



The Mesophragmatica Group of Species of *Drosophila*

Author(s): Danko Brncic and Susi Koref Santibanez

Source: *Evolution*, Vol. 11, No. 3 (Sep., 1957), pp. 300-310

Published by: Society for the Study of Evolution

Stable URL: <http://www.jstor.org/stable/2405794>

Accessed: 04/02/2010 16:01

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=ssevol>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Society for the Study of Evolution is collaborating with JSTOR to digitize, preserve and extend access to *Evolution*.

<http://www.jstor.org>

THE MESOPHRAGMATICA GROUP OF SPECIES OF DROSOPHILA

DANKO BRNCIC AND SUSI KOREF SANTIBAÑEZ¹

Catedra de Biología, Escuela de Medicina, Universidad de Chile, Santiago, Chile

Received January 31, 1957

INTRODUCTION

In their monograph published in 1952, Patterson and Stone knew of 613 described species of *Drosophila*. The number of known species has been growing rapidly in recent years. This growth is due to two causes. First, the *Drosophila* fauna of some previously unexplored regions is being investigated. Secondly, some of the old "species" are being analyzed with the aid of genetic, cytological, and ecological techniques. In several instances, such analysis has disclosed the existence of extremely interesting groups of very closely related, and yet biologically quite clearly independent, sibling species which were previously confused under one species name. The *obscura* species group (Dobzhansky and Epling, 1944; Dobzhansky, 1951; Buzzati-Traverso and Scossierolli, 1952), the *virilis* group (Patterson and Stone, 1952), and the *willistonii* group (Burla *et al.*, 1949) are examples.

The neotropical faunal region contains apparently the greatest diversity of species of *Drosophila*. The study of *Drosophila* of this region is still in an early exploration stage. Many territories have never been studied for *Drosophila*, and the nature of most of the described species is inadequately understood. The present article reports the results of a study of the evolutionary status of a cluster of related species, which may be called the *mesophragmatica* species group from the oldest described species *Drosophila mesophragmatica* Duda. Some species of this group are quite common in parts of Peru,

Bolivia, Chile, and Argentina. The six species which we are able to distinguish are extremely favorable as materials for genetic and evolutionary studies. They are easily reared in the laboratory, and their chromosomes are easily stained and analyzed in microscopic preparations. Finally, a comparative investigation of these species discloses interesting evolutionary relationships.

A REVIEW OF THE TAXONOMIC STATUS

The name *Drosophila mesophragmatica* Duda (1927) belongs to a species collected at La Paz (Bolivia) and at Cuzco (Peru), and described by its author on the basis of examination of pinned and dried specimens. In 1947, Pavan and da Cunha found at Campos de Jordão (Brazil) some flies which seemed to fit Duda's description of *mesophragmatica*, and which they used for a redescription of this species. Jaeger and Salzano (1953) described a form which is very abundant in the state of Rio Grande do Sul (Brazil), in Uruguay, and in a part of Argentina under the name of *Drosophila gaucha*. Finally, Brncic (1957) reported the existence in Chile of a species which seemed morphologically rather similar to that of Pavan and da Cunha, as well as to that of Jaeger and Salzano.

Owing to the kindness of Professor C. Pavan of the University of São Paulo and of Professor Cordeiro of the University of Porto Alegre, we have obtained stocks from Campos de Jordão and from Rio Grande do Sul. The crosses between them, as well as the crosses with the Chilean species, revealed that both Brazilian forms belong to the same species. The hybrids between them are completely fer-

¹ This work has been supported in part by a grant from the Rockefeller Foundation.

tile, and no differences can be found in the salivary gland chromosomes. On the other hand, hybrids between the Brazilian and the Chilean strains are completely sterile, and some chromosomal differences between these strains are observed. This leads to the conclusion that, although the Brazilian and the Chilean forms are almost indistinguishable morphologically, they most probably represent two different specific entities.

Now, which of these species corresponds to *D. mesophragmatica* Duda? Fortunately, thanks to the efforts of Mr. J. Stiffel, who collected material in the neighborhood of La Paz, Bolivia, in 1955, it was possible to study about 100 specimens of flies resembling *D. mesophragmatica* from Duda's type locality. Later in the same year, one of the authors (Brncic) collected similar flies at Cuzco, Peru. This material proved to contain four distinct species.

By means of morphological, cytological and breeding analysis, it has been found that one of the Bolivian species is identical with the Brazilian one. Other two species also found in Bolivia are very similar to the first, but they failed to cross with it or with each other. On closer examination, it was found that they can be distinguished by several minor morphological features. Among the flies from Cuzco, Peru, one of the forms found is identical to one of the Bolivian species, while the other, although it has most traits in common with the forms mentioned, is clearly a new species in the group.

Comparing all the flies with the original description of Duda, we conclude that the form found both in Cuzco and in La Paz, the type localities given by Duda, is the one which agrees best with the type species. It is redescribed in this paper under the name of *D. mesophragmatica*, Duda. The name, *D. gaucha* Jaeger and Salzano, is maintained for the Brazilian species, including the one redescribed by Pavan and Da Cunha as *D. mesophragmatica*. The Chilean form is a sibling

species which is named *D. pavani* (Brncic, 1957). The other two members of the group are described as *D. altiplanica* (Bolivia) and *D. orkui* (Peru) by Brncic and Koref (1957). A sixth species, collected in March 1957 at Machu Pichu (Peru), by Dr. Marta Breuer of the University of São Paulo, Brazil, and in April, 1957, by Brncic in the same locality is described under the name of *D. viracochi* Brncic and Koref (1957).

Of the six species mentioned in this paper, samples of the populations have been analyzed from the following localities: *D. mesophragmatica* from Cuzco (Peru) and La Paz (Bolivia); *D. gaucha* from Campos de Jordão, São Paulo (Brazil), Porto Alegre (Brazil), Cordoba (Argentina) and San Luis (Argentina); *D. pavani* from the Chilean provinces of Atacama (Copiapo and Vallenar), Coquimbo (La Serena, Vicuna, Paihuano, Ovalle), Santiago (Bellavista and Arrayan), Colchagua (Los Alpes) and from Mendoza and San Luis, both in Argentina; *D. altiplanica* from La Paz (Bolivia); *D. orkui* from Cuzco (Peru), and *D. viracochi* from Machu Pichu (Peru).

The cultures of all these species are maintained on the usual *Drosophila* culture medium; the cytological studies of the metaphase and salivary gland chromosomes are made with the aid of the acetorceine squash method.

MORPHOLOGY OF THE SPECIES OF THE MESOPHRAGMATICA GROUP

The following are the common traits of the six species which can be included in the *mesophragmatica* group: Brown forms; arista with 7 to 9 branches; carina prominent and sulcate; 8 rows of acrostichal hairs; mesonotum pollinose with faint longitudinal stripes; abdominal tergites with transversal bands, interrupted in the midline and diffusely spread out towards the lateral angles; anterior Malpighian tubes free; posterior fused with continuous lumen; members of the subgenus *Drosophila*.

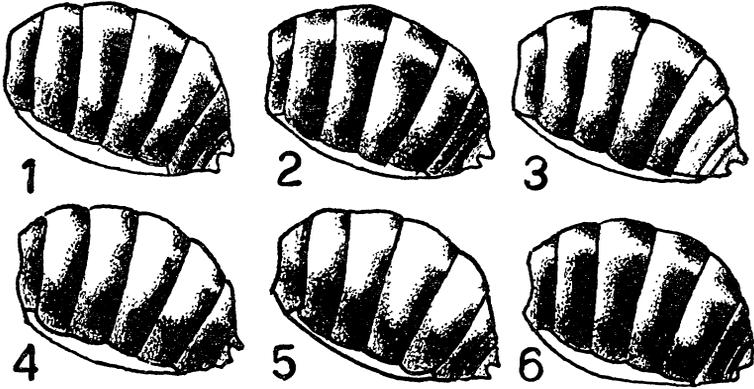


FIG. 1. Color patterns of the abdomen of *D. pavani* (1), *D. gaucha* (2), *D. mesophragmatica* (3), *D. altiplanica* (4), *D. orkui* (5), and *D. viracochi* (6).

Drosophila mesophragmatica Duda, 1927

The essential characteristics of this species are as follows: Arista with 7 to 8 branches, 8 being the usual number; Antennae brown; third joint pilose and darker than the other two. Front brown. Space between the ocelli blackish, forming a triangle. Bases of all orbital and vertical bristles dark brown, almost undistinguishable in color from the rest of the front, only slightly pollinose. The anterior orbital about the same size as posterior; middle orbital about $\frac{1}{3}$ to $\frac{1}{2}$ the length of other two. Only one prominent oral bristle; second one about $\frac{1}{4}$ to $\frac{1}{3}$ length of the first. Carina prominent and sulcate, gradually broadening below. Face grayish yellow. Cheeks grayish yellow, with some pollinosity, their greatest width about $\frac{1}{5}$ to $\frac{1}{4}$ greatest diameter of eye. Eyes wine red with dark pilosity.

Acrostichal hairs in 8 regular rows. No prescutellars. Anterior scutellars divergent. Mesonotum dark brown, pollinose. Very faint diffuse darker streaks inside and outside the dorsocentral rows. Scutellum dark brown. Pleuras very dark brown, with darker sutures. Sternite index about 0.7. Legs tannish brown; apical bristles on first and second tibiae, preapical on all three. Abdomen light yellow with dark brown bands on the posterior margins of each tergite, interrupted

in the middle, and covering a little less than $\frac{1}{2}$ of the segment width. On the lateral margins, the bands expand forwards reaching the anterior border of the tergite and forming solid black areas. In females the last abdominal segment almost entirely yellow, or only slightly darkened.

Wings clear, slightly tannish. Veins light brown; anterior crossvein slightly clouded, posterior crossvein a little more clouded. Apex of first costal section with two prominent bristles of equal length; third costal section with heavy bristles on its basal $\frac{1}{6}$ to $\frac{1}{5}$. Costal index about 3.3; 4th vein index about 1.4; 5x index about 1.0; 4c index about 0.70.

Length body about 2.9 to 3.6. Wings about 2.8 – 3.1 mm. Testes yellow with about 3 to 4 inner and 5 outer coils. Spermatic pump with two posterior diverticula. Ventral receptacle with about 30 coils. Spermathecae cherry-shaped, brown, chitinized, with a strongly marked base.

Drosophila gaucha Jaeger and Salzano, 1953

The description of this species was based on specimens collected at Muitos Capoës, Rio Grande do Sul, Brazil, in June 1952. According to a personal communication from the authors, the species is abundant in the South of Brazil, in

Uruguay, and Argentina. It is easily distinguished from *D. mesophragmatica* by several characteristics: General color lighter, yellowish brown; markings of the abdomen fainter and more diffuse; all segments in the female of the same color; third costal section with heavy bristles on its basal $\frac{1}{4}$ or less.

Drosophila pavani Brncic, 1957

This species is difficult to distinguish from *D. gaucha* by its morphological characteristics; nevertheless, when both forms are examined simultaneously under the microscope they may be separated by some minor details: In *D. gaucha* the bases of the orbital and vertical bristles cannot be distinguished clearly from the neighboring regions, nor do they have the silvery reflections of the Chilean species; 5x index in *D. pavani* is 1.32 ± 0.13 in males and 1.27 ± 0.14 in females, while in *D. gaucha* it is 1.09 ± 0.08 in males and 1.02 ± 0.07 in females. The external genitalia of the males are also different in both species; the lower margin of the clasper is a little straighter in *D. pavani*; the lower margin of the genital arch is strongly convex and forms a prominence in the Brazilian species, while in *D. pavani* this convexity is not so pronounced.

Drosophila altiplanica Brncic and Koref, 1957

This species differs from *D. mesophragmatica* in the following main characters: Arista with about 8 to 9 branches, 9 being most frequent; last two tarsal segments blackish; posterior dark brown bands on the abdominal segments thinner and apparently uninterrupted in the midline; the last segments of the females with the same markings as the others; the ventral receptacle in the females with about 40 to 45 coils.

Drosophila orkui Brncic and Koref, 1957

This species is darker in color than the other members of the group; the mesonotum is dull dark brown, darker in the

midline and a little more strongly striped than the others; sterno-index about 0.5 — 0.6; legs tannish brown with darkened coxae; third costal section with heavy bristles on its basal $\frac{1}{4}$ to $\frac{1}{3}$.

Drosophila viracochi Brncic and Koref, 1957

Differs from the other species of the group in having only 7 branches in the arista, and in having the anterior scutellar bristles convergent.

Excepting *D. gaucha* and *D. pavani*, the species members of the group can be distinguished by examination of their external morphology. The following key may be used for recognition of the species:

1. Anterior scutellar bristles divergent 2
 Anterior scutellars convergent *D. viracochi*
2. Third costal section with heavy bristles on its basal $\frac{1}{2}$ or less 3
 Third costal section with heavy bristles on its basal $\frac{1}{4}$ or more 4
3. Arista with 7 to 8 branches; costal index 3.3; dark bands on the posterior margins of the tergites clearly interrupted in the middle *D. mesophragmatica* Duda.
 Arista with 8 to 9 branches; costal index about 4; dark bands on the posterior margins of the tergites, diffusely or faintly interrupted in the midline *D. altiplanica* Brncic and Koref
4. Mesonotum dull dark brown, darker in the midline with several faint light stripes, legs tannish brown with coxae darkened *D. orkui* Brncic and Koref.
 Mesonotum brown; legs yellow *D. pavani* Brncic, or
 D. gaucha Jaeger and Salzano.

GEOGRAPHIC DISTRIBUTION

Data on the geographic distribution of the six known members of the *mesophragmatica* group are represented in figure 2.

D. mesophragmatica has been reported from Bolivia (La Paz) and from Peru (Cuzco and Machu Pichu); *D. orkui* and *D. viracochi* have been collected only in Peru (Cuzco and Machu Pichu, respectively); *D. altiplanica* is described from Bolivia; *D. gaucha* has been found in Southern Brazil, in Uruguay, Argentina and Bolivia; and *D. pavani* in Chile, and



FIG. 2. Known geographic distribution of the six members of the *mesophragmatica* group.

in a part of Argentina close to the Eastern slope of the Andes.

Summarizing, *D. viracochi*, *D. mesophragmatica* and *D. orkui* are sympatric in Peru (Cuzco); *D. mesophragmatica*, *D. altiplanica* and *D. gaucha* are sympatric in Bolivia (La Paz), while *D. gaucha* and *D. pavani* overlap in a small region in Argentina (province of San Luis).

According to a personal communication from Professor Wheeler, of the University of Texas, specimens very similar to *D. altiplanica* or *D. orkui* have been collected by Dr. W. B. Heed in the mountains near Bogota, Colombia, at about 11,000 feet of

altitude. In any case, with the exception of *D. gaucha*, most of the species of this group seem to be fundamentally Andean. Its members are abundant in nature, and in some places they are the dominant species of *Drosophila*. For example, at some collecting spots near Cuzco, Peru, the members of this group made up a 51.35% to a 95.23% of the total *Drosophila* flies obtained. The same situation seems to exist at La Paz, Bolivia, although there are no exact quantitative data from there. In the north-central part of Chile, *D. pavani* is the most abundant species, and in some collections it forms up to three-

quarters of all individuals of *Drosophila* found (Atacama). Professors Pavan and Cordeiro inform us that *D. gaucha* is relatively scarce in Brazil. In Argentina it is probably more abundant. It seems to

live by preference at certain altitudes. For example, in the "Sierra" of Cordoba (Argentina) it makes up 31.84%, and in the "Sierra" of San Luis (Argentina) 16.8% of the specimens of the genus.

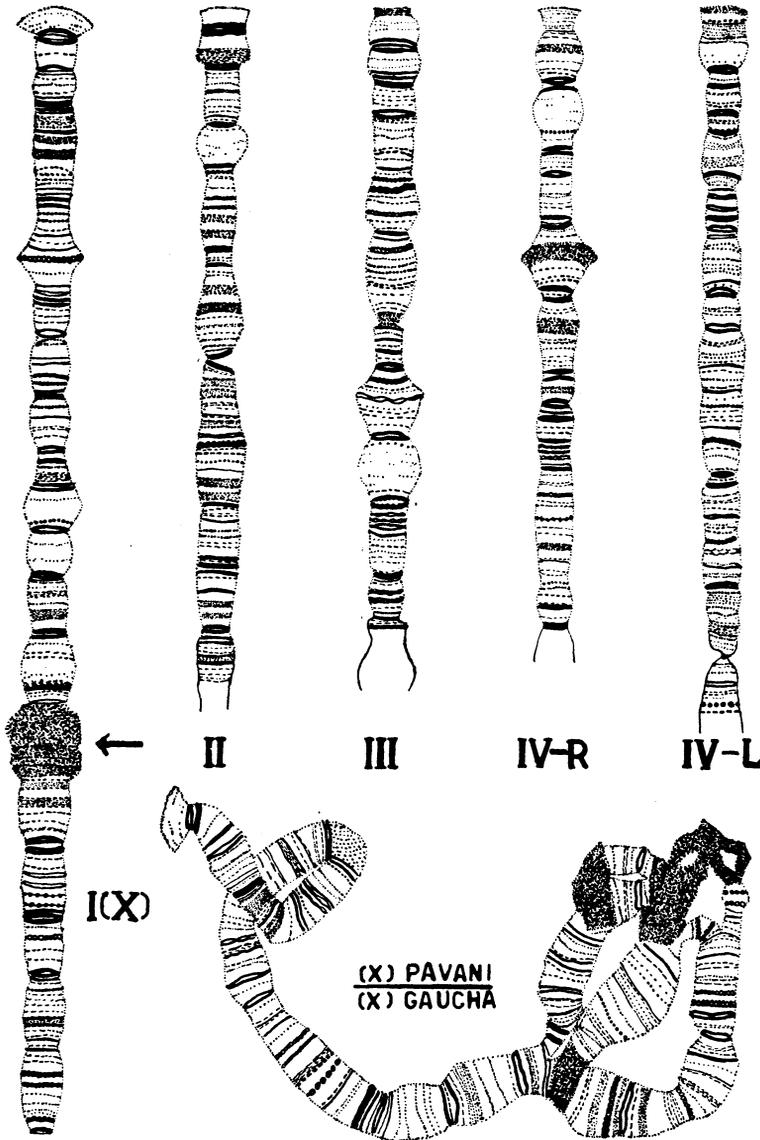


FIG. 3. The X-chromosome of *D. pavanii* and the distal portions of the autosomes of *D. pavanii* and *D. gaucha*. The arrow indicates the heterochromatic zone of the X-chromosome, the location of which distinguishes *D. pavanii* from the other members of the group. The double inversion in the lower part of the figure occurs in the hybrid X-chromosomes in the cross *D. pavanii* by *D. gaucha*.

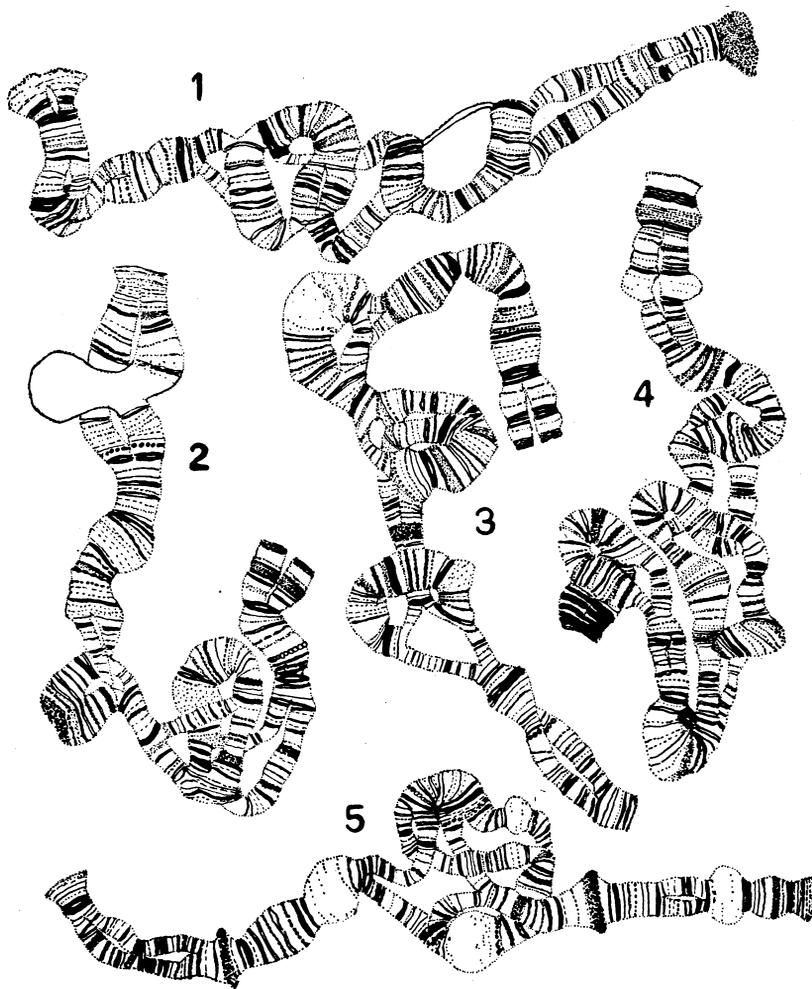


FIG. 4. Gene homologies and inversions found in the hybrids between *D. gaucha* and *D. mesophragmatica*. 1. X-Chromosome; 2. Left arm of the fourth chromosome; 3. The third chromosome; 4. The second chromosome; 5. Right arm of the fourth chromosome.

CHROMOSOMES

Pavan and da Cunha (1947) and Jaeger and Salzano (1953) have studied the karyotype of *D. gaucha* and Brncic (1957) that of *D. pavani*. The metaphase chromosomes of the *mesophragmatica* group are shown in figure 5. *D. pavani*, *D. gaucha* and *D. viracochi* all have one pair of V shaped chromosomes, 3 pairs of rods, one of which is the X-Y pair, and one pair of dots. *D. altiplanica* has the same basic chromosomal configuration, although

its dots are slightly elongated, and one of the pairs of rods is bent, giving the impression of small V's. *D. mesophragmatica* and *D. orkui* both have one pair of V's and four pairs of rods, one of which is shorter than the rest. The sex pair also corresponds to one of the pairs of rods.

In contrast to what is observed in the metaphase plates, the structure of the salivary gland chromosomes is very similar in all six species. There are 5 long euchromatic arms which converge to-

wards a large heterochromatic chromocenter, in which is embedded a small strand, corresponding to the dot-like chromosome. Figure 3 shows the distal free ends of the euchromatic arms, as they are seen in *D. pavani* and *D. gaucha*. Slight differences in the disc patterns in these arms permit the identification of the species from cytological preparations. The homologies between *D. pavani* or *D. gaucha* and *D. mesophragmatica's* chromosomes may also be seen in figure 4.

The fact that in the salivary gland chromosomes of *D. mesophragmatica* and *D. orkui* there are only 5 euchromatic arms instead of 6, as should be expected according to the metaphase plates, may indicate that one of the rods, probably the shortest one, corresponds to the dot observed in the other members, which has been modified through the addition of extra heterochromatin, as has been suggested by Wharton (1943) for other species. On the other hand, the fact that *D. altiplanica* has the same basic chromosomal configuration, when theoretically it should have 6 euchromatic strands, as one of the pairs of rods has been replaced by a pair of V's, indicates that in this case the shape does not reflect the position of the centromere, and that these chromosomes are most probably acrocentric instead of metacentric. The V-like

shape could be due to the presence of a secondary constriction.

REPRODUCTIVE ISOLATION

A study of the reproductive isolating mechanisms which prevent the exchange of genes between closely related species is essential for an understanding of the evolutionary status of these species. Evidence is available to show that the natural populations of the six species of *mesophragmatica* group are reproductively isolated. No gene exchange is taking place between these species, even when they are sympatric. This applies as well to the sibling species, *D. gaucha* and *D. pavani*.

Individual as well as mass culture crosses have been tried out between all the members of the *mesophragmatica* group (see table 1). Virgin females were aged in isolation for 5–8 days before being placed with males of other species. The flies were then kept either at 16° or at 25° C. If no larvae appeared, the females were dissected after exposures to the males for periods up to 30 days. The ventral receptacles of the females were examined under the microscope for the presence of spermatozoa.

D. gaucha and *D. pavani* mate freely under the laboratory conditions. Hybrids are produced in almost all crosses of these species, but they are nearly always

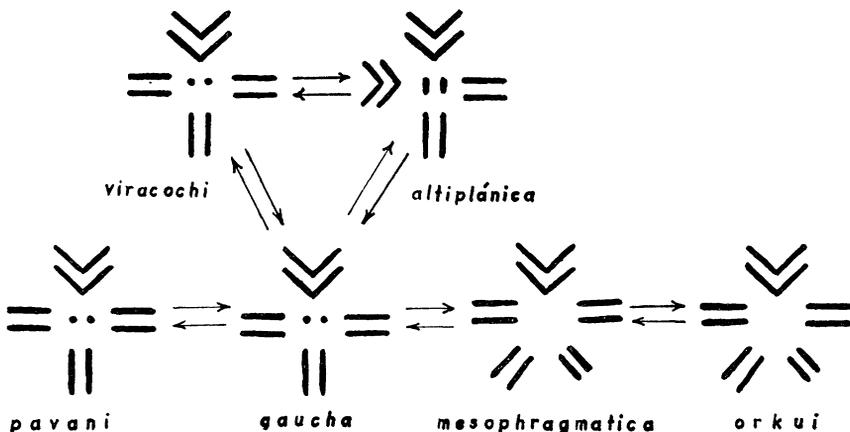


FIG. 5. Metaphase plates and hypothetical phylogenetic relationships of the six members of the *mesophragmatica* group.

TABLE 1. Production or non-production of hybrids in crosses between different species of the mesophragmatics species group

Males	Females					
	<i>mesophragmatica</i>	<i>gaucha</i>	<i>pavani</i>	<i>orkui</i>	<i>altiplanica</i>	<i>viracochi</i>
<i>mesophragmatica</i>		none	few pupae	none	none	none
<i>gaucha</i>	few pupae		♀ ♀ sterile, some ♂ ♂ occasionally fertile	none	none	none
<i>pavani</i>	few pupae	sterile ♀ ♀ and ♂ ♂		none	none	
<i>orkui</i>	none	none	none		none	none
<i>altiplanica</i>	none	none	none	none		none
<i>viracochi</i>	none	none	none	none	none	

sterile. The hybrid flies may copulate with each other or with representatives of the parental species; however, spermatozoa occasionally found in the ventral receptacles of hybrid females are inactivated. Only in two instances, F_1 hybrid males from the cross *pavani* ♀ by *gaucha* ♂ were fertile when backcrossed to *pavani* females. Other crosses which have produced a few hybrids are *mesophragmatica* ♀ by *gaucha* ♂ and *mesophragmatica* ♀ by *pavani* ♂. Occasionally some larvae are found in the cultures, and they form scattered pupae, which die without giving rise to adult hybrids.

All other crosses produce no progeny whatever. However, the failure to produce progeny is not due to lack of copulation. In fact, inseminated females can be found in most crosses, but the few sperms which can be seen in the ventral receptacles are always inactive. The eggs laid by such females are always unfertilized. The most effective reproductive isolating mechanism operative in these crosses is, therefore, the inviability of the

spermatozoa in the sperm receptacles of females of foreign species.

PROBABLE PHYLOGENETIC RELATIONSHIPS IN THE MESOPHRAGMATICA SPECIES GROUP

The six species of the *mesophragmatica* group are obviously closely related. They are morphologically very close, and *D. gaucha* and *D. pavani* are sibling species which cannot be distinguished by any of the traits commonly used in *Drosophila* taxonomy. Nevertheless, the reproductive isolation seems to be complete. The areas of *D. gaucha* and *D. pavani* overlap in a part of Argentina, but no indications of even occasional hybridization have been observed. *D. gaucha*, *D. mesophragmatica* and *D. altiplanica* are sympatric in Bolivia, and *D. mesophragmatica*, *D. orkui* and *D. viracochi* are sympatric at Cuzco, Peru.

Since most of the species fail to produce hybrids, it is not possible to make detailed comparisons of the gene arrangement in their chromosomes by observing

the pairing of homologous chromosomes in the hybrids. A comparative study of the chromosomes in metaphase plates and in salivary gland cells permits, nevertheless, some inferences concerning the possible phylogenetic relationships between the species of the group. Figure 5 indicates the probable phylogenetic arrangement.

The sibling species *D. gaucha* and *D. pavani* are obviously the closest relatives. Figure 5 shows that their metaphase chromosomes are identical. However, the gene arrangement in their chromosomes has diverged appreciably, as shown in figure 3. The hybrids show a double overlapping inversion in the basal part of the X-chromosome. Because of these inversions, a large heterochromatic section which is submedian in *D. pavani* is subbasal in *D. gaucha*. This trait, easily visible in preparations of the salivary gland chromosomes, distinguishes *D. pavani* from *D. gaucha*. In fact, it distinguishes *D. pavani* from the other four species as well, since in all members of the group, except *D. pavani*, the heterochromatic section in the X-chromosomes occupies a subbasal position.

D. viracochi has, like *D. gaucha*, the heterochromatic section in the X-chromosome in a subbasal position. The former species is, on this basis, considered closer to *D. gaucha* than to *D. pavani*, and it is placed accordingly in figure 5. *D. mesophragmatica* and *D. orkui* are probably related, since they have identical metaphase configurations, although they do not cross and differ in some externally visible traits. Since the crosses of *D. mesophragmatica* to *D. gaucha* and *D. pavani* produce a few hybrids which die in the pupal stage, it may be inferred that these species are closer to each other than they are to *D. orkui*. The study of the chromosomes in the salivary glands of the hybrids gives very interesting results, shown in figure 4. The evolutionary divergence between *D. mesophragmatica* and *D. gaucha* has involved formation of paracentric inversions. In fact every chromosome differs in the gene arrange-

ment from the corresponding chromosome in the other species. There exist multiple inversions, as well as a lack of pairing of certain sections, the latter apparently due to lack of homology between some of the bands.

Since *D. altiplanica* has failed to cross to any other species, it is difficult to establish its position securely. The V shape acquired by one of the pairs of rods also separates this species from the rest of the group. The metaphase configuration, nevertheless, suggests that *D. altiplanica* is near to *D. gaucha* and *D. viracochi*.

SUMMARY

Six species of the subgenus *Drosophila*, living in South America, have been included in the new *mesophragmatica* species group: *D. mesophragmatica* Duda, *D. gaucha* Jaeger and Salzano, *D. pavani* Brncic, *D. altiplanica* sp. nov., *D. orkui* sp. nov., *D. viracochi* sp. nov.

With the exception of *D. gaucha* and *D. pavani*, which exhibit only cryptic morphological differences, all the other members can be distinguished by their external characteristics.

The six species show varying degrees of reproductive isolation. *D. gaucha* and *D. pavani* mate freely under laboratory conditions, but the hybrids are always sterile. Hybrids between *D. mesophragmatica* females and *D. gaucha* or *D. pavani* males are rarely produced and develop only to the pupal stage. Most of the other species copulate, but the sperm are rapidly inactivated, and the eggs which the females lay are not fertilized. In addition, there is good chromosomal and genetic evidence to show that no gene exchange takes place in the natural populations of the six species of the group, in spite of the fact that some are sympatric in certain regions, including the two sibling species *D. pavani* and *D. gaucha*.

All six species have five pairs of chromosomes in the metaphase plates. *D. gaucha*, *D. pavani* and *D. viracochi* have one pair of V's, three pairs of rods and

one pair of dots. In *D. mesophragmatica* and *D. orkui*, the dots are transformed by addition of heterochromatin into a pair of rods. In *D. altiplanica* one of the rods has acquired the shape of a medium-sized V, probably due to the presence of a secondary constriction.

The study of the salivary gland chromosomes has revealed that the most important changes related to speciation in this group involve paracentric inversions and additions or losses of heterochromatin. The analysis of the chromosomes permits the establishment of a hypothetical phylogenetic relationship between the species of the group.

ACKNOWLEDGMENTS

The authors wish to express their gratitude to the Rockefeller Foundation for the grants which have supported these studies. They are also greatly indebted to Professor Theodosius Dobzhansky of Columbia University for his constructive criticism, his valuable suggestions, and for his help in the preparation of the manuscript; to Miss Adriana Casanova for her technical aid; to Drs. Pavan and Da Cunha of the University of Sao Paulo, and to Drs. Cordeiro and Salzano of the University of Rio Grande do Sul, Brazil, who kindly provided the stocks and valuable data on *D. gaucha*; to Dr. Wheeler of the University of Texas for his suggestions concerning the descriptions of the species; to Dr. J. M. Cei of the University of Cuyo, Mendoza, and to the many colleagues at the Estación Agrícola Experimental de la Molina, Perú, to the USA Agricultural Research Mission in Perú, and to the Public Health Service of Perú, all of whom

helped in the collecting trips in these countries.

LITERATURE CITED

- BRNCIC, D. 1957. Las especies chilenas de *Drosophilidae*. [Editorial Universitaria.] Imprenta Stanley, Santiago, Chile.
- , AND S. KOREF. 1957. The *mesophragmatica* group of the genus *Drosophila* with description of three new species. *Biologica (Chile)*, 22: 63–72.
- 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.
- BUZZATI-TRAVERSO, A., AND R. E. SCOSSIROLI. 1955. The *obscura* group of species of the genus *Drosophila*. *Advances in Genetics*, 7: 47–92.
- DOBZHANSKY, TH., AND C. EPLING. 1944. Contributions to the genetics, taxonomy and ecology of *Drosophila pseudoobscura*. P.N.-A.S., 34: 137–141. *Carne. Inst. Publ., Wash.*, 554: 1–183.
- . 1951. *Genetics and the Origin of Species*. (Third Ed.) Columbia University Press, New York.
- DUDA, O. 1927. Die Sudamerikanischen *Drosophiliden* unter Berücksichtigung auch der anderen Neotropischen sowie Nearktischen Arten. *Arch. Naturgesch.*, 91 A. 11–12: 1–229.
- JAEGER, C. P., AND F. M. SALZANO. 1953. *Drosophila gaucha*, a new species from Brazil. *Rev. Brazil. Biol.*, 13: 205–208.
- PAVAN, C., AND A. B. DA CUNHA. 1947. Especies brasileiras de *Drosophila*. *Bol. Fac. Fil. Cien. e Letras Univ. S. Paulo*. 86. *Biol. Geral.*, 7: 3–46.
- PATTERSON, J. T. 1943. The *Drosophilidae* of the Southwest. *Univ. Texas Publ.* 4313: 7–216.
- , AND W. STONE. 1952. *Evolution of the Genus Drosophila*. The Macmillan Co., New York.
- WHARTON, L. T. 1943. Analysis of the metaphase and salivary chromosome morphology within the genus *Drosophila*. *Univ. Texas Publ.* 4313: 282–319.