

FURTHER STUDIES ON CHROMOSOMAL VARIABILITY IN THE COMPLEX TAXON *Drosophila serido* (DIPTERA, DROSOPHILIDAE)

Deborah Tosi¹ and Fábio de Melo Sene²

ABSTRACT

Chromosomal arrangements were analyzed in 70 isofemale lines of the *Drosophila serido* taxon originating from 14 different locations. Four new polymorphic arrangements were detected and described in addition to those reported in the literature. The fixed arrangement $2e^8$, heretofore considered to be restricted to *D. borborema*, was also detected in populations from Central-Western Brazil. Data suggesting that these populations of the Central-Western region have reached a degree of differentiation that permits us to consider them as distinct species are discussed. Some of the conclusions reached by Tosi (Masters Thesis, Instituto de Biociências, USP, 1982) were modified, especially by recognizing that the 2Y inversion reported by this investigator indeed corresponds to two inversions: inversion $2x^7$ in Northeastern Brazil, and $2j^9$ in Northern Argentina.

Even though the available data do not cover the entire area of *D. serido* distribution, they support the idea of mosaic differentiation from a single population that may have been isolated in "refugia" owing to the paleoclimatic cycles of the quaternary period.

INTRODUCTION

Drosophila serido (Vilela and Sene, 1977) presents a wide geographic distribution (Vilela *et al.*, 1980, 1983; Sene *et al.*, 1982, 1988; Vilela, 1983; Fontdevila *et al.*, 1988; Silva and Sene, 1989) throughout areas of dry vegetation in South

¹ Departamento de Biologia, Instituto de Biociências, USP, Caixa Postal 11.461, 05499 São Paulo, SP, Brasil.

² Departamento de Biologia, Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, 14049 Ribeirão Preto, SP, Brasil. Send correspondence to F.M.S.

America ("caatinga", dunes, rocky fields, "chaco" and transition areas) and is always associated with the presence of Cactaceae, which represent their breeding sites (Pereira *et al.*, 1983; Wasserman *et al.*, 1983; Fontdevila *et al.*, 1988). The fly belongs to the *D. buzzatii* cluster, *mulleri* complex, *mulleri* subgroup of the *repleta* group (Wasserman, 1982; Ruiz *et al.*, 1982; Wasserman and Richardson, 1987; Fontdevila *et al.*, 1988).

Studies of heterochromatin patterns and morphology of metaphase chromosomes (Baimai *et al.*, 1983), polytene chromosomes (Tosi *et al.*, 1982; Ruiz *et al.*, 1982; Wasserman and Richardson, 1987), aedeagus morphology (Silva, A.F.G. and Sene, F.M. (unpublished results) and reproductive isolation (Bizzo, 1983) have shown marked differences among populations from different areas, though the geographic patterns of the characteristics of each marker do not coincide fully (Sene *et al.*, 1982, 1988).

Fontdevila *et al.* (1988) described the populations of Bolivia and Northern Argentina as a new species, *D. koepferae*, thus elevating *D. serido* to a Superspecies Taxon consisting of two species: *D. serido* (Brazil) and *D. koepferae* (Argentina and Bolivia).

Because of these features of polymorphism and polytypy, this taxon is excellent material for ecologic-adaptative, population differentiation and speciation studies. Its wide distribution throughout the dry areas of South America and ecologic fidelity to cactus plants make this taxon very useful for the study of the influence of paleoclimatic cycles of the quaternary period that were responsible for the expansion and contraction of dry vegetation, forming areas of population isolation and shelters. These cycles, which must have played an important role in the differentiation of tropical populations in South America (Bigarella *et al.*, 1975; Ab'Saber, 1977; Vanzolini, 1981), appear to have also been responsible for the differentiation and structure of *D. mercatorum pararepleta* (Sene, 1986) and of the *D. serido* taxon (Sene *et al.*, 1982, 1988).

The data presented here were obtained by Tosi in 1982. The delay in publication was due to the complexity of the problem and to the fact that we were aware of other studies being conducted on this species that would alter the conclusions reached by Tosi (1982). Data published by Ruiz *et al.* (1982), Wasserman and Richardson (1987) and Fontdevila *et al.* (1988) provided additional information that was not available at the time of Tosi's studies (1982). This has permitted reanalysis of our data and their presentation in a manner compatible with present knowledge.

The use of chromosomal inversions as phylogenetic markers is based on the fact that inversions are extremely rare events considered to be unique within a group of species. The same inversion present in different populations indicates common ancestry or an ancestor-descendant relationship between them (Painter, 1934; Sturtevant and Dobzhansky, 1936; Wasserman, 1960, 1963). Even though they indicate a

phylogenetic relationship, inversions by themselves do not indicate the direction of evolution. Only in certain cases as in Hawaiian *Drosophilidae*, have the phylogenetic relationships determined through inversions been related to evolutionary direction by geomorphological dating (Carson *et al.*, 1970, 1982).

MATERIAL AND METHOD

We analyzed the polytene chromosomes of 70 isofemale lines, each one originating from a single wild female collected at 14 different locations throughout the area of distribution of *D. serido*. The flies were trapped on banana and orange bait fermented with baker's yeast and placed in hanging cans, or in plastic bags, or on the ground according to the techniques of Sene *et al.* (1981b). The collecting sites and the respective lines are listed in Table I.

Twenty to forty pairs from the strain to be analyzed were distributed among tubes measuring 3 cm in diameter and 10 cm high containing *Drosophila* culture medium, 4 pairs to a tube. Twenty larvae from each tube were used for analysis. Chromosome preparations were obtained from salivary glands of 3rd-instar larvae by the classical technique of squashing in lactoacetic orcein. Chromosomes were photographed with a photomicroscope for the identification of chromosome sequences.

To identify the arrangements detected in the second chromosome (chromosome 2) and compare them with those already reported in the literature we used the following technique: on the basis of the breakpoints of the inversions described by Ruiz *et al.* (1982) and Wasserman and Richardson (1987), we constructed a map for chromosome 2 of *D. serido* similar to that prepared by Wasserman and Richardson (1987). The basic scheme used in all studies of this kind, including the present one, is the chromosome map of *D. repleta* presented by Wharton (1942). Thus, we constructed chromosomes with the following band order:

Standard *D. serido* — 2 a b d² e² s⁶ x⁷

Standard *D. borborema* — 2 a b d² e² s⁶ e⁸

Standard *D. koepferae* — 2 a b d² e² s⁶ j⁹

On the basis of these standards, we located on the chromosome map the breakpoints of the polymorphic inversions described by the above authors, i.e.:

D. serido — 2 a⁸, 2 a⁸ b⁸, 2 c⁸, 2 d⁸

D. koepferae — 2 l⁹, 2 k⁹, 2 m⁹, 2 n⁹, 2 u⁹, 2 v⁹, 2 x⁹, 2 w⁹.

For the arrangements detected in chromosomes 3, 4 and 5 we used the same technique as for chromosome 2. However, since in the *repleta* group these chro-

Table 1 - Collection sites and number of isofemale lines of each localization analyzed in the present study.

| Code | Country or State in Brazil | Name and geographical localization | Collection date | Collectors | Number of isofemales lines | Type |
|------|----------------------------|---|-----------------|-------------------------|----------------------------|------|
| A16 | Bahia | Milagres (12°51'S, 39°53'W) | Nov., 24 1976 | F.M. Sene <i>et al.</i> | 4 | I |
| A19 | Bahia | Ibotirama (12°16'S, 43°04'W) | Nov., 27 1976 | F.M. Sene <i>et al.</i> | 1 | IV |
| A53 | Paraguay | Bella Vista (22°12'S, 56°26'W) | April 05, 1977 | F.M. Sene/C.R. Vilela | 1 | IV |
| A55 | M.Gr. Sul | Bela Vista (22°06'S, 56°34'W) | April, 05 1977 | F.M. Sene/C.R. Vilela | 4 | IV |
| A77 | Bahia | Cafarnaum (11°28'S, 41°22'W) | Jan., 22 1978 | F.M. Sene/C.R. Vilela | 1 | I |
| A95 | Minas Gerais | Cardeal Mota (19°18'S, 43°35'W) | June, 02 1978 | F.M. Sene/C.R. Vilela | 2 | IV |
| B20 | Argentina | Tapia (Tucuman) (26°32'S, 65°22'W) | Oct., 25 1978 | F.M. Sene/C.R. Vilela | 5 | III |
| B25 | Argentina | Famatina (La Rioja) (29°01'S, 67°10'W) | Oct., 29 1978 | F.M. Sene/C.R. Vilela | 2 | III |
| B26 | Argentina | Famatina (La Rioja) (29°06'S, 67°10'W) | Oct., 29 1978 | F.M. Sene/C.R. Vilela | 2 | III |
| B31 | Argentina | Puerto Tirol (Chaco) (27°18'S, 59°09'W) | Oct., 30 1978 | F.M. Sene/C.R. Vilela | 6 | II |
| B32 | Argentina | Resistencia (Chaco) (27°17'S, 58°48'W) | Oct., 30 1978 | F.M. Sene/C.R. Vilela | 1 | II |
| B49 | Bahia | Barreiras (12°07'S, 43°04'W) | Oct., 12 1979 | F.M. Sene/G.R. Martho | 5 | IV |
| B50 | Bahia | Ibotirama (12°16'S, 43°04'W) | Oct., 12 1979 | F.M. Sene/G.R. Martho | 10 | IV |
| B53 | Bahia | Milagres (12°51'S, 39°53'W) | Oct., 15 1979 | F.M. Sene/G.R. Martho | 14 | I |
| B58 | Bahia | Paulo Afonso (09°18'S, 38°17'W) | April, 12 1980 | F.M. Sene/C.R. Vilela | 8 | I |
| B59 | Pernambuco | Petrolina (09°23'S, 40°32'W) | April, 16 1980 | F.M. Sene/C.R. Vilela | 4 | IV |

mosomes have a much lower degree of variability we were also able to use as reference the photographic map of the chromosomes of *D. mercatorum mercatorum* presented by Sene *et al.* (1981a).

RESULTS

As mentioned earlier, the present paper represents the full publication of data obtained by Tosi in 1982 and partially presented by Sene *et al.* in 1982 and 1988. The data were obtained from the analysis of 70 isofemale lines derived from collections at 14 different localizations. These 14 locations (Figure 1) do not cover the entire area

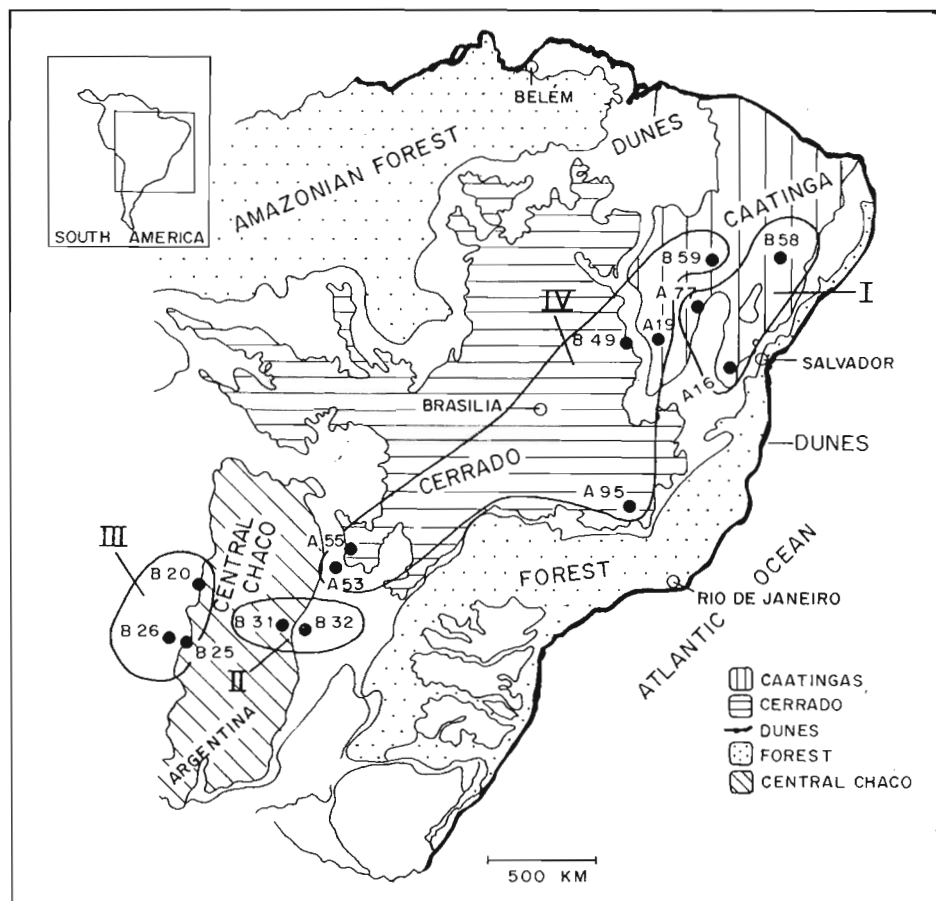


Figure 1 - Map showing the location of the collection sites divided in terms of the 4 types of chromosome structure found. The main types of vegetation are also indicated.

of distribution of this taxon, which was shown in previous studies by Vilela *et al.* (1980, 1983), Sene *et al.* (1982, 1988), Vilela (1983), Fontdevila *et al.* (1988), and Silva and Sene (1989).

Analysis of the chromosomal composition of these 70 isofemale lines revealed the presence of fixed ancestral arrangements and polymorphic arrangements; most of the latter were linked to chromosome 2, which is the most variable chromosome in the *repleta* group (Sene *et al.*, 1981a; Wasserman, 1982; Sene and Santos, 1988). At the time Tosi carried out her work (1982), none of these arrangements had been described and new codes were used to designate them. Later, Ruiz *et al.* (1982) and Wasserman and Richardson (1987) described most of the arrangements following the designation used by Wasserman in his studies on the *repleta* group (Wasserman, 1954, 1960, 1962, 1982). We are presenting in Table II the designations previously given by our group and the corresponding ones used in the present paper.

Table II - Correspondence between the designations for the chromosome arrangements used by Tosi (1982), and in the present paper.

| Designations used by Tosi (1982), and Sene <i>et al.</i> (1982, 1988) | Designation used in the present paper according to Ruiz <i>et al.</i> (1982) and Wasserman and Richardson (1987) |
|--|--|
| "2W" | 2e ⁸ |
| "2Y"* | 2x ⁷ (Brazilian <i>D. serido</i>) |
| "2Y"* | 2j ⁹ (Southern <i>D. serido</i> or <i>D. koepferae</i>) |
| "2b" | 2b ⁸ |
| "2c" | 2a ⁸ |
| "2f" | 2l ⁹ |
| "2g" | 2k ⁹ |
| "2h" | 2m ⁹ |
| "2i"** | 2n ⁹ |
| "3a" | 3k ² |
| "4a" | 4m |
| "5b" | 5w |

* In the studies by Tosi (1982), and Sene *et al.* (1982, 1988), the "2Y" inversion was considered to be fixed in populations from Northeastern Brazil and Northern Argentina. A review of the material in preparation for the present paper revealed that the inversion occurring in Brazil is not the same as that occurring in Argentina, though the breakpoints are close. This is in agreement with the data obtained by Ruiz *et al.* (1982) and Wasserman and Richardson (1987).

** The "2i" inversion, though present in the material studied by Tosi in 1982, was not described in that study.

Other arrangements detected by Tosi (1982) but not yet designated with the nomenclature employed by Wasserman will be presented with quotation marks in the present paper, using the same designations given in the original studies (Tosi, 1982; Sene *et al.*, 1982, 1988). When possible, the breakpoints of the inversions in chromosome 2 were determined on the basis of the basic chromosomes of *D. serido* and *D. borborema* presented by Wasserman and Richardson (1987) and Ruiz *et al.* (1982). The inversions are listed below:

"2a" – (Figure 2) – Breakpoints (C2c – E1d)

"2d" – (Figure 3)

"2e" – (Figure 3)

"5a" – (Figure 4) – Breakpoints (C3a – F1a)

Figure 5 shows chromosome 2 of *D. serido* homozygous for the $2e^8$ ("2W") arrangement.

The chromosome constitution detected in the strains from the different areas analyzed is shown in Table III.

These results lead us to maintain the division of these populations into the same four types as presented by Sene *et al.* (1988), except that differences in fixed arrangements were now found between type I and types II and III. Even though no difference in fixed arrangements exists between types II and III, we have maintained the latter subdivision based on the presence of different polymorphic arrangements until new data clarify the situation. The geographic distribution of these types is shown in Figure 1.

These data alter the chromosome constitution of the *D. buzzatii* cluster presented by Wasserman and Richardson (1987). The main alteration is the presence of the fixed arrangement $2e^8$, which heretofore was thought to be present only in *D. borborema*, in type IV of *D. serido*. Table IV and Figure 6 were constructed from the data obtained in the present study added to all of the data available in the literature.

DISCUSSION

Analysis of the chromosome composition of 70 isofemale lines from 14 different locations throughout the area of geographic distribution of *D. serido* was initially presented by Tosi (1982). Intensive studies carried out in parallel and after 1982 led to changes in the information available in 1982 (Ruiz *et al.*, 1982; Wasserman and Richardson, 1987; Fontdevila *et al.*, 1988). Reanalysis of the data obtained by Tosi in 1982 in the light of the new information led to a change in the conclusions reached in the 1982 work and partially discussed by Sene *et al.* (1982, 1988). The main changes were: 1. we recognize that the populations from Northeastern Brazil

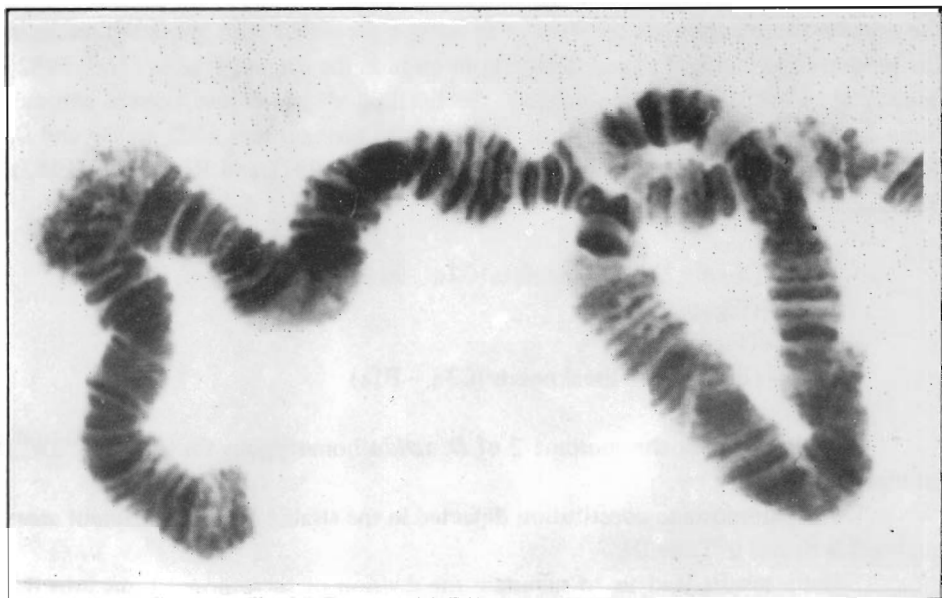


Figure 2 - Photograph of arrangement "2a" in heterozygosis.

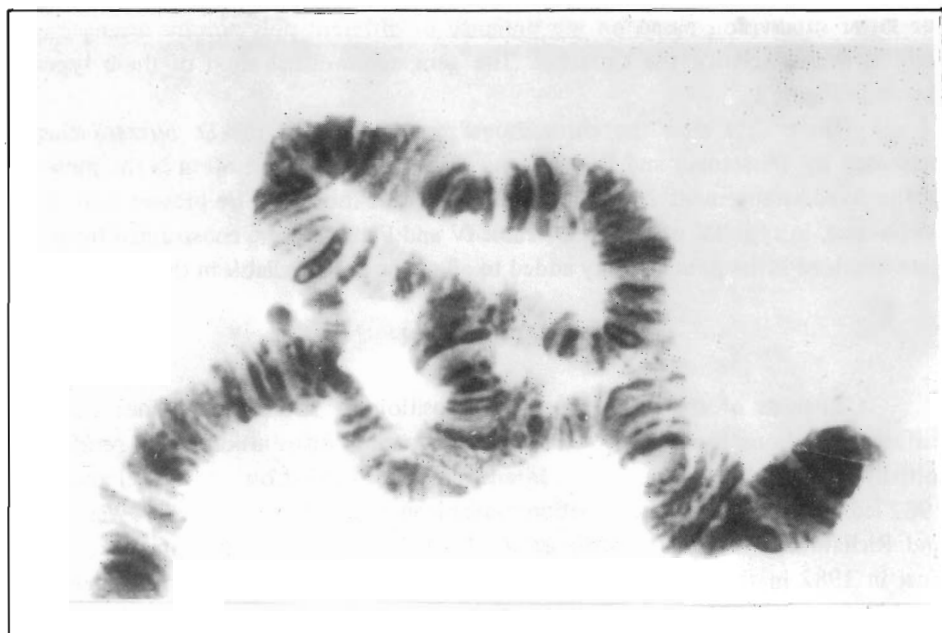


Figure 3 - Photograph of arrangement "2d"/"2e" in heterozygosis.

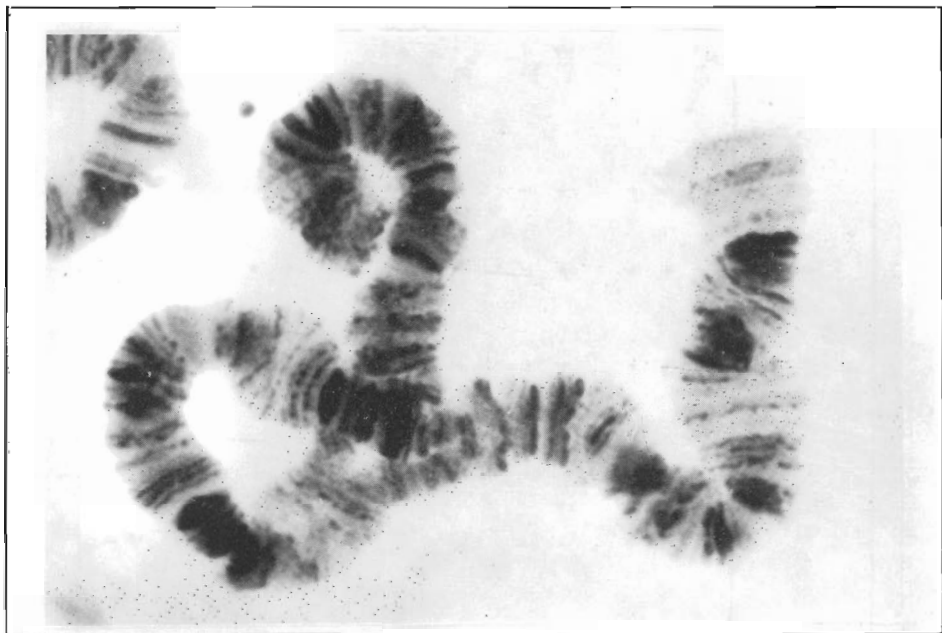


Figure 4 - Photograph of arrangement "5a" in heterozygosis.

and Northern Argentina do not have the same fixed "2Y" chromosomal arrangement. Indeed, the arrangement called "2Y" by Tosi (1982) represents two different inversions though with very close breakpoints: $2x^7$ in Northeastern Brazil and $2j^9$ in Northern Argentina; 2. the population from Cafarnaum, State of Bahia, which was reported by Tosi (1980) to have the ancestral arrangement of the complex, actually presents the $2x^7$ arrangement. This result, confirmed by Wasserman and Richardson (1987), slightly changes the idea that the Diamantina Plateau, part of "Serra do Espinhaço", is a barrier separating the populations with the $2e^8$ arrangement from those with the $2x^7$ arrangement. This situation of possible sympatry may be extended further to the north of Cafarnaum, since Silva and Sene (1989) found that flies having type A aedeagus ($2x^7$ arrangement) were sympatric with type B ($2e^8$ arrangement) in Petrolina, State of Pernambuco.

Thus, Figure 1 in the present paper shows a change in the geographic distribution of the chromosome types shown in Figure 3. in the paper by Sene *et al.* (1982) and in Figure 2 in the paper by Sene *et al.* (1988).

The present study increases by four the number of polymorphic inversions known for this species and shows the presence of inversion $2e^8$, which was previously thought to be restricted to *D. borborema* (Wasserman and Richardson, 1987), in populations of Central and Western Brazil, called "type IV" by Sene *et al.* (1988).

Table III - Chromosome arrangements of *D. serido* in the different strains analyzed in the present paper.

| Type | Locality | Number of isofemale lines | X a b c | 2 a b d ² s ⁶ e ² | 3b | 4 | 5 | Polymorphism |
|------|----------------------------|---------------------------|---------|--|----|---|---|---|
| I | A16/B53 - Milagres - BA | 18 | + | x ⁷ | + | + | + | 2a ⁸ , 2a ⁸ /b ⁸ |
| I | A77 - Cafarnaum - BA | 1 | + | x ⁷ | + | + | + | |
| I | B58 - Paulo Afonso - BA | 8 | + | x ⁷ | + | + | + | 2a ⁸ |
| II | B31 - Puerto Tirol - Arg. | 6 | + | j ⁹ | + | + | + | "2d/e", "5a" |
| II | B32 - Resistencia - Arg. | 1 | + | j ⁹ | + | + | + | "2d/e", "5a" |
| III | B20 - Tapia - Arg. | 5 | + | j ⁹ | + | + | + | 2l ⁹ , 2k ⁹ , 2m ⁹ , 2n ⁹ , 3k ² , 4m, 5w |
| III | B25/B26 - Famatina - Arg. | 4 | + | j ⁹ | + | + | + | 2l ⁹ , 2k ⁹ , 2m ⁹ , 2n ⁹ |
| IV | A19/B50 - Ibotirama - BA | 11 | + | e ⁸ | + | + | + | "2a" |
| IV | A53 - Bella Vista - Parag. | 1 | + | e ⁸ | + | + | + | "2a" |
| IV | A55 - Bela Vista - MS | 4 | + | e ⁸ | + | + | + | "2a" |
| IV | A95 - Cardeal Mota - MG | 2 | + | e ⁸ | + | + | + | |
| IV | B49 - Barreiras - BA | 5 | + | e ⁸ | + | + | + | "2a" |
| IV | B59 - Petrolina - PE | 4 | + | e ⁸ | + | + | + | "2a" |

Table IV - Chromosome constitution of the *D. buzzatii* cluster. (1) Sene *et al.* (1988); (2) Wasserman and Richardson (1987); (3) Fontdevila *et al.* (1988); (4) Wasserman (1982); (5) Ruiz *et al.* (1982); (6) Ruiz *et al.* (1984; (7) Present paper; (8) Sene *et al.* (1982); (9) Barker *et al.* (1985).

| Species and Types | Xabc | 2ab d ² s ⁶ e ² | 3b | 4 | 5 | Polymorphisms |
|---|------|--|----|---|---|--|
| <i>D. buzzatii</i> | + | + | + | + | g | 13 inversions (4, 5, 6, 8, 9) |
| <i>D. borborema</i> | + | e ⁸ | + | + | + | 2f ⁸ , 2f ⁹ /e ⁸ , 2f ⁸ , 2h ⁸ (2) |
| <i>D. serido</i> - Type I (1) - (Brazilian <i>D. serido</i>) (2) | + | x ⁷ | + | + | + | 2a ⁸ , 2a ⁸ /b ⁸ (2,7), 2c ⁸ /d ⁸ (2) |
| - Type II (1) | + | j ⁹ | + | + | + | "2de", "5a" (7) |
| - Type III (1) - Southern <i>D. serido</i> | + | j ⁹ | + | + | + | 2k ⁹ , 2l ⁹ , 2m ⁹ , 2n ⁹ , 3k ² |
| (2) - <i>D. koeppferae</i> (3) | | | | | | 4m, 5w (5, 7) |
| - Type IV (1) - (Central-Western - Brazilian <i>D. serido</i>) (7) | + | e ⁸ | + | + | + | "2a" (7) |

(1) = Sene *et al.*, 1988; (2) = Wasserman and Richardson, 1987; (3) = Fontdevila *et al.*, 1988; (4) = Wasserman, 1982; (5) = Ruiz *et al.*, 1982; (6) = Ruiz *et al.*, 1984; (7) = Present paper; (8) = Sene *et al.*, 1982; (9) = Barker *et al.*, 1985.

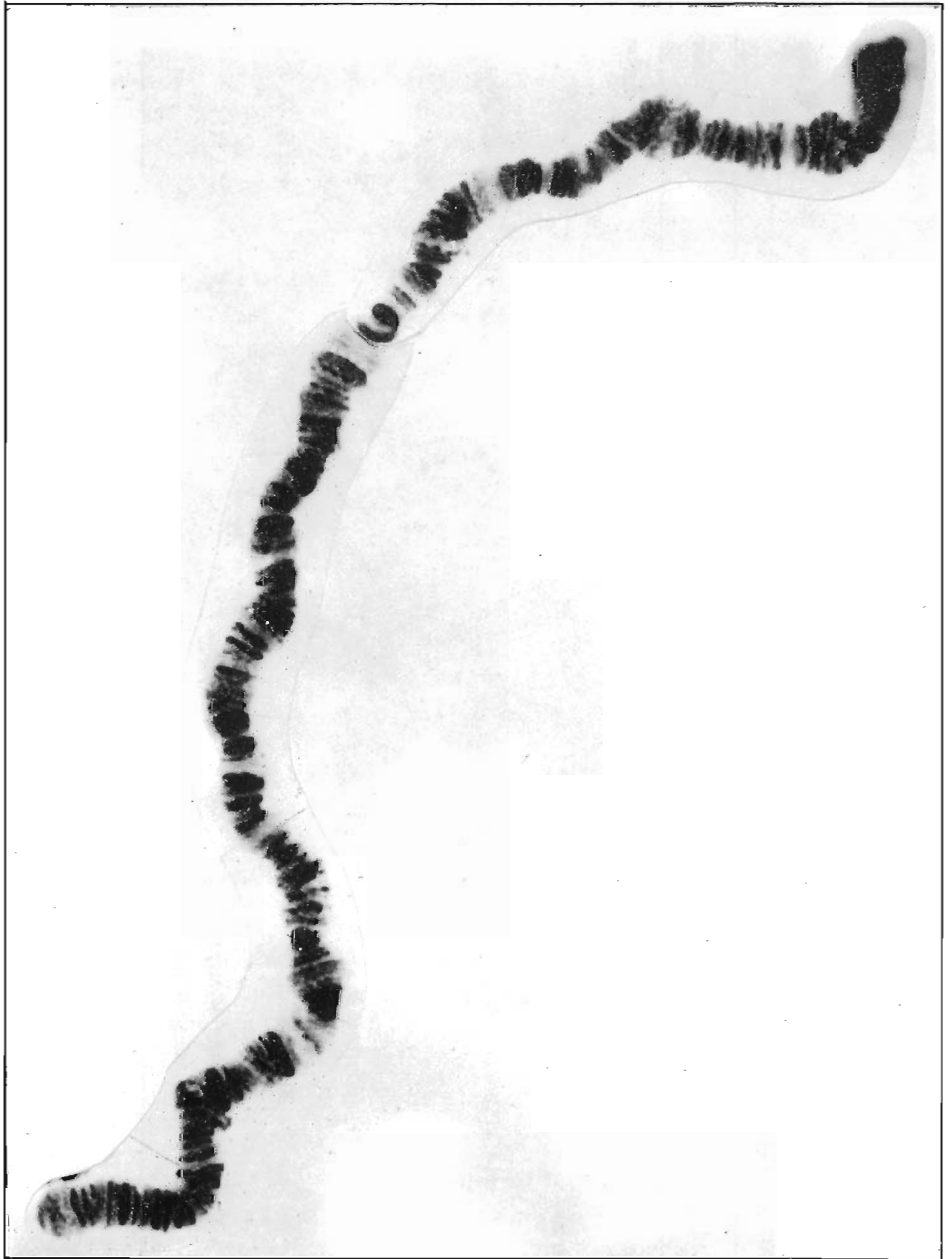
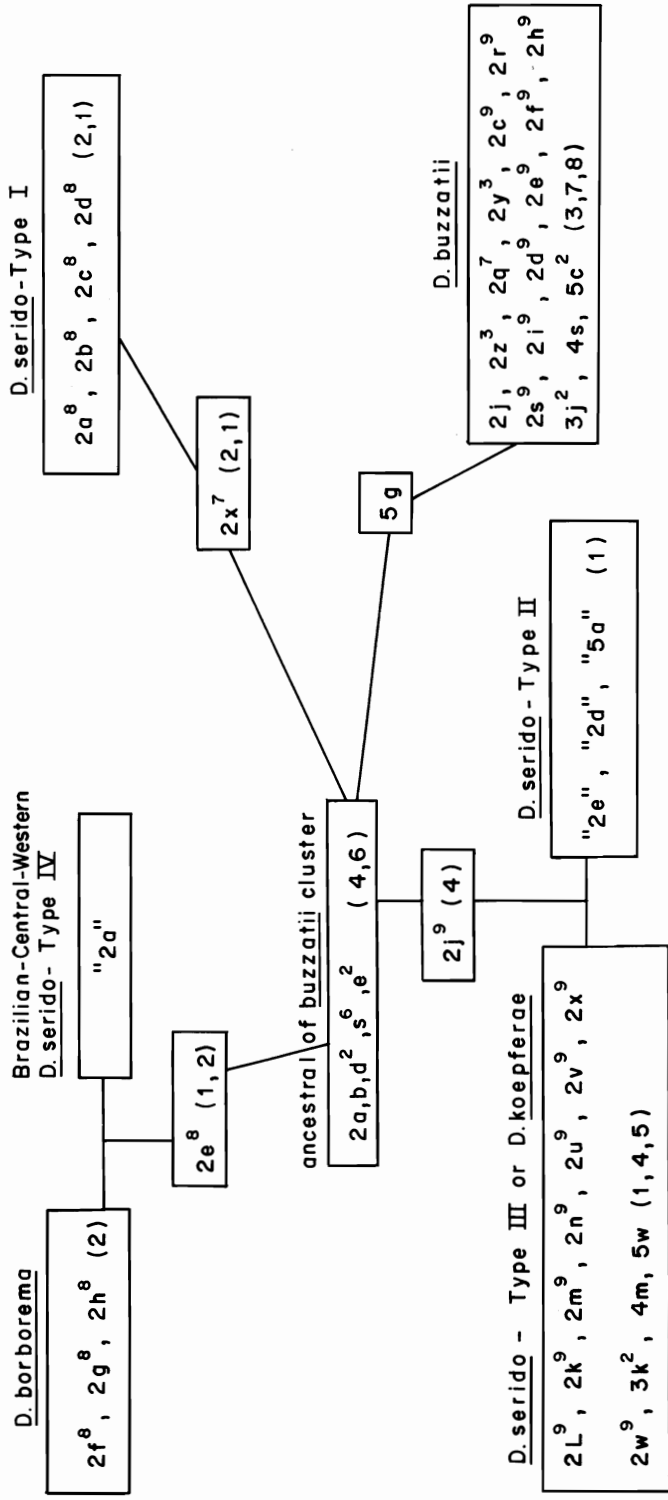


Figure 5 - Photograph of chromosome 2 of *D. serido* homozygous for the $2e^8$ ("2W") arrangement.



(1) = present paper; (2) = Wasserman & Richardson, 1987; (3) = Ruiz et al., 1984; (4) = Ruiz et al., 1982; (5) = Fontdevila et al., 1988; (6) = Ruiz et al., 1981; (7) = Sene et al., 1982; (8) = Barker et al., 1985.

Figure 6 - Diagram of chromosome arrangements in the *D. buzzatii* cluster. (1) - present paper; (2) - Wasserman and Richardson (1987); (3) Ruiz et al. (1984); (4) - Ruiz et al. (1988); (5) - Fontdevila et al. (1988); (6) - Ruiz et al. (1981); (7) - Sene et al. (1982); (8) - Barker et al. (1985).

These type IV populations also show differentiation in aedeagus morphology and were characterized as type B by Silva and Sene (1989) on the basis of this trait. They also show reproductive isolation from most of the other *D. serido* populations (Bizzo, 1983; Sene *et al.*, 1988). These characteristics would be sufficient to permit these populations to be described as a new species. However, before this can be done a better analysis will be needed of the sympatric situations detected by Silva and Sene (1989) in collections made at B59-Petrolina, State of Pernambuco and A95-Cardeal Mota, State of Minas Gerais. At present we shall continue to call this population "Central-Western Brazilian *D. serido*" type IV in terms of polytene chromosomes, type B in terms of aedeagus morphology, and type II in terms of reproductive isolation.

The populations of Northeastern Argentina (B31-Resistência and B-32-Puerto Tirol) seem to be isolated from the populations along the slopes of the Andes in the Tucumán and La Rioja Provinces, where the populations of *D. koepferae* are found (Vilela *et al.*, 1980). They present the $2j^9$ inversion that is fixed in *D. koepferae*, but have different polymorphic arrangements. The type D aedeagus found in these populations (Silva and Sene, 1989) appears to be similar to that found by Fontdevila *et al.* (1988) in Bolivian populations, which they also described as *D. koepferae*. This suggests that the distribution of Puerto Tirol and Resistência populations may be continuous to that of *D. koepferae*, not through the Central Chaco (Vilela *et al.*, 1980) but by-passing it to the north through Paraguay and Bolivia. Further collections in this region may clarify the problem.

Analysis of all the markers used thus far in the study of these populations is indicating a type of mosaic differentiation, suggesting that all of these populations differentiated more or less simultaneously from the isolation of populations of the same species previously showing continuous geographic distribution. This isolation must have occurred during the paleoclimatic cycles of the quaternary period with the expansion of humid vegetation and the retraction of dry vegetation, including Cactaceae. Since at least four such cycles occurred during the quaternary period, all of them superimposed in the same area, it is difficult to determine if the differentiation of the *buzzatii* cluster was the consequence of one or more cycles (Sene, 1986; Sene *et al.*, 1988).

The presence of relict populations of *D. buzzatii* in the caatinga of Northern Brazil is additional evidence of these cycles, which was accompanied by differentiation at the isoenzyme level and loss of variability at the chromosome level in *D. buzzatii* (Barker *et al.*, 1985).

The presence of arrangement $2e^8$, fixed in *D. borborema* whose distribution is limited to the caatinga of Northeastern Brazil (Sene *et al.*, 1982; Vilela *et al.*, 1983) and also fixed in the Central-Western Brazilian populations, represents additional evidence of mosaic differentiation, which practically rules out the possibility of simple phylogenetic ties between these populations.

Even though the present study has significantly extended the area of this taxon that has been analyzed chromosomally, it still leaves unstudied all of the populations in Southern and Southeastern Brazil where the species occurs along the coast, with separate populations in the dunes, and in the hinterland, where it occurs in "islands" or "refugia" of dry areas containing Cactaceae in the States of São Paulo, Paraná, Santa Catarina and Rio Grande do Sul.

ACKNOWLEDGMENTS

We are grateful to Dr. J.M. Amabis for constant help with the inversion analyses, to Drs. M.A.Q.R. Pereira, C.R. Vilela and F.C. Val and to our colleagues A.F.G. Silva and N.M.V. Bizzo for suggestions and encouragement. Marcos R. de Souza prepared the map.

Research supported by FAPESP, CNPq, FINEP and University of São Paulo.

RESUMO

Foram analisados os arranjos cromossômicos de 70 "isofemais lines" do Taxon *D. serido* originados de 14 localidades diferentes. Além dos arranjos já descritos na literatura foram encontrados, e descritos, mais 4 arranjos polimórficos. Foi encontrado também o arranjo fixo $2e^8$, até então restrito a *D. borborema*, nas populações da região centro-oeste do Brasil. Foram discutidos os dados que sugerem que estas populações da região centro-oeste tenham atingido um grau de diferenciação que permita que elas sejam descritas como uma espécie distinta. Algumas conclusões de Tosi (Masters Thesis, Instituto de Biociências, USP, 1982) foram alteradas, principalmente com o reconhecimento de que a inversão "2Y" daquele trabalho, na realidade são duas inversões: - inversão $2x^7$, no nordeste do Brasil, e $2j^9$ no norte da Argentina.

Os dados disponíveis embora ainda não cubram toda a área de distribuição da espécie, reforçam a idéia de diferenciação em mosaico a partir de uma única população que teria sido isolada em "refúgios" em decorrência dos ciclos paleoclimáticos do período quaternário.

REFERENCES

- Ab'Saber, A.N. (1977). Espaços ocupados pela expansão dos climas secos da América do Sul, por ocasião dos períodos glaciais quaternários. *Paleoclimas* 3: 1-19.
- Baimai, V., Sene, F.M. and Pereira, M.A.Q.R. (1983). Heterochromatin and karyotypic differentiation of some neotropical cactus-breeding species of the *Drosophila repleta* species group. *Genetica* 60: 81-92.
- Barker, J.S.F., Sene, F.M., East, P.D. and Pereira, M.A.Q.R. (1985). Allozyme and chromosomal polymorphism of *Drosophila buzzatii* in Brazil and Argentina. *Genetica* 67: 161-170.
- Bigarella, J.J., Andrade-Lima, D. and Riehs, P.J. (1975). Considerações a respeito das mudanças paleoclimáticas na distribuição de algumas espécies vegetais e animais no Brasil. *An. Acad. Brasil. Cienc.* 41 (Supl.): 411-464.

- Bizzo, N.M.V. (1983). Estudo sobre a biologia e isolamento reprodutivo em *Drosophila serido*. Master Thesis. Instituto de Biociências, USP, São Paulo.
- Carson, H.L., Hardy, D.E., Spieth, H.T. and Stone, W.S. (1970). The evolutionary biology of the Hawaiian Drosophilidae. In: *Evolution and Genetics in Honor of Theodosius Dobzhansky*. (Hecht, M.K. and Steere, W.C., eds.). Appleton-Century-Crofts, New York, pp. 437-543.
- Carson, H.L. and Yoon, J.S. (1982). Genetics and Evolution of Hawaiian *Drosophila*. In: *The Genetic and Biology of Drosophila* (Ashburner, M., Carson, H.L. and Thompson Jr., J.N., eds). Vol 3b. Academic Press, London, pp. 297-344.
- Fontdevila, A., Pla, C., Hasson, E., Wasserman, M., Sanchez, A., Naveira, H. and Ruiz, A. (1988). *Drosophila koepferae*: A new member of the *Drosophila serido* (Diptera, Drosophilidae) Superspecies Taxon. *Annals of the Entomol. Soc. of America* 81 (3): 380-385.
- Painter, T.S. (1934). Salivary chromosomes and the attack on the gene. *J. Hered.* 25: 465-476.
- Pereira, M.A.Q.R., Vilela, C.R. and Sene, F.M. (1983). Notes on breeding and feeding sites of some species of the *repleta* group of the Genus *Drosophila* (Diptera, Drosophilidae). *Ciênc. Cult.* 35 (9): 1313-1319.
- Ruiz, A. and Fontdevila, A. (1981). Ecología y Evolution del subgrupo *mulleri* de *Drosophila* en Venezuela y Colombia. *Acta Cient. Venezolana* 32: 338-345.
- Ruiz, A., Fontdevila, A. and Wasserman, M. (1982). The Evolutionary history of *D. buzzatii*. III. Cytogenetic Relationships Between Two Sibling Species of the *buzzatii* cluster. *Genetics* 101: 503-518.
- Ruiz, A., Naveira, H. and Fontdevila, A. (1984). La Historia Evolutiva de *Drosophila buzzatii*. IV. Aspectos citogenéticos de su polimorfismo cromossômico. *Genet. Iberica* 36: 13-35.
- Sene, F.M. (1986). Geographic and ecological pattern of chromosome polymorphism in *Drosophila mercatorum pararepleta*. *Rev. Bras. Genet.* IX: 573-591.
- Sene, F.M., Amabis, J.M., Carson, H.L. and Cyrino, T.H.F.S. (1981a). Chromosome polymorphism in *Drosophila mercatorum pararepleta* in South America. *Rev. Bras. Genet.* IV: 1-10.
- Sene, F.M., Pereira, M.A.Q.R., Vilela, C.R. and Bizzo, N.M.V. (1981b). Influence of different ways to set baits for collection of *Drosophila* flies in three natural environments. *Dros. Inf. Service* 56: 118-121.
- Sene, F.M., Pereira, M.A.Q.R. and Vilela, C.R. (1982). Evolutionary aspects of cactus breeding *Drosophila* species in South America. In: *Ecological Genetics and Evolution* (Barker, J.S.F. and Starmer, W.T., eds.). Academic Press, Sydney Austrália, pp. 97-106.
- Sene, F.M., Pereira, M.A.Q.R. and Vilela, C.R. (1988). Contrasting patterns of differentiation inferred from traditional genetic markers in the process of speciation. *Pacific Science* 42: 81-88.
- Sene, F.M. and Santos, T.H.F. (1988). Chromosomal variability in *Drosophila paranaensis* from Brazil, South America. *Evolución Biológica* 2: 261-271.
- Silva, A.F.G. and Sene, F.M. Morphological geographic variability in *Drosophila serido* (Diptera, Drosophilidae). *Rev. Bras. Ent.*, (submitted).
- Sturtevant, A.H. and Dobzhansky, T.H. (1936). Inversions in the third chromosome of wild races of *Drosophila pseudoobscura* and their use in the study of the history of the species. *Proc. Natl. Acad. Sci.* 22: 448-450.

- Tosi, D. (1982). Análise das inversões cromossômicas de *D. serido*. Masters Thesis. Instituto de Biociências, USP, São Paulo.
- Vanzolini, P.E. (1981). A quasi-historical approach to the natural history of the differentiation of reptiles in tropical geographic isolates. *Papéis Avulsos Zool.* (São Paulo) 34: 189-204.
- Vilela, C.R. (1983). A revision of the *Drosophila repleta* species group (Diptera, Drosophilidae). *Rev. Bras. Ent.* 27: 1-114.
- Vilela, C.R. and Sene, F.M. (1977). Two new neotropical species of the *repleta* group of the genus *Drosophila* (Diptera, Drosophilidae). *Rev. Bras. Ent.* 30: 295-299.
- Vilela, C.R., Sene, F.M. and Pereira, M.A.Q.R. (1980). On the *Drosophila* fauna of Chaco and East Slopes of Andes in Argentina. *Rev. Bras. Biol.* 40: 837-841.
- Vilela, C.R., Pereira, M.A.Q.R. and Sene, F.M. (1983). Preliminary data on the geographical distribution of *Drosophila* species within morphoclimatic domains of Brazil. II. The *repleta* group. *Ciênc. Cult.* 35: 66-70.
- Wasserman, M. (1954). Cytological studies of the *repleta* group. *Univ. Tex. Publ.* 5422: 130-152.
- Wasserman, M. (1960). Cytological and phylogenetic relationship in the *repleta* group of the genus *Drosophila*. *Proc. Natl. Acad. Sci. USA* 46: 842-859.
- Wasserman, M. (1962). Cytological studies of the *repleta* group of genus *Drosophila*: the *mulleri* subgroup. *Univ. Tex. Publ.* 6205: 85-117.
- Wasserman, M. (1963). Cytology and phylogeny of *Drosophila*. *Amer. Natur.* 97: 333-352.
- Wasserman, M. (1982). Evolution and speciation in selected species groups. The *repleta* species group. In: *The Genetics and Biology of Drosophila* (Ashburner, M., Carson, H.L. and Thompson Jr., J.N., eds.). Vol. 3b. Academic Press, NY. pp. 61-139.
- Wasserman, M., Fontdevila, A. and Ruiz, A. (1983). Potential gene exchange between South American *Drosophila* species, with a description of a new species in the *D. repleta* group. *Ann. Entomol. Soc. Amer.* 76: 675-677.
- Wasserman, M. and Richardson, R.H. (1987). Evolution of Brazilian *Drosophila mulleri* complex species. *The Journal of Heredity*, 78: 282-286.
- Wharton, L.T. (1942). Analysis of the *repleta* group of *Drosophila*. *Univ. Tex. Publ.* 4228: 23-52.

(Received June 30, 1989)