* This research was supported in part by the Office of Naval Research, and by Higgins funds allotted to Princeton University. Permission is granted for reproduction and use by the United States Government.

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DROSOPHILA PAULISTORUM, A CLUSTER OF SPECIES IN STATU NASCENDI[*, †]

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One hundred years ago Darwin wrote that "... species are only strongly marked and permanent varieties, and that each species first existed as a variety ...." Species of sexual and cross-fertilizing organisms arise mostly through gradual divergence and reproductive isolation of subspecies (= geographic races or varieties). Evidence of this are numerous "borderline cases," in which subspecies have almost reached the degree of divergence and of reproductive isolation met with among species. In turn, the most interesting among "borderline cases" are chains of intergrading subspecies, the terminal links of which coexist sympatrically, in the same territory, with little or no interbreeding taking place. In the territories in which they live together, these divergent forms behave, then, like true species; and yet they appear to be only races if the connecting links are considered. Gene exchange between the terminal links remains possible, and may actually be taking place, via the connecting chain of subspecies.

Several examples of circular chains of subspecies have been observed, chiefly in birds and insects (reviews in Mayr[1] and Rensch[2]). A beautiful case in a species of salamander has recently been added by Stebbins.[3, 4] The first instance in the genus *Drosophila* is to be reported in the present article. According to Patterson and Stone's review,[5] the genus *Drosophila* contained 613 described species in 1952. Several race-species borderline cases have been observed, but in none of these have sympatrically coexisting forms been found connected by chains of allopatric races. Since many species of *Drosophila* are favorable as materials for genetic experimentation, the borderline race-species situation may, it is hoped, be analyzed here more fully than has been possible elsewhere.

Position of Drosophila paulistorum among its Relatives.—The five sibling species, *D. paulistorum*, *D. willistoni*, *D. equinoctialis*, *D. tropicalis*, and *D. insularis* are practically indistinguishable by inspection of their external morphology, [6, 7] although Spassky[8] recently found slight differences in the male genitalia which enable him to classify living males. The species can, however, be identified by their chromosomes, as seen in the cells of larval salivary glands. Furthermore, they are completely isolated reproductively. Sexual isolation is so strong that cross-insemination rarely succeeds, and no viable hybrids are produced except in the crosses involving *D. insularis*. Even these hybrids are wholly sterile. *D. insularis* is known only from some of the islands in the Lesser Antilles, but the other four species are widely distributed in the American tropics, all of them being sympatric in the basin of the Amazon and in the part of South America lying north of the Equator. *D. paulistorum* occurs from southern Brazil to Central America (Guatemala) and Trinidad. In many parts of this large area it is one of the commonest species of the genus, especially in the superhumid tropical rainforest climates.

D. willistoni is a unified species, in the sense that strains of any geographic origin can easily be crossed with strains from anywhere else, and produce fully viable and fertile hybrids. *D. tropicalis* is differentiated into at least two subspecies, the hybrids between which are sterile as males.[9] Nothing is known about possible differentiation of *D. equinoctialis*. The remarkable differentiation of *D. paulistorum* is described below.

Material.—We have in our laboratory strains of *D. paulistorum* from the following 25 localities (the numbers in the following list correspond to those on the map in Fig. 1): (1) Tikal, Guatemala, May, 1958, Sophie Dobzhansky Coe; (2) Lancetilla,

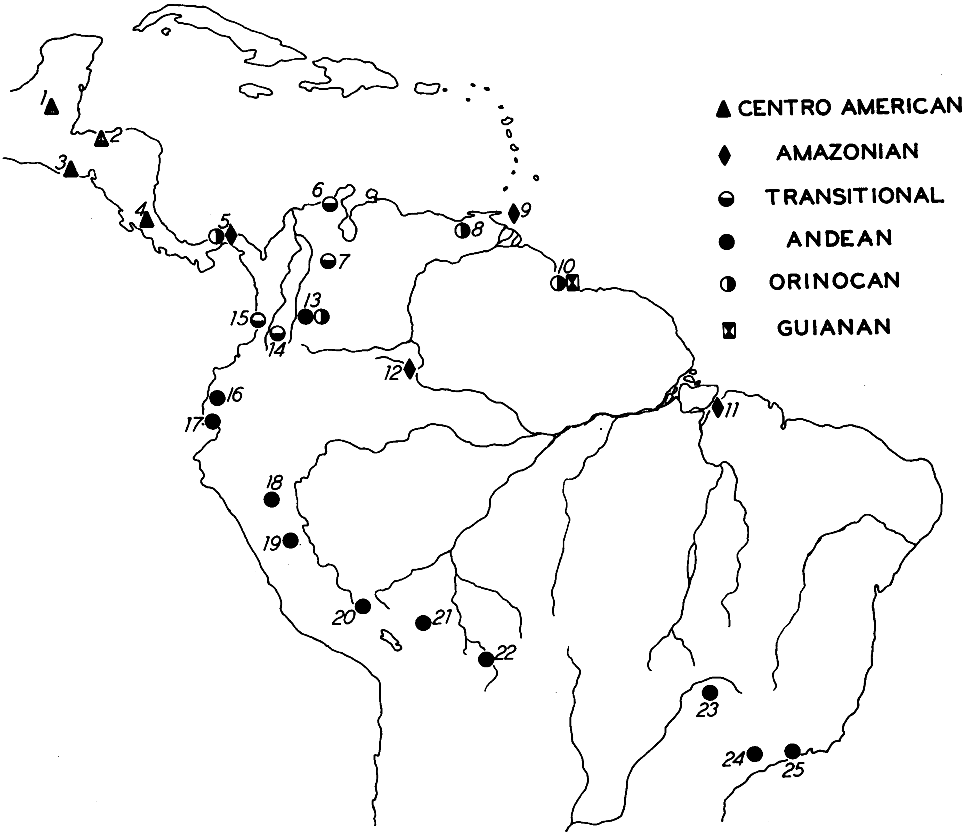

FIG. 1.— Geographic origin of the strains of *Drosophila paulistorum*. The numbers of the localities on this map correspond to those in Figures 2–4 and in the text.

Honduras, May, 1954, W. B. Heed; (3) San Salvador, August, 1954, W. B. Heed; (4) Turrialba, Costa Rica, August, 1956, W. B. Heed; (5) Barro Colorado, Panama, August, 1956, W. H. Heed; (6) Santa Marta, Columbia, September, 1956, H. L. Carson and M. Wasserman; (7) Bucaramanga, Columbia, September, 1956, H. L. Carson and M. Wasserman; (8) Caripe, Venezuela, November, 1956, M. Wasserman; (9) Arima Valley, Trinidad, February, 1956, W. B. Heed; (10) Georgetown, British Guiana, July, 1957, W. B. Heed; (11) Belem, Brazil, July, 1952, Th. Dobzhansky; (12) Içana, Brazil, August, 1952, C. Pavan and Th. Dobzhansky; (13) Llanos near Villavicencio, Columbia, March, 1958, Th. Dobzhansky; (14) Palmira, Colombia, March, 1958, M. Wheeler and Th. Dobzhansky; (15) Buenaventura, Columbia, March, 1958, Th. Dobzhansky; (16) Santo Domingo de los Colorados, Ecuador, March, 1958, M. Wheeler and Th. Dobzhansky; (17) Pichilingue, Ecuador, March, 1958, M. Wheeler and Th. Dobzhansky; (18) Tarapoto, Peru, September, 1956, C. Pavan and Th. Dobzhansky; (19) Tingo Maria, Peru. September, 1956, C. Pavan and Th. Dobzhansky; (20) Urubamba, Peru, September, 1956, C. Pavan and Th. Dobzhansky; (21) Coroico, Bolivia, April, 1958, M. Wasserman; (22) Santa Cruz de la Sierra, Bolivia, April, 1958, M. Wasserman; (23) Ituitaba and Araguari, Minas Gerais, Brazil, August, 1957, M. Breuer; (24) Cantareira, São Paulo, Brazil, January, 1958, C. Pavan; and (25) Angra dos Reis, Brazil, May, 1956, Th. Dobzhansky.

The older strains, the progenitors of which were collected in 1956 or earlier were derived each from a single wild female fertilized in nature. The Peruvian strains (localities Nos. 18–20) are progenies of the populations kept in laboratory population cages for about a year, the founders of which came from several dozen wild strains from a given locality mixed together. The newer strains, started in 1957 and 1958, were prepared as follows. Separate strains were established from each wild female collected in a given locality. These strains were then intercrossed chainwise, i.e., A × B, B × C, ... Y × Z, Z × A. If all crossed yielded fertile F_1 progenies the strains were pooled in a single mixed population from each locality. Sometimes two groups of strains were found, interfertile within but intersterile between groups. Two pooled strains were then established (i.e., Llanos-A and Llanos-B).

First Series of Experiments.—Attempts to intercross strains of *D. paulistorum* yield a variety of results. Some crosses go easily, and produce fertile F_1 hybrids; others fail to give any hybrid offspring; still others produce in F_1 fertile female but sterile male hybrids. Systematic intercrosses were started in the fall of 1956 and in 1957 with the 16 strains then available. The results are summarized in Figure 2.

The experiments were arranged as follows: about a dozen virgin females from one strain and a like number of males from another were placed together in a culture bottle at room temperature. If no larvae appeared in the food within a week, the flies were transferred, without etherization, to a fresh culture bottle, and left there for another week. If no progeny appeared, the cross was considered as having failed; such failures are marked in Figure 2 by the sign *O*. If the progeny did appear, the hybrid flies were allowed to develop, and a dozen or more pairs of them were placed in a fresh culture. If F_2 larvae appeared, the F_1 hybrids were evidently fertile; such fertile crosses are marked in Figure 2 by an *F*. If no F_2 larvae appeared after a week, the parents were transferred to a fresh culture and left

♂ \ ♀	HONDURAS	SALVADOR-A	SALVADOR-B	COSTA RICA	PANAMA-A	TRINIDAD	BELEM	IÇANA	TARAPOTO	TINGO MARIA	URUBAMBA	ANGRA	BUCARAMANG	SANTA MARTA	CARIPE	PANAMA-B
2. HONDURAS		F		F	O	O	O	O	ST	ST		ST	ST		ST	ST
3. SALVADOR-A	F		F	F	O		O	O	ST		ST			F		ST
3. SALVADOR-B	F	F			O	O	O			ST		ST			ST	F
4. COSTA RICA	F		F		O			O			ST	ST	F	F		ST
5. PANAMA-A	O	O	O	O		F	F	F	ST	O	O	ST	O	O	O	O
9. TRINIDAD		O		O	F		F		O	O	O		O	O		O
11. BELEM	O	O		O	F	F		F	ST		ST			O	O	O
12. IÇANA	ST	O	O		F	F	F		O	O		ST	O		O	ST
18. TARAPOTO	O	ST	O	ST	O		O	O			F	F		ST		O
19. TINGO MARIA		ST		ST		O	O		F			F	F		O	ST
20. URUBAMBA	ST				O	O		O		F		F		ST		ST
25. ANGRA	ST	ST		ST		O	O		F	F			O	ST	ST	
7 BUCARAMANGA		O		ST	O	O	ST		F	F	F	F		ST	O	O
6. SANTA MARTA	F		F		O			ST	ST	ST		ST	F		F	O
8. CARIPE	O	ST	O	ST	O	O	O	ST	ST	O	ST		O	O		F
5 PANAMA-B	ST	ST	ST		O	O	O	O	ST	ST	ST	ST	F	O	F	

FIG. 2.—First series of experiments. Outcome of the crosses between strains of different geographic origin. O—no progeny produced; ST—male F_1 hybrids sterile; F—hydrids fertile.

there for another week. The nonappearance of a progeny was taken to mean that one or both sexes of the F_1 hybrids are sterile. Such crosses are marked in Figure 2 by *ST*. Separate experiments showed that the sterile sex is the male.

The geographic origin of the strains, shown in Figure 1, must be taken into consideration in an analysis of the data reported in Figure 2. A group of "Centro-American" strains are easily intercrossed and yield fertile hybrids; these are the strains from Honduras (the locality No. 2 in Fig. 1), two strains from El Salvador (No. 3), and one from Costa Rica (No. 4). The "Amazonian" group consists of strains from Belem (No. 11), Icana (No. 12), Trinidad (No. 9), and Panama-A (No. 5); these strains also yield fertile hybrids easily. A third, "Andean-South Brazilian," group comes from the eastern slope of the Andes in Peru (localities Nos. 18, 19, and 20), and from Angra dos Reis in southern Brazil (No. 25). The strains of this group also interbreed freely. However, intercrosses of strains belonging to the different groups either fail altogether (*O* in Fig. 2) or yield sterile hybrid males (*ST*).

This situation may suggest the existence of three reproductively isolated, although morphologically identical, sibling species: the Centro-American, the Amazonian, and the Andean. This interpretation is excluded by finding four other strains from Santa Marta (No. 6 in Fig. 1) and Bucaramanga (No. 7) in Colombia, Caripe, in Venezuela (No. 8), and Panama-B (No. 5). Figure 2 shows that Santa Marta gives fertile hybrids with the Centro-American group but not with the Andean group; the Bucaramanga strain is fertile with the Andean group, with Santa Marta, but only with Costa Rica in the Centro-American group. Caripe is fertile with Santa Marta but not with Bucaramanga, and produces sterile hybrids or none with the Centro-American and the Andean groups. Panama-B is fertile with Caripe; its females give fertile hybrids with one of the two strains from El Salvador, and its males do likewise with Bucaramanga. Attempts to cross Panama-B to other strains give sterile hybrids or none.

Perhaps the most important fact is that the two strains, A and B from Panama, have refused to cross entirely, despite repeated trials. Since both strains are derived from progenitors collected in Barro Colorado Island, this locality must harbor two sympatric, and yet completely reproductively isolated, populations of *D. paulistorum.* These populations behave, then, like full-fledged species. And yet they can exchange genes, because each of them can be crossed to other populations with which they produce at least fertile female hybrids. In fact, crosses can be arranged connecting the two Panama populations without yielding any sterile hybrids at all (see below).

The matings which produce no hybrids at all (marked by an *O* in Fig. 2) fail because of a complete sexual isolation between the strains involved. This has been established by dissection of the surviving females which were exposed for two weeks to foreign males, and examination of their seminal receptacles under a microscope. No sperm was found in the hundreds of females dissected. There is an incomplete sexual isolation also between at least some of the strains which produce sterile hybrids (*ST* in Fig. 2). We have dissected the females from some of these crosses after the hybrids have appeared, and found usually one or two inseminated females, the rest remaining virgins. This is evidently the explanation of the erratic character of some of the results; thus, the females of the Amazonian strains always refuse to accept males of the Centro-American and Andean groups, but Amazonian males occasionally inseminate some females of the latter two groups. Perhaps, any two strains may eventually be made to produce hybrids. Whether any of the inter-group crosses yielding sterile hybrids are entirely free of sexual isolation remains to be determined.

The nature of the sterility of the hybrid males is also not known in detail. It can, however, be stated that the testes of these males contain no spermatozoa and only abnormal spermatids, and their seminal vesicles are always empty.

Second Series of Experiments.—The experiments reported above made it clear that the species *D. paulistorum* is broken up into at least three incipient species, plus some connecting, or transitional, populations. In 1958 one of us (Th. D.) was able to collect further material in Colombia and in Ecuador. Drs. M. Wheeler and M. Wassermann of the University of Texas have contributed invaluable material from Panama, British Guiana, and Bolivia; Drs. C. Pavan and A. B. da Cunha have sent new strains from southern Brazil. A second series of experimental crosses has been carried out in 1958, using the same procedure as described above,

♂ \ ♀	GUATEMALA	HONDURAS	COSTA RICA	PANAMA-A	TRINIDAD	BELEM	PANAMA-B	PANAMA-C	LLANOS-A	CARIPE	GUIANA-A	GUIANA-B	SANTA MARTA	BUCARAMANGA	PALMIRA	BUENAVENTURA
1. GUATEMALA		F	F	O	ST			ST	ST	ST	ST	O	F	O		ST
2. HONDURAS	F		F	O	O			ST		ST			F		O	
4. COSTA RICA	F					O	ST		ST		O	ST		O		O
5. PANAMA-A	O		O		F		O		O		O			ST	O	O
9. TRINIDAD			O			F	O	O	O		O	O		O	O	O
11. BELEM	O	O		F	F			O		O			O		F	
5. PANAMA-B	ST	ST				O		F	F	F	F		ST	O	O	ST
5. PANAMA-C		ST	ST	O	ST		F		F	F	F			O	O	ST
13. LLANOS-A	ST	F				ST	ST	ST		ST	O	O	F	O	O	
8. CARIPE			ST	O	O		F	F	ST		F		ST		F	ST
10. GUIANA-A	O	ST		O		O		F	F	F		O	ST		O	
10. GUIANA-B	ST	ST		O	O			O	ST	O	O		ST		ST	
6. SANTA MARTA			F	O	O			O			O			F	O	F
7. BUCARAMANGA	O	ST				ST		ST	O	ST	O	ST				
14. PALMIRA			F	O	O		O		O					F		ST
15. BUENAVENTURA	ST	ST				O		ST	ST	ST	ST	O	F		O	
13. LLANOS-B	ST	ST		ST		ST	ST	O	O	ST	ST	ST	ST	F		
16. SANTO DOMINGO	F		O	O	ST		ST		F					F		ST
17. PICHILINGUE	ST	ST				O		ST	ST	ST	ST	O	F	ST	F	ST
19. TINGO MARIA	ST	ST				O		O		ST	ST	ST	ST		F	
21. COROICO			ST	O	O		O		O					F		F
22. SANTA CRUZ	ST	ST				ST		O		O	ST	F	ST		F	
23. MINAS GERAIS			ST	ST	O		ST		ST							F
24. SÃO PAULO	ST	ST				O		ST		ST	ST	O	ST	F	F	
25. ANGRA			ST	O	O		O		ST					F		F

FIG. 3.—Second series of experiments. Outcome of the crosses between strains of different geographic origin. O—no progeny produced; ST—male F_1 hybrids sterile; F—hybrids sterile.

except that no dissections and examinations of the sperm receptacles were made. The results are summarized in Figures 3 and 4, and in map form in Figure 1.

(*a*) *Centro-American group*, Guatemala to Costa Rica. Fully fertile *inter se* and with Santa Marta, Colombia. The strain from Tikal, Guatemala, collected

♀ / ♂	SANTA MARTA	BUCARAMANGA	PALMIRA	BUENAVENTURA	LLANOS-B	SANTO DOMINGO	PICHILINGUE	TINGO MARIA	COROICO	SANTA CRUZ	MINAS GERAIS	SÃO PAULO	ANGRA
1. GUATEMALA	F	O		ST		ST	ST	ST	ST		ST		F
2. HONDURAS	F		O			ST		ST	F		ST	ST	ST
4. COSTA RICA		O		O	ST		O	ST	ST	ST		ST	ST
5. PANAMA-A		ST	O	O	O		O	ST		ST		ST	
9. TRINIDAD		O	O	O	O		O	ST		ST		ST	
10. BELEM	O		F			ST			ST		ST		ST
5. PANAMA-B	ST	O	O	ST	ST		O	ST		O		ST	
5 PANAMA-C		O	O	ST		ST			ST		ST		ST
13. LLANOS-A	F	O	O	O	O	ST	ST	ST		ST	ST	ST	ST
8. CARIPE	ST	O	F	ST		ST		O	ST		ST		ST
10. GUIANA-A	ST		O			ST			ST	ST	ST		ST
10. GUIANA-B	ST		ST			ST		ST	ST	ST	ST	O	ST
6. SANTA MARTA		F	O	F		ST	F		O		ST		ST
7. BUCARAMANGA					F		O	F		F		F	
14. PALMIRA		F		ST	F	F			F		F		F
15. BUENAVENTURA	F		O		ST		F	ST		ST		F	
13. LLANOS-B	ST	F	F			F	O	F		F		F	
SANTO DOMINGO		F		ST	F				F		F		F
17. PICHILINGUE	F	ST	F	ST		F		ST		ST		ST	
19. TINGO MARIA	ST		F			F			F		F		F
21. COROICO		F		F	F		F				F		F
22. SANTA CRUZ	ST		F			F		F	F			F	
23. MINAS GERAIS				F	F		F			F			F
24. SÃO PAULO	ST	F	F			F		F	F		F		
25. ANGRA		F		F	F		F			F		F	

FIG. 4.—Second series of experiments. Outcome of the crosses between strains of different geographic origin. O—no progeny produced; ST—male F_1 hybrids sterile; F—hybrids fertile.

by Mrs. Sophie Dobzhansky Coe, yields fertile hybrids also with Santo Domingo, Ecuador. The strain from Costa Rica is fertile with Palmira, Colombia.

(*b*) *Amazonian group,* Panama to Para. Fertile *inter se,* and with only one other strain, from Palmira, Columbia (Transitional group, No. 14). Amazonian females accept males chiefly from the Andean group, but amazonian males are more successful with females of all other groups.

(*c*) *Andean-South Brazilian group*, Llanos of Colombia, Andes of Ecuador, Peru, and Bolivia, southern Brazil. There is some incipient differentiation even within this group, since the males from Pichilingue, Ecuador, yield sterile F_1 hybrid sons when mated to Peruvian, Bolivian, or Brazilian females (Fig. 4). Pichilingue females produce fertile hybrids with Peruvian, Bolivian, and Brazilian males. Otherwise this group gives fertile hybrids only with some of the strains of the Group F (Transitional), but sterile ones with other strains of the Transitional and other groups.

(*d*) *Orinocan group*, Panama, Llanos and Colombia, Venezuela, British Guiana. Fertile *inter se*, except that Llanos-A males produce sterile sons with females of the other strains, and Llanos-A females produce sterile sons with males from Caripe, Venezuela. The Llanos-A strain is also fertile with Honduras of the Centro-American groups, with Santo Domingo of the Andean group, and with Santa Marta of the Transitional group.

(*e*) *Guianan*, a single strain, Guiana-B from near Georgetown, British Guiana. Thus far, we have succeeded in obtaining fertile hybrids between this strain and only one other, that of the Andean group, from Santa Cruz, Bolivia. Guiana-B males are accepted by females of the other groups except the Amazonian, but the male hybrids produced are sterile.

(*f*) *Transitional group*, Colombia localities Nos. 6, 7, 14, and 15 (Fig. 1). Fertile *inter se*, except that the strains from Palmira and from Buenaventura are difficult to cross, and when crossed produce sterile sons. This group deserves its name because at least some of its members produce fertile hybrids with at least some members of every other group, except the Guianan group. Here we have, then, a genetic bridge which connects the gene pools of the other groups. A glance at the map in Figure 1 shows that Group F is geographically also bridging the other groups.

Conclusions and Summary.—The geographic distributions of the six groups, or subspecies are, as shown in Figure 1, generally distinct. However, in at least three localities representatives of two groups occur together, sympatrically, and yet remain incapable of interbreeding. These localities are: (1) Barro Colorado Island, Panama, where groups B and D have been found, (2) Llanos near Villavicencio, Colombia, groups C and D, and (3) Georgetown, British Guiana, groups D and E. In all these cases the sympatric populations yield no hybrid progenies, and even no cross-insemination, in laboratory experiments in which they have no possibility of mating within their own race.

Inability of sympatric Mendelian populations to interbreed and to exchange genes is *prima facie* evidence that these populations belong to different species. Nevertheless, we are obliged to conclude that *D. paulistorum* is, considered as a whole, a single species. This is not because its component populations, whether reproductively isolated or not, are not distinguishable by the morphology. The compelling evidence comes from the existence of bridging populations, which do produce fertile hybrids when crossed to other populations which are reproductively isolated from each other. With the strains at our disposal, it may be necessary to make as many as four consecutive crosses in order to connect two otherwise non-interbreeding populations without encountering sterility of, at least, the male hybrids (e.g. between Panama-A and Panama-B). Since female hybrids are mostly fertile, the gene exchange becomes facilitated; generally no more than two consecutive crosses are needed to open a channel for gene exchange. *D. paulistorum* is a single inclusive Mendelian population. No matter to what group a strain giving rise to a favorable mutation or a gene combination may belong, the mutation of the gene combination will, at least potentially, be able to diffuse in other populations and to become the property of the species as a whole. To what extent such a potentiality is actually realized is, of course, a separate question. We hope to be able to shed some light on it by another study.

Comparison of *D. paulistorum* with other race-species borderline case, that of the frog *Rana pipiens*, suggests itself. As shown by the brilliant studies of Moore,[10] the northern populations of this species (from New England) yield inviable hybrids when crossed to southern populations (Texas or Florida). Viable hybrids are, however, formed by geographically adjacent populations. *R. pipiens* is an inclusive Mendelian population, a single species, and, at least potentially, a unit of evolutionary change. One can imagine the situation in *R. pipiens* coming to resemble that in *D. paulistorum,* if the frog populations like those of New England migrated to some territory and met there expanding populations like those of Texas, and both coexisted sympatrically without effective gene exchange. If this were to happen together with preservation of the present genetic connection in the eastern United States, we would be led to conclude that the specific unity of *R. pipiens* is not forfeited. On the other hand, suppose that only populations like the present inhabitants of New England and Texas were preserved and became sympatric without breakdown of reproductive isolation; that would mean emergence of two genetically closed systems, two species. A parallel event would be disappearance of the populations of *D. paulistorum* which now inhabit the northwestern part of the continent of South America (Colombia and, perhaps, Panama). What remained would, perhaps, be five independent species (here, however, a caveat: the populations of central and eastern Brazil having not been studied, we do not know whether the Amazonian and the Andean groups are, or are not, connected there).

Whether two Mendelian populations, or groups of populations, are distinct species or only races is frequently in doubt. Most of these doubtful cases can be resolved unambiguously if sufficient evidence, observational and experimental, becomes available. A minority are, however, true borderline cases; in these the process of species splitting has, on our time level, reached the critical stage of transition from race to species. *D. paulistorum* is one species; it is also a cluster of species *in statu nascendi;* it bespeaks the correctness of Darwin's opinion that "each species first existed as a variety."

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