

Characterization and distribution of supernumerary chromosomes in 23 colonies of *Partamona helleri* (Hymenoptera, Apidae, Meliponinae)

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ABSTRACT

Partamona helleri has from zero to three supernumerary chromosomes. Analysis of 23 colonies demonstrated that there are two different types of supernumerary chromosomes, a submetacentric chromosome, which we called B₁ type, and a smaller acrocentric chromosome which was designated B₂ type. These chromosomes were differently distributed among individuals of the same colony and among individuals of different colonies. In some colonies, we also observed heteromorphism in the second pair of chromosomes, which may be related to the origin of the supernumerary chromosome system of this species.

INTRODUCTION

Populations of several plant and animal species often include individuals which, in addition to the normal diploid complement, bear extra chromosomes with peculiar characteristics (Jones and Rees, 1982). The genetic role of these supernumerary chromosomes, or B chromosomes, varies among the different species studied. They have been implicated with changes in chiasma frequency and distribution in rye, *Secale cereale* (Jones and Rees, 1967), with leaf striping in maize, *Zea mays* (Staub, 1987), seed germination of *Allium schoenoprasum* with less water (Plowman and Bougourd, 1994), and antibiotic resistance in the fungus *Nectria hemaetococca* (Miao *et al.*, 1991).

In the Hymenoptera, supernumerary chromosomes have been found in four ant species: *Leptothorax spinosior*, which has a supernumerary chromosome system ranging from 0 to 12 (Imai, 1974), *Podomyrma*

adelaide with six to seven supernumeraries (Imai *et al.*, 1977), and *Pseudolasius* sp.2 and *Prenolepsis jerdoni* in which six to 11 supernumeraries have been found (Imai *et al.*, 1984). These chromosomes have also been detected in the bee *Partamona cupira* (= *Partamona helleri*), which has zero to three supernumerary chromosomes (Costa *et al.*, 1992). Another example is the supernumerary chromosome of the parasitoid wasp *Nasonia vitripennis*, called PSR (paternal sex ratio), which transmitted only via sperm, induces the condensation and posterior elimination of the paternal chromosome set, except itself, in fertilized eggs. Because of the haplodiploid sex determination system, such haploid eggs develop into males (Nur *et al.*, 1988).

Characterization of the supernumerary chromosomes of a species is of great importance for the understanding of cytological behavior (stability or accumulation) and their effect on the individuals which bear them (Henriques-Gil *et al.*, 1984). The characterization of the PSR chromosome of *Nasonia vitripennis* by Nur *et al.* (1988) is a clear example of this, as it made possible further molecular characterization and the formulation of hypotheses about the origin and action

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mechanism of this chromosome by Eickbush *et al.* (1992).

MATERIAL AND METHODS

We reanalyzed the data obtained by Costa *et al.* (1992) for 16 colonies collected in Viçosa (20°35' LS, 42°52' LW), São Miguel do Anta (20°42' LS, 42°43' LW), and Guaraciaba (20°35' LS, 43°00' LW), all of them in the State of Minas Gerais, Brazil. Seven new colonies were also analyzed, six from Viçosa and one from Juiz de Fora (21°46' LS, 44°21' LW), also in Minas Gerais.

Cytogenetic analysis was made of the cerebral ganglion and/or gonads of larvae in the prepupal or white-eyed pupa stage, according to the technique of Imai *et al.* (1988). C-band analysis was done according to Sumner (1972), as modified by Pompolo and Takahashi (1990). At least 10 metaphases per slide were examined and those of good quality were photographed with a Zeiss photomicroscope using Agfa Copex Pan A.H.U. film.

RESULTS

The normal chromosome number ($n = 17$; $2n = 34$) was found in 11 of the 23 colonies analyzed. The variations in the remaining colonies and the distribution of the supernumeraries within and among the colonies were designated (Table I).

Metaphase analysis demonstrated the presence of two types of supernumerary chromosomes in *P. helleri*, a submetacentric chromosome, designated B_1 type, and a smaller acrocentric one, which we called B_2 type (Figure 1).

C-banding data demonstrated that the supernumeraries of *P. helleri* (= *P. cupira*) have heterochromatin in the pericentromeric region, in agreement with the observations reported by Costa *et al.* (1992). However, in two of the colonies studied (PX and PU), the B_1 type supernumerary showed two different patterns: one with pericentromeric heterochromatin and the other with heterochromatin along its entire length. Additionally, in some pairs of homologous chromosomes of the normal complement hetero-

chromatin was also present in regions other than the pericentromeric areas (Figures 2 and 3). Unfortunately, we were unable to get a good C-band pattern for the B_2 type chromosome due to its small size.

Karyotype analysis demonstrated a size difference between the long arms of the homologues of the second pair, characterizing heteromorphism in the normal karyotype of some colonies of the species (Figures 1 and 2).

DISCUSSION

The origin of supernumerary chromosomes is still widely debated. Volobujev (1981) suggested two hypotheses to explain the origin of these chromosomes. One proposes that they are a result of structural rearrangements that occurred during evolution in the ancestral karyotype. The other suggests that they result from autosomal or sexual chromosomes that underwent nondisjunction, followed by a process of genetic inactivation. The heteromorphism detected in the second pair of chromosomes in some colonies of *P. helleri* may be related to the origin of supernumerary chromosomes in this species according to the first hypothesis of Volobujev (1981).

The variation in the distribution of B_1 and B_2 type supernumerary chromosomes detected in the

Table I - Diploid number, female gametes, and putative male gametes involved in the production of the different numerical polymorphisms detected in *Partamona helleri*.

Colony designation	Diploid number	F Gametes queen	Putative M gametes	Karyotypes detected
PB, PC, PU, PL, PR, PX	34 and 35	$n = 17$ and $17 + B_1$	$n = 17$	$2n = 34$ and $34 + B_1$ $n = 17$ and $17 + B_1$
PI, PN	35	$n = 17$	$n = 17 + B_2$	$2n = 34 + B_2$ $n = 17$
PT	35 and 36	$n = 17$ and $17 + B_2$	$n = 17 + B_1$	$2n = 34 + B_1$ and $34 + B_1 + B_2$
PM	36	$n = 17$	$n = 17 + B_1 + B_2$	$2n = 34 + B_1 + B_2$ $n = 17 + B_1 + B_2$ and $17 + B_1$
PA	35, 36 and 37	$n = 17, 17 + B_1$ and $17 + B_1 + B_1$	$n = 17 + B_2$	$2n = 34 + B_2, 34 + B_1 + B_2$ and $34 + B_1 + B_1 + B_2$
PO	34, 35 and 36	$n = 17, 17 + B_1, 17 + B_2$ and $17 + B_1 + B_2$	$n = 17 + B_1$	$2n = 34 + B_1, 34 + B_1 + B_1, 34 + B_1 + B_2$ and $34 + B_1 + B_1 + B_2$

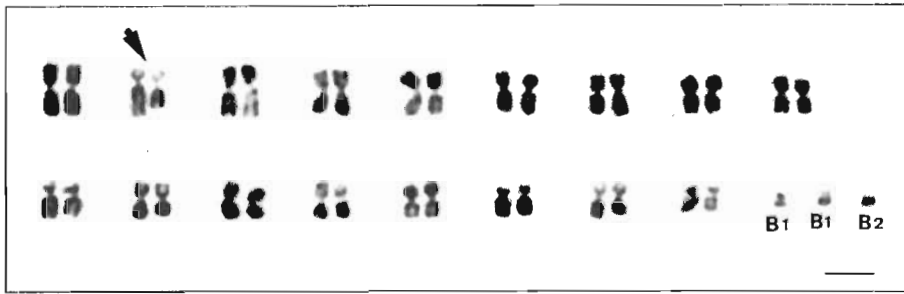


Figure 1 - Karyotype of colony PA of *Partamona helleri* ($2n = 34 + B_1 + B_1 + B_2$) obtained by conventional staining, showing supernumerary chromosomes. The arrow points to a heteromorphism at the second pair of the normal complement. Horizontal bar = 5 μm .

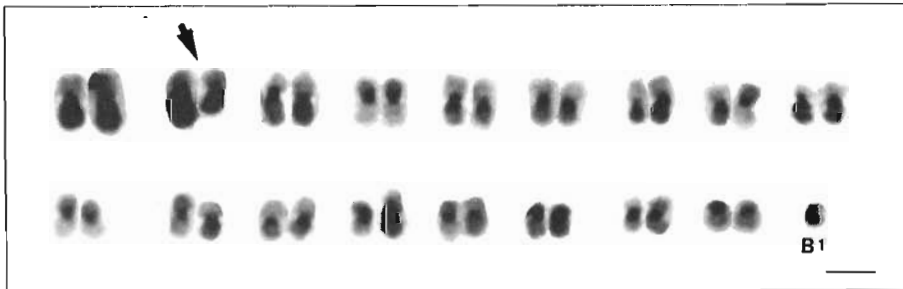


Figure 2 - Karyotype of colony PX of *Partamona helleri* ($2n = 34 + B_1$) obtained by the C-band technique. The arrow points to the heteromorphism detected in the second pair of the normal complement. Horizontal bar = 5 μm .

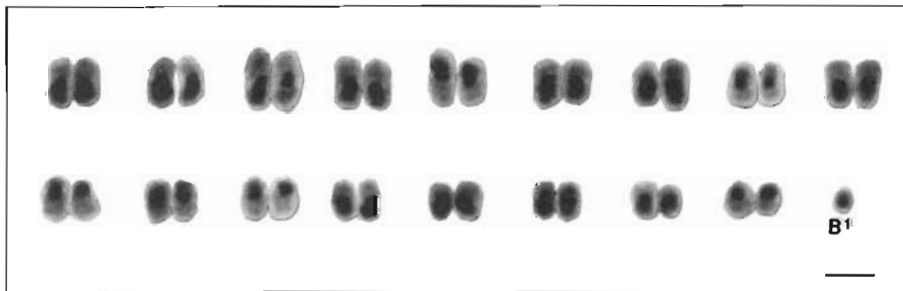


Figure 3 - Karyotype of colony PU of *Partamona helleri* ($2n = 34 + B_1$) obtained by the C-band technique, showing the distribution of heterochromatin along the supernumerary chromosome B_1 . Horizontal bar = 5 μm .

populations could be a result of how these chromosomes were inherited in the colonies studied. According to Costa *et al.* (1992), the origin of the different polymorphic colonies detected in *P. helleri* is due to the production of gametes with different chromosome numbers by the queen and of only one type of gamete by males. Our data support this hypothesis. Table I presents the different types of gametes that may have produced the numeric polymorphism observed in *P. helleri*.

We observed no apparent phenotypic effect due to the presence of these extra chromosomes. However, there may be a mechanism which controls

their accumulation because individuals with more than three supernumeraries were not observed (Figure 1 and Table I). According to Henriques-Gil *et al.* (1984), the mechanisms controlling the number of supernumerary chromosomes in the populations may be related to the differences between them, variations in their cytologic behavior and in their effects on the individuals which bear these chromosomes.

On the basis of the karyotypes detected in colony PM, the males could not have descended from a queen producing only gametes with $n = 17$ (Table I). Thus, these males may have been produced from non-fertilized eggs laid by workers, since workers have the two supernumerary types. Although *Partamona* workers usually have barely developed ovaries (Sakagami *et al.*, 1963), the rare occurrence of this phenomenon gives support to this possibility.

Since the supernumerary chromosomes found in *P. helleri* have no apparent prejudicial effect, we believe that they may persist in the populations, just as happens in the majority of the species that carry supernumerary chromosomes. The rarity in the Hymenoptera may be more related to the scarcity of cytogenetic data in this order than with the possible effects of the supernumeraries. In the case of the Meliponinae, only 75 species out of the 300 which compose this subfamily have already been studied at a cytogenetic level.

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RESUMO

Partamona helleri possui um sistema de cromossomos supranumerários que varia de 0 a 3. A análise de 23 colônias demonstrou que há dois diferentes tipos de cromossomos supranumerários: um submetacêntrico que denominamos tipo B₁ e outro menor e acrocêntrico, o qual foi designado tipo B₂. Estes cromossomos estão distribuídos diferentemente entre indivíduos da mesma colônia e entre indivíduos de colônias diferentes. Foi também observado um heteromorfismo no segundo par do cariótipo de algumas colônias de *P. helleri*, o qual pode estar relacionado com a origem do sistema de cromossomos supranumerários desta espécie.

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