Again we emphasize that the interpretation yields only the fact that the lower bound for the mean yield strength is lower slightly above 300 km than below 300 km; similar comparisons apply to the depths slightly above and below 550 km. Strengths are not compared at widely separated depths.

No statistical analysis of these results has as yet been made. The statistical properties of the curve may modify the interpretation.

[1] Gutenberg, B., "The energy of earthquakes," *Quart. J. Geol. Soc. London,* **112,** 1–14 (1956).

[2] Gutenberg, B., *Physics of the Earth's Interior* (New York: Academic Press, 1959), p. 202.

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*THE SUPERSPECIES DROSOPHILA PAULISTORUM**

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Drosophila paulistorum is genetically perhaps the most complex, but also one of the most interesting, species of its genus. Dobzhansky and Spassky[1] found that some strains of this species fail to cross with certain morphologically similar strains; other strains intercross but produce fertile female and sterile male hybrids; and still other strains cross as easily as do females and males from the same strain, and yield fertile progenies. Dobzhansky and Spassky divided the strains at their disposal into five races or incipient species, which do not intercross or produce sterile male progenies, and a sixth, Transitional race, each strain of which is fertile with at least one other race. Most remarkable of all, in three localities (Barro Colorado in Panama, Llanos of Colombia, and Georgetown in British Guiana), two races were found to coexist side by side, apparently without gene exchange. These sympatric but reproductively isolated "races" behave, then, as full-fledged species. And yet the Transitional race, and also the transitional strains discovered by Malogolowkin,[2] show that a gene flow between these "species" is at least potentially possible. *Drosophila paulistorum* is a superspecies, as defined by Mayr.[3] Accession of new material from some critically important portions of the distribution area of *Drosophila paulistorum* now permits a more thorough, though still far from exhaustive, analysis of the situation.

Materials.—Samples of the populations of *D. paulistorum* were collected in 39 localities or groups of localities shown on the maps in Figures 1 and 2 and listed below. The wild-collected flies were sent to the laboratory in New York, where each female was placed in a separate culture and allowed to produce progeny. The progenies from the same locality were intercrossed chainwise, A ♀ × B♂, B ♀ × C♂ . . . Z ♀ × A♂. If all the crosses succeeded and gave fertile F_1 offspring, the progenies of several females were combined in as many strains as seemed possible to maintain. If some of the crosses failed or gave sterile progenies, further tests were arranged to discover which lines belong to the same Mendelian population. A total of 97 strains were available for the experiments (this number does not include the strains maintained by Dr. C. Malogolowkin at Columbia University). The number of possible intercrosses of 97 strains being prohibitively large (9,312), only about one

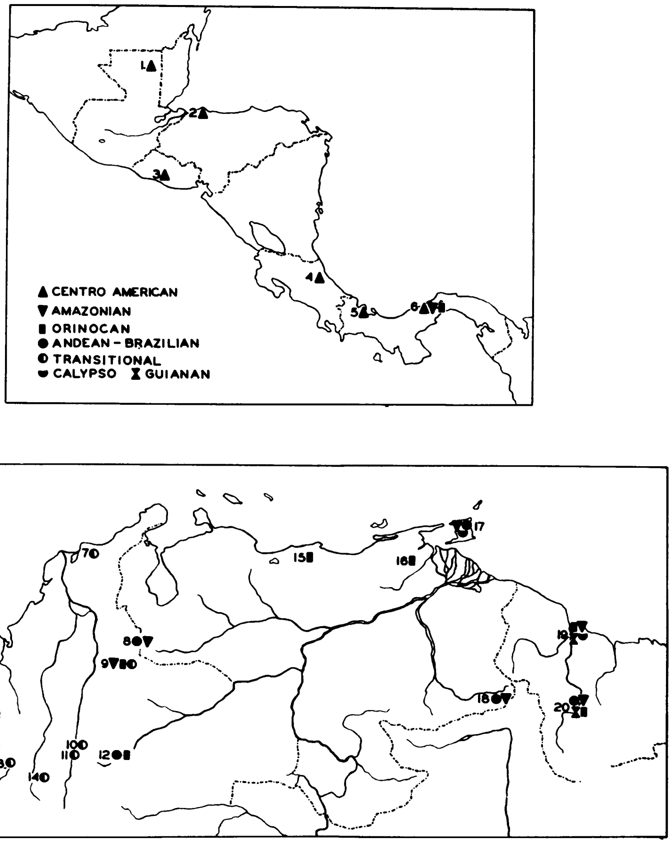

Fig. 1.—The geographic distribution of the races of *Drosophila paulistorum* in Central and South America.

tenth of them were actually made, chosen so as to make the properties of each strain reasonably clear.

In the following list of localities, the letters DS and M indicate that data concerning these population samples can be found in the papers of Dobzhansky and Spassky[1] and of Malogolowkin.[2] (1) Tikal, Guatemala, DS; (2) Lancetilla, Honduras, DS; (3) San Salvador, DS; (4) Turrialba, Costa Rica, DS; (5) Boquete, Chiriqui Prov., Panama, S. B. Pipkin, collector, 2 lines; (6) Barro Colorado, Madden Forest, Piña in Fort Sherman Reservation, Cerro Campana, Goofy Lake in Cerro Azul, El Real in Darien Province, Panama, S. B. Pipkin, collector, 18 lines combined in 11 strains; (7) Santa Marta, Colombia, DS; (8) Cucuta, Colombia, A. S. Hunter, collector, 10 lines combined in 4 strains; (9) Bucaramanga, Colombia, DS, and 7 lines collected by A. S. Hunter, combined in 3 strains; (10) Mesitas del Colegio, Colombia, A. S. Hunter, collector, 22 lines combined in 3 strains; (11) Girardot, Colombia, A. S. Hunter, collector, 6 lines in 2 strains; (12) Llanos south of Villavicencio, Colombia, DS; (13) Palmira, Colombia, DS; (14) Buenaventura, Colombia, DS; (15) Tuy near Araguita, Venezuela, Th. Dobzhansky, collector, 3 lines in 1 strain; (16) Caripe, Venezuela, Th. Dobzhansky, collector, 17 lines in 6 strains; (17) Simla and Sangre Grande, Trinidad, Th. Dobzhansky, collector,

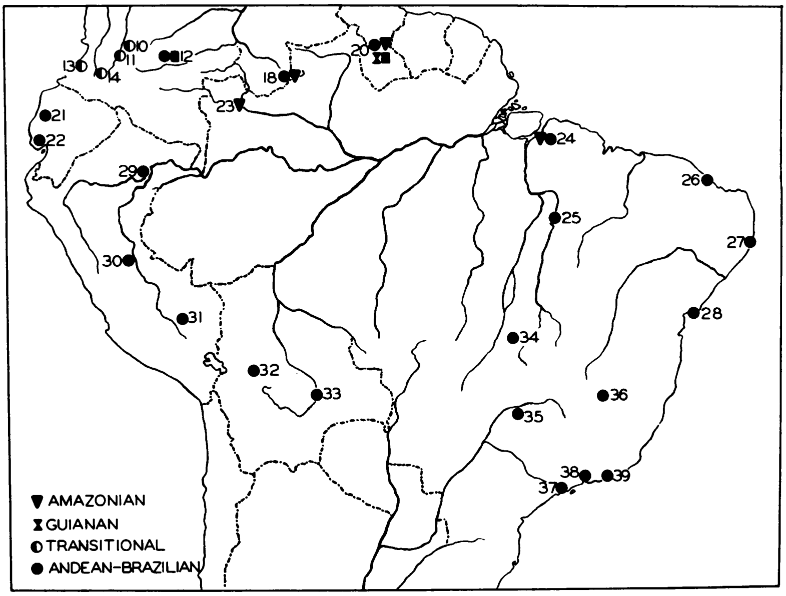

Fig. 2.—The geographic distribution of the races of *Drosophila paulistorum* in South America.

52 lines in 11 strains; (18) Santa Elena de Uairen, Venezuela, Th. Dobzhansky, collector, 35 lines in 11 strains; (19) vicinity of Georgetown, British Guiana, DS, Th. Dobzhansky, collector, 23 lines in 12 strains; (20) Apoteri, British Guiana, Th. Dobzhansky, collector, 20 lines in 9 strains; (21) Santo Domingo, Ecuador, DS; (22) Pichilingue, Ecuador, DS; (23) Içana, Amasonas, Brazil, DS; (24) Belém, Pará, Brazil, DS, M; (25) Carolina, Brazil, M; (26) Ceará, Brazil, M; (27) Recife, Brazil, M; (28) Bahia, Brazil, M; (29) Tarapoto, Peru, DS; (30) Tingo Maria, Peru, DS; (31) Urubamba, Peru, DS; (32) Coroico, Bolivia, DS; (33) Santa Cruz, Bolivia, DS; (34) Goias, Brazil, M; (35) Ituitaba and Araguari, Minas Gerais, Brazil, DS; (36) Cerra do Cipo, Minas Gerais, Brazil, M; (37) São Paulo, Brazil, DS; (38) Angra dos Reis, Brazil, DS; (39) Rio de Janeiro, Brazil, M.

The Crosses.—The technique of the experimental intercrosses of the strains from the above localities was the same as described by Dobzhansky and Spassky.[1] Some crosses yielded no progeny, others gave sterile F_1 hybrid males, and still others gave fertile hybrids. The results can be summarized best as follows. *D. paulistorum* is a complex of seven races or incipient species: (1) Centro-American, (2) Amazonian, (3) Andean-South Brazilian, (4) Orinocan, (5) Guianan, (6) Calypso, and (7) Transitional. Strains which belong to the same race produce fertile hybrids of both sexes, with the exception of the following three crosses between strains of the Transitional race: Santa Marta (7) ♀ × Mesitas (10) ♂, Santa Marta ♀ × Bucaramanga (9) ♂, and Palmira (13) ♀ × Santa Marta ♂. The sterility of the F_1 hybrid males in these crosses appears to be a special case, explored by Ehrman.[4] Several crosses within the Orinocan race recorded by Dobzhansky and Spassky[1] as giving sterile hybrids or no progeny gave fertile progenies in subsequent tests. On the other hand, Carmody *et al.*[5] demonstrated that some matings of strains belonging to the same race, but coming from different localities, succeed less easily than do matings within a strain. However, these rudiments of sexual isolation within a race rarely approach the degree of reproductive isolation between the races.

The results of the interracial crosses are summarized in Table 1. Females of the Orinocan race with males of the Amazonian, and females of the Amazonian with males of all other races, rarely give hybrid progenies. Other matings succeed more easily, but give sterile male hybrids. The fact that must be stressed is, however, that every race has produced a fertile progeny in at least one interracial cross. This is particularly true of the Transitional race, but occasional fertility is found also in crosses not involving the Transitional race. These exceptional crosses indicate the existence of transitional strains like those found by Malogolowkin[2] (her crosses are, however, not included in the data in Table 1). We hope to report on the behavior of the transitional strains in a separate publication.

TABLE 1

NUMBERS OF INTERRACIAL CROSSES WHICH GIVE NO PROGENY (O), FERTILE FEMALE BUT STERILE MALE HYBRIDS (S), AND FERTILE HYBRIDS (F)

Races	O	S	F
Amazon. ♀ × Andean ♂	33	7	—
" × Orinoc. ♂	47	5	—
" × Guianan ♂	13	5	—
" × Calypso ♂	8	—	—
" × Cent.-Am. ♂	24	2	—
" × Trans. ♂	20	7	—
Andean ♀ × Amazon. ♂	20	19	—
" × Orinoc. ♂	14	5	—
" × Guianan ♂	11	2	—
" × Calypso ♂	—	2	1?
" × Cent.-Am. ♂	1	15	2
" × Trans. ♂	—	6	13
Cent. Am. ♀ × Amazon. ♂	12	6	—
" × Andean ♂	1	9	—
" × Orinoc. ♂	3	12	—
" × Guianan ♂	—	2	—
" × Calypso ♂	—	1	—
" × Trans. ♂	2	9	4
Orinoc. ♀ × Amazon. ♂	160	2	4?
" × Andean ♂	4	14	—
" × Guianan ♂	8	1	1
" × Cent.-Am. ♂	4	14	—
" × Trans. ♂	12	10	1
Guianan ♀ × Amazon. ♂	6	—	—
" × Andean ♂	1	4	—
" × Orinoc. ♂	2	1	—
" × Cent.-Am. ♂	3	1	—
" × Trans. ♂	3	2	—
Calypso ♀ × Amazon. ♂	9	1	—
" × Andean ♂	1	6	1 ?
" × Orinoc. ♂	2	2	—
" × Guianan ♂	3	—	—
" × Cent.-Am. ♂	—	3	—
" × Trans. ♂	2	3	—
Trans. ♀ × Amazon. ♂	12	4	1
" × Andean ♂	0	4	5
" × Orinoc. ♂	6	6	2
" × Cent.-Am. ♂	5	6	5

Geographic Distribution.—The maps in Figures 1 and 2 show two salient facts. First, in some localities in the northern part of the South American continent, from Panama and the Llanos of Colombia to British Guiana and to the mouth of the Amazon, two or more races coexist sympatrically. At Apoteri (20) and Georgetown (19), British Guiana, four sympatric races are found; in Panama (6), Bucaramanga (9), and Trinidad (17) there are three sympatric races each; at Cucuta (8), in Llanos of Colombia (12), in Santa Elena (18), and Belém (24), there are at least two each. Where collections were made personally by one of the authors (Th. Dobzhansky), care was taken to mark the exact location of the collecting grounds, and the records show conclusively that representatives of different races (incipient species) do live in close proximity. Secondly, some races are allopatric. Over large territories only a single race is found. This conclusion is, of necessity, based on negative evidence. More extensive collecting might discover sympatric occurrence of races in some territories in which only a single race is now known. There is every reason, however, to think that each race has a distribution area different from all others.

Sexual Isolation between Sympatric and Allopatric Strains.—When two or more species of sexually reproducing and cross-fertilizing organisms share the same territory, their populations are exposed to the risk of hybridization and gene exchange. If such gene exchange leads to production of adaptively inferior genotypes, natural selection may favor genetic constitutions which hinder or prevent hybridization. On the other hand, the gene exchange and introgression may weaken the reproductive isolation, and eventually lead to fusion of previously separate populations. Experiments have been made to test whether the sexual isolation between sympatric strains of a given pair of races is, on the average, greater or smaller than that between allopatric strains of the same races.

The technique adopted was the so-called "male-choice" method (see Carmody *et al.*[5] for details). Briefly, groups of 10 virgin females of each of two races (i.e., a total of 20 females) were aged for 3–4 days after hatching, marked for recognition by clipping a part of one of their wings, and confined for 24–48 hr with males of one of the two races. All the females were then dissected, and their sperm receptacles were examined for the presence or absence of sperm. For statistical reasons, only those batches in which no fewer than 6 and no more than 14 of the 20 females were inseminated were included in the counts. In the following list, the strains used are indicated by numbers, which correspond to those on the maps in Figures 1 and 2 and in the locality list above.

Sympatric combinations: Amazonian × Orinocan: 6 × 6, 9 × 9, 19 × 19, 20 × 20; Amazonian × Andean: 17 × 17, 18 × 18, 20 × 20; Orinocan × Andean: 20 × 20; Centro-American × Amazonian: 6 × 6.

Allopatric combinations: Amazonian × Orinocan: 6 × 9, 6 × 15, 6 × 16, 9 × 15, 9 × 16, 9 × 19, 9 × 20, 15 × 17, 15× 18, 15 × 19, 16 × 17, 16 × 18, 17 × 19, 18 × 19, 19 × 20; Amazonian × Andean: 6 × 20, 9 × 17, 9 × 20, 17 × 18, 17 × 19, 18 × 19, 9 × 18, 18 × 20, 19 × 20; Orinocan × Andean: 9 × 20, 15 × 17, 16 × 17, 16 × 18, 17 × 20, 18 × 19; Centro-American × Amazonian: 6 × 17.

The results of the tests of sexual isolation are summarized in Table 2. The "homogamic" matings are those between females and males of the same strain, and "heterogamic" are those between different strains. The isolation coefficients are all positive (the plus signs are omitted). The important point is that these coefficients tend to be higher for the sympatric than for the allopatric strains. Of the eight pairs of figures in the last column in Table 2, the coefficient is higher for the sympatric strains in seven cases, and equal in one case (Amazonian & Andean, with Andean males). Combining all the sympatric crosses, we have the isolation coefficient +0.84, and for the total of allopatric crosses +0.72.

The conclusion is warranted that the isolation which decreases the chances of production of hybrid offspring is stronger between sympatric than between allopatric populations of the same pairs of incipient species. This conclusion is consistent with the findings of Dobzhansky and Pavlovsky,[6] that each race has mostly or exclusively the chromosomal polymorphs of its own, not found in the populations of other races. The only exception to this rule is the Transitional race, which shares chromosomal polymorphisms with the Andean-Brazilian race; these two races are most easily crossable (Table 1), and the distribution area of the Transitional

TABLE 2

NUMBERS OF INSEMINATED (+) AND UNINSEMINATED (−) FEMALES IN SYMPATRIC (SYM.) AND ALLOPATRIC (ALLO.) HOMOGAMIC AND HETEROGAMIC MATINGS

Females	Males	Origin	Homogamic		Heterogamic		IC*
			+	−	+	−	
Amaz. + Orin.	Amaz.	Sym.	103	43	8	132	0.84
" "	"	Allo.	359	136	58	507	0.76
" "	Orin.	Sym.	95	32	4	118	0.92
" "	"	Allo.	341	132	53	418	0.73
Amaz. + And.	Amaz.	Sym.	95	53	12	133	0.78
" "	"	Allo.	167	61	29	193	0.69
" "	And.	Sym.	76	22	7	88	0.84
" "	"	Allo.	219	58	19	238	0.84
Orin. + And.	Orin.	Sym.	32	17	4	45	0.78
" "	"	Allo.	117	58	44	128	0.44
" "	And.	Sym.	20	17	1	36	0.89
" "	"	Allo.	134	41	31	142	0.62
C.-Am. + Amaz.	C.-Am.	Sym.	12	8	0	14	1.00
" "	"	Allo.	42	17	2	55	0.89
" "	Amaz.	Sym.	18	2	0	20	1.00
" "	"	Allo.	46	4	6	31	0.70
Total		Sym.	451	194	36	586	0.84
"		Allo.	1425	507	242	1712	0.72

* IC = isolation coefficient.

race is a geographic extension of the area of the Andean-Brazilian race (Fig. 2). It is also consistent with the findings of Malogolowkin,[2, 7] that transitional strains of the Andean race, which give fertile hybrids with the Amazonian race, occur where the Andean race is the sole representative of its species (or superspecies). Ehrman[8] has shown that the genetic basis of the sexual isolation in *D. paulistorum* is polygenic; it is, then, not difficult to visualize a process of natural selection that encourages the spread in sympatric populations of incipient species of the genes which limit or prevent the reproductive wastage resulting from gene flow between these populations.

Summary.—*Drosophila paulistorum* is a superspecies composed of seven races or incipient species. The interest of the situation lies precisely in that these seven may be considered about equally legitimately as very distinct races or as very closely related species. Each race inhabits a geographic area different from the others, but the areas of some of the races overlap. Where two or more "races" share a common territory, they apparently do not interbreed and thus behave like full-fledged species. However, the Transitional race and transitional strains yield fertile hybrids with some other races. Gene flow between the incipient species is therefore possible, although it is questionable whether it is actually taking place.

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*BIOSYNTHESIS OF CELL WALL MUCOPEPTIDE BY A PARTICULATE FRACTION FROM STAPHYLOCOCCUS AUREUS**, †

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Mucopeptides have been defined chemically as those polymers which contain N-acetyl muramic acid, N-acetyl glucosamine, and a characteristic peptide generally composed of D-and L-alanine, D-glutamic acid, either L-lysine or diaminopimelic acid, and in some cases glycine or aspartic acid.[1, 2] These glycopeptides are essential structural components of the cell walls of bacteria and related organisms such as blue-green algae, rickettsia, the psittacosis group of viruses, and the actinomyces (see review[3]). The mucopeptide of *S. aureus* H contains a polysaccharide "backbone" composed of N-acetyl muramic acid and N-acetyl glucosamine. Attached to the polysaccharide are ester-linked acetyl groups and a peptide composed of L-alanine, D-glutamic acid, L-lysine, D-alanine, and about 5 glycine residues. There is evidence that considerable cross-linkage occurs between peptide chains.[4–6] Such extensive cross-linkage between mucopeptide chains would explain the strength these materials give to the wall.

Nucleotide-bound sugars, which are frequently precursors of simple polysaccharides, have recently been shown to be precursors of more complex polysaccharides as well.[7, 8] That synthesis of mucopeptide may be similar to polysaccharide synthesis was thus suggested some years ago by the observation that interference with the growth of staphylococci by penicillin led to accumulation within the cells of 3 uridine nucleotides.[9] The structure of the largest compound, uridine diphospho-N-acetyl-muramyl-L-alanyl-D-glutamyl-L-lysyl-D-alanyl-D-alanine (UDP-muramyl-peptide) is shown in Figure 1.[9, 10] Since N-acetyl muramic acid and these amino acids are components of the mucopeptide, the 3 uridine compounds have been implicated as precursors of mucopeptide.[11] The composition of the smaller nucleotides suggested that they may be intermediates on a pathway leading to formation of the largest nucleotide-muramyl-peptide. Indeed, Ito and Strominger[12] have demonstrated that a pathway for the formation of UDP-muramyl-peptide from UDP-N-acetyl muramic acid exists in staphylococci. The alternate transfer of muramyl-peptide and N-acetyl glucosamine from their respective uridine nucleotides to an acceptor mucopeptide would thus make the initial polymerization of mucopeptide "backbone" comparable to synthesis of polysaccharide. Subsequent addition of glycine to the polymer and the introduc-