A. carinata* populations in the analysis of male genital measurements and palar peg numbers. Symbols for populations as in Fig. 2.

analyses), and separated the Swiss population very clearly as a distinct unit. Of the others the rock pool populations, and the northern Finnish and central Swedish populations formed two clear sets, while the Icelandic and British populations remained somewhat apart from each other. Great differences between the populations in size of genitalia were also evident when the length of the left paramere was plotted against wing length. A common linear relation existed between the two variables for most populations, but the relative paramere lengths were somewhat smaller in the British males and much greater in the Swiss males.

The second canonical variable described the form of the tip of the right paramere, the number of palar pegs being a contributory factor. The rock pool populations were again separated from the others, but within this set the western Swedish population was further separated from the other two rock pool populations. The third canonical variable was a function of number of palar pegs and separated the western Swedish and central Swedish populations from the others. The fourth canonical variable was correlated with the length of the distal projection of the right paramere. It explained only 4 % of the variance, but functioned as an additional factor in separating the western Swedish population from the two other rock pool populations.

Result of the classification of the populations according to the discriminatory spaces in the analyses are given in Table 4. In all cases most individuals were placed in the right population, which indicates that the populations are phenetically distinct. Occasional misplaced individuals were mostly specimens of atypical size, and only between the rock pool populations were misclassifications apt to occur for other reasons also.

Table 4. Classification of the *A. carinata* individuals. Symbols for populations as in Table 1.

| Origin of individuals | | Number of individuals placed in IC | BR | NF | CS | WS | ES | SF | SA |
|---|---|---|---|---|---|---|---|---|---|
| ♂♂ | IC | 48 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| | BR | 0 | 46 | 1 | 3 | 0 | 0 | 0 | 0 |
| | NF | 0 | 0 | 42 | 3 | 0 | 0 | 2 | 3 |
| | CS | 0 | 3 | 6 | 36 | 0 | 0 | 1 | 0 |
| | WS | 0 | 0 | 0 | 0 | 42 | 3 | 5 | 0 |
| | ES | 0 | 0 | 0 | 0 | 3 | 34 | 6 | 0 |
| | SF | 0 | 0 | 2 | 0 | 9 | 7 | 32 | 0 |
| | SA | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 46 |
| ♀♀ | IC | 48 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| | BR | 0 | 49 | 0 | 0 | 0 | 0 | 0 | 1 |
| | NF | 0 | 0 | 47 | 0 | 0 | 0 | 1 | 2 |
| | CS | 0 | 1 | 0 | 42 | 0 | 1 | 0 | 0 |
| | WS | 1 | 0 | 0 | 0 | 39 | 4 | 6 | 0 |
| | ES | 0 | 0 | 0 | 1 | 5 | 37 | 5 | 0 |
| | SF | 1 | 0 | 1 | 0 | 1 | 5 | 42 | 0 |
| | SA | 0 | 1 | 3 | 1 | 1 | 0 | 1 | 43 |

*Characters of the Pyrenean specimens*

Since the Pyrenean sample included only eight males, only preliminary comparison with the other populations was attempted. Values of the canonical variables were calculated from the sample mean vectors and coefficients of Tables 1 and 3. Results with means of the original variables are shown in Table 5, and the sample means are also placed in Figs. 2—4. On the basis of the wing and leg measurements the population clearly seemed to have affinities with the Swiss, northern Finnish, central Swedish and British populations. The less important canonical variables, however, showed the sample to be a separate unit. In the genital characters the first canonical variable placed the sample as an average type, differing clearly from the Swiss population. The second canonical variable separated the sample most clearly in the direction opposite to the rock pool populations.

## 4. Discussion

The geographic areas inhabited by *A. carinata* are rather different from each other. Ecologically they can be grouped as follows:

Table 5. Numerical data on the Pyrenean sample of *A. carinata*. Abbreviation Rc. = right clasper.

| Wing and leg measurements | $\bar{x}$ ±SD |
|---|---|
| Middle claw | 1.15 ±0.05 |
| Wing, total | 6.54 ±0.16 |
| Hind tarsus 1 | 2.27 ±0.09 |
| Fore tarsus | 0.98 ±0.02 |
| Hind tibia | 1.75 ±0.04 |
| Middle leg, total | 7.03 ±0.14 |
| Hind tarsus 2 | 1.02 ±0.05 |
| Hind leg, total | 6.85 ±0.18 |
| Canonical variables | |
| 1st | −5.91 |
| 2nd | −22.32 |
| 3rd | 19.56 |
| 4th | 16.57 |
| 5th | −24.15 |

| Measurements of genitalia and palar pegs | $\bar{x}$ ±SD |
|---|---|
| Rc. basal part | 0.422 ±0.019 |
| Rc. distal part | 0.290 ±0.020 |
| Palar peg number | 34.75 ±1.84 |
| Rc. proximal projection | 0.027 ±0.004 |
| Rc. distal projection | 0.086 ±0.018 |
| Left clasper, total | 1.200 ±0.024 |
| Canonical variables | |
| 1st | 40.43 |
| 2nd | −1.51 |
| 3rd | 13.44 |
| 4th | −5.71 |

— The Icelandic and British populations live in areas strongly influenced by the Atlantic Ocean, the former in a variety of water bodies, the latter mainly in peat pools. The summer season is long, but temperatures are relatively low. The pools are often deep, with plenty of soft bottom sediment.

— The northern Finnish and central Swedish populations live in arctic conditions where the summer is short and cold. The water bodies inhabited are usually large and deep, with varying amounts of bottom sediment. Local populations are often short-lived, since the summer is barely long enough for larval development and the winter kills large proportions of the overwintering adults.

— At high altitudes in the Pyrenees and Alps the conditions closely resemble those of the arctic areas. However, the species also occupies pools at somewhat lower altitudes, and dispersal from these would quickly restore local populations which became extinct at higher altitudes.

— The rock pool populations live in an environment very different from all other habitats. The summer season is relatively long, and in small pools the temperature may fluctuate widely, with daily maxima frequently exceeding 30°C. The high temperature allows very rapid development of larvae, and a partial second generation is produced. The breeding pools are more or less temporary, thus necessitating strong ability for dispersal. There is a seasonal change of habitat, for the adults overwinter in deeper ponds (Pajunen & Jansson 1969, Pajunen 1972, 1977).

In the multivariate analysis of wing and leg measurements the first two canonical variables, explaining about 80 % of the total variation, separated the populations into sets which corresponded to the ecological grouping. Thus, the analysis seemed to indicate adaptation of the populations to their environments. The most distinct entity comprised the three rock pool populations. A somewhat less homogeneous, but nevertheless clearly recognizable group was formed by the arcto-alpine populations, including the northern Finnish, central Swedish, and Swiss populations. The small Pyrenean sample also clearly belonged to this group. The Icelandic and British populations fell outside the two groups as two separate units. The most important character in the grouping was the length of the middle claw. A short claw may be an adaptation to a hard bottom and a thin layer of soft detritus in the rock pools. In other habitats, where the depths are greater, aquatic vegetation may be present and the bottom is covered with a thick layer of detritus; here a longer claw may be advantageous for grasping supports. *A. germari* (Fieber), a species very closely related to *A. carinata*, inhabits larger and deeper water bodies (Weber 1965), and possesses long claws. The length of the claw has been used as a diagnostic character in separating the larvae of the two species (Jansson 1969).

The second canonical variable, measuring general body size, may reflect only the availability and abundance of suitable food. In Iceland, on the other hand, *A. carinata* is the only Corixid species and occupies a wide variety of habitats, and this may be linked with the small size of the individuals.

The third and fourth canonical variables are more difficult to connect with environmental factors. Increase in length of hind tibia with increasing body length, as indicated by the third variable, might be connected with use of the hind legs in ventilation and cleaning of the abdomen, but possible adaptive value for faster swimming could also be considered. The two variables seem to group the populations in a way which might correspond to their geographic origin. The third variable indicates a marked heterogeneity within the set of rock pool populations, and also very effectively separates the Swiss population from all the others. The fourth variable further separates the northern Finnish and central Swedish populations from the others, and also the small Pyrenean sample from the other arcto-alpine populations.

Heterogeneity of the ecological grouping was further supported by multivariate analysis of the male genital characters. Variation between the populations showed an obvious geographic pattern. Size of genitalia separated the populations along a southeast-northwest axis, and structure of the tip of the right paramere roughly along a southwest-northeast axis. The third and fourth canonical variables further contributed to the separation of members of the ecological groups. The western Swedish population was separated from the other two rock pool populations towards the northern Finnish and central Swedish populations, but it also seemed to have affinities with the Icelandic population, from which the main separating factors were differences in size. Both the Swiss and the Pyrenean populations appeared as distinct units, but differed from the other populations in the same direction. In general, the results of the canonical variable analysis conform very well with the results obtained in crossbreeding experiments between the same populations (JANSSON 1978b).

The distribution of *A. carinata* in Fennoscandia is largely the result of a northward invasion of the species during and after the Late Glacial period. LINDBERG (1944) suggested that the species dispersed rapidly and inhabited any temporary water bodies that were available. Gradual land upheaval in connection with vegetational changes then destroyed suitable inland habitats, and the coastal populations became separated from the more northern populations. The rock pool environment probably resembles the type of temporary habitat available during the Late Glacial period, and requires adaptations similar to those which were then necessary for efficient colonization: sufficient ability to disperse, high reproductive capacity, and a behavioural repertoire adequate for coping with the rapidly fluctuating size of the temporary environment (PAJUNEN & JANSSON 1969, PAJUNEN 1972, 1977). Thus, the coastal populations can be regarded as extant fragments of the Late Glacial fauna (BRINCK 1966).

Deduction of common ancestry from phenetic similarities is always hazardous, but differences persisting in spite of overall similarities imposed by similarities of the environment probably indicate less close kinship. The three rock pool populations apparently form a heterogeneous group. Eastern Swedish and southern Finnish populations appeared to be very similar, as was also indicated by crossbreeding experiments (JANSSON 1978b): the largest stretch of open water, some 30 km between the two countries, does not seem to act as a geographic barrier to *A. carinata*. Between the eastern and western Swedish populations, on the other hand, there is a clear distributional gap, as the species has not been found in southern Sweden (OSSIANNILSSON 1946, BERGGREN 1971, COULIANOS & OSSIANNILSSON 1976). Both crossbreeding experiments and morphometric differences between the rock pool populations indicate that the Swedish west coast and the Baltic areas may have been colonized separately and from different sources.

According to JANSSON (1978b), the southern Finnish and eastern Swedish populations are closely related to the northern Finnish and central Swedish populations. The canonical variable analysis, on the other hand, indicated affinities between the western Swedish and central Swedish populations. Thus, the present-day distribution of the species in northern Fennoscandia may be a result of mixing of populations originating from two different sources, one having a common origin with the western Swedish, the other with the southern Finnish and eastern Swedish populations.

Analyses of wing and leg measurements united the Swiss (and Pyrenean) population(s) with the northern Finnish and central Swedish populations into an arcto-alpine group. The grouping was purely ecological, however, since the genital characters broke it up completely. The southern montane populations are glacial relicts, and have been isolated from the northern populations since the last glaciation. In crossbreeding experiments with the northern populations the Swiss population was found not to produce viable progeny (JANSSON 1978b), and it is thus not surprising that the populations were also clearly separated by the canonical variable analysis.

BROWN (1944) drew attention to the scarcity of Corixids in the Faroe Islands in spite of apparent suitability of habitats for several species common in Britain. He suggested that *A. carinata* in the Faroe Islands, as well as in Iceland, is a survival from adverse periods when most other species were exterminated, i.e. a species which has survived in the glacial refuges. Unfortunately we had no specimens from the Faroes, and lack of other species is probably a significant ecological factor affecting the Icelandic population and possibly interfering with the morphometric comparison. However, the Icelandic and British populations differed in many respects from all the other populations and in the same direction, thus indicating relatively close kinship between the two, and discouraging the theory that the species survived in refuges in Iceland during the last glaciation.

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