

## Viability of progeny in experimental crosses between geographically isolated populations of *Arctocoris carinata* (C. Sahlberg) (Heteroptera, Corixidae)

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JANSSEN, A. 1978: Viability of progeny in experimental crosses between geographically isolated populations of *Arctocoris carinata* (C. Sahlberg) (Heteroptera, Corixidae). — Ann. Zool. Fennici 15:77—83.

Crossbreeding experiments between eight geographically more or less isolated populations of *Arctocoris carinata* indicated that the populations of Lapland and the Scandinavian Range are rather closely related to the coastal populations of southern Finland and eastern Sweden. The population of the Swedish west coast, in contrast, seems to be genetically remote from the other Fennoscandian populations, and may have had more recent connections with the British population. Both the British and Icelandic populations seemed rather distant from the population of southern Finland. The most drastically different of the populations tested, however, was the population of the Swiss Alps, which, when crossed with the populations of Iceland and southern Finland, produced mainly inviable larvae.

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### 1. Introduction

Among the theories of speciation the most widely accepted is that known as allopatric speciation, whereby new species are thought to evolve through geographic isolation of populations. During the period of isolation the populations may acquire characteristics which prevent crossbreeding if the barriers disappear.

In Europe the Corixid *Arctocoris carinata* inhabits water bodies at high altitudes, in arctic regions, and in certain coastal areas. Its range is split into several well-isolated areas (Fig. 1): Iceland, the Faroe Islands, the northern parts of the British Isles, Lapland and the Scandinavian Range, the Swedish W and E coasts, the Finnish SW coast, the Pyrenees, and the Alps (POISSON 1935, 1957, BROWN 1944, LINDBERG 1944, FRISTRUP 1945, OSSIANNILSSON 1946, STICHEL 1955, MACAN 1956, SOUTHWOOD & LESTON 1959). The species has also been reported from the Caucasus Mountains (POISSON 1935, STICHEL 1955, WEBER 1965) but, according to ŠTYS (1975), these records probably concern a related species, *A. armeniaca*

ŠTYS. STICHEL (1955) also reported *A. carinata* from Kamchatka, but further studies are needed to confirm these records.

The patchy distribution of *A. carinata* in Europe is clearly a result of climatic and related changes that have occurred since the last glaciation, and the populations existing today must have been isolated from each other for several thousands of years. Yet only the population occurring in the Pyrenean Range has been described as a separate subspecies, *A. carinata pyrenaica* Poisson (POISSON 1957), on account of morphological characteristics. JANSSEN (1978), however, has shown that the characteristics on which the subspecies *pyrenaica* was separated from the nominate form are within the limits of the variation found in all populations and do not justify ranking of the Pyrenean population as a distinct subspecies.

To investigate the effects of the long isolation on populations of *A. carinata*, live specimens were brought to the laboratory from several localities. The present paper concerns the genetic differentiation reflected by crossbreeding experiments between some of the populations.

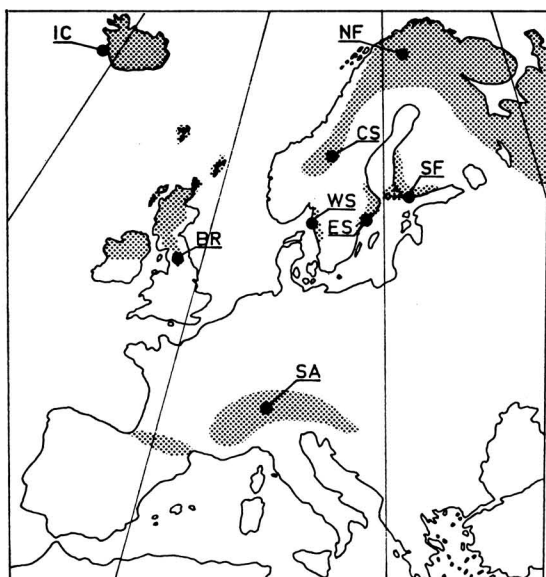


Fig. 1. Distribution of *A. carinata* in Europe. Dots indicate localities sampled (see text).

## 2. Material and methods

The populations used in the experiments were as follows (abbreviations used in the text are given in parentheses): Icelandic (IC), British (BR), northern Finnish or Lappish (NF), central Swedish (CS), western Swedish (WS), eastern Swedish (ES), southern Finnish (SF), and Swiss Alpine (SA) (Fig. 1). Exact collecting localities were:

IC: Iceland, Gullbringusýsla, Hafnarfjörður, 21. IX.1972.

BR: England, Westmorland, Dufton Fell (national grid ref. 35/728275), 5.X.1973.

NF: Finland, Enontekiö, Sarvisoiavi (grid 27°E 763:30), 21. IX. 1975.

CS: Sweden, Härjedalen, Saxvallbygget, 18.IX.1975.

WS: Sweden, Bohuslän, Skaftö, Kristineberg Zoological Station, Island of Långö, 28.VIII.1973.

ES: Sweden, Södermanland, Askö, Askölaboratoriet, Island of Persö, 17.IX.1975.

SF: Finland, Hanko, Tvärminne Zoological Station, the islands Brännskär and Långskär (grid 27°E 664:29), 5.X.1972, 15.X.1973, and 15.X.1975.

SA: Switzerland, Canton Graubünden, Lenzerheide, 18.VIII.1972.

Like most species of Corixidae, *A. carinata* overwinters as the adult, breeding the following spring and early summer (PAJUNEN & JANSSON 1969a, 1969b, PAJUNEN 1972, 1977). The specimens for the present study were collected in late summer and early autumn, too late for immediate crossbreeding experiments. For overwintering, the bugs were placed in plastic vessels (24 × 15 × 10 cm, with about 3 l of water), males and females separately, and kept for 1–3 months in constant

temperature cabinets at 5°C and a photoperiod of 8 hrs light and 16 hrs dark. When transferred to 20°C and a reversed photoperiod the bugs showed sexual activity in less than a week, and in about 2 weeks the females began to lay eggs. Under these conditions the bugs reproduced continuously and, for instance, during winter 1972–73 the Icelandic population produced five successive generations.

In the cultures both adults and larvae were fed on freezer-stored Chironomid larvae. At 20°C the bugs were fed daily, but at 5°C weekly feeding was considered adequate. Excess food was removed every now and then, and bacterial growth on the water surface was prevented by continuous ventilation from aquarium ventilators.

The culture vessels were provided with pieces of rock and moss: *A. carinata* females lay their eggs in small crevices in the rocks, or between leaves of mosses. Because the species is an active predator as both larva and adult, and will eat its own eggs and younger larvae, the substrate provided for egg-laying was transferred to other vessels daily. When the first developing larvae reached the third instar, no more eggs were transferred to these vessels, and the parental culture was also terminated.

On reaching the adult stage, the insects were sexed daily and males and females were transferred to separate vessels. In this way they were prevented from mating, and could be used for further experiments.

As some of the populations were sampled in 1972, and others in 1973 or 1975, not all combinations could be tested. In all breeding experiments the P generation consisted of 5 males and 5 females. Fertility of the F<sub>1</sub> generation was tested in backcrosses arranged like the original crosses except that the number of F<sub>1</sub> individuals available was often less than in the original set (cf. Table 1). If the number of F<sub>1</sub> individuals exceeded 10 males and 10 females, the individuals used in the backcrosses were taken at random and the excess specimens were not used.

As a basis for comparison of the success of the crosses, simultaneous intrapopulation cultures were set up as controls. Specimens for backcrosses were obtained both from the control cultures and by keeping some of the original specimens at 5°C until needed (up to 6 months).

## 3. Results

Crossbreeding experiments between the populations were arranged in three groups, I: IC, SF and SA (winter 1972–73), II: BR, WS and SF (winter 1973–74) and III: NF, CS, ES and SF (winter 1975–76). The populations tested in group I were all geographically far from each other, in group II they were much closer, and in group III only two populations were actually geographically isolated, but two rather distantly situated localities from each of these were tested (cf. Fig. 1). The only population that could be tested with all other populations was the nearby SF population. Results of the experiments are shown in Table 1, and discussed in detail below.

Table 1. Progeny from crosses between different *A. carinata* populations. IC = Icelandic, BR = British, NF = northern Finnish, CS = central Swedish, WS = western Swedish, ES = eastern Swedish, SF = southern Finnish, and SA = Swiss Alpine population. A and B = P generation male and female populations, respectively; e = eggs laid, but no larvae observed; ne = no eggs observed; V = larvae observed up to the fifth instar, but no adults emerged; — = not tested; numbers in parentheses indicate repeated tests.

Group	P generation	F <sub>1</sub>	Number of individuals (♂♂/♀♀) obtained in backcrosses			
	A × B 5 ♂♂ × 5 ♀♀	♂♂/♀♀	F <sub>1</sub> ♂♂ with A ♀♀ B ♀♀		F <sub>1</sub> ♀♀ with A ♂♂ B ♂♂	
I	IC × SF	9/5	4/3	—	1/0	0/1
	SF × IC	3/5	—	2/6	4/5	0/1
	SA × IC (1)	2/1	—	1/1	—	—
	SA × IC (2)	0/1	—	—	—	ne
	SA × SF (1)	0/1	—	—	—	V
	SA × SF (2)	V	—	—	—	—
II	BR × WS	8/9	1/7	e	2/4	4/1
	BR × SF	7/4	3/3	4/8	e	3/3
	WS × BR	5/6	4/2	2/0	4/4	2/4
	WS × SF	0/1	—	—	—	3/4
	SF × BR	8/8	1/1	0/4	2/4	3/2
	SF × WS (1)	0/3	—	—	e	ne
	SF × WS (2)	1/2	—	—	—	—
III	NF × ES	15/18	3/3	19/18	17/15	18/16
	NF × SF	11/8	6/13	4/5	V	11/14
	CS × NF	12/13	—	14/12	—	10/4
	CS × ES	14/25	—	13/20	16/16	17/14
	CS × SF	24/24	—	24/13	26/21	8/8
	ES × NF	24/16	14/17	14/7	15/16	6/10
	ES × CS	15/6	21/9	—	12/6	—
	ES × SF	21/36	21/20	27/33	28/23	23/22
	SF × NF	17/15	11/8	18/15	15/27	17/18
	SF × CS	8/11	24/8	—	20/11	—
	SF × ES	20/15	16/24	17/18	14/9	16/18

### Group I

Crosses between the IC and SF populations gave meagre results in the F<sub>1</sub> generation. Backcrosses seemed to do well in the beginning, with plenty of larvae hatching from the eggs laid in every combination tested. However, by the time the insects reached the adult stage, their number had decreased to a single specimen in three of the cultures, and in the other vessels to fewer than 10.

About half of the SA specimens were collected as fifth instar larvae and they suffered high mortality during transportation from Switzerland. During the overwintering period mortality was also high, particularly among the females, which generally reach the adult stage somewhat

later than the males in Corixidae (cf. PAJUNEN & JANSSON 1969a, JANSSON & SCUDDER 1974), and had thus had no time for developing the fat body necessary for overwintering. Therefore, no experiments could be arranged with SA females.

Somewhat unexpectedly, a fair number of SA males survived in the overwintering conditions, and crosses were possible with both IC and SF females. In both cultures large numbers of larvae hatched out, but most of them died before reaching the third instar, and altogether only four adults were obtained. The only female from the cross SA × IC died on the third day after emergence, but the two males survived long enough for further tests. The backcross with IC females gave a fair number of first instar larvae, but again most of these died before reaching the third instar, and only one male and one female emerged as adults. These two were left together in their vessel, and lived for nearly 2 months, but produced no offspring. The cross of SA × SF gave only one adult, a female. This was backcrossed to SF males, but none of the offspring reached the adult stage. In this backcross also, mortality was highest in larvae of the second instar, and only two larvae reached the fifth instar before dying.

Both SA × SF and SA × IC experiments were repeated, but again with meagre results (Table 1), and again the larvae died mainly in the second instar. In the former cross none of the progeny reached the adult stage, and in the latter cross one adult female was obtained. When backcrossed to IC males, this female was not observed to lay any eggs.

### Group II

Crosses between BR and WS or BR and SF gave slightly more promising results than those between the more distant populations. However, in two of the backcross combinations (BR-WS males with WS females and BR males with BR-SF females), no larvae hatched from the eggs laid, and in the other backcrosses the scores were also meagre.

More surprisingly, however, the offspring of crosses between the two rock pool populations (WS and SF) were also poorly viable. In the cross WS × SF no one stage of larval development was particularly fatal, but an initially good number of larvae simply decreased

throughout the experiment and only one female specimen reached the adult stage. This female was backcrossed to SF males and the result, seven adults, was about "normal" as compared with progenies of other backcrosses made that year.

The reverse cross, SF  $\times$  WS, gave three adult females. No stage was particularly fatal in this culture either, but larval development was unusually slow. Ordinarily the first adults emerge about 6 weeks after the first larvae appear in the vessels, but in this case more than 11 weeks elapsed before any adults were obtained. In the backcross of two of the females with SF males no larvae hatched from the few eggs laid, and the remaining female, when backcrossed with WS males, was not observed even to lay any eggs.

The original experiment (SF  $\times$  WS) was repeated, and again only three adults were obtained. Unfortunately these could not be tested further because larval development was again delayed, and the specimens emerged late in spring when the cultures had to be discontinued for the summer.

### Group III

In this group the results of all combinations were clearly better than in any of the previous experiments, and only two cultures (NF  $\times$  SF and SF  $\times$  CS) produced fewer than 20 individuals. In the cross SF  $\times$  CS no larval stage was observed to be particularly difficult, but in the NF  $\times$  SF a high proportion of specimens seemed to die as fifth instar larvae or recently emerged adults. Further, although in general backcrosses in group III produced fair numbers of offspring, the backcross of NF-SF females with NF males gave no adults. In this experiment no particularly difficult stage for the larvae was observed, but their number decreased throughout the experiment, the last five dying in the fifth instar.

In two other backcrosses that gave fewer than 10 offspring, the NF population was also involved: NF-ES males with NF females, and NF-SF males with SF females.

### Control experiments

In the control experiments arranged for comparison of the success of the crossbreeding experiments the F<sub>1</sub> generation on average comprised some 35 adults, and in the F<sub>2</sub> generation

Table 2. Progeny in control cultures of the various *A. carinata* populations (5 ♂♂ and 5 ♀♀ in both original and F<sub>1</sub> cultures). Explanations as in Table 1.

Population	F <sub>1</sub> (♂ ♂ / ♀ ♀)	F <sub>2</sub> (♂ ♂ / ♀ ♀)
IC	11/18	16/18
BR	11/12	—
NF (1)	16/26	14/11
NF (2)	19/19	13/16
CS	24/19	18/24
WS	11/9	—
ES (1)	12/16	12/18
ES (2)	18/24	—
SF (1)	22/17	15/10
SF (2)	23/28	16/26
$\bar{x}$	35.5	32.9
SD	9.97	7.08

(counted in only 7 cultures) the score was about 33 adults (Table 2). In addition, attempts were made to culture the SA population, but the score was only nine adults. Since the meagre result was obviously due to the early collecting time, which caused difficulties in the "overwintering" of females, the result is not comparable with the other data and is not included in the calculations. Similar difficulties were also experienced in the first attempts to culture the NF and CS populations in 1972 and 1973, respectively. In both these attempts the populations were sampled in late August, and the numerous fifth instar larvae in the samples suffered high mortality during transport. Further, overwintering of adults in the laboratory failed almost totally, and the populations could not be included in the tests carried out during the winters of 1972 and 1973. In 1975 both populations were sampled later in the season, and no difficulties were experienced in overwintering or control cultures.

In the cultures which produced numerous offspring, older larvae preyed on younger ones even though amply provided with Chironomid larvae. When the number of fifth instar larvae reached about 30–40 individuals, the younger larvae suddenly disappeared, and all remaining specimens emerged as adults within about a week. In contrast, in cultures with small numbers of larvae the youngest ones were often at the third instar when the first adults emerged, and in such cases more than 3 weeks elapsed between the emergence of the first and last adults.

#### 4. Discussion

In the rock pool habitats of the archipelagoes of southern Finland and eastern and western Sweden, *A. carinata* often reaches very high population densities (cf. PAJUNEN 1977). In other parts of its range the species inhabits larger, more permanent water bodies. No estimates exist for population densities in these biotopes, but frequently the collection of sufficient material for the present study required considerable effort, which indicates that population densities were rather low. In the laboratory cultures the average number of offspring obtained in the control experiments, some 35 adults per vessel, would be equivalent to almost 1000 individuals/m<sup>2</sup>. This is more than six times as much as the highest estimate for fifth instar larvae in rock pools (PAJUNEN 1977), and even higher when compared to densities in larger ponds. Yet the results of the control cultures, if grouped according to type of habitat, give no reason to believe that the size of the original water body affected the scores: On average, the F<sub>1</sub> generation comprised 36 offspring for the rock pool populations, and 35 for the others (the Swiss population excluded).

In rock pools the numbers of individuals reaching the adult stage are limited mainly by food shortage and cannibalism (PAJUNEN 1977). In the laboratory cultures these factors were counteracted by abundant feeding, and the effect of cannibalism was not significant until the number of fifth instar larvae reached 30–40 individuals per vessel. According to PAJUNEN (pers. comm.), in rock pools the population level can also be boosted high above natural levels by artificial feeding.

According to earlier experience of rearing various Corixidae, *A. carinata* is one of the easiest species to culture in the laboratory (cf. JANSSEN 1969, JANSSEN & SCUDDER 1972, PAJUNEN & SUNDBÄCK 1973, PAJUNEN 1975). Thus, the control cultures can be considered representative of breeding under the steady conditions prevailing, and the results of the crossbreeding experiments can be compared with them.

Of the 56 possible combinations between the eight populations, only 21 were tested. In Fig. 2 the results are expressed as a function of the distance between the sampling localities, and it is seen that in general within distances

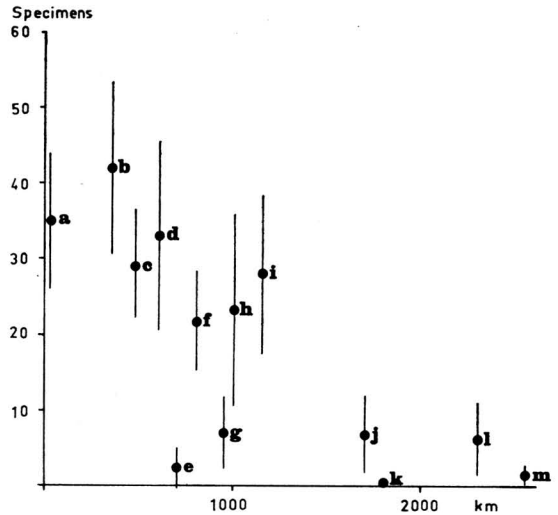


Fig. 2. Success of crosses and backcrosses ( $\bar{x} \pm SD$ ) between the various *A. carinata* populations as a function of distance between the sampling localities. a = control cultures, b = ES & SF, c = CS & ES, d = CS & SF, e = WS & SF, f = NF & CS, g = BR & WS, h = NF & SF, i = NF & ES, j = BR & SF, k = SF & SA, l = IC & SF, m = IC & SA.

of less than about 1200 km the crosses were successful, but for greater distances the results were meagre. Exceptions to this general trend were that the western Swedish population gave very poor results in crosses with the southern Finnish population and only slightly better with the British population, although the respective distances were only some 700 and 950 km.

Success in the crossbreeding experiments can be considered to express genetic closeness of the populations. Since the different combinations gave very different scores, it can be inferred that during geographic isolation the populations have evolved in different directions. In the north, the northern Finnish and central Swedish populations bred rather well with the eastern Swedish and southern Finnish populations, thus indicating that the populations of Lapland and the Scandinavian Range have apparently had fairly recent connections with the coastal populations of southern Finland and eastern Sweden. The populations of Iceland, Britain, and the Swedish west coast, on the other hand, gave poor results when crossed with the southern Finnish population. Unfortunately no crosses could be made between the Icelandic and



British populations, because specimens were not obtained during the same year, and thus nothing can be said about possible connections between the two. However, the observation that the Swedish west coast population gave slightly better results with the British population than with the southern Finnish population indicates that the western Swedish population may have had more recent connections with the British than with the other Fennoscandian populations.

The Swiss population, in repeated tests, gave practically no viable offspring with either the Icelandic or the southern Finnish populations. In contrast to all other crosses, the larvae suffered very high mortality at the second instar. This result is particularly interesting because under the same conditions *A. carinata* produces viable and fertile hybrids with the related *A. germari* (Fieber) (JANSSON, in preparation). The inference is that although there are no obvious morphological differences between the Alpine and the northern populations

of *A. carinata*, the Alpine population has acquired characteristics which function effectively as a postzygotic isolating mechanism that would prevent crossbreeding with the northern populations if the ranges were once again to overlap. Thus, according to the biological species concept, the Alpine population is approaching the point at which it could be considered a separate species.

*Acknowledgements.* I wish to express my sincere gratitude to the following colleagues for invaluable help during my collecting trips to the various countries: Dr. A. R. HILL (Glasgow, Scotland), Dr. A. INGOLFSSON (Reykjavik, Iceland), Dr. B.-O. JANSSON (Askölaboratoriet, Sweden), Dr. T. T. MACAN (Windermere, England), Dr. C. SPEICH (Zürich, Switzerland), and the late Dr. B. SWEDMARK (Kristineberg Zoological Station, Sweden). Dr. B. LINDBERG and Mr. P. HILIVIRTA assisted during collecting trips to Lapland. I am also grateful to Dr. O. HALKKA for criticism of the manuscript. Financial aid for the collecting trips was obtained from the Emil Aaltonen Foundation (Tampere, Finland) and the Nordic Council for Terrestrial Ecology.

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Received 17. I. 1978

Printed 20. VI. 1978