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GEOGRAPHY OF THE SIBLING SPECIES RELATED TO *DROSOPHILA WILLISTONI*, AND OF THE SEMISPECIES OF THE *DROSOPHILA PAULISTORUM* COMPLEX¹

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The six sibling species of *Drosophila willistoni* group are among the most favorable, and at the same time challenging materials for studies on the genetics of speciation processes. The species are *D. willistoni* Sturtevant, *D. paulistorum* Dobzhansky & Pavan, *D. pavlovskiana* Kastritsis & Dobzhansky, *D. equinoxialis* Dobzhansky, *D. tropicalis* Burla & da Cunha, and *D. insularis* Dobzhansky. Burla et al. (1949) found slight morphological differences that were insufficient for identification of single individuals, but Spassky (1957) noted differences in the male genitalia which do permit such identification. Unambiguous discrimination is also possible through examination of the gene arrangements in the chromosomes of larval salivary glands (Burla et al., 1949; Dobzhansky et al., 1950), and of the variant enzymes detected by electrophoresis (Ayala et al., 1970). Owing to ethological isolation, cross-mating of the species occurs rarely, although under laboratory conditions some cross-inseminations can be obtained (Burla et al., 1949). Intercrosses of *D. insularis* females with *D. tropicalis* and *D. willistoni* males, and occasionally with *D. paulistorum*

and *D. equinoxialis* males, give viable but completely sterile hybrids (Dobzhansky et al., 1957). *D. paulistorum* and *D. pavlovskiana* produce sterile male but fertile female hybrids (Kastritsis and Dobzhansky, 1966). Obtaining not only viable but even fertile hybrids with complete chromosome pairing has been claimed for other combinations of the sibling species, but such claims have not been confirmed in experiments conducted in our laboratory (chiefly by Dr. L. Ehrman).

The most interesting differences between the species are those in geographic distribution and in the degree of intraspecific diversity. *D. insularis* and *D. pavlovskiana* are narrow endemics, the former on some of the islands of the Lesser Antilles and the latter in Guyana. The other four species occur over vast territories in the American tropics, and as will be shown below live sympatrically in most parts of their distribution areas. Although *D. willistoni* has the widest distribution, from Florida to Argentina, strains from anywhere intercross easily, and with a single exception yield fertile hybrids. The exception is a population sample from Lima, Peru; it produces sterile male hybrids with some, though not all, conspecific strains from other localities (Dobzhansky, 1965). *D. paulistorum* presents a contrasting situation. It is a super-species composed of at least six semispecies, or incipient species. Ethological isolation between the semispecies is sufficient to enable some of them to coexist sympatrically in many localities, as will be shown below. Hybrids of the semispecies obtained in the laboratory are sterile as males but fertile

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as females (Dobzhansky and Spassky, 1959; Dobzhansky et al., 1969; Perez-Salas et al., 1970). *D. tropicalis* consists of at least two subspecies, *tropicalis* and *cubana*, in South America and the West Indies respectively. There is little ethological isolation between them, but male hybrids are sterile (Townsend, 1954). The presently available data give no sufficient reason to treat *tropicalis* and *cubana* as separate species. *D. equinoxialis* is insufficiently known, but according to unpublished data of one of us (F. Ayala), strains from Puerto Rico give sterile male hybrids with those from South America. According to an unpublished thesis of Dr. G. Carmody, there may be a seventh sibling species, two strains of which have been obtained from Colombia and one from Brazil, which crosses with some but not with other strains of both *D. paulistorum* and *D. equinoxialis*. This matter requires further study.

Fragmentary data on the geographic distributions of the species and semispecies of the *willistoni* group have been published in the papers referred to above. The purpose of the present article is to collate these, as well as much unpublished information, and to derive from this information whatever inferences the data permit concerning the evolutionary status of the forms under consideration.

COLLECTION AND DIAGNOSIS

The population samples were made by sweeping with a collecting net over baits, usually of fermenting bananas but sometimes of wild fruits fallen to the jungle floor. In addition to the population samples collected by the authors of the present article, many colleagues kindly sent us *willistoni*-like flies from their collections. The early samples in Brazil (1943–1956) were made by the members of a cooperative research project, including Professors C. Pavan and A. B. da Cunha (Univ. of São Paulo), Ch. Malogolowkin and A. G. L. Cavalcanti (National Univ., Rio de Janeiro),

A. R. Cordeiro (Univ. Rio Grande do Sul), C. L. Birch (Univ. Sydney, Australia), B. Battaglia (Univ. Padua, Italy), and Th. Dobzhansky, then of Columbia University. Between 1954 and 1963 Professors H. L. Carson (Washington Univ.), W. B. Heed (Univ. Arizona), and M. Wasserman (Queens College) furnished samples from Central America, West Indies, and northern South America; Professor S. B. Pipkin (George Washington Univ.) sent many samples from Panama and some from Colombia between 1958 and 1964, and Professor A. J. Gallo (Faculdade de Filosofia, São José do Rio Preto) from the vicinity of the latter town in 1968–1970.

Until 1953, the species were diagnosed mainly by inspection of the chromosomes in the larval salivary glands in the progenies of single wild-collected females. Thereafter, both wild-collected males and sons of wild-collected females were classified according to the morphology of their genitalia, mostly by B. Spassky. From 1969 on, enzyme variants detected by electrophoresis were also used. The cytological, morphological, and biochemical diagnoses agree in better than 99% of the determinations. Occasional doubts can always be resolved by outcrosses to known species strains.

The existence of the semispecies in *D. paulistorum* was discovered first in 1957 (Dobzhansky and Spassky, 1959). The semispecies in the early collections were distinguished only in the few strains that were conserved in the laboratory. In the more recent collections, all strains, each descended from a single wild-collected female, are tested by crossing to each other (by chain crosses) or by outcrossing to tester strains known to belong to certain semispecies. The results of the tests are as a rule quite unambiguous—fertile hybrids of both sexes are obtained in crosses to one and only one tester, while the crosses to other testers give either no progenies or sterile male hybrids. The exceptions are, of course, most interesting. Strains of the Transitional group may or may not yield

sterile male hybrids in crosses with other Transitionals, or with Centroamerican, or with Andean-Brazilian strains (Dobzhansky et al., 1969). A strain from the vicinity of San Martin, in the Llanos of Colombia, was giving fertile hybrids with the strains of the Orinocan semispecies when tested in 1958, but later produced sterile progenies with the same strains (Dobzhansky and Pavlovsky, 1967). Kastritsis (1966, 1967) found that the semispecies can also be distinguished cytologically, but this is too laborious to be used routinely for diagnosis. Pasteur (1970) has found statistically significant differences among the semispecies in several morphological characters. The largest differences occur in tibia/wing length ratio and in clasper tooth numbers. The morphological differences, however, cannot be used for diagnostic purposes since there is considerable overlap among the semispecies.

GEOGRAPHY OF THE SIBLING SPECIES

Percentages, rounded off to the nearest integer, of the four siblings (*D. willistoni*, *D. paulistorum*, *D. equinoxialis*, and *D. tropicalis*) in samples from different localities are shown in Table 1. Small samples, in which the frequencies may be unreliable, are reported only for localities for which larger samples are unavailable. Otherwise small samples are ignored, or in some instances pooled together, as seems reasonable. In some localities collections have been made at different seasons or in different years, thus giving information about the seasonal or other variability of the species incidence.

In Table 1, the localities are arranged generally from North to South and from West to East. It can be seen (Figure 1) that the distribution of *D. willistoni* extends further both northward and southward than that of any of its siblings. *D. willistoni* alone has been found in Florida, in Uruguay and in Argentina. On the Greater Antilles (Cuba, Haiti, Puerto Rico, Jamaica) it coexists with *D. equinoxialis*

and *D. tropicalis*, which may outnumber *D. willistoni* in the samples. On the Lesser Antilles, excepting Trinidad, *D. willistoni* lives either alone or in the company of *D. insularis*. Three strains of this latter species were obtained from St. Kitts, one from St. Lucia, and four from Montserrat. It is quite possible that *D. insularis* will be found also on other islands of the Lesser Antilles chain. Contrary to the islands of the Antilles, which in geological history were never connected with any continent or with each other, Trinidad is geologically a part of South America. It is, therefore, not unexpected that it has all four siblings, like the neighboring Venezuela and Guyana. The very small sample from north-central Mexico (Axtla) had only *D. willistoni* (collected by Professor J. A. Moore), but further south there appear *D. equinoxialis* and *D. tropicalis*. The northernmost locality of *D. paulistorum* is Tical, in Guatemala (collected by Dr. S. D. Coe). From there down to central Brazil the four sibling species are sympatric. In southern Brazil, from São Paulo southward, only *D. willistoni* and *D. paulistorum* are found; the southernmost locality of *D. tropicalis* is São Jose do Rio Preto (Professor A. J. Gallo, collector). In the southernmost state of Brazil, Rio Grande do Sul, *D. paulistorum* is rare, and further southward it has not been found at all. Thus, *D. paulistorum* does not extend as far north, but it does live further to the south, than *D. equinoxialis* and *D. tropicalis*. *D. pavlovskiana* is a rare endemic in Guyana. Only two strains of it were collected near Georgetown (in 1957 and 1963), one at Apoteri, at the junction of the Essequibo and Rupununi rivers, in 1963, and one in the Kanuku Mountains in 1970 by Mr. Carl Hopkins.

One would like to know whether the sibling species are differentiated ecologically. More than a quarter of a century of sampling these populations in nature and breeding them in the laboratory has yielded some information, though not as much as desirable. The siblings which live

TABLE 1. Percentages of the four sibling species in different collections.

Locality	Dates	<i>willistoni</i>	<i>paulistorum</i>	<i>equinoxialis</i>	<i>tropicalis</i>	Number examined
<i>Mexico and Central America</i>						
Axtla, S. L. Potosi, Mexico	Sep 46	100	—	—	—	5
Cuernavaca, Mexico	Jun 63	53	—	18	29	17
Tehuacan, Mexico	Jan 63	60	—	—	40	10
Tical, Guatemala	May 58	94	2	3	2	65
Lancetilla, Honduras	Apr 54	11	—	34	55	135
El Salvador, Salvador	May 54	35	2	45	18	246
El Salvador, Salvador	Aug 54	8	8	74	9	74
Turrialba, Costa Rica	Aug 56	22	28	34	16	64
La Lola, Costa Rica	Aug 56	1	4	64	30	138
San Isidro, Costa Rica	Aug 56	44	8	47	—	36
Santa Ana, Costa Rica	Aug 56	11	—	89	—	54
Boquete, Panama	Aug 58	50	30	20	—	10
Central Panama	Feb	20	< 1	27	53	421
Central Panama	Apr	4	—	60	36	245
Central Panama	May–Jun	33	2	41	24	298
Central Panama	Aug–Oct	12	13	49	26	271
Central Panama	Nov–Dec	7	9	80	4	661
El Real, Panama	Dec 62	5	3	91	1	79
Jaque, Panama	Feb 69	20	< 1	27	52	426
<i>Florida and West Indies</i>						
Lake Placid, Florida	?	100	—	—	—	104
Cuba	Feb 56	49	—	19	32	63
Haiti	Feb 56	53	—	30	18	57
Jamaica	Feb 56	54	—	31	15	254
Jamaica	Jul 58	84	—	1	15	138
Grand Cayman	Jan 67	13	—	83	4	71
Yunque, Puerto Rico	Feb 56	63	—	6	31	54
Yunque, Puerto Rico	Nov 57	42	—	50	9	141
Mayaguez, Puerto Rico	Nov 57	73	—	19	8	26
St. Thomas, V. I.	Aug 56	100	—	—	—	9
St. Kitts	Jan 56	100	—	—	—	77
Montserrat	Dec 63	100	—	—	—	92
St. Lucia	Jan 56	100	—	—	—	105
St. Vincent	Aug 56	100	—	—	—	9
Barbados	Jan 56	100	—	—	—	115
Port of Spain, Trinidad	Aug 56	82	—	18	—	17
Tabaquite, Trinidad	Aug 56	52	—	39	10	31
Simla, Trinidad	Feb 63	73	22	5	—	237
Simla, Trinidad	Jan 69	62	38	—	—	516
Sangre Grande, Trinidad	Feb 55	76	15	9	—	55
Sangre Grande, Trinidad	Feb 63	64	4	24	8	50
St. Isabel, Trinidad	Jan 69	72	28	—	—	54
Mora Forest, Trinidad	Feb 69	75	25	—	—	63
<i>Colombia</i>						
Chocó, Teresita	Feb 69	13	2	53	33	737
Chocó, Condoto	Feb 67	—	100	—	—	200
Valle, Malaga	Feb 69	10	90	—	—	80
Buenaventura	Mar 58	51	49	—	—	41
Palmira	Mar 58	88	5	—	7	75
Rio Raposo	Jun 63	—	100	—	—	41
Turbo	Feb 67	< 1	1	10	88	311
Monteria	Mar 58	8	—	4	89	159
Cordoba	Feb 67	—	—	17	83	18
Piojó	Feb 67	42	—	12	46	24

TABLE 1. Continued.

Locality	Dates	<i>willistoni</i>	<i>pauistorum</i>	<i>equinoxialis</i>	<i>tropicalis</i>	Number examined
<i>Colombia</i>						
St. Marta, Sea Level	Sep 56	7	—	63	31	59
St. Marta, Las Nubes	Aug 56	19	77	4	—	114
St. Marta, Las Nubes	Feb 67	65	4	—	31	319
Bucaramanga	Sep 56	78	2	18	2	124
Llanos, San Martín	Mar 58	73	3	14	10	156
La Macarena	Feb 68	25	1	61	13	288
Valparaiso	Feb 68	60	23	8	9	379
Mitú	Feb 68	45	41	11	2	175
Leticia	Feb 68	12	43	41	3	236
<i>Ecuador</i>						
Pichilingue	Mar 58	58	4	—	38	55
Santo Domingo	Mar 58	72	6	—	22	18
<i>Venezuela</i>						
Perijá, Machiques	Jan 63	—	—	5	95	19
Perijá, Machiques	Nov 67	—	11	89	—	153
Vigía	Jan 69	25	55	16	4	113
Barrancas, Barinas	Apr 69	16	11	35	39	385
Mérida	Dec 56	94	3	—	3	67
Barquisimeto	Jan 70	14	7	29	50	70
Sarare	Nov 67	14	2	45	39	98
Rancho Grande	Nov 68	13	85	2	—	143
Tuy	Jan 63	11	3	79	8	112
Guatopo	Aug 69	27	71	< 1	1	311
Marrero	Aug 69	51	4	27	17	138
Caripe	Jan 63	88	10	—	2	174
Caripe	Aug 69	89	11	—	—	46
Puerto Ayacucho	Nov 68	57	10	33	—	427
S. F. Atabapo	Dec 69	49	5	47	—	109
Ocamo	Nov 68	50	37	14	—	131
S. Elena Uairén	Jan 63	81	19	—	—	176
<i>Guyana</i>						
Georgetown	Aug 57	17	24	43	17	37
Georgetown	Feb 63	28	9	63	—	192
Apoteri	Feb 63	91	8	1	—	209
Skeldon	Feb 63	85	—	6	9	34
Kanuku Mts.	May 70	89	6	3	1	206
<i>Northern Brazil</i>						
Marco	Feb 68	11	9	39	41	150
Tefé	Nov 69	19	7	71	3	493
Içana	Sep 52	15	29	52	4	197
Uaupés	Sep 52	13	2	83	2	120
Tapuruquara	Nov 69	28	64	8	—	640
Uraricoara, Rio Branco	Apr 49	67	32	1	1	111
Mucajaí, Rio Branco	Apr 49	42	9	35	14	173
Moura & Anavilhanas	Apr 49	49	43	5	3	100
Manaus	Nov 69	72	23	4	< 1	248
Santarém	Nov 69	87	4	< 1	9	407
Macapá	Nov 69	38	—	18	44	79
Tracajatuba	Nov 69	14	—	1	85	84
Amapá	Jun 52	63	25	10	1	156
Marajó, Oriente	Jul 52	34	23	5	39	173
Belém	Oct–Nov 48	14	76	11	—	74

TABLE 1. Continued.

Locality	Dates	<i>willistoni</i>	<i>paulistorum</i>	<i>equinoxialis</i>	<i>tropicalis</i>	Number examined
<i>Northern Brazil</i>						
Belém	May 49	37	47	5	11	150
Belém	Sep 49	20	80	—	—	80
Belém	Jun 52	33	64	1	3	140
Belém	Aug 52	37	54	1	7	135
Belém	Nov 69	10	48	6	36	395
S. Luís, Maranhão	Apr 56	74	25	—	1	135
Rosário	Apr 56	56	42	—	2	113
Imperatriz	Aug 49	96	3	—	1	104
Carolina	Aug 49	89	11	—	—	37
<i>Northeastern Brazil</i>						
Floriano, Piauí	Feb 53	72	15	9	4	164
Aratuba, Ceará	Apr 56	92	3	—	5	74
Maranguape	Apr 56	46	51	—	4	81
Guaramiranga	Apr 56	90	9	—	1	102
Natal	Apr 56	100	—	—	—	130
Paraíba	Nov 55	97	2	—	1	113
Olinda	Nov 55	100	—	—	—	67
Recife	Nov 55	96	4	—	—	90
Recife	Apr 56	76	23	—	1	160
Salvador	Feb 49	100	—	—	—	280
Catuni	Feb 49	100	—	—	—	150
Catuni	Dec 51	100	—	—	—	64
Barreiras	Jan 53	77	11	—	11	108
Ilhéus	Jan 52	98	2	—	—	222
<i>Central and Southern Brazil</i>						
Palmares, Acre	Jan 49	54	41	2	3	116
Cruzeiro do Sul	Jan 49	50	30	7	13	319
Porto Velho	Jan 49	32	49	13	6	53
Palma, Goiás	Nov 48	95	1	—	4	76
Monjolinho	Nov 48	89	11	—	—	144
Bôa Esperança M.G.	Jan 53	98	2	—	—	58
Gov. Valadares	Oct 52	56	43	—	1	100
Rio de Janeiro	Nov 52	57	43	—	—	177
Angra dos Reis	Jun 55	77	23	—	—	699
Mogi, S.P.	Sep 48	92	8	—	—	37
Mogi, S.P.	Oct 48	85	15	—	—	79
Mogi, S.P.	Dec 48	43	57	—	—	157
Mogi, S.P.	Feb 49	77	23	—	—	128
Mogi, S.P.	Apr 49	84	16	—	—	89
Vila Atlântica	Sep 48	49	51	—	—	143
Vila Atlântica	Nov 48	22	78	—	—	172
Vila Atlântica	Jan 49	51	49	—	—	119
Vila Atlântica	Mar 49	82	18	—	—	122
Vila Atlântica	May 49	67	33	—	—	176
Pirassununga	Sep 48	82	18	—	—	57
Pirassununga	Oct 48	93	7	—	—	107
Pirassununga	Dec 48	98	2	—	—	108
Pirassununga	Feb 49	93	7	—	—	110
Pirassununga	Apr 49	92	8	—	—	100
Pirassununga	Jun 47	100	—	—	—	99
S.J. Rio Preto	Sep-Oct 68	100	—	—	—	34
S.J. Rio Preto	Nov-Dec 68	99	< 1	—	1	536
S.J. Rio Preto	Jan 69	99	< 1	—	< 1	1983
S.J. Rio Preto	Mar 70	79	21	—	—	672

TABLE 1. Continued.

Locality	Dates	<i>willistoni</i>	<i>paulistorum</i>	<i>equinoxialis</i>	<i>tropicalis</i>	Number examined
<i>Central and Southern Brazil</i>						
Paranaguá	Mar 49	83	17	—	—	29
Iguassu	Mar 49	100	—	—	—	134
Reuter, R.G.S.	Jan 48	100	—	—	—	27
Santo Angelo	May 49	100	—	—	—	27
Ponta Grossa	Apr 51	100	—	—	—	107
<i>Peru, Bolivia</i>						
Tarapoto	Sep 55	57	38	1	4	77
Urubamba	Sep 55	3	97	—	—	30
Tingo Maria	Sep 55	50	46	< 1	3	248
Lima	Apr 59	100	—	—	—	92
Coroico	May 58	3	97	—	—	66
Santa Cruz	May 58	76	18	—	6	100
<i>Argentina, Uruguay</i>						
Melo, Ur.	May 51	100	—	—	—	34
Tucuman	Mar 52	100	—	—	—	118
Buenos Aires	Mar 52	100	—	—	—	56
La Plata	Mar 52	100	—	—	—	43

sympatrically in the enormous area, from Mexico to southern Brazil, are attracted to the same natural and artificial baits. The possibility of differential attraction to different baits cannot, however, be ruled out. Detailed examination of the data reported in Table 1 shows that *D. paulistorum* is most at home in superhumid tropical forests. It is the dominant species on the rainy west coast of Colombia (Condoto, Malaga, Rio Raposo), the commonest or second commonest on the Upper Amazon, Rio Negro, and their tributaries (Mitu, Leticia, Tapuruquara, Moura, but curiously not at Tefe), and at Belem in Para. It becomes rare in the dry northeastern Brazil (except in the humid mountains of Maranguape), but emerges again as the commonest or second commonest species on the humid coast of São Paulo (Vila Atlantica).

D. equinoxialis and *D. tropicalis* are most at home in relatively drier forests alternating with savannas (Caribbean coasts of Colombia, Venezuela, and Guyana, but not in eastern, central, and southern Brazil, where these species become rare or absent). *D. willistoni* is found almost everywhere, including man-modified environments. It

is nevertheless not a "domestic" species (Dobzhansky, 1965), being far outnumbered near human habitations by *D. simulans*, *D. ananassae*, *D. latifasciaeformis*, *D. sturtevantii*, and some species of the *repleta* group.

The greater prevalence of *D. willistoni*, relative to its siblings but not to other species of *Drosophila*, in habitats disturbed by man is quite striking. The former often can, and the latter usually cannot, be found in fruit orchards and similar places. Where samples collected at different seasons are available, *D. paulistorum* is usually more frequent during the rainy and *D. willistoni* during the dry seasons (see especially the samples from southern Brazil). In the Cordillera Oriental of the Andes of Colombia, *D. willistoni* seems to reach higher elevations than the other siblings.

The Semispecies of Drosophila paulistorum

Table 2 reports the semispecies found in the samples of populations of *D. paulistorum*. It can be seen that many samples in Table 1 are not mentioned in Table 2,



FIG. 1. The known geographic distribution of the six sibling species of *D. willistoni* group.

and a few of those in Table 2 are not in Table 1. The reason is that the semispecies were not distinguished in the early collections, and some samples of *D. paulistorum* came from collections in which the proportions of the other siblings were not recorded. Where only a single strain was preserved in the laboratory, or only a few

strains were studied from nature, the semispecies diagnosed are marked by plus signs, instead of percentages. The most interesting part of the geographic area of *D. paulistorum*, in which several semispecies occur, is mapped in Figure 2. Not shown on the map is a portion of Central America where only the Centroamerican semispecies is

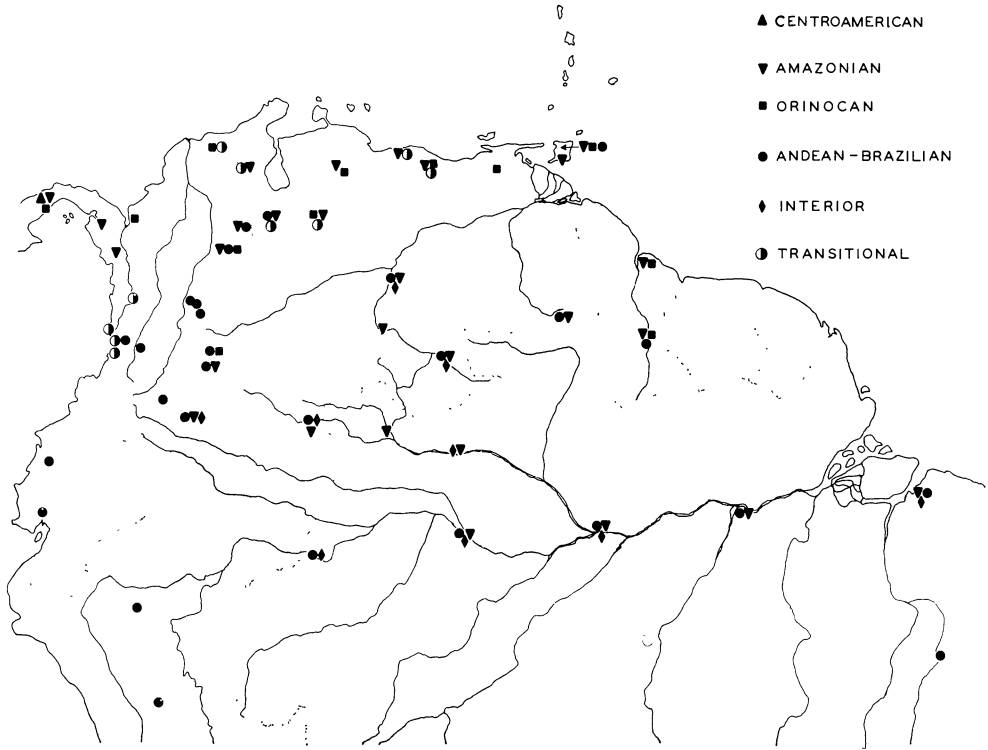


FIG. 2. The known geographic distribution of the semispecies of *D. paulistorum*.

found, and northeastern, central and southern Brazil, Peru and Bolivia, where only the Andean-Brazilian semispecies occurs. The distribution areas of the semispecies are well differentiated, although in some places two or three semispecies occur sympatrically.

The Centroamerican semispecies occurs alone in Guatemala, Honduras, El Salvador, Costa Rica and western Panama. In central Panama (Canal Zone and adjacent areas) the Amazonian and Orinocan semispecies are also found. The Transitional populations, which are closely related to Centroamerican, occur alone on the superhumid west coast of Colombia (see Chocó, Malaga, Raposo), together with Orinocan on the St. Marta Massif, and with Andean-Brazilian and Amazonian in northern Venezuela. As shown by Dobzhansky et al. (1969), some transitional strains produce

fertile, while others produce sterile F_1 male hybrids with Centroamerican, with Andean-Brazilian and with each other. It must be noted that the strains from Vigía and Barinas, which are shown in Table 2 as Transitionals were not tested as extensively as the others.

The Andean-Brazilian semispecies has by far the largest distribution area—from northeastern Colombia (Cucuta, Bucaramanga) and the adjacent part of Venezuela (Vigía), Trinidad, Central Guyana (Apoteri), down to southern Brazil (São Paulo, Parana, Rio Grande Sul), and from the Andean chains of Colombia, Ecuador, Peru and Bolivia, to the Atlantic coast of Brazil. Moreover, in much of this area this semispecies lives alone. However, it does coexist sympatrically with Amazonian, with Orinocan, or with Interior along the Amazon, and especially to the north of that

TABLE 2. *The presence (+), or percentages, of the semispecies of Drosophila paulistorum in different collections.*

Locality	Centro-american	Transitional	Andean-Brazilian	Amazonian	Orinocan	Interior	Numbers examined
<i>Central America</i>							
Tical, Guatemala	+	—	—	—	—	—	1
Lancetilla, Honduras	+	—	—	—	—	—	1
San Salvador, El Salvador	+	—	—	—	—	—	2
Turrialba, Costa Rica	+	—	—	—	—	—	1
Boquete, Panama	+	—	—	—	—	—	2
Almirante, Panama	+	—	—	—	—	—	2
Central Panama	21	—	—	53	26	—	19
El Real, Panama	—	—	—	+	—	—	1
<i>Trinidad</i>							
Simla 1963	—	—	2	88	10	—	52
Simla, 1969	—	—	—	98	2	—	148
Mora Forest	—	—	—	100	—	—	12
<i>Colombia</i>							
Chocó, Teresita	—	—	—	100	—	—	15
Chocó Condoto	—	100	—	—	—	—	200
Valle, Malaga	—	100	—	—	—	—	66
Buenaventura	—	—	+	+	—	—	2
Rio Raposo	—	100	—	—	—	—	41
Turbo	—	—	—	—	+	—	1
Santa Marta	—	50	—	—	50	—	4
Bucaramanga	—	—	+	+	+	—	7
Cucuta	—	—	30	70	—	—	10
Llanos, San Martin	—	—	75	—	25	—	4
La Macarena	—	—	+	+	—	—	2
Fusagasuga	—	—	+	—	—	—	2
La Mesa	—	—	100	—	—	—	27
El Colegio	—	—	100	—	—	—	22
Girardot	—	—	100	—	—	—	100
Palmira	—	—	+	—	—	—	1
Gigante	—	—	100	—	—	—	4
Valparaiso	—	—	29	2	—	69	90
Mitu	—	—	2	51	—	47	132
Leticia	—	—	25	—	—	75	105
<i>Venezuela</i>							
Perija, Machiques	—	3	—	97	—	—	77
Vigia, Zea	—	74	18	8	—	—	50
Barinas	—	10	—	83	7	—	42
Barquisimeto	—	—	—	100	—	—	7
Sarare	—	+	—	—	+	—	2
Rancho Grande	—	90	—	10	—	—	150
Tuy	—	—	—	—	+	—	3
Guatopo	—	4	—	96	—	—	167
Caripe	—	—	—	—	100	—	21
Puerto Ayacucho	—	—	50	33	—	17	30
S. F. Atabapo	—	—	—	100	—	—	5
Ocamo	—	—	3	17	—	80	30
S. Elena Uairen	—	—	88	12	—	—	33

TABLE 2. Continued.

Locality	Centro-american	Transitional	Andean-Brazilian	Amazonian	Orinocan	Interior	Numbers examined
<i>Guyana</i>							
Georgetown	—	—	—	28	72	—	18
Apoteri	—	—	15	75	10	—	17
Kanuku Mts.	—						
<i>Northern Brazil</i>							
Marco	—	—	79	—	—	11	14
Tefé	—	—	4	4	—	92	26
Içana	—	—	—	+	—	—	1
Tapuruquara	—	—	—	47	—	53	346
Manaus	—	—	3	95	—	3	38
Santarém	—	—	11	89	—	—	9
Belém	—	—	1	99	—	1	157
Carolina	—	—	+	—	—	—	1
Maranguape	—	—	100	—	—	—	13
Recife	—	—	100	—	—	—	18
Salvador	—	—	100	—	—	—	9
<i>Central and Southern Brazil</i>							
Goiania	—	—	+	—	—	—	2
Cerra do Cipó, M. G.	—	—	+	—	—	—	5
Xingu	—	—	100	—	—	—	12
Rio de Janeiro	—	—	100	—	—	—	45
Angra dos Reis	—	—	+	—	—	—	1
S. J. Rio Preto	—	—	100	—	—	—	141
Cantareira	—	—	+	—	—	—	1
Paranaguá	—	—	+	—	—	—	1
São Pedro, R. G. S.	—	—	+	—	—	—	1
<i>Ecuador, Peru, Bolivia</i>							
Pichilingue	—	—	+	—	—	—	1
Santo Domingo	—	—	+	—	—	—	1
Tarapoto	—	—	+	—	—	—	1
Urubamba	—	—	+	—	—	—	1
Tingo Maria	—	—	+	—	—	—	1
Coroico	—	—	+	—	—	—	1
Santa Cruz	—	—	+	—	—	—	1

river and the upper Orinoco. It is the Andean semispecies which reaches fairly high elevations in the Andes of Colombia (La Mesa, El Colegio, and Fusagasuga to the west and southwest of Bogota). The type specimen of *D. paulistorum* belongs to the Andean-Brazilian semispecies. The type locality is Mogi das Cruzes, São Paulo, Brazil (Burla et al., 1949).

The Amazonian semispecies extends from Panama and Trinidad to the estuary of the Amazon and Tocantins. It is the common-

est semispecies in the watersheds of Rio Negro and Orinoco, as well as along the Amazon. However, it has not been found on the upper Amazon (Solimões) at Leticia and Marco, and was relatively rare at Tefe. Amazonian is sympatric with Orinocan, Interior or Andean-Brazilian semispecies, and seems to occur nowhere alone. In contrast to this, Orinocan and Interior have never been found together. Orinocan seems to be confined to the Caribbean coast north of the Llanos of Colombia and Venezuela,

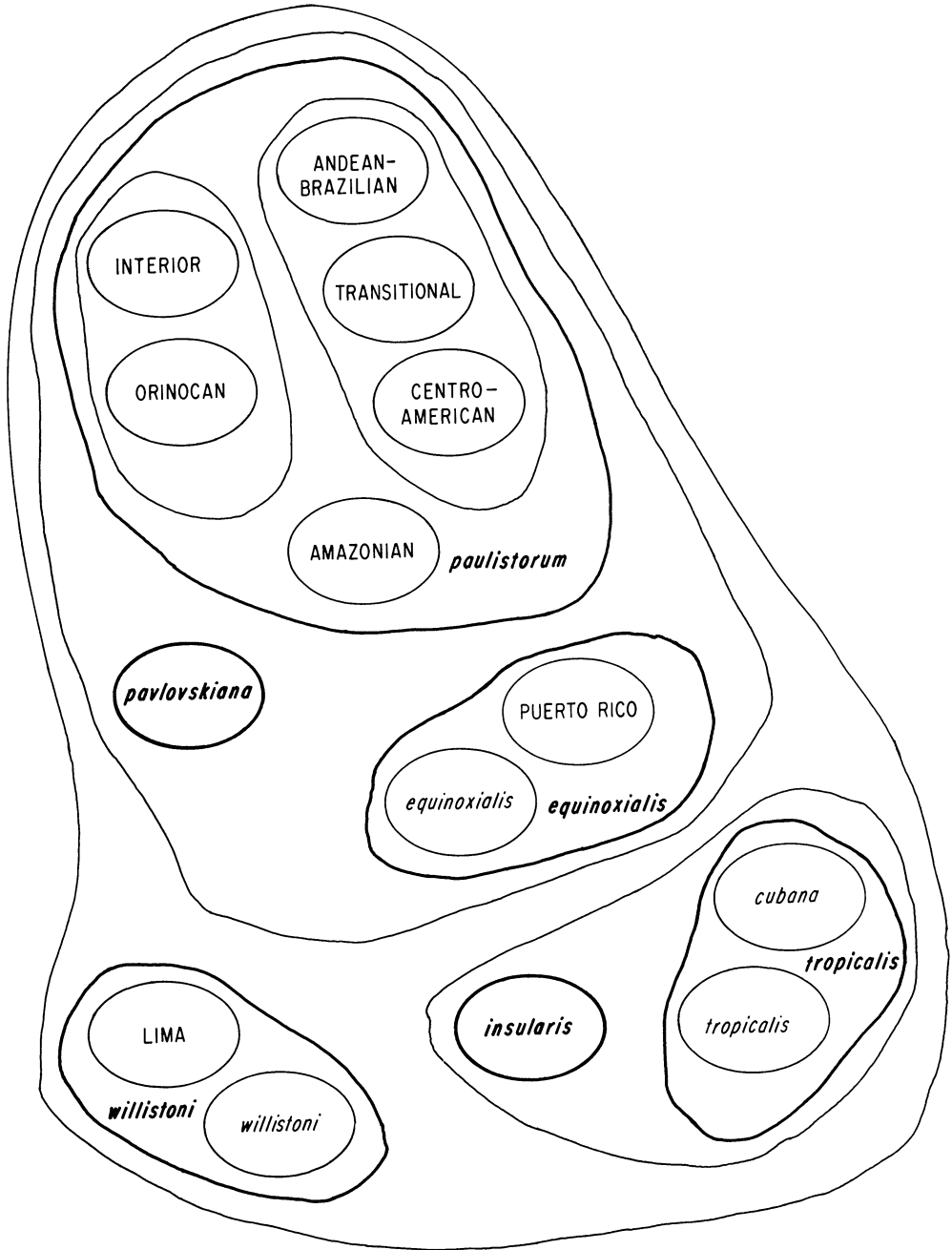


FIG. 3. Diagram showing relationships within the *D. willistoni* group of sibling species.

while Interior lives south of the Llanos, on the upper Orinoco, Rio Negro, upper Amazon, and their tributaries. A single Interior female was however collected at Belem. The unfortunately very small collection near San Martin, in the Llanos of Colombia, contained a female the progeny of which gave fertile hybrids with Orinocan in 1958, but sterile hybrids in 1963 and thereafter (Dobzhansky and Pavlovsky, 1967). It may well be that this strain, coming from a geographically intermediate place was also genetically intermediate between the Orinocan and Interior semispecies. These semispecies are more closely related to each other than any other pair of semispecies (Perez-Salas et al., 1970).

DISCUSSION

In the present article we are dealing with two levels of evolutionary divergence. First, the six sibling species are complexes of Mendelian populations reproductively completely isolated from each other. Secondly, the semispecies of *D. paulistorum* are only emerging as genetically closed systems, though some of them are already capable of sympatric coexistence. It is likely that the divergence of the semispecies is more recent than that of the sibling species. Certain inferences seem to be warranted by the available information. Figure 3 shows schematically the evolutionary relationships within the *D. willistoni* group of sibling species.

D. paulistorum, *D. equinoxialis* and *D. pavlovskiana* are genetically, cytologically and biochemically closer to each other than to the remaining siblings. Their geographic distributions are appreciably different. *D. paulistorum* is a southern form, most at home in superhumid tropical forests. *D. equinoxialis* has a more northerly distribution, tending towards somewhat drier country, savannas and gallery forests. *D. pavlovskiana* is a rare endemic, known only from Guyana. The three species may have been originally native and allopatric in equatorial South America, Central America,

and the Guyana Shield respectively. *D. tropicalis* and *D. insularis* are also closely related; the latter is probably an insular offshoot of the former. The placement of *D. willistoni* is difficult. Its distribution area includes those of all its siblings, and it is not clearly related more intimately to any one of them than to the others.

Haffer (1967, 1969), Vuilleumier (1965) and other investigators have analyzed and attempted to provide a historical explanation of the geographic distribution patterns of groups of closely related species, and of subspecies of polytypic species of birds in tropical America. Some of these patterns, particularly that of the *Crax rubra* species group (Vuilleumier, 1965), are remarkably parallel to that of the semispecies of *D. paulistorum*. According to Haffer, "during several dry climatic periods of the Pleistocene and post-Pleistocene, the Amazonian forest was divided into a number of smaller forests which were isolated from each other by tracts of open, nonforest vegetation." The alternating isolated and rejoining forests provided "refuge areas" for organisms dependent on humid tropical forest environments, and resulted in "a rapid differentiation of the Amazonian forest fauna in geologically very recent times." *D. paulistorum* is such an organism. The semispecies of *D. paulistorum* may be correlated with Haffer's refuge areas.

Dobzhansky et al. (1969) and Perez-Salas et al. (1970) reached the tentative conclusion that Transitional populations (they are too heterogeneous to be regarded a separate semispecies) are probably the least modified remnants of the ancestral *D. paulistorum*. They are found alone in Haffer's Chocó refuge and in the mountains near the Caribbean coast of Colombia and Venezuela. The Centroamerican semispecies is a near relative of Transitional, and corresponds to Haffer's Centroamerican refuges. Orinocan and Amazonian semispecies resemble in present distributions *Crax daubentoni* and *C. alector* (Vuilleumier, 1965), and may be derived from

Haffer's Catatumbo, Imeri, Guyana or Belém refuges. Interior semispecies corresponds either to Napo or to Imeri refuges. The Andean-Brazilian may have greatly expanded from the East Peruvian refuge, or from further south and southeast.

It is interesting and probably significant that the premating (ethological) isolation is appreciably stronger, at least on the average, in those semispecies which in most of their distribution areas live sympatrically with other semispecies. Thus, Amazonian females rarely accept Andean males, while Andean females cross to Amazonian males more easily (Dobzhansky and Pavlovsky, 1967, and references therein). The isolation between Amazonian and Orinocan, which are largely sympatric, is strong in both directions while Orinocan females accept Andean males again less easily than Andean females accept Orinocan males. Centroamerican and Transitional strains from the western coast of Colombia show the least ethological isolation from the other semispecies, since they are largely allopatric.

Interior shows least isolation from its nearest relative, Orinocan, with which it is largely allopatric, and most isolation from Amazonian, with which it is sympatric (Perez et al., 1970). It should also be noted that the cytological differentiation of the semispecies does not always parallel the degree of reproductive isolation between them (Kastritsis, 1966, 1967, and private communication).

SUMMARY

The known geographic distributions of the six sibling species of *Drosophila willistoni* group, and of the six semispecies of the *D. paulistorum* complex, are outlined in Tables 1 and 2, and in Figs. 1 and 2. A tentative historical explanation of the geographic and other relationships between the semispecies is proposed.

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LITERATURE CITED

- AYALA, F. J., C. A. MOURÃO, S. PEREZ-SALAS, R. RICHMOND, AND TH. DOBZHANSKY. 1970. Enzyme variability in the *Drosophila willistoni* group. I. Genetic differentiation among sibling species. Proc. Nat. Acad. Sci. U.S. 67:225-232.
- BURLA, H., A. B. DA CUNHA, A. R. CORDEIRO, TH. DOBZHANSKY, C. MALOGOLOWKIN, AND C. PAVAN. 1949. The *willistoni* group of sibling species of *Drosophila*. Evolution 3:300-314.
- DOBZHANSKY, TH. 1957. Genetics of natural populations. XXVI. Chromosomal variability in island and continental populations of *Drosophila willistoni* from Central America and the West Indies. Evolution 11:289-293.
- . 1963. Species of *Drosophila*. The Hooker Lecture. Proc. Linnean Soc. London 174:1-12.
- . 1965. "Wild" and "domestic" species of *Drosophila*. In H. G. Baker and G. L. Stebbins (eds.) *The Genetics of Colonizing Species*, Academic Press, New York.
- DOBZHANSKY, TH., H. BURLA, AND A. B. DA CUNHA. 1950. A comparative study of chromosomal polymorphism in sibling species of *D. willistoni* group of *Drosophila*. Amer. Natur. 84:229-246.
- DOBZHANSKY, TH., L. EHRMAN, AND O. PAVLOVSKY. 1957. *Drosophila insularis*, a new sibling species of the *willistoni* group. Univ. Texas Publ. 5721:39-47.

- DOBZHANSKY, TH., AND O. PAVLOVSKY. 1969. Experiments on the incipient species of the *Drosophila paulistorum* complex. *Genetics* 55: 141-156.
- DOBZHANSKY, TH., O. PAVLOVSKY, AND L. EHRMAN. 1969. Transitional populations of *Drosophila paulistorum*. *Evolution* 23:428-492.
- DOBZHANSKY, TH., AND B. SPASSKY. 1959. *Drosophila paulistorum*, a cluster of species in *statu nascendi*. *Proc. Nat. Acad. Sci. U.S.* 45: 419-428.
- EHRMAN, L., AND C. PETIT. 1968. Genotype frequency and mating success in the *willistoni* species group of *Drosophila*. *Evolution* 22: 649-658.
- HAFNER, J. 1967. Speciation in Colombian forest birds west of the Andes. *Amer. Museum Novitates*, No. 2294, 57 pp.
- . 1969. Speciation on Amazonian forest birds. *Science* 165:131-137.
- KASTRITSIS, C. D. 1966. A comparative chromosome study in the incipient species of the *Drosophila paulistorum* complex. *Chromosoma* 19:208-222.
- . 1967. A comparative study of the chromosomal polymorphs in the incipient species of the *Drosophila paulistorum* complex. *Chromosoma* 23:180-202.
- KASTRITSIS, C., AND TH. DOBZHANSKY. 1966. *Drosophila pavlovskiana*, a race or a species? *Amer. Midl. Natur.* 78:244-248.
- PASTEUR, G. 1970. A biometrical study on the semispecies of the *Drosophila paulistorum* complex. *Evolution* 24:156-168.
- PEREZ-SALAS, S., R. C. RICHMOND, O. PAVLOVSKY, L. EHRMAN, AND TH. DOBZHANSKY. 1970. The interior semispecies of *Drosophila paulistorum*. *Evolution* 24:519-527.
- SPASSKY, B. 1957. Morphological differences between sibling species of *Drosophila*. *Univ. Texas Publ.* 5721:48-61.
- TOWNSEND, J. I. 1954. Cryptic subspeciation in *Drosophila* belonging to the subgenus *Sophophora*. *Amer. Natur.* 88:339-351.
- VUILLEUMIER, F. 1965. Relationships and evolution within the Gracidae. *Bull. Museum Comp. Zool. Harvard Univ.* 134:1-27.