

Cytogeography of three parallel Robertsonian polymorphisms in the water-hyacinth grasshopper, *Cornops aquaticum* (Orthoptera: Acrididae)

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Abstract. *C. aquaticum* (Acrididae: Leptysminae) inhabits water-hyacinths in the Neotropical region. The blue-flowered water-hyacinth, *Eichhornia crassipes*, has been introduced elsewhere without its natural enemies and has become a weed; recently *C. aquaticum* was considered as a possible biological control agent. In this work, six populations were sampled and cytologically studied. *C. aquaticum* has $2n = 23$ chromosomes in males and 24 in females, with an X0/XX sex determination system. All chromosomes are acro-telocentric and the basic karyotype includes three Robertsonian (Rb) translocations between pairs 1/6, 2/5, and 3/4. These polymorphisms are restricted to the lower course of the Paraná river, between Rosario and Buenos Aires. Fusion frequencies increase southwards, thus showing a geographical cline. The polymorphisms mostly accord with Hardy-Weinberg and gametic phase equilibria. The rearrangements cause a drastic chiasma repatterning in the fusion bivalents (or trivalents) which reduces the proximal chiasma frequency. Recombination is also reduced due to the loss of independent segregation. A recombination index that takes into account both these factors correlates negatively with the number of pairs of chromosomes affected by fusions among populations, which does not accord with the “central-marginal” pattern.

INTRODUCTION

The water-hyacinth grasshopper *Cornops aquaticum* (Orthoptera: Acrididae) is a Neotropical grasshopper that lives in close association with plants of the genera *Eichhornia* and *Pontederia*, on which this species feeds and lays eggs (Adis & Junk 2003, Adis et al., 2004). Early in the XXth century the blue-flowered water-hyacinth, *Eichhornia crassipes*, was introduced into other continents (mainly Africa) as an ornamental. Free of natural enemies, it has become the “World’s Worst Water Weed”, choking dams, overgrowing lakes and rivers and preventing people free access to water (Center et al., 2002). Biological control was attempted by introducing weevils that feed on water-hyacinth, but the result is so far disappointing (Albright et al., 2004). Therefore *C. aquaticum* was considered as a possible biological control agent, and is the main one for many workers, because of ecological considerations. Nowadays, it is being studied for possible release in South Africa (Oberholzer & Hill, 2001). However, its cytogenetics remains largely unknown; only two reports describe the chromosome number of this species (Mesa, 1956; Mesa et al., 1982), both of which indicate that the chromosome number for *C. aquaticum* is the typical one for acridoid grasshoppers, modified by the occurrence of three centric fusions; however, it is not known whether the centric fusions are polymorphic or polytypic. Recently, De Franca Rocha et al. (2004) described in more detail the standard karyotype of *C. aquaticum* and 4 other leptysmine grasshoppers from Brazil, but did not find the Robertsonian (Rb) translocations. As Rb polymorphisms are likely to be important features of the genetic system of a species, and given the

ecological importance of *Cornops aquaticum*, it was decided to undertake a population cytogenetic study of this species. In a previous study (Colombo, 2007), the chiasma effects of the Robertsonian rearrangements were described, and in the present contribution behaviour and geographical distribution of these polymorphisms is analysed.

MATERIAL AND METHODS

In this study, six Argentinian populations and a Caribbean one were sampled and cytologically studied. The Caribbean population is in Trinidad and Tobago (13 males); the Argentinian ones, from north to south: Corrientes (46 males), Santa Fe (42 males), Rosario (19 males), San Pedro (12 males), Zárate (27 males), and Tigre (14 males) (see map in Fig. 1). Testes were dissected and fixed in ethanol-acetic acid (3 : 1). Cytological analysis was performed by squashing some follicles in propionic haematoxylin. Male meiosis was studied; chiasmata were registered in 10 metaphase I plates per individual and classified as proximal, interstitial or distal with respect to the centromere. Data were processed using the STATISTICA (StatSoft-Inc, Tulsa, OK, USA) package. Gametic phase equilibrium was tested by using the GENEPOP (Laboratoire de Génétique et Environnement, Montpellier, France) package. In order to identify the pairs involved in Rb translocations in each individual, trivalents or submetacentric bivalents with terminal chiasmata were carefully measured; it is true that when there are interstitial or proximal chiasmata the pairs of chromosomes involved in the rearrangement cannot be identified, but otherwise they are readily and accurately identifiable without ambiguity.

The Tosto & Bidau (1991) recombination index, which takes into account the number of segregating units, plus the number of interstitial – or proximal, in the case of submetacentric chromosomes – chiasmata, are correlated with geographic variables.

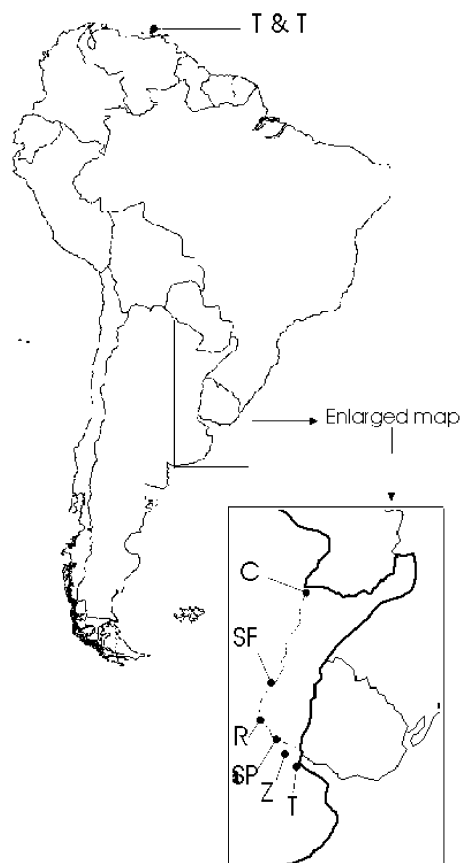


Fig. 1. Map of South-America, plus detail of the River Plate region, showing the location where the population samples of *Cornops aquaticum* were collected. T & T – Trinidad and Tobago; C – Corrientes; SF – Santa Fe; R – Rosario; SP – San Pedro; Z – Zárate; T – Tigre.

The segregating units may be bivalents, the X univalent or, in this case, trivalents.

RESULTS

The karyotype

As stated earlier by Mesa (1956) and Mesa et al. (1982), and recently by De Franca Rocha et al. (2004), *C. aquaticum* has $2n = 23$ chromosomes in males and 24 in females, with an XO/XX sex determination system. This study revealed that all chromosomes of this basic karyotype are acro-telocentric and we numbered them from 1 to 11, according to their size (Fig. 2). Pairs 9, 10, and 11 are distinctly small; the others range from large to medium-



Fig. 2. Karyograms of three different male karyotypes of *Cornops aquaticum*. A – basic karyotype, with $2n = 23$, all chromosomes acro/telocentric; B – karyotype of an individual from the Zárate population, heterozygote for the 1/6 and 2/5 centric fusions, $2n = 21$; C – karyotype of an individual from the Tigre population, homozygote for all three centric fusions, $2n = 17$.

sized. This basic karyotype includes three Rb translocations (= centric fusions) between chromosome pairs 1 and 6 (fusion 1/6), 2 and 5 (fusion 2/5), and 3 and 4 (fusion 3/4), which occur in different frequencies depending on the population (Figs 2 and 3).

Population cytogenetics

The polymorphisms are restricted to the lower course of the Paraná river, between Rosario and Buenos Aires, which are less than 300 km apart, a small distance when compared to the area colonized by this species, between 23°N and 35°S (i.e. from Mexico to Argentina). Of course it is exceedingly difficult to sample a species with such a wide geographical distribution. Only one population that is not Argentinian was included in this study: a sample from Trinidad and Tobago. No Rb polymorphism was found in this population. The northernmost Argentinian sample was from Corrientes, in the middle course of the Paraná river, which also turned out to be monomorphic and without fusions. Two hundred km further south, in Santa Fe, there were 0.12 fusions per individual (fpi); in Rosario this value is still low (0.11 fpi) and then increases noticeably southwards (San Pedro: 1.25 fpi; Zárate: 3.07 fpi). Tigre, the southernmost population, has 5.14 fpi and shows a very high frequency of fusions (the maximum possible is 6 fpi). Although no Uruguayan population was studied, it is known that these polymor-

TABLE 1. Frequencies of fused chromosomes in the different population samples of *Cornops aquaticum*, along with their latitude and longitude.

Population	Fusion 1/6	Fusion 2/5	Fusion 3/4	Latitude	Longitude
Trinidad and Tobago	0	0	0	10.30°N	61.31°W
Pernambuco, Brazil*	0	0	0	8.03°S	34.54°W
Corrientes	0	0	0	27.30°S	58.49°W
Rosario	0.026	0.026	0	33.00°S	60.39°W
San Pedro	0.25	0.20	0.25	33.59°S	59.41°W
Zárate	0.521	0.542	0.438	34.07°S	59.02°W
Tigre	0.884	0.846	0.884	34.35°S	58.34°W

*Source: De Franca Rocha et al., 2004.

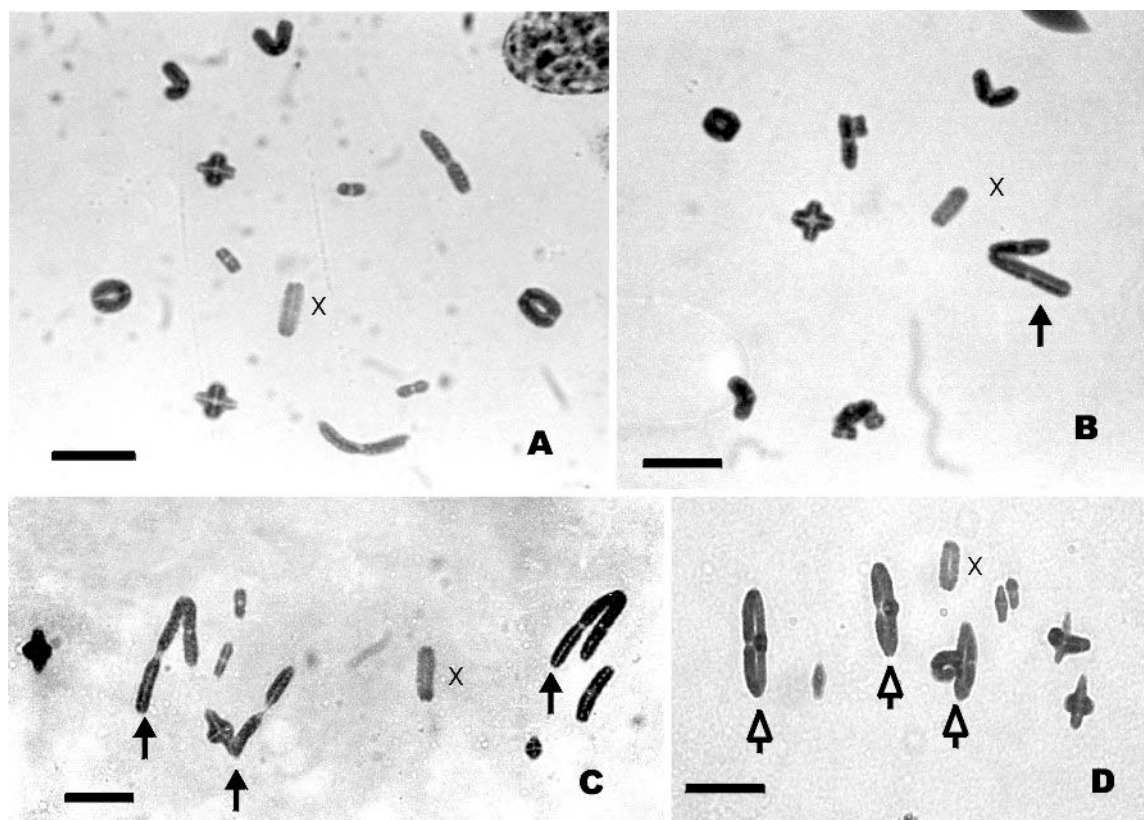


Fig. 3. Metaphase I plates of male *Cornops aquaticum* with different karyotypes. A – basic homozygote without fusions from Corrientes; B – heterozygote for the 1/6 centric fusion from San Pedro; C – heterozygote for all three centric fusions from Zárate; D – homozygote for all three centric fusions from Tigre. Full arrows – trivalents. Empty arrows – Robertsonian bivalents. Bar = 10 μ m.

phisms are present in that country since the original report by Mesa (1956) was of a Uruguayan population collected at latitude 30°S.

The karyotype frequencies are given in Table 1. Between Rosario and Tigre, the fusion frequencies show a significant regression with latitude ($P = 0.023$). Adjustments using the expected frequencies, calculated using the Hardy-Weinberg formula, were made to the two most polymorphic populations, i.e. those from San Pedro and Zárate. The fusion karyotypes, when considered separately, were in keeping with the Hardy-Weinberg values except for fusion 1/6, which exhibited a significant excess

of heterozygotes in Zárate (Table 2); when considered pairwise, they were all in gametic phase equilibrium.

Chiasma studies

Chiasma frequency and distribution was studied in three groups of chromosomes: (a) acro-telocentric bivalents of unfused homozygotes; (b) trivalents of heterozygotes; (c) meta-submetacentric bivalents of fused homozygotes. Chiasmata were classed as proximal (P), interstitial (I) or distal (D) with respect to the centromere. The details of this chiasma study are given in Colombo (2007).

TABLE 2. Comparison of observed karyotype frequencies with those expected according to the Hardy-Weinberg equilibrium in the San Pedro and Zárate polymorphic populations. F – fused chromosome; U – unfused chromosome; O – observed frequency; E – expected frequency. * – statistically significant. n.s. – not significant.

Fusion 1/6 karyotype			Fusion 2/5 karyotype			Fusion 3/4 karyotype					
UU	UF	FF	UU	UF	FF	UU	UF	FF			
(a) San Pedro											
O:	1	2	7	O:	1	3	6	O:	0	5	5
E:	0.4	3.2	6.4	E:	0.6	3.75	5.63	E:	0.63	3.75	5.62
$\chi^2_{(1)} = 0.44$		$P > 0.05$ ns		$\chi^2_{(1)} = 1.41$		$P > 0.05$ ns		$\chi^2_{(1)} = 1.12$		$P > 0.05$ ns	
(b) Zárate											
O:	4	17	3	O:	8	10	6	O:	4	13	7
E:	6.5	11.9	5.53	E:	7	11.9	5.1	E:	4.6	11.8	7.5
$\chi^2_{(1)} = 4.22$		$P < 0.05^*$		$\chi^2_{(1)} = 0.61$		$P > 0.05$ ns		$\chi^2_{(1)} = 0.22$		$P > 0.05$ ns	

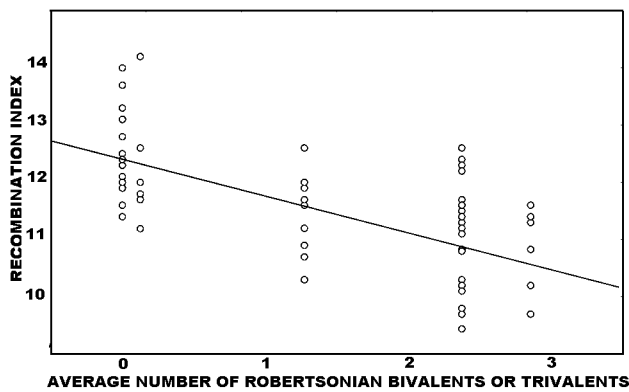


Fig. 4. Graph of the relationship between the individual index of recombination (Y axis) and the average number of fusion bivalents (or trivalents) (X axis) (see text for further explanation).

An index of recombination used by Tosto & Bidau (1991), which consists of the number of bivalents (or segregating blocks, such as trivalents or the X univalent) plus the number of interstitial chiasmata (or, in metacentrics, of proximal and interstitial chiasmata), clearly correlates significantly with the number of fusions per population, and more significantly with the numbers of pairs of chromosomes involved in the centric fusions (Fig. 4).

DISCUSSION

Cytogenetic implications of the Robertsonian rearrangements

It is well known that structural heterozygosity produces problems at meiosis in heterozygotes of chromosomal rearrangements, either in pericentric or paracentric inversions, whole arm reciprocal translocations (WARTs), and Rb translocations (Hewitt, 1979). In the latter case, the commonest irregularity consists of incorrect orientation of the fusion trivalent, which increases if chiasma frequency on the trivalent is high, and if these chiasmata are proximally located (Baker & Bickham, 1986; Bidau, 1991; Searle, 1993). Thus if a fusion polymorphism is to become established in a natural population it needs a high degree of preadaptation, namely by few, distally located chiasmata (Bidau & Mirol, 1988). Another possibility is that chiasmata become redistributed in fusion carriers. This is usually the case in *Leptysma argentina*, another leptysmine grasshopper, where both an inter- as well as an intrachromosomal redistribution of chiasmata is apparent (Colombo, 1989, 1990, 1993), whereas in *Dichroplus pratensis* (Melanoplinae: Acrididae) only the affected chromosomes repattern their chiasma distribution (Bidau, 1990). This was attributed to impaired synapsis due to spatial problems in heterozygotes (Martí & Bidau, 2001). However, the fact that chiasma redistribution also occurs in fusion homozygotes of *L. argentina* has led to the supposition that a different, possibly genetic, effect of the metacentric chromosome may be influencing chiasma distribution in the trivalent (Colombo, 1990).

In *Cornops aquaticum*, the chiasma redistribution affects both fusion homozygotes and heterozygotes,

which causes a severe reduction in the amount of recombination in the populations with a high frequency of metacentrics, both due to the lack of independent segregation and suppression of proximal chiasmata. Darlington (1939) proposed an index of recombination, which consisted of the haploid number of chromosomes plus chiasma frequency. However, not all chiasmata contribute to recombination to the same degree. Arguably, interstitial chiasmata result in a higher level of recombination than terminal chiasmata – unless there are metacentric bivalents or fusion trivalents. In that case, proximal chiasmata also contribute significantly to recombination.

Earlier (Colombo, 1992) we developed an index of recombination that took into account both chiasma position and haploid number of chromosomes (or segregating units, such as trivalents) and applied it to a population sample for which the chiasma distribution had been accurately recorded in diplotene bivalents (Colombo, 1993). As chiasma position is rarely known in such detail, we made correlations with other, simpler indexes of recombination, which indicated that the most accurate is that developed by Tosto & Bidau (1991), which takes into account bivalent (or trivalent) number, interstitial and proximal chiasmata of meta- or submetacentric chromosomes (Colombo, 1992). This index (obtained using data from Colombo, 2007) is highly significantly correlated with fusion number. An even higher degree of correlation was found with the number of chromosomal pairs affected by fusions – assuming no difference between a trivalent and a fused bivalent. It could be argued that this number is included in the index, and so a correlation is expected. However, if there was no change in chiasma distribution, i.e. if chiasmata were still mostly proximal, the correlation would have been very weak, or insignificant.

The central-marginal model challenged

In natural populations of *Drosophila* it is known that the most central populations (both from an ecological and geographical point of view) tend to be more polymorphic for paracentric inversions, and the marginal populations tend to monomorphism. This is termed the “central-marginal model” (Powell, 1997). Cunha & Dobzhansky (1954) proposed, on the basis of data obtained from studies on *Drosophila willistoni*, that the level of inversion polymorphism is directly related to the diversity of the habitat occupied by the populations. The idea is that the greater environmental diversity, the more inversions there are due to diversifying selection. Another explanation of the central-marginal pattern, proposed by Carson (1958), states that central populations are well adapted and hence recombination disrupts coadapted combinations of genes. As inversions suppress recombination in heterozygotes, the low frequency of inversions in marginal populations reflects the need for new combinations of genes in populations that are challenged by environmental instability.

However, in the species of grasshoppers studied, this does not seem to apply. In *Trimerotropis pallidipennis*, a grasshopper with pericentric inversion polymorphisms

(Colombo & Confalonieri, 1996), there is a clear correlation between the inverted sequences and minimum temperature, at least in Argentinian populations. That causes lowland and northern populations to have a high frequency of inversions, whereas high mountain and southern populations have a high frequency of the standard, acrocentric chromosomes. No hint of a central-marginal distribution was found, but the most polymorphic populations were from areas with intermediate temperatures (Confalonieri, 1995).

In the grasshopper *Leptysma argentina*, which has a centric fusion polymorphism, the southern populations have the highest fusion frequency and the lowest degree of recombination (Colombo, 1989), but in many aspects it could be said that these southern populations are marginal for a species whose distribution is mainly tropical and subtropical.

However, the case of *Dichroplus pratensis* seems to be different. This species is polymorphic and/or polytypic for seven different Rb translocations throughout Argentina, and all of them cause a chiasma repatterning leading to a reduction in recombination (Bidau, 1990). Bidau & Martí (2002, 2005) found that heterozygosity is highest in central populations and lower in clearly marginal populations, such as those in Northern Argentina and Patagonia; this geographic pattern is interpreted by the authors as a central-marginal one.

In *Cornops aquaticum*, this does not seem to be the case. It is clear that the mouth of the Paraná river is a marginal environment for this species – in fact, it is by far the southernmost point of its distribution – and yet it is here that the highest frequency of centric fusions was found. In addition, populations from the centre of the geographical distribution, such as those from the state of Pernambuco in Brazil, at latitude 8°S (De Franca Rocha et al., 2004), and Trinidad and Tobago at latitude 10.30°N (this paper) do not show any chromosomal polymorphism. In this case recombination is lowest in the most marginal population, which clearly does not conform to the central-marginal model. A possible, though speculative, explanation of this cline, is that the submetacentric chromosomes bear different genes to those on the standard, acrocentric chromosomes (this is possible due to the reduction in recombination in trivalents). These genes are coadapted (in the sense of Dobzhansky, 1951) and as recombination is suppressed among them they constitute supergenes as in the case of chromosome inversions (Ford, 1971). Some supergenes may be favoured in southern (i.e. with a cooler climate) populations, others in northern populations. The geographical distribution of *C. aquaticum* reinforces this hypothesis. In the northern hemisphere the northernmost boundary of its distribution is around latitude 23°N, whereas in the southern hemisphere the southernmost limit is about latitude 35°S. Probably the difference is caused by the fact that in the south there are big rivers (Paraná and Uruguay) that transport the water-hyacinths southwards. Thus the Rb translocations may allow the southern populations to live in a climate that the species normally cannot withstand.

In species of *Drosophila* where a clinal variation of inversions is found – notably in *D. subobscura* (Prevosti et al., 1988) – similar clines tend to develop wherever this species is transported accidentally by man. In fact, a north-south cline for paracentric inversions in Europe is repeated along the Pacific coast of North-America, and a south-north cline along the Pacific coast of South-America. This invasion of the New World by an Old World species is referred to by Ayala et al. (1989) as “a grand experiment in evolution”. As *C. aquaticum* is about to be introduced into South-Africa as a biological control agent (Oberholzer & Hill, 2001) it is tempting to say that the clines similar to those found in South-America will develop in South-Africa, if the founder populations contains Rb polymorphisms. We look forward to the outcome of this new “experiment in evolution”.

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