

# THE INTERRELATIONSHIPS OF THE INCIPIENT SPECIES WITHIN THE *DROSOPHILA PAULISTORUM* COMPLEX

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*Drosophila paulistorum* Dobzhansky and Pavan is a species, or a superspecies, possessing remarkably complex and interesting genetic architecture. As shown by Dobzhansky and Spassky (1959), *D. paulistorum* consists of six races or incipient species, at least five of which are, in varying degrees, reproductively isolated from each other. These five (Andean-South Brazilian, Amazonian, Orinocan, Guianan, and Central American) cross with difficulty and produce progenies consisting of fertile daughters and sterile sons. The sixth, Transitional race, consists of strains which can be crossed to each other and to at least one other race, the crosses yielding fertile progenies. As demonstrated by Ehrman (1960, 1961), the genetic basis of the hybrid male sterility is a maternal effect which makes all sons of the mothers carrying racially mixed karyotypes sterile, while the sexual (behavioral) isolation is determined polygenically, the sexual compatibility being a function of the proportions of the genes of the different races which the individuals carry.

Each race has its own geographic distribution area, although in several places the areas overlap and in these places two or even three races coexist sympatrically without interbreeding. Such sympatric populations behave as though they were full-fledged species, and yet gene exchange between them is still possible by way of the Transitional race (and of the transitional strains described below). The distributional relationships between the races and the reproductive characteristics of the populations of *D. paulistorum* obviously demand further study, and the present article reports observations and experiments on

the populations in different parts of Brazil.

## MATERIALS AND METHODS

New population samples of *D. paulistorum* have been collected in eight localities in Brazil: Belém, Pará, January, 1961, L. E. Magalhães and Bruce Wallace; Carolina, Maranhão, January, 1961, L. E. Magalhães and Bruce Wallace; Maranguape, Ceará, March, 1961, C. Malogolowkin; Recife, Pernambuco, November, 1960, C. Malogolowkin; Salvador, Bahia, July, 1960 and March, 1961, C. Malogolowkin; Goiania, Goiás, March, 1961, C. Malogolowkin; Cerra do Cipó, Minas Gerais, February, 1961, C. Malogolowkin; Rio de Janeiro, Guanabara, September, 1960, C. Malogolowkin.

Strains were established from single females collected in nature. The numbers of the original strains were as follows:

|            |         |
|------------|---------|
| Belém—71   | Bahia—9 |
| Carolina—2 | Goiás—2 |
| Ceará—13   | Cipó—5  |
| Recife—18  | Rio—45  |

These strains were crossed individually to three other strains, namely Belém (Amazonian race, obtained from the laboratory of Professor Th. Dobzhansky, at Columbia University, derived from ancestors collected at Belém in 1948), Angra (Andean-South Brazilian race, obtained from the same laboratory, collected at Angra dos Reis in 1956) and Ceará (undetermined race, obtained from the laboratory of C. Pavan, derived, probably, from ancestors collected by Dobzhansky in 1956). Some of the crosses resulted in no progeny, while some gave sterile and other fertile male hybrids. According to the behavior observed, the

|                          |          | AMAZONIAN |      |      |      |      |          | ANDEAN-SOUTH BRAZILIAN |         |      |          |       |          |      |      |       |         |      |        |      |       |      |          |          |   |
|--------------------------|----------|-----------|------|------|------|------|----------|------------------------|---------|------|----------|-------|----------|------|------|-------|---------|------|--------|------|-------|------|----------|----------|---|
|                          |          | BELEM-A   | " -B | " -C | " -J | " -L | PANAMA-A | TRINIDAD               | BELEM-K | " -D | CAROLINA | CEARA | RECIFE-A | " -B | " -C | BAHIA | GOIAS-A | " -B | CIPO-A | " -B | RIO-A | " -B | URUBAMBA | LLANOS-B |   |
| AMAZONIAN                | BELEM-A  |           | F    |      | F    | F    | F        | F                      | O       | S    |          | S     |          |      |      | O     | S       |      |        |      |       |      |          |          |   |
|                          | " -B     |           |      | F    | F    | F    |          | F                      | O       |      | S        | O     | S        |      | S    | O     | S       | S    |        |      |       |      |          |          |   |
|                          | " -C     |           | F    | F    |      | F    | F        | F                      | O       | S    |          |       |          |      |      | S     |         |      |        |      |       |      |          |          |   |
|                          | " -J     |           | F    | F    | F    |      | O        | F                      | O       | S    | S        | O     |          |      | O    | O     | S       | O    | S      | O    | O     | O    | O        | O        | S |
|                          | " -L     |           | F    | F    | F    |      |          | F                      | F       | O    | O        | O     |          | O    | O    | S     |         | O    | O      | O    | O     | O    | O        | O        | S |
| ANDEAN - SOUTH BRAZILIAN | PANAMA-A |           | F    | F    | F    | F    |          |                        | O       | O    | O        | O     | O        | O    | O    | O     | O       | O    | O      | O    | O     | O    | O        | O        | O |
|                          | TRINIDAD |           | F    | F    | F    | F    |          |                        | O       | O    | O        | O     | O        | O    | O    | O     | O       | O    | O      | O    | O     | O    | O        | O        |   |
|                          | BELEM-K  |           | O    | O    | O    | O    | O        | O                      |         | S    | S        | O     | S        | S    | O    | O     | O       | O    | O      | O    | S     | O    | S        | O        | O |
|                          | " -D     |           | S    |      | S    | S    | S        | S                      | O       |      |          | F     | F        | F    | F    | F     |         | F    |        | F    | F     |      |          |          |   |
|                          | CAROLINA |           | S    |      |      | S    | S        | S                      | O       |      |          | F     | F        |      | F    | F     | F       | F    | F      | F    | F     | F    | F        | F        | F |
|                          | CEARA    |           | O    | S    | S    | O    | S        | S                      | O       | O    | F        | F     |          | F    | F    | F     | F       | F    | F      | F    | F     | F    | F        | F        | F |
|                          | RECIFE-A |           |      |      | S    | S    | S        | S                      | O       |      |          | F     |          | F    |      | F     | F       | F    | F      | F    | F     | F    | F        |          |   |
|                          | " -B     |           |      | S    |      | O    | S        | S                      | O       | O    | S        | F     | F        |      | F    | F     | F       | F    | F      | F    | F     | F    | F        | F        | F |
|                          | " -C     |           |      | S    |      |      | S        | S                      | O       | F    |          | F     | F        |      | F    | F     | F       | F    | F      | F    | F     | F    | F        | F        | F |
|                          | BAHIA    |           | S    | S    | S    | S    | S        | S                      | O       | O    | F        | F     | F        | F    | F    | F     | F       | F    | F      | F    | F     | F    | F        | F        | F |
|                          | GOIAS-A  |           |      | S    |      | S    | S        | S                      | O       | F    |          | F     | F        |      | F    | F     | F       | F    | F      | F    | F     | F    | F        | F        | F |
|                          | " -B     |           |      | S    |      | S    | S        | O                      | S       | O    |          | F     | F        |      | F    | F     | F       | F    | F      | F    | F     | F    | F        | F        | F |
|                          | CIPO-A   |           |      | S    |      | S    | S        | S                      | O       | F    | F        | F     | F        |      | F    | F     | F       | F    | F      | F    | F     | F    | F        | F        | F |
|                          | " -B     |           |      | S    |      | S    | S        | S                      | O       |      |          | F     | F        |      | F    | F     | F       | F    | F      | F    | F     | F    | F        | F        | F |
| RIO-A                    |          |           | S    |      | S    | S    | O        | S                      | O       |      | F        | F     | F        |      | F    | F     | F       | F    | F      | F    | F     | F    | F        | F        |   |
| " -B                     |          |           | S    |      | S    | O    | O        | O                      | O       | F    | F        | F     | F        |      | F    | F     | F       | F    | F      | F    | F     | F    | F        | F        |   |
| URUBAMBA                 |          | O         | O    | O    | O    | O    |          |                        | O       | F    | F        | F     | F        | F    | F    | F     | F       | F    | F      | F    | F     | F    | F        | F        |   |
| LLANOS-B                 |          | O         | O    | O    | O    | S    |          |                        | S       | F    | F        | F     | F        | F    | F    | F     | F       | F    | F      | F    | F     | F    | O        | F        |   |

FIG. 1. Outcomes of crosses of the new strains of *Drosophila paulistorum* to each other and to tester strains of the Andean-South Brazilian and the Amazonian races. O = no hybrids produced; S = sterile F<sub>1</sub> hybrids; F = fertile F<sub>1</sub> hybrids.

strains were then combined in the following 19 stocks:

Belém A, B, C, D, J, K, L    Bahia  
 Carolina                      Goiás A, B  
 Ceará                         Cipó A, B  
 Recife A, B, C                Rio A, B

These 19 stocks served as material for a study of their crossability and fertility with each other and with the following standard strains maintained in the laboratory of Th. Dobzhansky (see Dobzhansky and Spassky, 1959):

*Amazonian*: Panamá A, Trinidad, Belém  
*Orinocan*: Panamá B, Guiana A  
*Andean-South Brazilian*: Llanos B, Urubamba, Angra  
*Transitional*: Santa Marta, Bucaramanga, Palmira, Buenaventura  
*Guianan*: Guiana B

The tests were arranged as follows: about ten virgin females were kept with a similar number of males for about ten days at room temperature. If no larvae appeared, the flies were transferred without etherization to a fresh culture bottle and

left there for ten more days. If no progeny appeared the cross was considered to have failed. Where hybrids were produced, a group of a dozen or more hybrids of each sex was transferred without etherization to a new bottle, left there for ten days, and transferred again to fresh food. Failure to produce progeny indicated sterility of the hybrids, and as shown by other experiments this sterility affected only the hybrid males.

#### *Preliminary Tests*

As indicated above, all strains were initially crossed to the Belém, Angra, and Ceará tester strains. The results were as follows: the strains from Carolina, two strains from Belém, 18 strains from Recife, one strain from Goiás, three strains from Cipó, and 43 strains from Rio de Janeiro crossed and produced fertile hybrids with the Angra and with the Ceará tester strains, but failed to cross to the Belém tester strain. One Goiás strain, two strains from Cipó, and two strains from Rio crossed to all three tester strains, but produced sterile  $F_1$  hybrid males with the Belém tester strain. All these strains belong to the Andean-South Brazilian race. The 13 new strains from Ceará and nine from Bahia crossed to and gave fertile hybrids with all three testers; as will be shown below, these strains also belong to the Andean-South Brazilian race, but at least some of them have properties "transitional" to the Amazonian race. Sixty-eight of the new Belém strains crossed and produced fertile hybrids with the Belém tester strain, and failed to cross or produced sterile male hybrids with Angra and with the tester Ceará. These belong to the Amazonian race. Finally, one strain from Belém failed to cross to the Ceará and Belém tester strains, but produced sterile hybrids with Angra. This is presumably a representative of a new race, the properties of which are now being further tested.

On the basis of the behavior shown in the above crosses, the original strains were consolidated into the 19 strains enumerated above, which then served for further tests.

#### *Main Experiment*

The results of the main series of crosses are shown in figs. 1 and 2, in which the strains are grouped according to the races to which they belong. The symbol "O" means that the cross failed to produce  $F_1$  hybrid offspring; "S" stands for production of sterile male hybrids; "F" for production of fertile hybrids; and absence of a symbol means that the cross has not been made. Fig. 1 shows that Belém A, B, C, J, and L produce fertile hybrids with each other, and with the Amazonian race strains Panamá A and Trinidad. They fail to cross, or give sterile male hybrids, with the remainder of the strains listed in figs. 1 and 2, including with the Transitional race. These are strains of the Amazonian race.

Belém D, Ceará, Recife, Bahia, Goiás, Cipó, and Rio strains form another group. They cross and produce fertile hybrids with each other and with the Urubamba and Llanos B tester strains of the Andean-South Brazilian race (fig. 1). They fail to cross, or produce sterile male hybrids with the Orinocan, Centro-American, Guianan, and Amazonian races (fig. 2). Their behavior with the Transitional race is more complex and interesting (fig. 2). The females of the new strains cross easily and produce fertile hybrids with Bucaramanga, Palmira, and Buenaventura males, except that the Rio B ♀ × Bucaramanga ♂ cross yields sterile sons. With Santa Marta (Transitional) males the hybrid progenies are sterile, except the crosses Ceará ♀ × Santa Marta ♂ and Goiás A ♀ × Santa Marta ♂ which give fertile progenies of both sexes (fig. 2). The reciprocal crosses, Santa Marta females to males of the new strains, all give sterile male hybrids, while the crosses of the Bucaramanga, Palmira, and Buenaventura females to males of the new strains give some fertile and some sterile hybrids, or produce no hybrids at all, as shown in fig. 2.

The conclusion that may be drawn is that the Brazilian strains tested, including Belém D but not the other Belém strains, belong to the Andean-South Brazilian race.

|                          |            | AMAZONIAN     |             |         |              |          |           |           |          |          |          | ANDEAN - SOUTH BRAZILIAN |             |         |              |          |               |           |          |          |          |             |             |         |              |          |             |           |          |          |          |        |   |   |  |  |
|--------------------------|------------|---------------|-------------|---------|--------------|----------|-----------|-----------|----------|----------|----------|--------------------------|-------------|---------|--------------|----------|---------------|-----------|----------|----------|----------|-------------|-------------|---------|--------------|----------|-------------|-----------|----------|----------|----------|--------|---|---|--|--|
|                          |            | +♂            |             |         |              |          |           |           |          |          |          | +♀                       |             |         |              |          |               |           |          |          |          |             |             |         |              |          |             |           |          |          |          |        |   |   |  |  |
|                          |            | SANTA MARTA   | BUCARAMANGA | PALMIRA | BUENAVENTURA | PANAMA-B | GUIANA-A  | GUATEMALA | SALVADOR | HONDURAS | GUIANA-B | SANTA MARTA              | BUCARAMANGA | PALMIRA | BUENAVENTURA | PANAMA-B | GUIANA-A      | GUATEMALA | SALVADOR | HONDURAS | GUIANA-B | SANTA MARTA | BUCARAMANGA | PALMIRA | BUENAVENTURA | PANAMA-B | GUIANA-A    | GUATEMALA | SALVADOR | HONDURAS | GUIANA-B |        |   |   |  |  |
| AMAZONIAN                | BELEM - A  | O             | S           | S       | S            | O        | O         | O         | O        | O        | S        | O                        | O           | O       | O            | O        | S             | O         | O        | O        | O        | O           | O           | O       | O            | O        | O           | O         | O        | O        | O        | O      | O |   |  |  |
|                          | " - B      | S             | S           | S       | S            | O        | O         | S         | O        | O        | S        | O                        | O           | O       | O            | O        | O             | O         | O        | O        | O        | S           | O           | O       | O            | O        | O           | O         | O        | O        | O        | O      | O |   |  |  |
|                          | " - C      | O             | S           | S       | S            | S        | O         | S         |          | S        | S        | O                        | O           | O       | O            | O        | O             | O         | S        | S        | O        | O           | O           | O       | O            | O        | O           | O         | O        | O        | O        | O      | O |   |  |  |
|                          | " - L      | O             | S           | S       | S            | S        | O         | O         | O        | O        | S        | S                        | O           | O       | O            | O        | O             | O         | O        | O        | S        | S           | O           | O       | O            | O        | O           | O         | O        | O        | O        | O      | O | O |  |  |
|                          | " - K      | S             | O           | O       | O            | O        | O         | O         | S        |          | O        | O                        | O           | O       | O            | O        | O             | O         | O        | O        | O        | O           | O           | O       | O            | O        | O           | O         | O        | O        | O        | O      | O |   |  |  |
|                          | " - D      | S             | F           | F       | F            | S        | F         | S         | S        | S        | S        | S                        | F           | F       | F            | S        | S             | O         | S        | S        | S        | S           | S           | F       | F            | F        | S           | S         | O        | S        | S        | S      | O |   |  |  |
| ANDEAN - SOUTH BRAZILIAN | CAROLINA   | S             | F           | F       | F            | S        | S         | S         | S        | S        | S        | F                        | F           | F       | S            | S        | S             | S         | S        | S        | S        | S           | F           | F       | F            | S        | S           | S         | S        | S        | S        | S      |   |   |  |  |
|                          | CEARA      | F             | F           | F       | F            | S        | S         | S         | S        | S        | S        | F                        | F           | S       | S            | S        | S             | S         | S        | S        | S        | S           | F           | F       | S            | S        | S           | S         | S        | S        | S        | O      |   |   |  |  |
|                          | RECIFE - A |               | F           | F       | F            | S        | S         | S         | S        | S        | O        | S                        | O           | F       | O            | S        | S             | S         | S        | S        | S        | S           | O           | F       | O            | S        | S           | S         | S        | S        | S        | O      |   |   |  |  |
|                          | " - B      | S             | F           | F       | F            | S        | S         | S         | S        | S        | O        | S                        | O           | F       | F            | S        | S             | O         | S        | S        | O        | S           | O           | F       | F            | S        | S           | O         | S        | S        | S        | O      |   |   |  |  |
|                          | " - C      | S             | F           | F       | F            | S        | S         | S         | S        | S        | O        | S                        | O           | S       | F            | S        | O             | S         | S        | S        | O        | S           | O           | S       | F            | S        | O           | S         | S        | S        | S        | O      |   |   |  |  |
|                          | BAHIA      | S             | F           | F       | F            | S        | F         | S         | S        | S        | O        | S                        | F           | O       | O            | S        | S             | S         | S        | S        | O        | S           | F           | O       | O            | S        | S           | S         | S        | S        | S        | O      |   |   |  |  |
| ANDEAN - SOUTH BRAZILIAN | GOIAS - A  | F             | F           | F       | F            |          | S         | S         | S        | S        | O        | S                        | F           | F       | F            | S        | S             | S         | S        | S        | S        | F           | F           | F       | S            | S        | S           | S         | S        | S        | O        |        |   |   |  |  |
|                          | " - B      | S             | F           | F       | F            |          | S         | S         | S        |          | S        | S                        | F           | F       |              | S        | S             | S         | S        | S        | S        | F           | F           |         | S            | S        | S           | S         | S        | S        | O        |        |   |   |  |  |
|                          | CIPO - A   | S             | F           | F       | F            | S        |           | S         | S        | S        | O        | S                        | S           | F       | S            | S        | S             | S         | S        | S        | S        | S           | F           | S       | S            | S        | S           | S         | S        | S        | O        |        |   |   |  |  |
|                          | " - B      |               | F           | F       | F            | S        | S         | S         | S        | S        | O        | S                        | O           | F       | S            | S        | S             | S         | S        | S        | S        | O           | F           | S       | S            | S        | S           | S         | S        | S        | O        |        |   |   |  |  |
|                          | RIO - A    | S             | F           | F       | F            | S        |           | S         | S        | S        | O        | S                        | O           | O       | O            | S        | S             | S         | S        | S        | S        | O           | O           | O       | S            | S        | S           | S         | S        | S        | O        |        |   |   |  |  |
|                          | " - B      | S             | S           | S       | S            | S        | S         | S         | S        | S        | O        | S                        | F           | F       | F            | O        | S             | S         | S        | S        | S        | F           | F           | F       | O            | S        | S           | S         | S        | S        | O        |        |   |   |  |  |
|                          |            | TRANSI-TIONAL |             |         |              |          | ORIN-OCAN |           |          |          |          | CENTR. AMER              |             |         |              |          | TRANSI-TIONAL |           |          |          |          | ORIN-OCAN   |             |         |              |          | CENTR. AMER |           |          |          |          | GUIAN. |   |   |  |  |

FIG. 2. Crosses of the new strains of *Drosophila paulistorum* to tester strains of the Transitional, Orinocan, Centro-American, and Guianan races. (See fig. 1 for an explanation of the symbols.)

The only exceptional situations observed (fig. 1) are, first, that the Llanos B females gave no progenies with Rio A males, and that the cross Recife B ♀ × Belém D ♂ gave sterile hybrid sons. The crosses to the other races gave the results shown in fig. 2. The crosses to the Centro-American, Amazonian, and Guianan races either failed or produced sterile progenies. So did the crosses to the Orinocan race, except that the progenies of Belém D ♀ × Guiana A ♂ and Bahia ♀ × Guiana A ♂ were slightly fertile in one experiment but sterile in another.

#### Transitional Strains

The preliminary tests and the main ex-

periment gave results which appear to be in disagreement on some points. Ceará and Bahia strains (Andean-South Brazilian race) gave, in the preliminary tests, fertile male hybrids with the Belém tester strain (Amazonian race), while in the main experiment Ceará and Bahia failed to cross or produced sterile hybrids with the new Belém strains and with Panamá A and Trinidad (Amazonian race, fig. 1). The inference that Belém, Ceará, and Bahia populations contain genotypes with different properties as far as crossability is concerned has subsequently been tested and confirmed by the following experiments.

The Belém tester strain is the progeny of

|         | ♂     |         |      |      |      |      |      | ♀     |         |      |      |      |      |      |
|---------|-------|---------|------|------|------|------|------|-------|---------|------|------|------|------|------|
|         | CEARA | BELEM-D | " -A | " -B | " -C | " -L | " -J | CEARA | BELEM-D | " -A | " -B | " -C | " -J | " -L |
| BAHIA-1 | F     | F       | S    |      | S    | S    |      | F     | F       | O    | O    | O    | S    |      |
| " -2    | F     | F       | F    | S    | S    | S    | S    | F     | F       | O    | S    | O    | O    | O    |
| " -3    | F     | F       | S    | S    | F    | S    | S    | F     | F       | O    | O    |      | O    | O    |
| " -4    | F     | F       | S    | S    | S    | S    | S    | F     | F       | O    | O    | O    | O    | O    |
| " -5    | F     | F       | F    | S    | S    | S    | S    | F     | F       | O    | O    | O    | O    | O    |
| " -6    | F     | F       | S    | S    | F    | S    | S    | F     | F       | O    | O    | O    | O    | O    |
| " -7    | F     | F       | S    | S    | F    | S    | S    | F     | F       | O    | O    | O    | O    | O    |
| " -8    | F     | F       | F    |      | S    | S    | S    | F     | F       | O    | O    | O    | O    | O    |

FIG. 3. Intercrosses of the strains from Belém, Pará, to those from Bahia and from Ceará.

flies collected at Belém, as stated above, in 1948. Ceará and Bahia strains used in the main experiment are combinations of 13 and nine strains respectively pooled together (see above). Some of the original strains were still maintained when the apparently contradictory results came to light. It was accordingly resolved to test the behavior of the unmixed strains.

The relevant experiments are reported in fig. 3. When Belém or Ceará females are crossed to Bahia 1—Bahia 8 males, the results are simple and consistent. Except for Belém D and Ceará, which belong to the Andean-South Brazilian race, the crosses either fail or produce sterile hybrid sons. The reciprocal crosses are more complex. In the first place, all the crosses yielded hybrids easily. The hybrids of Belém D with Ceará were fertile as expected. But so were the hybrid males from the crosses Bahia 2 ♀ × Belém A ♂, Bahia 3 ♀ × Belém C ♂ (few hybrids fertile), Bahia 5 ♀ × Belém A ♂, Bahia 6 ♀ × Belém C ♂, Bahia 7 ♀ × Belém C ♂, Bahia 8 ♀ × Belém A ♂. It is clear that the Bahia and Belém populations contain genotypes which can, and those which cannot produce fertile hybrids when crossed. So does apparently the Ceará population, since it produced fertile hybrids with the Belém tester strain. Whether or not the fact this latter strain has been maintained for many generations under

laboratory conditions has anything to do with its peculiar behavior is an open question. The other strains which showed the transitional behavior were newly collected ones; note that the preliminary experiments were carried out when these strains were only a few generations removed from their wild progenitors.

*The Belém K Strain*

As shown in figs. 1 and 2, the Belém K strain proved to be difficult to cross to either sympatric or to allopatric strains of both the Andean-South Brazilian and the Amazonian races. No better success was obtained in crosses of Belém K to the tester strains of the other four previously known races. The few hybrids produced were sterile. This makes it probable that Belém K is a representative of a new, seventh, race of *D. paulistorum*, and that three sympatric races of this species live in the vicinity of Belém, apparently without effective interbreeding. The properties of the Belém K strain are being studied further by Mr. George Carmody in this laboratory.

DISCUSSION

Much further collecting and experimentation will be needed to elucidate fully the distributional relationships and the genetic structure of the races (or incipient species) of the *Drosophila paulistorum* complex. The data reported in the present article, however, in conjunction with those

of Dobzhansky and Spassky (1959), make some aspects of the situation clear. The Andean-South Brazilian race inhabits the largest territory, extending from southern Brazil (Rio Grande do Sul) to Central Brazil (Goiás, Carolina), northeastern Brazil (Bahia, Recife, Ceará), to the estuary of the Amazon (Belém), to Bolivia, Perú, Ecuador, and trans-Andean Colombia (Llanos). At Belém the Andean-South Brazilian race meets the Amazonian, and a third race represented by our Belém K strain; the three races coexist at Belém sympatrically without interbreeding. In Llanos the Andean-South Brazilian meets the Orinocan race, again without interbreeding; so do the Orinocan and Guianan races at Georgetown, British Guiana (Dobzhansky and Spassky, 1959, Carmody et al., 1962). The situation in the Amazon valley (the Amazonian Hylea) is unclear; the strain collected at Içana (upper Rio Negro) by Dobzhansky belongs to the Amazonian race, but more material would be needed from this vast and biologically rich territory to ascertain whether some of the other races are found there as well.

It is now becoming evident that the Transitional race found in Colombia by Dobzhansky and Spassky is really an appendage of the Andean-South Brazilian race. The data of these authors (1959) as well as my own (fig. 2), show that most of the available strains of the Transitional race hybridize and produce fertile hybrids with most of the Andean-South Brazilian strains. Only the Santa Marta (northern Colombia) strain gives fertile hybrids with the Centro-American race but not with the Andean-South Brazilian race (except for Goiás A, as shown in fig. 2). Of course, Santa Marta gives fertile hybrids also with the other Transitional race strains. More important still, the cytological data of Dobzhansky and Pavlovsky (in press) show that the gene arrangements in the chromosomes of the Transitional race are like those in the Andean, and differ from those in all other races.

The transitional strains described in the

present article are distinct from the Transitional race of Dobzhansky and Spassky. These strains are transitional between the Amazonian and the Andean-South Brazilian races, since they cross and produce fertile  $F_1$  hybrids with both. There is, however, no known population which would, as a whole, have these "transitional" properties. Fig. 3 shows that only some of the Bahia strains produce fertile hybrids with only some of the Belém strains, and then while one cross is fertile, its reciprocal gives sterile hybrids or fails altogether. Other Bahia strains show no indication of a "transitional" behavior; the Bahia population as a whole clearly belongs to the Andean-South Brazilian, not to the Amazonian race. Similarly, the Belém tester strain of the Amazonian race, the ancestors of which were collected at Belém by Dobzhansky in 1948, gives fertile hybrids not only with Bahia but also with Ceará strains. Some of the other Amazonian strains of the Belém, 1961, collection are and others are not crossable to Bahia, but none equals the easy crossability of the old Belém tester strain.

The most interesting, and I believe most significant, fact is that in no single instance have transitional strains been found in localities in which two or three of the incipient species coexist sympatrically. Belém D strain of the Andean-South Brazilian race shows a virtually complete reproductive isolation from all Belém strains of the Amazonian race. But some of the latter are crossable to and produce fertile hybrids with the allopatric Andean strains from Bahia and from Ceará. In central and western Colombia where Dobzhansky and Spassky (1959) found the Transitional race, no other race has been located; however, in Llanos, east of the Andes, they found the Andean and the Orinocan, but not the Transitional race. This argues against the otherwise possible hypothesis that the Transitional race and transitional strains are results of introgressive hybridization between the other races. If this were so, Belém and Llanos would be the

logical places to find crossable transitional strains of the Andean-South Brazilian and Amazonian (or, respectively, the Andean-South Brazilian and Orinocan) races. If transitional strains were living regularly in the zones of overlap of different races, this would offer further opportunities for introgression and for possible fusion of the incipient species. But this is not the case. What is actually observed is that the crossable strains of the different incipient species are always allopatric, and consequently do not endanger the integrity and the genetic divergence of the latter. Conversely, where the races or incipient species are actually sympatric, their reproductive isolation is found to be at its strongest. The rather obvious inference is that this intensified isolation is a product of natural selection tending to suppress the gene exchange between divergent populations (Dobzhansky, 1958).

#### SUMMARY

Tests of crossability and hybrid fertility were made with 165 new strains of *Drosophila paulistorum* collected chiefly in central and northeastern Brazil. The crossability of these strains to each other and to the standard tester strains of the six known races or incipient species of *D. paulistorum* complex, and the fertility of the resulting hybrids, were studied. The new strains belong to the Andean-South Brazilian, to the Amazonian, and to a new (seventh) race. Some of the strains proved to be transitional between the Andean-South Brazilian and the Amazonian races, in the sense that these strains can be crossed to and produce fertile hybrids with strains of both races. However, transitional strains have never been found in localities in which two or more of the races occur sympatrically. On the contrary, in these zones of sympatric overlaps the reproductive isolation between

the incipient species is most nearly complete.

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