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Reproductive isolation and experimental hybridization between Arctocorisa carinata and A. germari (Heteroptera, Corixidae)

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A. carinata (C. Sahlberg) and *A. germari* (Fieber) are close to each other morphologically, and presumably also genetically. They are partly sympatric, their habitat isolation is partial, their breeding seasons overlap, and in both species both sexes produce stridulatory signals during the mating season, stridulating activity being maximal at night. However, the signals are species- and sex-specific. In *A. germari*, laboratory experiments showed that exchange of acoustic signals between the sexes is an essential part of mating behaviour; in *A. carinata*, in contrast, males were frequently observed to attempt copulation without preceding acoustic signalling, and they often managed to copulate forcibly even with unreceptive females or females of other species.

Experimental crosses gave viable hybrids between *A. carinata* and *A. germari*, and one viable hybrid was even obtained between *A. carinata* and *Sigara distincta* (Fieber). Morphologically the hybrids had intermediate characters, and the acoustic signals of the *Arctocorisa* hybrids were also intermediate. In backcrosses of *Arctocorisa* hybrids the males were almost totally sterile; in contrast, the females produced fertile offspring when backcrossed to *A. germari* males, but sterile offspring when backcrossed to *A. carinata* males. Thus, in experimental crosses between *A. carinata* males and *A. germari* females postmating isolation was strong and behavioural isolation weak, but in crosses between *A. germari* males and *A. carinata* females the weak postmating isolation was counteracted by strong isolation in acoustic behaviour.

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1. Introduction

In numerous cases among insects, closely related species differ only slightly in morphological characters, and the correct mate selection seems to be ensured by differences in mating behaviour. The water bug family Corixidae is a case in point; frequently several morphologically close species may be caught in a single water body, but no hybrids are found.

The only thoroughly studied isolating mechanism in Corixidae involves premating exchange of stridulatory signals between the two sexes (Jansson 1972, 1973a, 1976). Yet, although by no means all species of the family are able to stridulate, only one example is known of other than acoustically induced approach of the two sexes, namely visual display of males reinforced by acoustic mounting signals (Jansson 1975).

During evolutionary studies on geographically isolated populations of *Arctocorisa carinata* (C. Sahlberg) (Jansson 1978a, 1979a) I observed that although the species does stridulate, matings often occur without preceding acoustic signalling. The presence of the closely related *A. germari* (Fieber) in some of the collecting sites for *A. carinata* then prompted the present study on reproductive isolation between the two species.

A. carinata and *A. germari* are morphologically close. Females are almost indistinguishable, the clearest separating character being in the middle leg femur, where *A. carinata* has a row of long, slender hairs, but *A. germari* has only short hairs (e.g. Stichel 1955, Macan 1956). In males the

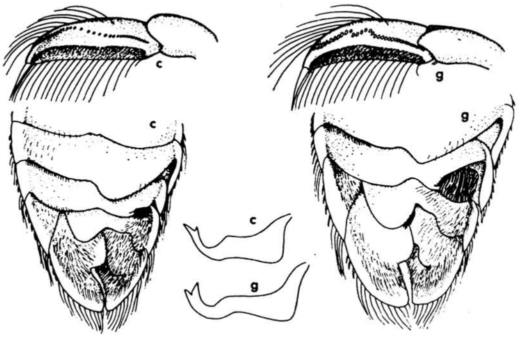

Fig. 1. Morphological characters of pala, dorsal view of abdomen, and shape of the right paramere in males of *A. carinata* (c) and *A. germari* (g).

species show more obvious differences: arrangement of the palar pegs, the dorsal view of the abdomen, and the shapes of the strigil and the right paramere (Fig. 1).

According to the records on the distribution of *A. carinata* and *A. germari*, in Europe the two are largely but not completely allopatric (e.g. Poisson 1935, 1957, Fristrup 1945, Ossiannilsson 1947, Macan 1956, Southwood & Leston 1959, Weber 1965, Coulianos & Osssiannilsson 1976, Nieser 1978, Jansson 1978a). *A. carinata* occurs in several geographically discrete areas: Iceland, the Faroe Islands, Scotland and the northern parts of England, the Swedish west coast, from the Swedish east coast to the Finnish south coast, from the Scandinavian Range through Lapland to northern Russia, and in the Pyrenees and the Alps. In addition, in the collections of the Leningrad Museum, USSR Academy of Sciences, I have seen specimens which indicate that along the Ural Mountains and the basin of the river Ob the range of *A. carinata* extends from the northern parts of European Russia as far south as the Magnetogorsk-Tobolsk area, while somewhat separately the species has also been found in the Altai region both in Russia and in Mongolia (see also Jaczewski 1960, Lansbury 1966); the records from the Caucasus Mountains seem to refer to *A. armeniaca* Štys (Štys 1975), and those from Kamchatka and the Kuril Islands to another species (Jansson 1979c).

A. germari occurs mainly in the north of Central Europe, but its range extends to the British Isles and Fennoscandia, with occasional records from rather far north in Lapland. The Leningrad Museum has a further series of specimens from the southern parts of the Urals, in the Tshelyabinsk-Tobolsk area. The absence of the species from most parts of European Russia, which is a well-studied area (Kerzhner, pers. comm.), indicates that the distribution of *A. germari* is likewise split into at least two isolated areas, i.e. western Europe and western Siberia. The record of *A. germari* from Mongolia (Jaczewski 1961) was based on a single female and may be incorrect, as the author himself stated. Thus, the ranges of *A. carinata* and *A. germari* overlap at least in England, Fennoscandia, and western Siberia.

2. Material and methods

Observations on the habitats of the two species were made during various field trips in Finland and Sweden, with occasional remarks on other countries as well. Laboratory experiments on behavioural and postzygotic isolation were carried out during the winter of 1974—75. For these tests the insects were collected in September 1974, *A. carinata* from SW Finland, Hanko, Tvärminne Zoological Station, rock pools of the archipelago, and *A. germari* from SW central Finland, Tampere, a building site where part of the basement excavation was temporarily filled with rainwater.

In the autumn both sexes of *A. carinata* and *A. germari* are sexually immature, and mating takes place in the spring (Crisp 1962a, 1962b, Pajunen & Jansson 1969). To ensure virginity of the females, the bugs were identified and sexed upon arrival at the laboratory, and overwintering was arranged separately. In general, the bugs were treated as in Jansson (1978a), and experiments on mating behaviour were begun in early January 1975. Crossbreeding experiments were then arranged from mid-January to mid-June according to the schedule shown in Table 1.

Table 1. The crossing schedule and terminology used. Symbols for genotypes: c = *carinata*, g = *germari*. The crosses are always expressed as *male* × *female*, and consequently in the hybrid genotypes the first letter refers to the parental male and the second to the parental female. In reciprocal crosses the numbers of specimens were 5 ♂♂ and 5 ♀♀ per vessel, but in some backcrosses the numbers of hybrids available were less than 5 (see Table 3). Where a backcross produced a progeny, this was called the B_1 generation, and if a further generation was obtained from intrabreeding of the B_1 generation this was called the B_2 generation.

Interspecific crosses	cc × gg	gg × cc
Resulting hybrids	cg	gc
Backcross combinations	cg × cc	gc × cc
	cg × gg	gc × gg
	cc × cg	cc × gc
	gg × cg	gg × gc
Progenies of backcrosses	B_1	B_1
Progenies of B_1 intrabreedings	B_2	B_2

Stridulatory signals of the bugs were recorded and analysed as described in Jansson (1979a), and to avoid temperature effects (Jansson 1974), all recordings were done at 20 ± 0.5°C. For tests on the diel periodicity of stridulating activity a set-up as explained in Jansson (1968, 1973b) was arranged to record a 5-min sample every hour for three consecutive days with each species.

3. Results

A. Habitats of the species

A. carinata lives in a variety of habitats from small, more or less temporary rock pools to permanent, relatively large and deep ponds and small lakes. Over most of its geographic range the species occupies the same water bodies throughout the year (Jansson 1978a, 1979a), but in the archipelagoes of southern Finland and eastern Sweden there is a seasonal change of habitat: overwintering occurs in deeper ponds which do not freeze through, and for the breeding season most individuals fly to small rock pools (Pajunen & Jansson 1969).

A. germari was reported from Finland for the first time fairly recently (Jansson 1967), the first catches regularly taking place in gravel pits and other artificial excavations in which relatively deep water bodies were formed. The only natural water where I have found *A. germari* during several summers in the 1970s is the pond described in Jansson & Pajunen (1978) for the southern Finnish population of *A. carinata*. In this particular pond *A. carinata* has overwintered in large numbers although found only in small numbers during the breeding season, whereas *A. germari*, though never very abundant, has inhabited the pond all the year round.

Elsewhere, I have caught occasional specimens of *A. germari* in the collecting sites described for the western and central Swedish populations of *A. carinata* in Jansson (1978a) and Jansson & Pajunen (1978), i.e. in Bohuslän and Härjedalen. Further, in northern Sweden I have caught *A. germari* near Arjeplog in Lule Lappmark, and Skröven in Norrbotten, and in museum collections I have seen specimens from two localities in northern Finland: LKem, Pallastunturi and Ks, Kuusamo; these localities are within the distributional range of *A. carinata* as well, and along the Scandinavian Range and in Lapland the two species thus seem so be sympatric over rather wide areas.

B. Breeding seasons

In southern Finland *A. carinata* has been observed to produce a partial second generation each summer (Pajunen & Jansson 1969, Pajunen 1977). In Lapland I have obtained only larvae or young teneral adults in late August and September; thus, the species obviously produces only one generation per summer in the north. For *A. germari* no exact life-cycle data are available from Finland, but finds of larvae as well as both old and young adults in August-September in southern Finland indicate that there is no seasonal isolation between the species.

C. Mating behaviour

Stridulatory signals

Both sexes of *A. germari* have well-developed stridulatory pegs on the fore-leg femora, but in *A. carinata* the pegs of the female are barely strong enough for stridulation (Fig. 2). In the laboratory the males of both species stridulated spontaneously, or in response to visual and acoustic stimuli from other specimens. When two or more males were stridulating to each other, the signalling was often followed by aggressive behaviour which, particularly in *A. carinata*, involved chasing and nudging. In both species the females stridulated only when sexually receptive and then only in response to the calls of conspecific males.

Audiospectrographic analysis revealed that the dominant frequency area of the sound was 3—4.5 kHz in all signals, but clear species- and sex-specific differences appeared in several other characteristics (Figs. 6—8, Table 2). Males of *A. carinata* produced only one kind of signal, i.e. structurally identical signals were produced both spontaneously and in response to various stimuli. This signal was basically a rather simple sequence of pulse-trains, but in the beginning and especially towards the end there were variable numbers of faster and louder pulse-trains. However, owing to the inconsistent variation in the location of the fast pulse-trains (cf. Jansson 1979a) the signal cannot be considered to be composed of two distinct pulse-train groups. The female signal of *A. carinata* consisted of sequences of monotonously repeated pulse-trains in 1—5 groups separated from each other by clear intervals. The signals were extremely faint, as would be expected from the

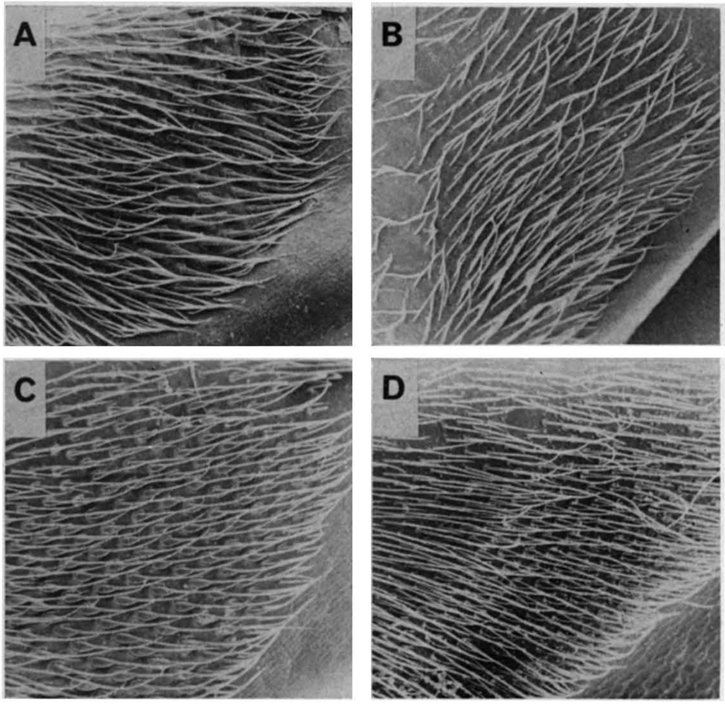

Fig. 2. Fore-femoral stridulatory pegs of *A. carinata* (A = ♂, B = ♀) and *A. germari* (C = ♂, D = ♀); magnification × 160. — Photographed in the SEM Laboratory, Faculty of Agriculture and Forestry, University of Helsinki.

structure of the stridulatory pegs, and the number of pulses per pulse-train was very small.

Males of *A. germari* produced two different signals: a spontaneous calling signal and an induced courtship signal (Figs. 6—7). The calling signal comprised a group of slow pulse-trains in the beginning, often some irregularities in the middle, and a group of fast pulse-trains at the end. The courtship signal was rather similar to the calling signal in the beginning, but there were no irregularities in the middle and the last pulse-trains, instead of being louder, appeared with gradually decreasing amplitude towards the end. The female signal was a relatively loud sequence of monotonously repeated pulse-trains in a single series (Fig. 8).

Table 2. Numerical data ($\bar{x}$ ± SD) on stridulatory signals of *A. carinata* and *A. germari*. Explanations: cls and cts = calling and courtship signals (in males of *A. germari*); s and f = slow and fast pulse-trains; a and b = first and subsequent pulse-train groups separately (in *A. carinata* females). The data for male signals of *A. carinata* are from Jansson (1979a), southern Finnish population. All signals were recorded at 20 ± 0.5 °C.

Species and sex	Signals analysed/ individuals in recordings	Number of pulse-train groups per signal	Signal duration (sec at 20°C)	Pulse-trains per signal	Pulses per pulse-train
A. carinata ♂♂	100/10	1	1.96±0.53	s 12.69±3.40 f 5.81±1.02	s 6.87±1.73 f 6.96±1.55
A. germari ♂♂	cls 40/8	2	2.82±0.52	s 15.87±3.07 f 13.35±4.88	s 7.88±1.57 f 5.10±0.95
	cts 42/8	1	3.46±0.80	31.29±7.94	6.90±1.70
A. carinata ♀♀	30/6	2.30±1.02	a 1.06±0.33[1] b 0.67±0.16[1]	a 10.97±2.81 b 7.26±1.60	2.45±0.83
A. germari ♀♀	40/8	1	5.15±0.79	47.48±6.93	6.44±1.50

[1] Duration of single pulse-train groups

Diel periodicity of stridulation

In the tests for diel periodicity of stridulating activity the males of both species stridulated at any time of day (Fig. 3). *A. germari* was a somewhat more active species in general, and its rhythm of activity showed a clearly nocturnal maximum. *A. carinata* showed some tendency to a two-peak periodicity, with one peak after dusk and another after dawn. However, differences between the species were far too slight to be considered functional in temporal isolation between the species.

Playback of male signals to females revealed no differences in the response of the latter either in darkness or in daylight: the receptive females responded by stridulating regardless of the light conditions.

Behavioural sequence of events leading to copulation

In *A. germari* mating behaviour usually followed the "normal" pattern for a species of Corixidae with ability to stridulate (Jansson 1973a): sexually mature males stridulated spontaneously, producing calling signals, and receptive females responded to these with agreement signals, according to which the males orientated towards them (Fig. 4). In the sand-lined basin used for the experiments this mechanism functioned very effectively, and the males seldom had to rely upon a second exchange of signals before finding the females. But in the few cases in which the males failed in the first attempt, they stopped and produced the structurally different courtship signal, and the females again responded with the agreement signal. In response to playback of recorded female signals the males gave courtship signals only.

Unreceptive females of *A. germari* did not usually respond to male signalling, and only when in close proximity to stridulating males did they swim away. The movements of these females rarely provoked males to chasing behaviour and, in general, males were observed to mount females almost exclusively in response to the female agreement signal (Fig.4).

In *A. carinata* the behaviour leading to copulation was more variable. Sometimes it followed the "normal" pattern, with exchange of signals between the sexes, but if a second exchange of signals was necessary before the males found the females, the males produced signals that were structurally identical to those produced spontaneously, except that the pulse-train rate was often slightly faster. Very often, however, acoustic signalling was partly or totally replaced by visual cues. Thus, if a male caught sight of a female, he either produced a signal and approached the female without waiting for the agreement signal, or simply swam towards her without any preceding acoustic signalling. Even receptive females (deemed receptive because not resisting when the males mounted) frequently omitted the agreement signal and responded simply by not escaping the stridulating and approaching males.

Visually induced approach of the males in *A. carinata* frequently led to attempts at copu-

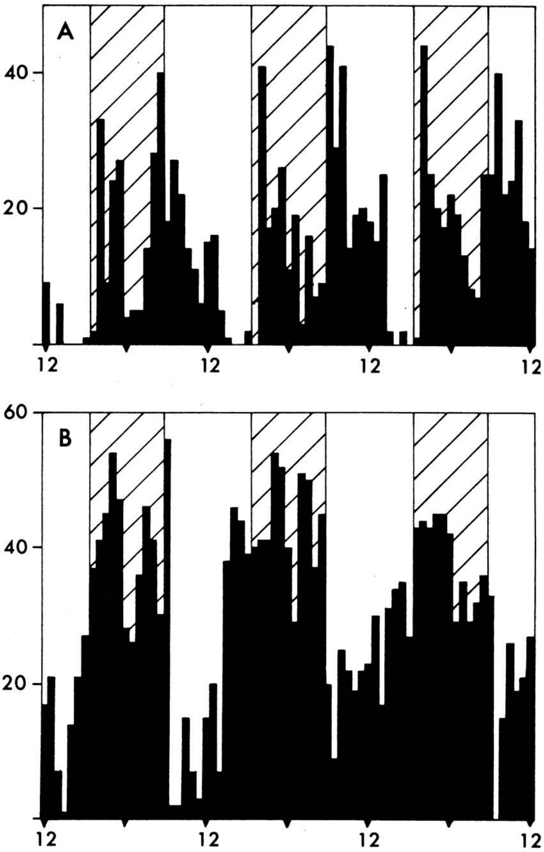

Fig. 3. Diel periodicity of male stridulating activity in *A. carinata* (A) and *A. germari* (B) in experiments with 10 ♂♂ and 10 ♀♀ per vessel at 21—23°C. Ordinate: Total number of signals recorded during a 5-min period every hour. Hatching = time between sunset and sunrise. Dates of experiments: A = 5.—9. IV. 1975, B = 30. III. — 3. IV. 1975.

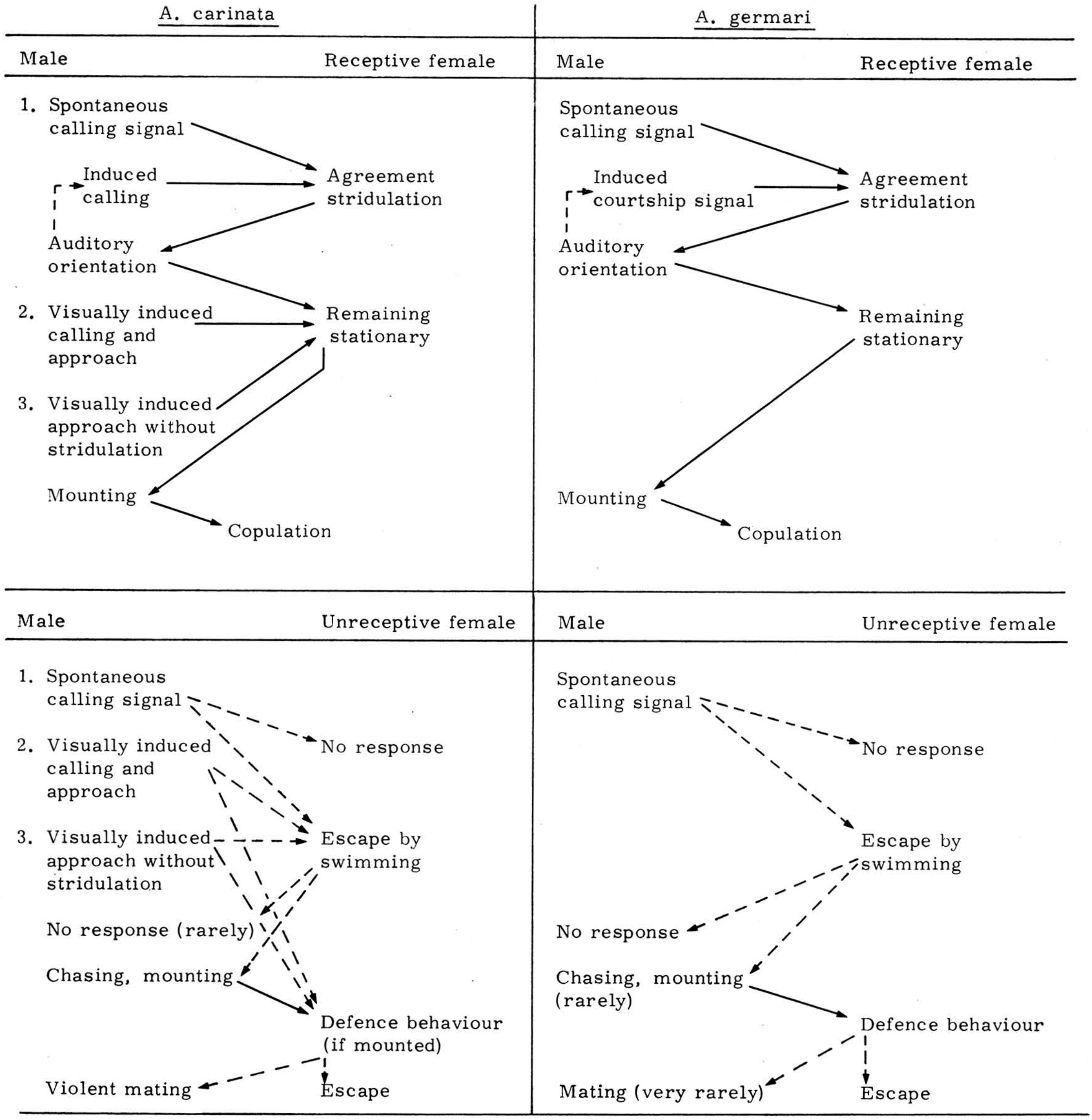

Fig. 4. Diagrams of sequences of events leading to copulation in *A. carinata* and *A. germari*.

lation with unreceptive females. Although such females tried to escape from the males by kicking vigorously with the hind legs (cf. Jansson 1973a), the males often managed to hold on and force them to mate. Also, when stridulating males were close to unreceptive females, the latter always responded by trying to swim away. This provoked a chasing reaction in the males, and they attempted to mount the females either when the latter were swimming or immediately after they stopped. In these cases, too, the males often managed to force the females to mate (Fig. 4).

When sexually active males of *A. carinata* were placed in a vessel with *A. germari* females, interspecific matings occurred in a few minutes. In the beginning the *A. germari* females fought vigorously against the *A. carinata* males, but once the males obtained genital contact the females calmed down and allowed the males to continue copulation. In the reverse combination, *A. germari* males with *A. carinata* females, the males had to be tricked to mount the females by playback of previously recorded *A. germari* female signals to the vessel; once this was done, interspecific matings occurred immediately, and receptive *A. carinata* females did not seem to resist the *A. germari* males.

D. Hybrid viability and fertility

When interspecific matings were obtained, the pieces of rock provided for egg-laying were transferred daily to separate vessels where the larvae were reared (cf. Jansson 1978a). Pure lines were also set up as control cultures. In the cross of *A. carinata* ♂♂ × *A. germari* ♀♀ the result was relatively good as compared to the control cultures, but in the reverse combination, *A. germari* ♂♂ × *A. carinata* ♀♀, only one hybrid individual survived to the adult stage (Table 3). The latter cross was repeated, and this time the score was eight hybrid adults. In the hybrid larvae, no one stage was observed to be particularly fatal, but initially good numbers of larvae simply decreased throughout the rearing. Further, about 25 % of the adult hybrids died within a week of emergence; these individuals are not included in Table 3.

Table 3. Results of experimental crosses between *A. carinata* and *A. germari*. Symbols for genotypes: c = *carinata*, g = *germari*. All crosses are given as ♂♂ × ♀♀, and in the hybrid genotypes the first letter refers to the parental male, the second to the female. Numbers in front of genotypes give the numbers of individuals per culture; numbers after the combinations (in parentheses) indicate repeated tests. Other explanations: e = eggs laid but no larvae observed; ne = not even eggs observed.

Interspecific crosses	Hybrids obtained (♂♂/♀♀)	Backcrosses of hybrid males	Progenies of back-crosses (B_1♂♂/♀♀)	Progenies of B_1 intra-breeding (B_2♂♂/♀♀)
5cc × 5gg	7/10	4cg × 5cc	e	–
5gg × 5cc (1)	0/1	3cg × 5gg	e	–
5gg × 5cc (2)	4/4	2gc × 5cc	2/2	1/0
		2gc × 5gg	e	–
		Backcrosses of hybrid females		
Control cultures:		5cc × 5cg	13/18	e
		3cc × 1gc (1)	1/2	ne
5cc × 5cc (F_1)	22/17	5cc × 2gc (2)	e	–
5cc × 5cc (F_2)	15/10	5gg × 5cg	10/12	8/5
5gg × 5gg (F_1)	21/23	5gg × 2gc	4/2	8/10

The fertility of the hybrids was tested in backcrosses, and the hybrid males turned out to be almost totally sterile. The males frequently mated with the females provided, and the females laid numerous eggs. However, in only one of the combinations did any larvae hatch from the eggs, and only four of these attained the adult stage. When these B_1 individuals were allowed to mate with each other, a few larvae appeared in the vessel, but only one survived long enough to emerge as an adult in the B_2 generation (Table 3).

The hybrid females, in contrast, appeared to be fertile in most backcrosses, and in some of the combinations the results were nearly as good as in the control cultures. When the B_1 progenies were cultured for further offspring, those originating from backcrosses to *A. carinata* males appeared to be sterile in both combinations, but those from backcrosses to *A. germari* males were able to produce further B_2 generations (Table 3).

E. Hybrid characters

Fig. 5 shows some morphological characters of the hybrid males, and examples of males obtained from the backcrosses. In most cases the hybrids were intermediate, and in backcrosses the characters shifted towards those of the species used as the parental representative. The only exception to this general trend appeared in the hybrids between *A. germari* males and *A. carinata* females: three out of four males showed characters closer to those of *A. carinata*. Rather interestingly, in the backcross experiments these were the most successful of the hybrid males in backcrosses with *A. carinata* females. However, the offspring were far fewer than in the control cultures, and in the B_2 generation the line terminated in a single individual (Table 3).

In the B_2 generation the morphological characters were in general similar to those of the B_1 generation. Here too, however, there was one exception: in the line of *A. germari* males with the *germari* × *carinata* hybrids the characters shifted further toward those of *A. germari*.

Like the morphological characters, the stridu-

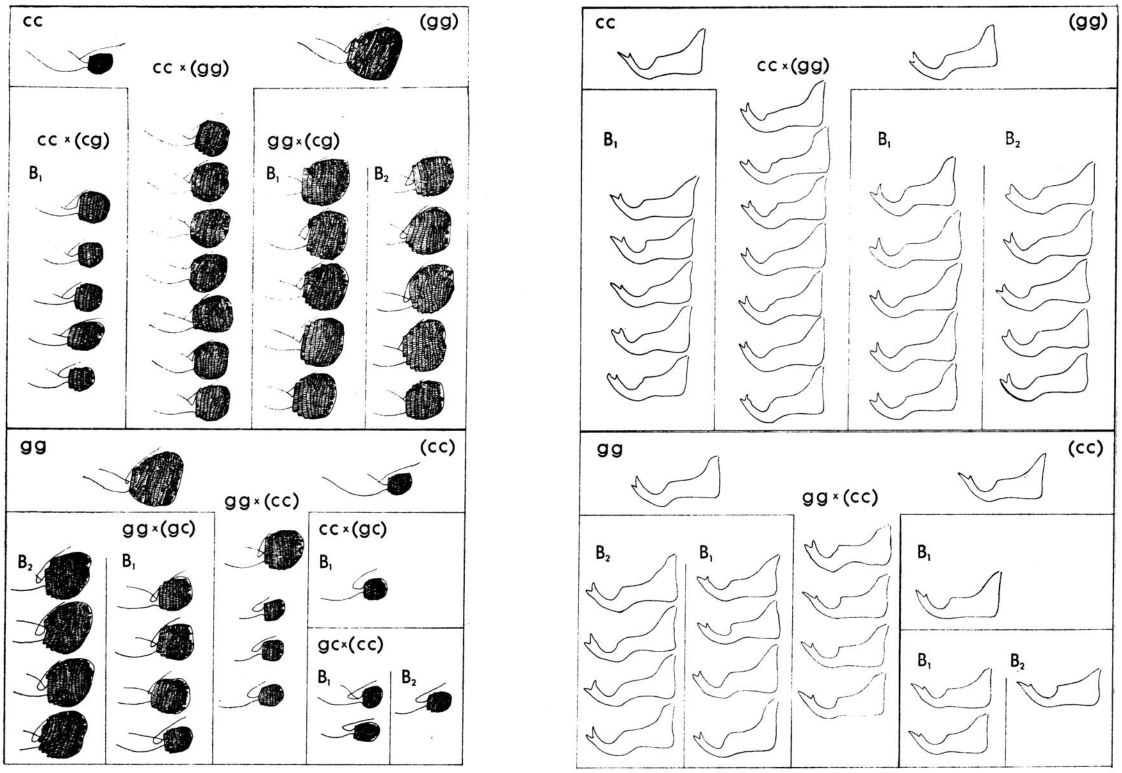

Fig. 5. Shape of strigil (left) and right paramere in males of *A. carinata* and *A. germari*, as compared with those of the hybrid males and some of the males from the B_1 and B_2 progenies. Symbols for genotypes: cc = *carinata*, gg = *germari*; represented by the parental female when shown in parentheses. The specimens are in the same order in the two drawings.

latory signals of the hybrids were intermediate in structure (Figs. 6—8, Table 4), and in backcrosses they shifted towards the signals of the parental species used. In the male calling signals the number of slow pulse-trains did not differ greatly between *A. carinata* and *A. germari*, and in the hybrids this feature also varied quite fortuitously (cf. Tables 2 and 4). On the other hand, the most conspicuous difference between the signals of the parental species, the number of fast pulse-trains per signal, placed the hybrids and the backcross progenies in a very consistent order: in both combinations the hybrids were closer to the parental female species, and the backcross progenies shifted close to the pure lines and in some of the combinations went even beyond these.

Tests of hybrid males with playback of various female signals revealed that distinct courtship signals were frequently produced only by the progeny from the cross of *A. carinata* ♂♂ × *A. germari* ♀♀. But although most of the signals from four of the males closely resembled the courtship signal of *A. germari* (Table 4), some of the courtship signals of the same males, as well as signals produced in the courtship situation by the remaining males from the same cross, appeared to be intermediate between calling and courtship signals: a series of about 20 slow pulse-trains was followed by 3—4 fast pulse-trains (Fig. 7). Of the other hybrids, only one male from the cross of *A. germari* ♂♂ × *A. carinata* ♀♀, and one male from the backcross of *carinata* × *germari* hybrid females to *A. carinata* males produced a few faint courtship signals (Table 4, Fig. 7). All other hybrid and backcross males responded to playback of the female signals with signals similar to those produced spontaneously; they were presumably unable to produce distinct courtship signals.

Table 4. Numerical data on some characteristics of the signals of *A. carinata* and *A. germari*, as compared with hybrids and B_1 individuals Symbols for the genotypes as in Table 3.

Genotype combination ♂♂ × ♀♀	Male calling signals: Signals analysed/ individuals in recordings	Number of pulse-trains per signal: Slow pulse-trains x̄ ± SD	Fast pulse-trains x̄ ± SD	Male courtship signals: Signals obtained/ specimens that produced distinct courtship signals	Pulse-trains per signal x̄ ± SD
cc × cc	100/10	12.69±3.40	5.81±1.02	0/0	0.0
cc × cg	15/3	15.00±5.79	5.40±2.70	3/1	18.00±8.18
gc × cc	17/2	14.00±1.15	5.86±1.57	0/0	0.00
gg × cc	22/3	10.55±4.12	5.90±3.04	4/1	23.27±6.70
cc × gg	50/5	13.58±3.81	8.46±5.26	26/4	27.27±6.21
gg × cg	29/3	14.14±4.88	12.90±4.18	0/0	0.00
gg × gc	26/3	14.00±2.45	20.00±4.38	0/0	0.00
gg × gg	40/5	15.87±3.07	13.35±4.88	42/5	31.29±7.94

Genotype combination ♂♂ × ♀♀	Female agreement signals: Signals analysed/ individuals in recordings	Number of pulse-trains per signal: First group x̄±SD	Subsequent groups x̄±SD	Pulses per pulse-train[2] x̄±SD
cc × cc	30/6	10.97±2.81	7.26±1.60	2.45±0.83
gg × cc	40/4	7.08±1.56	7.17±1.33[1]	3.79±1.22
cc × gg	87/9	15.76±8.98	0.00	5.83±2.01
gg × gg	40/5	47.48±6.93	0.00	6.44±1.50

[1] A second pulse-train group obtained from two individuals only, altogether six times.

[2] Measured from a sample of 20 signals from 4 individuals in each genotype combination.

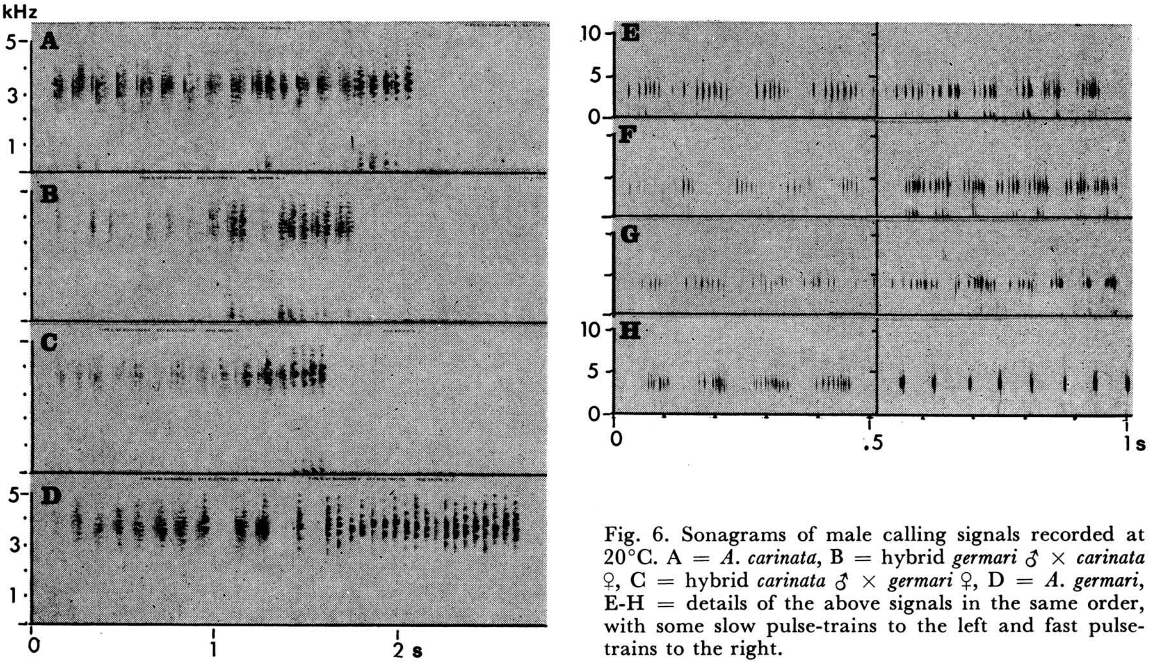

Fig. 6. Sonagrams of male calling signals recorded at 20°C. A = *A. carinata*, B = hybrid *germari* ♂ × *carinata* ♀, C = hybrid *carinata* ♂ × *germari* ♀, D = *A. germari*, E-H = details of the above signals in the same order, with some slow pulse-trains to the left and fast pulse-trains to the right.

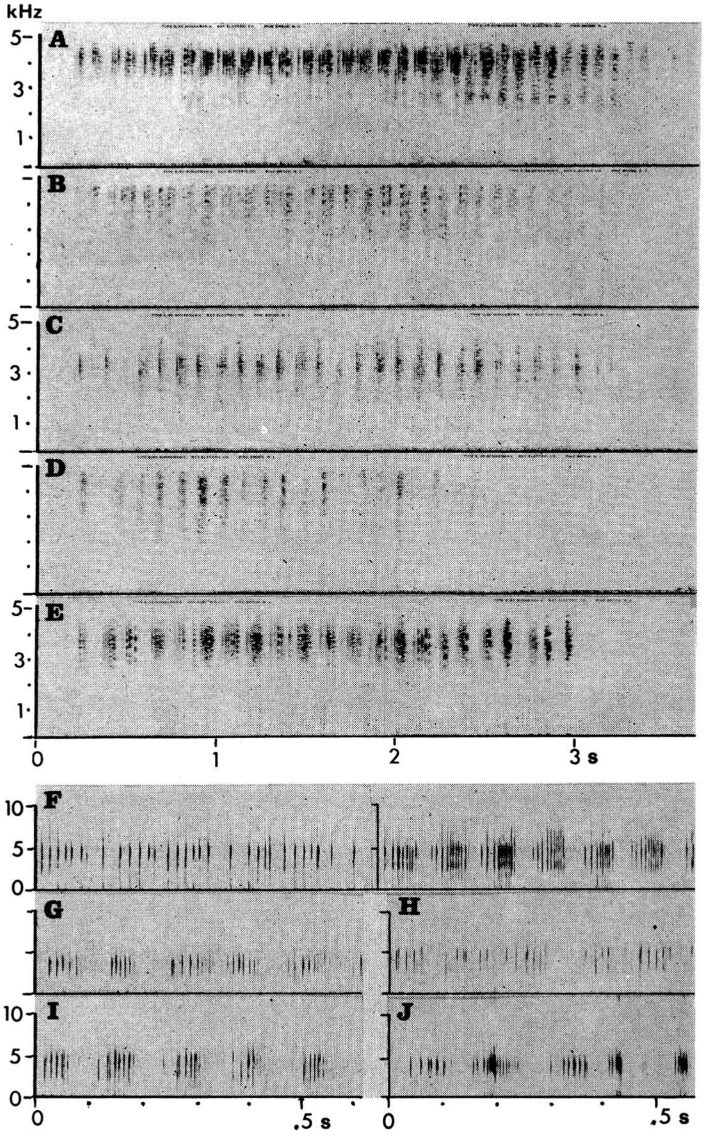

Fig. 7. Sonagrams of male courtship signals recorded at 20°C. A = *A. germari*, B = hybrid *carinata* ♂ × *germari* ♀, C = hybrid *germari* ♂ × *carinata* ♀, D = backcross hybrid *carinata* ♂ × *carinata* × *germari* ♀, E = intermediate signal between calling and courtship signals of a hybrid *carinata* ♂ × *germari* ♀, F-J = details of the above signals in the same order (in F details are shown from both the beginning and end of the *A. germari* signal, but in G-J only one spectrogram is given).

Of the 127 signals analysed from the hybrid females, only six included two pulse-train groups and all the rest only one group. In all these signals the number of pulse-trains per group was close to that of the *A. carinata* female signal (Table 4), and the amplitude of the signals was also very low, as in *A. carinata* (Fig. 8). In the number of pulses per pulse-train the hybrid females were of intermediate type, but in both combinations closer to the parental female species (Table 4). Signals of the backcross progenies were not recorded from the females because the specimens were used directly for the experiments in which their fertility was tested; obtaining of receptive and responding females would have required a period of isolation from males (Jansson 1973a).

In playback tests the parental species only occasionally responded to the signals of the hybrids, but the hybrids seemed to respond equally well to the signals of both parental species, as well as to the hybrid signals. How-

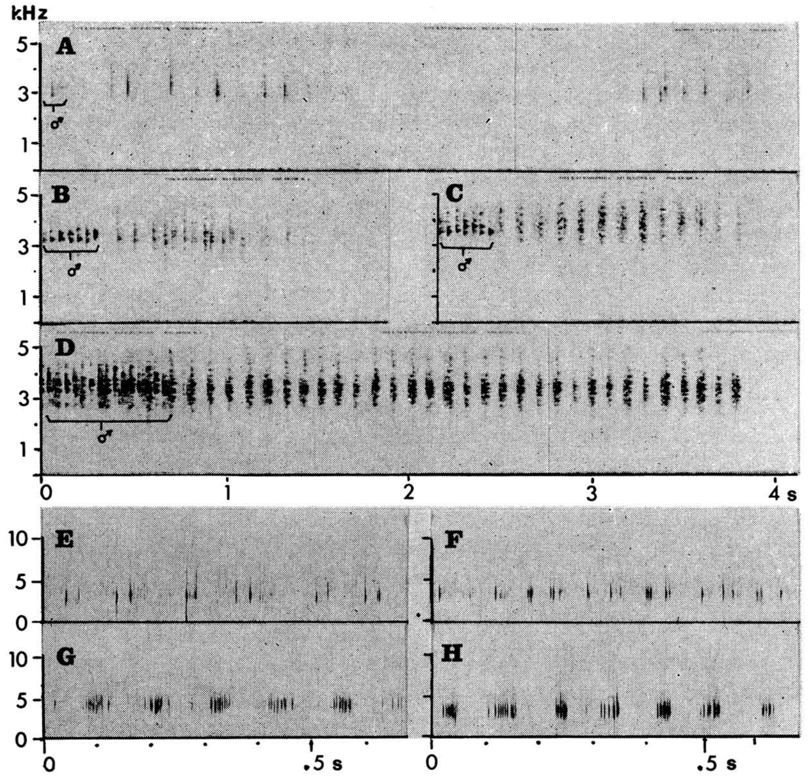

Fig. 8. Sonagrams of female agreement signals recorded at 20°C. A = *A. carinata*, B = hybrid *germari* ♂ × *carinata* ♀, C = hybrid *carinata* ♂ × *germari* ♀, D = *A. germari*, E-H = details of the above signals in the same order. In signals A-D the first traces to the left are the last pulse-trains of the male signals used to induce the females, showing how the female signal usually immediately follows the male call or even overlaps it.

ever, while the receptive females usually respond to the male calls by immediate stridulation or even begin their signal before the male call is completed (Fig. 8, Jansson 1973a, 1976), in the hybrid females, particularly those from the cross of *A. germari* ♂♂ × *A. carinata* ♀♀, the response was frequently delayed and the female signal did not begin until 1—2 sec after the male call had ended.

4. Discussion

Experimental crosses have revealed genetical differences between geographically isolated populations of *A. carinata* (Jansson 1978a). Thus, because the specimens of *A. carinata* and *A. germari* used in the present study were collected from Finland only, the distributional ranges of the species in Fennoscandia are the only ones relevant for consideration here.

Both *A. carinata* and *A. germari* readily colonize newly formed ponds with little or no aquatic vegetation. In Fennoscandia, *A. carinata* apparently occupied ponds some 10 000 years ago as these habitats became available during the Late Glacial period, but with climatic and related vegetational changes the species became extinct from wide areas inland, surviving only in the extreme habitats in the coastal rock pools and in ponds located at higher altitudes along the Scandinavian Range and in Lapland (Jansson 1978a, 1979a, Jansson & Pajunen 1978). *A. germari*, in contrast, is able to occupy the inland habitats, but seems to have reached Fennoscandia rather recently. Ossiannilsson (1947) reported the species only from the most southern province of Sweden, but Coulianos & Ossiannilsson (1976) already had records from Skåne and Öland in the south, and Lule Lappmark in the north. Further, during 1966—67 I collected large numbers of Corixidae from the Swedish west coast and did not find *A. germari*, but in 1973 I caught the species on a trip to Bohuslän. With my other records of *A. germari* from Sweden, I can thus add four more Swedish provinces to the distribution of the species: Bohuslän, Härjedalen, Pite Lappmark, and

Norrbotten. Similarly, in Finland *A. germari* was recorded for the first time rather recently, from Helsinki (Jansson 1967), and has been reported again from the same area (Huldén 1976), but I have since found it in three other localities in the south (N, Hanko; Ab, Masku; Ta, Tampere), and recently the species has been found in two localities in the north (LKem, Pallastunturi; Ks, Kuusamo). Thus the species has greatly expanded its range during the past few decades, and evidently the action of man in creating suitable ponds in gravel pits and other artificial excavations has favoured this expansion in Fennoscandia.

A. germari has been said generally to favour deeper waters than most species of Corixidae (e.g. Walton 1943, Crisp 1962b, Weber 1965). However, Crisp (1962b) also included *A. carinata* in the species found in deep waters and, indeed, in northern Fennoscandia I found it in large, deep ponds. Thus, the only areas of sympatric distribution where some degree of habitat isolation may be thought to exist between *A. carinata* and *A. germari* are the coastal areas of southern Finland and eastern and western Sweden, and even in these areas isolation is only partial; on the Swedish west coast I found a few specimens of *A. germari* in rock pools that contained *A. carinata* in abundance and on the Finnish south coast I have found *A. germari* continuously inhabiting one large pond in which *A. carinata* overwinters regularly, and some individuals of the latter species always remain to breed in this pond as well.

Mating behaviour in both species involves species- and sex-specific stridulatory signals which have the temporal characteristics of the signals that can function effectively in premating isolation of closely related species (Jansson 1973a). In *A. carinata*, however, the female signal is very faint and its functional significance as part of the mating behaviour of the species may be questioned; in the laboratory the males readily approached the females in response to visual cues. But the natural habitats of the species are ponds in which the bottom is covered by a layer of very soft detritus. The bugs usually hide in the detritus, and their chances of using visual cues for locating other specimens must be extremely limited. Thus, the female signal, despite its faintness, may be of great importance in pair formation. Alternatively, under natural conditions receptive females may actively search for males, as the female signal is functional only from a very short distance; no such approach of females to males was detected in the laboratory, but this was perhaps because there was little detritus in the vessels and the bugs were directly visible to each other. Receptive females have occasionally been observed to approach stridulating males in the genus *Cenocorixa* (Jansson 1973a), and the correlation of the loudness of the male signals with population densities in the geographically isolated populations of *A. carinata* (Jansson 1979a) may thus have adaptive significance: in low population densities louder signals would attract females from greater distances.

In various species of Corixidae males have been reported frequently to make attempts at mating in response to visual cues (Schaller 1951, Crisp 1962b, Finke 1968, Jansson 1968). However, these observations have all been made in the laboratory where the unreceptive females are evidently not able to hide and escape from the males nearly as effectively as in natural habitats. Further, when a female is receptive and produces agreement signals in response to male calls, echoes in aquaria prevent the males from finding the correct female (Jansson 1973a), and the excited males may then mount any individuals nearby; the latter may be swimming or stationary, males or females, or even specimens of other species (as was well demonstrated by inducing the *A. germari* males to mate with *A. carinata* females by playback of *A. germari* female calls). Among the numerous species of corixids that I have reared in the laboratory, *A. carinata* has been the only one so far in which the males have often been able to force resisting and evidently unreceptive females to mate. In all other species random mountings by the males have only occasionally led to copulation, and in these cases the females were probably close to becoming receptive and thus accepted the males somewhat prematurely. It seems probable that in laboratory conditions, where the females are too easily detectable, random mountings, which seldom lead to actual mating, tend to be greatly overestimated as part of true mating behaviour. According to Crisp (1962b), for instance, males of *A. germari* mount the females when the latter are swimming by, and genital contact takes place either when the pairs are swimming or when they come to the surface. Leston (in Haskell 1957) and Southwood & Leston (1959), although unable to describe the signals or explain their function, mentioned the ability of both sexes of *A. germari* to stridulate during the mating season. Stridulation was unknown to Crisp (1962b), but he stated that the minimum temperature at which the species mates is about 8 °C, which is probably its minimum temperature for stridulation (cf. Jansson 1974). Further, if males of *A. germari* mount unreceptive females in the laboratory (probably because echoes prevent finding of the correct, responding female), the pairs are unable to swim because of the defence behaviour (= kicking) of the female. Consequently, being lighter than water, the struggling specimens rise to the surface where they usually part. Parting of the specimens was also observed by Crisp (1962b), but he wrongly concluded that this was copulation when it was merely an attempt. Crisp (1962b) further mentioned that matings are easily observed in the field when the pairs come to the surface. It is true that a surface visit of a single specimen is easily distinguished from that of a mating pair. The male on the top obtains fresh air first, but then the pair has to turn sideways for the female to get fresh air too, and before the pair is able to dive again the turn to the normal swimming position requires some struggling. However, these visits to the surface have nothing to do with the initiation of copulation.

Despite the apparent effectiveness of stridulatory behaviour as part of premating isolation of Corixidae, interspecific pairing seems to occur readily under laboratory conditions (see also Jansson 1979b). On a couple of occasions I have even observed intergeneric matings, and occasionally wrong pairing seems to occur in natural conditions as well. For instance, in spring 1970 I was collecting corixids from a pond in Vancouver, British Columbia, when I caught a mating pair in which the male had black spots on the hind leg tarsi, but the female had concolorous hind legs. I preserved the specimens in a separate vial, and a closer study revealed that the male was *Callicorixa vulnerata* (Uhler), and the female *Cenocorixa blaisdelli* (Hungerford). Whether this copulation would have produced any hybrids is not known, and although I sampled the pond several times during the summer I never caught any abnormal specimens.

Another intergeneric mating occurred in my laboratory. During experimental crosses between geographically isolated populations of *A. carinata* (Jansson 1978a), I ran short of vessels when daily picking the newly emerged adults from the cultures. Temporarily, I stored some *A. carinata* males in a vessel where I had females of *Sigara distincta* (Fieber) for other studies. A couple of weeks later, when I removed the adult specimens, I found about a dozen first instar larvae in the vessel. The origin of these larvae was a mystery, and I wanted to check possible misplacing of *S. distincta* males in the vessel by rearing the larvae to be able to identify them. Development of the larvae was unusually slow, and only two of them reached the fifth instar. Finally, a male and a female emerged from these, but the female died a couple of days later. Microscopic inspection revealed that it was a hybrid between *A. carinata* and *S. distincta*. The male survived for several weeks, but because I had no suitable females available for backcross experiments, I had to terminate the culture. Some of the morphological characters of this hybrid specimen are shown in Fig. 9.

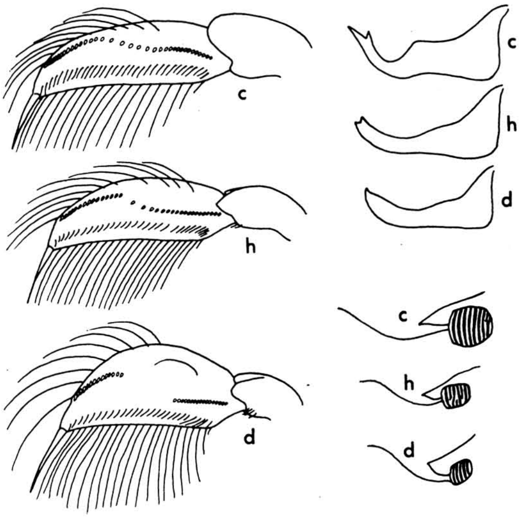

Fig. 9. Morphological characters of pala, right paramere, and strigil in males of *A. carinata* (c), *S. distincta* (d), and the hybrid between the two (h).

The best known and most thoroughly studied experimental hybridizations among insects are those carried out in the genus *Drosophila*. Patterson & Stone (1952) reviewed the known cases up to the early 1950s, and in several cases the fertility of the hybrids was comparable with my results on *Arctocorisa*: males were sterile, but females at least partly fertile. However, in the genus *Drosophila*, which includes several species groups, experimental crosses have generally been successful only within these groups and attempts to cross species from different groups (although within the genus) have been practically fruitless. In contrast, in my experiments a viable hybrid, although only one individual, was obtained between two genera, *Arctocorisa* and *Sigara*. The genus *Sigara* is generally considered to be a heterogeneous group of species, and includes several subgenera that differ too little morphologically to be ranked as genera (cf. e.g. Hungerford 1948). The genus *Arctocorisa*, on the other hand, was originally described as a subgenus of *Corixa* by Wallengren (1894), and included only *A. carinata* and *A. variegata* (= *A. germari*). The name was later raised to generic rank, but by various taxonomists it was used very freely and usually included several species now included in the genus *Sigara*. Hungerford (1948) finally fixed *Arctocorisa* as a generic name for two European and five North American species, and the genus, as then defined, is easily distinguished from the genus *Sigara*. However, my accidental hybridization between the two genera, even though it produced only one viable individual, casts some doubt on the significance of the characters used to separate the genera.

Southwood & Leston (1959) give the chromosome numbers of *A. carinata* and *A. germari* (and also *S. distincta*) as $22A + X + Y$. That the signal structure in the hybrid males was always closer to the parental female type indicates that some of the determining factors are carried either in the X chromosome or in the egg cytoplasm. As the signals of the hybrid females also showed a closer resemblance towards the parental female species, cytoplasmic inheritance seems more probable. Morphologically, a tendency towards characters of the parental female species was observed only in three males from the cross of *A. germari* ♂♂ × *A. carinata* ♀♀, while the fourth hybrid from the same cross showed intermediate characters (Fig. 5). Inheritance of the morphological characters in this particular cross indicates a complex genetic basis for the interspecific differences. The shift of characters still further towards those of the parental representative in the progeny of the B_1 generation supports this conclusion.

More or less fertile hybrids have been obtained in experimental crosses within some terrestrial genera of Heteroptera as well (e.g. Sailer 1953, 1954, 1955, Eyles & Blackith 1965), and in all these experiments differences in the mating behaviour of the species have delayed fertilization or otherwise caused difficulties in pair formation. In my experiments the *A. carinata* males willingly mated with the *A. germari* females (and apparently also with *S. distincta* females), but *A. germari* males mated with *A. carinata* females only when tricked by playback of *A. germari* female signals. The hybrid males were practically all sterile, and in the hybrid females the backcross lines with *A. carinata* males led to sterile progeny, and only the lines with *A. germari* males continued successfully. In both combinations, however, the hybrid females from the reciprocal crosses produced very faint signals, in this way resembling those of *A. carinata*, and if the *A. germari* males had had a choice, there would evidently have been selection against the hybrid females. Similarly, in the hybrid males the faintness of the signals and almost total lack of a courtship signal would probably have led to selection in favour of normal males. Thus, the results indicate that any weaknesses in the premating isolation between *A. carinata* males and *A. germari* females are offset by hybrid sterility, but between *A. germari* males and *A. carinata* females the weak postmating isolation is counteracted by the strong isolation in mating behaviour.

Strübing (1963) studied acoustic signals of hybrids between two species of *Euscelis* (Homoptera, Auchenorrhyncha), and found that the signals were intermediate, there being no differences between hybrids from reciprocal crosses. Backcrosses revealed great difficulties in pair formation, and only one combination gave any progeny; in morphological characters and acoustic signals these were identical with the parental species of the backcross. In contrast, in crosses between two species of *Teleogryllus* (Orthoptera, Gryllidae), Bentley & Hoy (1974) obtained results similar to those in the present paper. The intermediate characters of the hybrids were closer in both lines to those of the parental female species, and in backcrosses the characters shifted towards those of the pure line representative, although there were still some resemblances to the other species. Rather similar results with a few intermediate hybrids had already been obtained on gryllids by Fulton (1933), and also by von Hörmann-Heck (1957). In acridids, Perdeck (1958) even observed natural hybridization occasionally between two sibling species; the hybrids could easily be detected in the field by their intermediate song, and experimentally it was demonstrated that the hybrids were fully viable and fertile but were effectively isolated from both parental species by differences in acoustic signals.

Although the differences between *A. carinata* and *A. germari* in the sequence of events leading to copulation were observed in the laboratory, and the account given may to some extent have overemphasized the flexibility of the behaviour of *A. carinata*, the study indicates that the recent invasion of *A. germari* into Fennoscandia could lead to occasional interspecific matings between *A. carinata* males and *A. germari* females, but that matings between *A. germari* males and *A. carinata* females are highly improbable. The viability and fertility of some of the hybrids further indicate that the two species are genetically very close, as would be expected from the morphological likeness between the two. In fact, when these crosses are compared with experimental crosses between various geographically isolated populations of *A. carinata* (Jansson 1978a), the southern Finnish population of *A. carinata* seems to be genetically closer to *A. germari* than to the conspecific Swiss population. However, *A. carinata* and *A. germari* are distinct species, and while the present study stresses the importance of behavioural isolation, it further indicates that behavioural differences cannot be the only isolating mechanism between these two species.

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