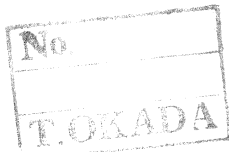


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/ TAXONOMIC RELATIONSHIPS WITHIN THE *DROSOPHILA VICTORIA*
SPECIES GROUP, SUBGENUS *PHOLADOEIS*

(DIPTERA: DROSOPHILIDAE)

SARAH BEDICHEK PIPKIN, *The Gorgas Memorial Laboratory, Panama, R. of P.*

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SARAH BEDICHEK PIPKIN, *The Gorgas Memorial Laboratory, Panama, B. of P.*

The victoria species group, designated by Wheeler (1949) and discussed by Mather (1955), has been investigated in order to clarify the taxonomic status of *D. lebanonensis* Wheeler 1949. This species was listed as a possible synonym of *D. victoria* Sturtevant 1942 by Wheeler (1959). In the course of study, a species belonging to the victoria group, kindly collected for the author in Tucson, Arizona by Dr. William B. Heed from the cottonwood, *Populus fremontii* Wats., proved to be smaller, shinier, and different in certain respects in the male genitalia from a laboratory strain originating from Prescott, northern Arizona, hitherto considered to be *D. victoria*. Meanwhile, a strain of the true *D. victoria* was collected from the type locality, Andreas Canyon, Palm Springs, California, by Dr. Lynn H. Throckmorton, and generously sent to the author. The Palm Springs *victoria* is one half millimeter shorter than the specimens from Tucson, slightly browner, and lacks the color polymorphism of the latter. Sturtevant (1942) states that strains considered to be *D. victoria*, collected by Professor J. T. Patterson in western United States and Mexico, differ slightly in the number of egg filaments and chromosomes from *victoria* from Palm Springs, California.

In the present study the Tucson species is described as *D. brooksi*, sp. nov. Reexamination of specimens of *victoria* from the type locality shows it to correspond closely with the original description (Sturtevant 1942). The species from Prescott called *victoria* by subsequent students (Patterson, 1943, Wheeler, 1947, 1949; Hsu, 1949; Pipkin, 1956; Mather, 1955, 1957) proves to be distinct and is here described as a subspecies of *lebanonensis* Wheeler 1949. The taxonomic relationships within the victoria species group are reviewed in the light of these findings.

¹ This work was supported by a research grant, RG 6813, from the United States Public Health Service.

Correction!

The species name "brooksi"
should read "brooksae"

The author collected several strains of the polymorphic species, *lebanonensis*, as well as *pattersoni* and *stonei* in The Lebanon during the years 1947 to 1949. A strain from Rasco, Jerusalem, Israel was obtained through the courtesy of Dr. Elisabeth Goldschmidt. *D. brooksi*, sp. nov., was collected in Tucson, Arizona by Dr. William B. Heed. The true *D. victoria* Sturtevant was collected by Dr. Lynn H. Throckmorton. The material from Prescott, Arizona was obtained through the courtesy of Dr. M. R. Wheeler. Slides for the study of male and female genitalia of the members of the victoria species group were prepared according to the method of Fairchild and Hertig (1948).

✓ *Drosophila (Pholadoris) brooksi*, sp. nov.

External characters of imagines. Male. Arista with 3 branches above, 2 below, in addition to the fork. Second and third joints of the antennae dark brown, the second joint with one bristle directed laterally, six bristles of varying lengths, directed ventrally; the third joint covered with short pale hairs. Front velvety dark brown; the lateral extremities of the lunula shining pale pruinose when viewed at an angle. Frontal triangle plainly delimited by a shallow groove, bearing on each side 6 mesially directed frontal hairs, the apical hair being flanked on each side by 2 short hairs; the groove delimiting the frontal triangle shining pale pruinose when viewed from an angle. Ocellar triangle black; anterior ocellar bristles divergent; ocelli pale pink. Orbits semi-shining, dark brown; orbital hairs 5. Proclinate orbital bristle equal to the posterior reclinate orbital: mid-orbital thin and $1/5$ the other two. One oral bristle prominent; the second, half the length of the first. Face dark brown, carina almost black, wider below, bulbous. Clypeus black, proboscis brown. Palps dark brown, almost black in old specimens; one subapical bristle and 4 shorter bristles on the lateral margin of the palps. Cheeks black; distance between the eye border and the base of the oral bristle $1/12$ the greatest diameter of the eye. Occiput dark brown. Eyes light maroon, darkening with age, with short pale pile. Greatest antero-posterior measurement of the eye $2/3$ the greatest dorso-ventral measurement.

Mesonotum and scutellum shining black; pleurae shining dark brown, thinly pollinose. Acrostichals in 6 rows; 4 bristles in the prescutellar row, the median pair definitely enlarged. Anterior scutellars divergent; distance from anterior to posterior dorsocentrals $4/9$ the distance between the two anterior dorsocentrals. Anterior sternopleural $6/7$ the posterior sternopleural and twice the mid-sternopleural. Halteres yellow. Apical bristles on first and second pairs of legs; preapicals on all three. Coxae and femora dark brown; tibiae and tarsi yellowish brown.

Wings unicolorous, tan; costal index approximately 2; fourth vein index 2.3; five x index 1.75; two bristles at the apex of the first costal section; third costal section with heavy hairs on the basal $6/11$.

Abdominal tergites shining black except for tergite 2, which is brownish medially; sternites gray. Hypopygium retracted into the abdomen, possessing the general characteristics of *D. lebanonensis* as figured by Hsu (1949); lobe-like process on the heel of the forceps prominent; primary teeth of forceps varying from 8 to 11; median 10; five bristles on the upper part of the genital arch (Fig. 1B); four to five bristles on the posterior margin of one concha of the hypandrium (Fig. 1A,C).

Female. Abdomen with black apical bands slightly more than one half the width of the tergites and extending to the lateral borders. Second tergite pale medially; apical bands of tergites 3, 4, 5 with fuzzy medial extensions. Ovipositor yellowish with 24 to 26 teeth (Fig. 1F).

Color polymorphism. The preceding description applies to the darkest color form of both sexes. In this species a balanced polymorphism of body color exists in nature and is maintained in laboratory cultures. The mesonotum of both sexes varies from shining black through dark brown to shining yellowish tan. The tan flies are also paler on the pleurae and bases of the legs. At the time of collection of about 300 individuals of this species, Dr. W. B. Heed estimated from 60 to 70% dark brown or black and from 40 to 30% light brown (personal communication). Exact counts were not made at this time because it was undesirable to etherize the flies as they are difficult to carry in culture. Three generations after the original collection, a sample of 117 flies was composed of 92 black or dark brown and 25 light brown. This color polymorphism was mentioned by Wheeler (1949) at a time when it was not realized that *brooksi* was a distinct species from the northern Arizona material.

Body length (etherized) male, 2.5 mm; female, 3 mm.

Length of wing, male, 2.5 mm; female, 2.7 mm.

Internal characters of imagines. Anterior malpighian tubules free and about twice as long as the posterior malpighian tubules; posterior malpighian tubules apposed but no continuous lumen. Testes elliptical, dull orange. Spermathecae with brown chitinized centers and pronounced apical indentation; ventral receptacle a short sac pressed against the ventral side of the uterus.

Eggs. With from 4 to 8 filaments; 35% with 5; 43% with 6; and 14% with 7 filaments (Table 2). Tips of filaments curly.

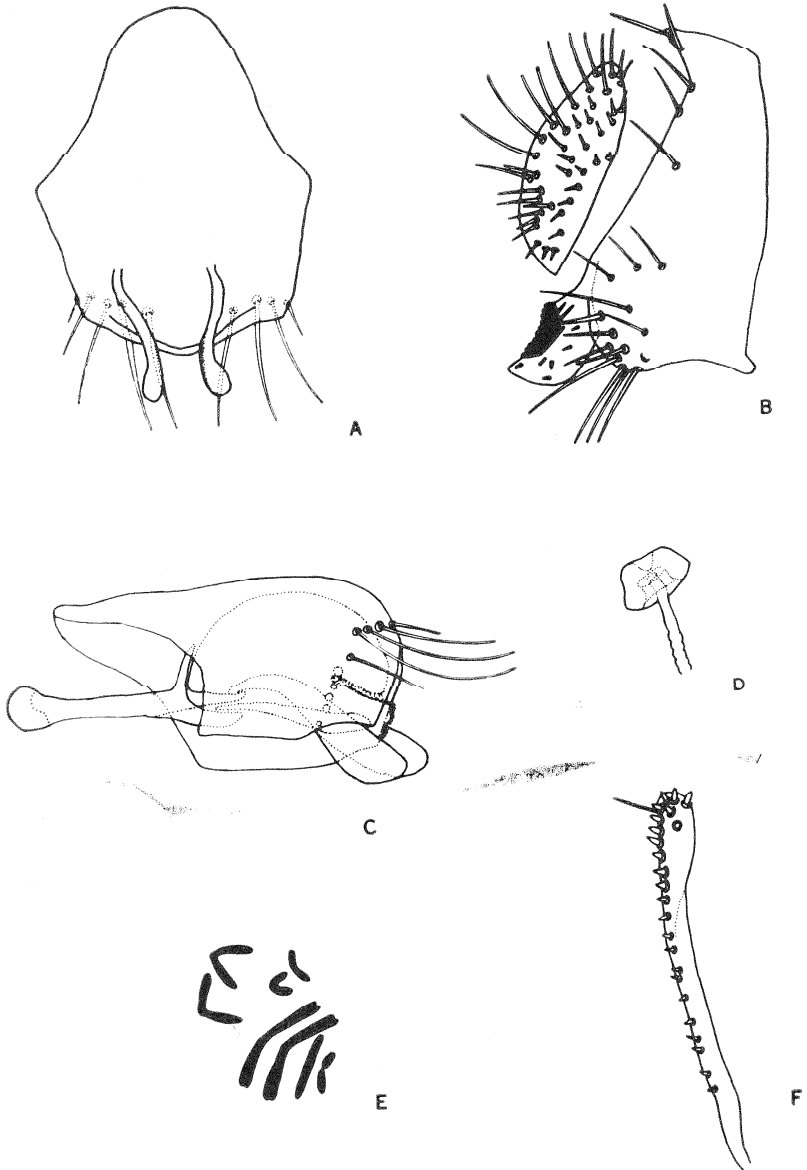
Larvae. White in color; skip; very active.

Puparia. Dull gold; each anterior spiracle with from 5 to 8 (median 7) very short pale filaments; stalk of anterior spiracle very short. Posterior spiracles contiguous, pale. Pupation either at the top or bottom of culture bottles.

Chromosomes. Larval brain preparations show males with one pair of large V's, one pair medium V's one pair small V's a rod-shaped X, a short rod-shaped Y chromosome with a pronounced constriction (Fig. 1E). Salivary gland chromosomes with 3 long arms, 2 medium arms, 2 short arms; a pronounced chromocenter; one gland larger than the other.

Physiological characteristics. Recovers rapidly from anaesthetization with ether; difficult to keep on standard culture medium.

Relationship. This species belongs to the victoria species group with *victoria*, *lebanonensis*, *pattersoni*, *stonei*, and *nitens*. *Brooksi* is closest to *victoria* Sturtevant (Palm Springs, California). *Brooksi* and *victoria* differ by the color polymorphism found in *brooksi*; the larger size (by $\frac{1}{2}$ mm.) of *brooksi*; the darker color of the dark color form of *brooksi*, *victoria* being browner; the larger size of the mid-sternopleural bristle in *brooksi*; presence of two hairs flanking the apical frontal hair in *brooksi* compared with one such hair in *victoria*; the different chromosome configuration in the two species; and the differences in number of egg filaments in the two species (see section on variation in egg filaments in the victoria group).



Distribution. Tucson, Arizona, collected May 25, 1960 from *Populus fremontii* Wats. by Dr. William B. Heed.

Types. Holotype male and a series of paratype males and females have been placed in the *Drosophila* Type and Reference Collection of The Genetics Foundation, The University of Texas, Austin, Texas.

Dedication. This species is named in honor of Mrs. Sarah Brooks Martin, the artist who prepared the color plates for Professor J. T. Patterson's *The Drosophilidae of the Southwest* and (with G. B. Mainland), *The Drosophilidae of Mexico*.

✓ *Drosophila* (*Pholadoris*) *lebanonensis casteeli*, subsp. nov.

External characters of imagines. Male. Arista with 3 branches above, 2 below, in addition to the terminal fork. Second and third joints of the antenna black, the second joint with one bristle directed laterally and 6 bristles directed ventrally, the third joint covered with short pale hairs. Front dark reddish brown, pollinose. Ocellar triangle and orbits black, semishining; ocelli brown. Small elevation interior to the base of the proclinate orbital bristle and also one at base of mid-orbital shining silvery when viewed at an angle. Frontal hairs arranged in two rows, forming a V, the apex of the V directed anteriorly, 7 frontal hairs on each side; 2 frontal hairs lateral to the apex of the V. Orbital hairs 5. Proclinate orbital bristle 4/5 posterior reclinate; mid-orbital 1/4 the proclinate orbital. One oral bristle prominent, the second half the length of the first. Face brown, carina black, wider below, bulbous. Clypeus black, proboscis tan. Palps tan, one subapical and three shorter bristles on the lateral margin of the palps. Cheeks tan, dark brown below. Distance between the eye border and base of the oral bristle 1/11 the greatest diameter of the eye. Eye maroon, darkening with age, with short pale pile. Greatest antero-posterior diameter 9/11 the greatest dorsoventral measurement of the eye. Occiput dark brown.

Mesonotum and scutellum semishining dark brown, without markings; pleurae dark brown, pollinose. Acrostichals in 6 rows; four hairs in the prescutellar row, the median pair definitely enlarged. Anterior scutellars divergent; distance from anterior to posterior dorsocentrals 4/7 the distance between the two anterior dorsocentrals. Anterior sternopleural 6/8 the posterior sternopleural; mid-sternopleural 5/8 the posterior. Halteres pale yellow. Coxae and femora of first pair of legs dark brown; dusky yellowish on second and third pairs of legs and on all three pairs of tibiae and tarsae.

Wings unicolorous tan; costal index, 2.2.; fourth vein index 2.6; five x index, 2. Two bristles at the apex of the first costal section; third costal section with heavy hairs on the basal 6/11.

Abdominal tergites shining black, the basal one somewhat less so, sternites dark gray. Hypopygium retracted into the abdomen; lobe like process on the heel of the forceps prominent; primary teeth of forceps vary from 11 to 14 (median 12); 3 prominent bristles on the upper part of the genital arch; 9 bristles on the posterior ventral margin of one concha of the hypandrium (Table 1).

Fig. 1, terminalia and chromosome configuration of *brooski*, sp. nov. A, hypandrium and conchae of male, dorsal view; B, genital arch and forceps of male; C, hypandrium and penis of male, side view; D, seminal receptacle of female; E, chromosomes, larval brain, male; F, vaginal plate of female.

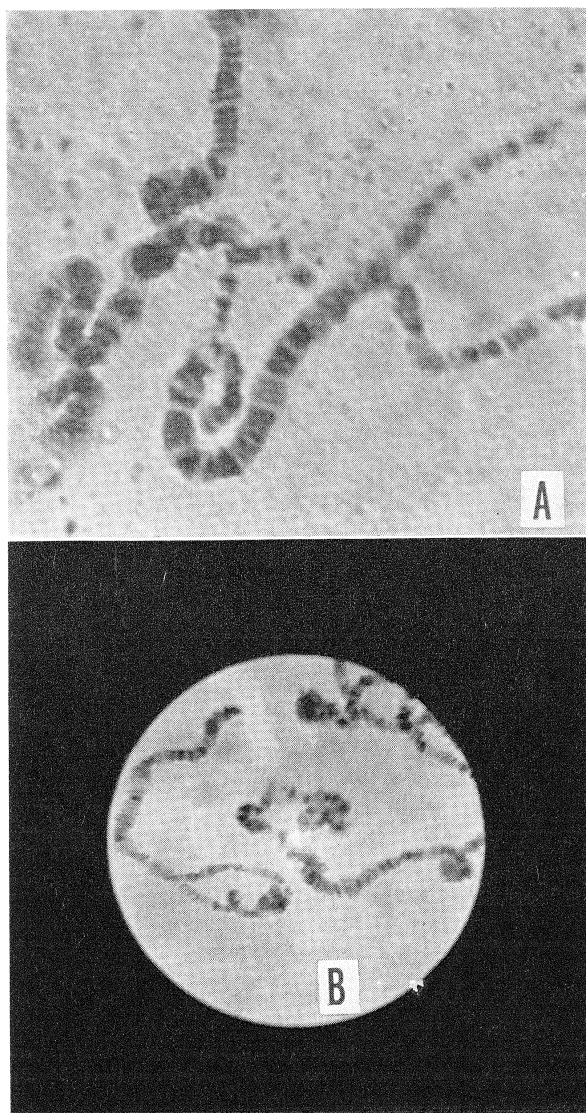


Fig. 2. Salivary chromosomes of hybrid larva of (A) *I. lebanonensis* and (B) *I. casteelei*, showing partial lack of pairing. Microphotographs by Dr. Alan C. Pipkin.

Female. Abdomen with broad shining dark brown apical bands covering the entire tergites 2, 3, 4. Corners only of tergites 5 and 6 are yellow as is the mid region of the circumanal tergite. Anterior-most sternite gray, remaining four paler. Ovipositor yellowish with 23 to 24 teeth.

Body length (etherized) male, 2.7 mm.; female, 3 mm.

Length of wing, male 2.5 mm; female 2.8 mm.

Internal characters of imagines. Anterior malpighian tubules free and much longer than the posterior, posterior tubules apposed without the formation of a continuous lumen. Testes elliptical, rusty brown in color. Seminal receptacles with brown chitinized centers; ventral receptacle a short sac pressed close to the ventral surface of the uterus.

Eggs. With from 5 to 8 filaments; 52% with 6 filaments; 36% with 7 filaments; 4% with 8 filaments (see Table 2).

Larvae. White in color; skip; very active.

Puparia. Golden; each anterior spiracle with from 5 to 6 branches; stalk of anterior spiracles very short. Posterior spiracles tightly apposed, golden yellow. Pupation is on the sides or near the plug of laboratory bottles.

Chromosomes. Larval brain preparations with 2 pairs large V's; one pair smaller V's; and one pair rods (Wharton, 1943). Salivary gland chromosomes with 3 long arms, 2 medium arms, 2 short arms; a pronounced chromocenter; one gland larger than the other.

Relationship. A subspecies of *D. lebanonensis* member of the victoria species group. *D. l. casteeli* lacks a light and dark mesonotum color polymorphism dependent upon an autosomal pair of alleles found in *l. lebanonensis* (Pipkin, 1956). The cheeks of *l. casteeli* are dark below; those of *l. lebanonensis*, entirely pale. The occiput, mesonotum, pleurae, and bases of legs are darker in *l. casteeli* than in the dark form of *l. lebanonensis*, but a mixture of the two forms could not be separated with complete accuracy. The testes of *l. casteeli* are rusty brown, whereas these are deep yellow in *l. lebanonensis*, a difference noted by Wheeler (1949).

Patterson and Stone (1952) cite numerous cases of gametic mortality in interspecific crosses as illustrating an isolating mechanism between closely related species. The possibility of sperm damage in crosses between *l. lebanonensis* and *l. casteeli* has been investigated. The results are presented in Table 4. For each of the crosses listed in this table, two day old females were exposed to males the same age for one hour only. Twenty-four hours later, the females were dissected and their seminal receptacles and vesicles examined for the presence of sperm. Table 4 gives the percentages of dissected females with motile sperm, non-motile sperm, disintegrating sperm, and no sperm. One hundred females were dissected in each case. According to Table 4, the percentage of females in which no sperm reach the receptacles and vesicle is somewhat higher in the crosses between subspecies than in the control crosses. Further, Table 4 shows a lower percentage of females with motile sperm and a higher percentage with non-motile and disintegrating sperm in the heterogametic crosses between *l. lebanonensis* and *l. casteeli* than in the control homogametic crosses.

TABLE 1. VARIATION IN NUMBER OF FORCEPS TEETH AND BRISTLES ON ONE SIDE OF THE HYPANDRIUM

species	forceps teeth	hypandrium bristles
victoria (palm spr.)	8-11 median 10	4
brooksi (tucson)	8-11 median 10	4,5
pattersoni (beirut)	10-13 median 11	5,6,7
stonei (sofar)	11-13 median 11	5,6
^{L.} lebanonensis	11-13 median 12	8,9,10
L.casteeli	11-14 median 12	9

Correction: The second species should read "*brooksae*."

This last difference is explained as owing to the deleterious effect of the secretions of the seminal receptacles or vesicle upon the alien sperm.

Larval salivary gland cells of hybrids between *l. lebanonensis* (Beirut strain) and the Prescott strain of *l. casteeli* were studied in acetoorcein preparations, each containing the glands of a single larva. In half of the preparations in which all chromosome arms could be followed, there was a complete pairing of all seven chromosome arms (3 long, 2 medium, and 2 short). The remaining preparations showed a complete lack of pairing in the medium length chromosomes, giving a total of 9 arms (3 long, 4 medium, 2 short); or a partial lack of pairing in one medium arm accompanied by a complete lack of pairing in the other medium arm (giving a total of 8 arms); or a partial lack of pairing in one medium arm accompanied by a partial lack of

pairing or by complete pairing in the other medium arm. Fig 2A and 2B are microphotographs illustrating partial pairing in two different hybrid larvae. The unpaired portions of the chromosome are seen to be half the thickness of the paired portions. One small inversion was found in a long arm of two preparations, and one medium-sized inversion was found in a different long arm of a hybrid between the two subspecies. A more thorough analysis of this lack of pairing and other structural differences in hybrid salivary cells is being undertaken.

A last difference between the subspecies *l. lebanonensis* and *l. castecli* is the presence of modifier(s) of the main pair of color alleles in polymorphic populations of *l. lebanonensis*, absent from *l. castecli* (Pipkin, unpublished). Furthermore, the modifier(s) producing a more extreme pale body color, introduced by the pale Beirut or Rasco strain of *l. lebanonensis* into hybrid populations of the two subspecies, do not become recombined so as to become expressed in 16 generations of such populations. Whether the modifier(s) are in one of the homologs which fails to pair regularly in the salivary gland chromosomes of the hybrid and presumably fails to undergo normal crossing over at meiosis, or whether the *l. lebanonensis* chromosome bearing the modifier(s) soon becomes lost from the hybrid population is not yet known. Further cytological work on such hybrid populations is being carried out.

Similarities between *l. lebanonensis* and *l. castecli* include the previously described range in number of teeth in the forceps and number of bristles on the posterior ventral border of the conchae, a like range in number of egg filaments, and similar crossability with *brooksi*. Further, the wing indices of the two subspecies are practically identical. A comparison of the wing indices, giving those of *l. lebanonensis* first, are as follows: costal index, 2, 2.2; fourth vein index, 2.8, 2.6; five x index, 2.2, 2. When *l. lebanonensis* females are crossed with *l. castecli* males, daily food transfers made, and all progeny hatching counted, the sex ratios are approximately equal. Seven such bottles gave the following sex ratios, males listed first: 124, 130; 115, 109; 116, 172; 177, 110; 138, 141; 111, 106; 70, 85. The reciprocal cross, *l. castecli* females crossed with *l. lebanonensis* males gave similar sex ratios, though the progeny hatch was lower owing to a mold infection: 23, 26; 30, 27; 47, 52. Deviations from a 50:50 sex ratio occurred in two bottles of the first cross, but they are opposite in direction. Hybrids between the two subspecies are fertile inter se and in either back cross, according to Table 3.

Distribution. The strain of *l. castecli* used in these studies was collected at Prescott, Arizona by collectors of The Genetics Foundation, The University of Texas, Austin, Texas. The same subspecies is believed to occur at Veyo, Utah and other points in New Mexico and Arizona listed in Wheeler (1949) under the name "*victoria*."

Types. Holotype male and a series of paratype males and females have been placed in the *Drosophila* Type and Reference Collection of the Genetics Foundation, The University of Texas, Austin, Texas.

TARIF 2. VARIATION IN NUMBER OF EGG FILAMENTS										
	2	3	4	5	6	7	8	9	10	total
victoria (palm springs)			1	4		25	4	3		37
brooksae (tucson)			6	26	28	9	2			71
pattersoni (beirut)		7	26	48	15	3	1			100
stonei (sofar)	3	6	16	33	19	3	1			81
<i>l.</i> lebanonensis (ain anub)				4	38	36	19	3		100
(rasco)				9	31	46	11	3		100
<i>l.</i> casteeli (prescott)				7	46	32	3			88

Dedication. *D. lebanonensis casteeli*, subsp. nov. is named in honor of the late Professor D. B. Casteel, Department of Zoology, The University of Texas.

RELATIONSHIP BETWEEN MEMBERS OF THE VICTORIA GROUP.
COMPARISON OF MALE AND FEMALE GENITALIA WITHIN THE GROUP

In order to further study the relationship between members of the victoria species group, the male and female genitalia of the members of this group available for study were reinvestigated. The forceps (primary clasper) and genital arch of *l. lebanonensis* and of *l. casteeli* were studied by Hsu (1949). Genital arches and forceps of *pattersoni* and of *stonei* were figured by Pipkin (1956). In all of the species of the victoria group studied, the penis and its apodeme, encased ventrally and laterally by the hypandrium and conchae, are located anterior to the genital arches and forceps. The hypandrium is continuous with its conchae. The apodeme of the penis is rod-like. The head of the penis is a hair-covered inverted bowl, the opening of which possesses a scalloped margin flanked by two clasper like lobes arising from the hypandrium. The surface of the head of the penis appears

to be made of small spindle shaped particles of chitin, each supporting a hair. The forceps is curved in all members of the victoria species group, in contrast with the straight forceps found in members of the coracina species group studied by Mather (1955). Drawings of male and female genitalia of *brooksi* appear in Fig. 1A, B, C, D, F. Aside from slight variations in dimensions of the hypandrium and penis, the main differences found among genitalia in the victoria species group consist in variations in the number of teeth in the forceps and in the number of bristles on the ventral posterior border of the conchae (Fig. 1A and C). Both the exact number of teeth in the forceps and the number of concha bristles vary slightly within a species and even on different sides of the same individual. Table 1 presents variation in the number of forceps teeth and the number of bristles on the ventral posterior border of one concha. Ten or more individuals of each species were examined to determine the extent of the variation. *Victoria* and *brooksi* are seen to possess the lowest number of concha bristles (4, for *victoria* and 4 to 5 for *brooksi*). A median of 11 to 12 forceps teeth is found in *pattersoni*, *stonei*, *l. lebanonensis*, and *l. casteeli*.

Females of the various members of the victoria group all possess a long bristle on each side near the apical end of the vaginal plates. From 6 to 8 (median 7) bristles are found distal to this long bristle. Proximal to the long bristle are from 15 to 20 short stubby bristles along the edges of the vaginal plates. Considerable variation in numbers of these bristles occurs within each species. These bristles are shown for *brooksi* in Fig. 1F.

VARIATION IN NUMBER OF EGG FILAMENTS IN THE VICTORIA SPECIES GROUP

A variation in number of egg filaments is characteristic of the victoria, coracina, maculosa, and levis species groups according to the work of Mather (1955). Table 2 presents information with respect to variation in number of egg filaments in the victoria group. For the group, a range of from 2 to 9 filaments occurs. The variation pattern is characteristic of each species. Thus the median number for *brooksi* is 6; for *pattersoni* and *stonei*, 5. Variations in egg filament number for both the Ain Anub and Rasco strains of *l. lebanonensis* and for the Prescott strain of *l. casteeli* do not differ statistically. Here the median classes are eggs with 6 and 7 filaments, respectively. These counts are in disagreement with Wheeler's 1949 count of filaments of the Ain Anub strain of *l. lebanonensis* (listed by him as being from "near Beirut"). The present author sent the Ain Anub strain to Dr. Wheeler in 1947; the Beirut strain was not sent to The Genetics Foundation, The University of Texas until 1960. Since the first dark strain of *l. lebanonensis* was collected in the mountain village of Ain Anub, it is better to refer to this strain by its collection locality. The present Beirut light strain is homozygous for the light color alleles and was derived from a heterozygous light strain collected in Beirut, Lebanon in 1947. Wheeler's finding the median egg fila-

TABLE 3. HYBRIDIZATION TESTS, VICTORIA GROUP

female parent	male parent				
	brooksae	pattersoni	stonei	l.lebanonensis	l.casteeli
brooksae	X	sterile	not made	larvae, few pupae	larvae, few pupae
pattersoni	3♂ 48♀ sterile	X	imagines sterile inter se, ♀ fertile to pattersoni ♂	larvae, pupae 2 imagines	larvae, pupae 2 imagines
stonei	not made	sterile	X	early larvae	sterile
l.lebanonensis	larvae, pupae	sterile	sterile	X	imagines fertile inter se and in back crosses
l.casteeli	larvae, few pupae	sterile	sterile	imagines fertile inter se and in back crosses	X

ment numbers to be 7 and 8 in the original Ain Anub strain indicates either a genetic change in the strain or influence of some environmental factor on the number of egg filaments. Twenty-five of the 37 eggs of *victoria* (Palm Springs) examined possessed 7 filaments. One filament was thick and split into two branches along its length at varying distances from its base. In 4 eggs the split was complete, resulting in 8 filaments: 3 eggs possessed 9 filaments. One egg possessed 4 filaments but the thick filament was split apically into 3 branches. Four eggs possessed 5 filaments, the thick filament being split apically into 3 branches. Sturtevant (1942) describes the eggs of *victoria* as having 8 filaments; this count agrees with the observations of the present author if the apical ends of the filaments are counted.

HYBRIDIZATION TESTS

Table 3 presents the results of hybridization tests within the *victoria* species group. Neither *nitens* nor *stonei* (culture lost in 1957) was available for testing with the newly described *brooksi*. Only preliminary tests have been made with *victoria*, owing to the difficulty of maintaining the stock on laboratory culture medium. All hybridization tests were made in standard 92 x 25 mm. culture vials, using corn meal medium, 20 females and 20 males to each vial. Daily food transfers were made for two weeks.

Females of the only yellow species, *pattersoni*, were the most successful, giving hybrid larvae, pupae, and few or many imagines in crosses with other members of the group. Pipkin (1956) found numerous hybrids produced by the cross of *pattersoni* females and *stonei* males. These hybrids were sterile *inter se*, but hybrid females were fertile when back-crossed with *pattersoni* males. Hybrids of a number of cultures of *pattersoni* females crossed with single dark *brooksi* males died as larvae or pupae, but one such culture yielded three males and 48 female. The *pattersoni-brooksi* hybrids were sterile *inter se*. The female hybrids were also sterile in back crosses with either *pattersoni* or *brooksi* males, whereas the male hybrids died before they could be tested in a back cross. Of the *pattersoni-brooksi* hybrids, 29 females and one male were intermediate in color between the "dark" of *brooksi* and "yellow" of *pattersoni*. Nineteen females and two male hybrids were shining yellow. Assuming the single dark *brooksi* parent male to have been heterozygous for the pale color allele, these results suggest a monogenic inheritance of the polymorphism in *brooksi* and an allelism between the "yellow" of *pattersoni* and the "pale" color allele of *brooksi*. *Pattersoni* females crossed either with *L. lebanonensis* or with *L. casteeli* produce hybrids usually dying as early larvae or pupae, but two imagines have hatched from each of these crosses (Pipkin, 1956). *Brooksi*, used as a female parent, gives hybrid larvae, a few of which pupate, with males of *L. lebanonensis* or *casteeli*. The reciprocal crosses, *L. lebanonensis* or *L. casteeli* females crossed with *brooksi* males, give a similar hybrid progeny, dying in larval or pupal stages. *Stonei* females rarely produce early larvae with *L. lebanonensis* males (Pipkin, 1956). Hybridization tests of females of *brooksi*, *pattersoni*, and *L. lebanonensis* crossed with males of *victoria* (Palm Springs) give no hybrid larvae though many eggs are laid in each case. Females of each of these species dissected after being with *victoria* males for two weeks showed no sperm in their seminal receptacles or vesicles. This does not mean that no copulation occurred, because the sperm could have disintegrated and been absorbed in this time.

In all of the cases in which interspecific hybrids occurred in Table 3, the crosses were characterised by sporadic success (but not by slowness of the hybrid larvae to appear after the cross was made), slow development of hybrid larvae, usual death of the hybrids in various larval or the pupal stages. Hybridization tests between the subspecies *L. lebanonensis* and *L. casteeli* have been discussed previously in this paper.

DISCUSSION

The present taxonomic studies have shown the male and female genitalia to be remarkably similar in the members of the *victoria* group studied. Considering the number of teeth in the forceps and the number of bristles on the posterior ventral border of the conchae of the hypandrium, the members fall into three pairs of closely related forms: *victoria* and *brooksi*; *pattersoni* and *stonei*; and, finally,

TABLE 4. PERCENTAGE FEMALES WITH SPERM DAMAGE IN CROSSES OF L. LEBANONENSIS AND L. CASTEELI

	motile sperm	non-motile sperm	disintegrating sperm	absence of sperm
<i>L. lebanonensis</i> ♀ x <i>L. casteeli</i> ♂	13	27	10	50
<i>L. casteeli</i> ♀ x <i>L. lebanonensis</i> ♂	7	11	15	67
<i>L. lebanonensis</i> ♀ x <i>L. lebanonensis</i> ♂	44	11	4	41
<i>L. casteeli</i> ♀ x <i>L. casteeli</i> ♂	50	22	0	28

L. lebanonensis and *L. casteeli*. The range in number of egg filaments likewise shows greater resemblance among these three pairs (with the exception of *brooksi* and *victoria*). Hybridization tests show that hybrids dying as larvae or pupae may result from crosses of species widely distant geographically. The close similarity of male and female genitalia in all the species studied shows that no mechanical isolation barrier to the success of these crosses exists. Mather (1957) found that transfer of sperm can take place between the maculosa species group (*novamaculosa* female) and the victoria group (*L. casteeli*, called "victoria" male).

The designation of *L. lebanonensis* and *L. casteeli* as subspecies rests chiefly upon the finding of sperm damage in crosses between the two and upon the lack of pairing of one chromosome pair in the salivary glands of the hybrids between these two forms. Lack of pairing in the salivaries of hybrids presumably means lack of pairing at meiosis, and consequent barrier to free recombination by crossing over, according to the work of Dobzhansky (1933) on hybrids between *pseudobscura* and *persimilis*. Wasserman (1954) states that in the salivaries of the closely related *arizonensis* and *mojavensis*, the region near the centromere of the X chromosome is usually unpaired. Townsend (1954) reports that "pairing is often complete," though certain inversions are present, in the salivary chromosomes of hybrids between

tropicalis tropicalis and *tropicalis cubana*. Pairing in the salivaries of hybrids of *pallidipennis pallidipennis* and *pallidipennis centralis* is complete, with one inversion present. (Patterson and Wheeler, 1947).

A part of the marked similarities between *l. lebanonensis* and *l. casteeli* is owing to their wide geographical separation. These two forms would probably not have diverged, owing to their free interbreeding capacity if they had remained in the same area. *Nitens* (Italy and Switzerland) is the nearest European relative of *l. lebanonensis* according to a morphological comparison. The two species differ in chromosome configuration, and *nitens* lacks a color polymorphism.

The members of the victoria species group are distributed in both Palaearctic and Nearctic regions. *Nitens* is known from Italy (Buzzati-Traverso, 1943) and Switzerland (Burla, 1948). *L. lebanonensis* is found in the Lebanon (Wheeler, 1949, Pipkin, 1953, 1956), and Israel (Goldschmidt, unpublished). *Pattersoni* and *stonei* occur in The Lebanon (Pipkin, 1956). A group of three species, *brooksi*, *victoria*, and *l. casteeli*, occur in the western United States. Wheeler (1949) states that extensive trap collections by the University of Texas group have not revealed a victoria species group member east of Nebraska. Further undescribed members of this group probably occur, as Sturtevant suggested (Sturtevant, 1942). The victoria group flies are not attracted to fruit baited traps as readily as many of the Sophophora and Drosophila. Most of the collections have been made from such traps. (Wheeler, 1949, Pipkin, 1953, Buzzati-Traverso, 1943). Dr. Throckmorton's collection of *victoria* was from the sap of *Populus fremontii* Wats., the flies refusing his fruit baited traps nearby (personal communication). *Brooksi* was likewise taken from the sap of this tree by Dr. Heed. A further study of the ecology of this group will prove profitable.

The existence of a Palaearctic and a Nearctic species polymorphic for light and dark mesonotum color (*l. lebanonensis* and *brooksi*) indicates similar mutability with similar survival value in related species. Sturtevant and Novitski (1941) noted similar mutations in a number of Drosophila species. Similar polymorphic abdominal patterns occur in the cardini group (Da Cunha, 1949; Stalker, 1953; Heed and Wheeler, 1957) and in the melanogaster group (Freire-Mai, 1949; Oshima and Taira, 1956; Moriwaki, 1952; Zürcher, 1958).

Gene exchange is possible between two of the Palaearctic victoria group species, *pattersoni* and *stonei*. Whether introgressive changes have occurred here is not known. It is interesting that a polymorphic species, *l. lebanonensis*, exists in the same area with its yellow and black relatives.

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