

## INCOMPATIBILITY TESTS IN THE *CULEX PIFIENS* COMPLEX PART I. AFRICAN STRAINS.

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Cytoplasmic incompatibility<sup>1</sup> in the *Culex pipiens* complex results in death of the embryos in certain crosses between allopatric populations. It has been observed in numerous combinations between strains from Europe, Asia and North America (Laven 1957, 1959, 1967b) and in Australia (Dobrotworsky 1955). In most of these cases strains are involved which belong to the subspecies *Culex pipiens pipiens*. Some crosses between this subspecies and *Culex pipiens fatigans* are also incompatible. Very few cases of incompatibility have been observed thus far in crosses between populations of the subspecies *Culex pipiens fatigans*.

For some time it was supposed that the incompatibility phenomenon might be restricted to the subspecies *Culex pipiens pipiens*. That this is not the case was first demonstrated by observations on African populations by Roubaud (1956). He crossed a strain from Dakar (Senegal) with one from Brazzaville (Congo) and got normal offspring in the pairing ♀ Brazzaville x ♂ Dakar, but no offspring in the opposite direction ♀ Dakar x ♂ Brazzaville. Service (1956) did not find incompatibility between strains from Nigeria and British Guinea and Rozeboom (1958) also between strains from North

America and from the Philippine Islands, but Krishnamurthy (1962 unpublished) has observed incompatibility between Indian populations from Trivandrum and Nagpur. The crossing ♀ Nagpur x ♂ Trivandrum was successful but ♀ Trivandrum x ♂ Nagpur gave no offspring.

The incompatibility phenomenon has attracted much interest in recent times because it has been proven as a means for genetical control of *Culex* populations (Laven 1967a). Systematic crossings of as many populations as possible will provide the basis for future applications. The present paper summarizes the information available for some African populations.

During a recent visit to different places in Western, Central and Eastern Africa I was able to collect living material from Thiès (Senegal), Brazzaville (Congo) and New Halfa (Sudan). Professor A. W. A. Brown (London, Ontario) provided me with a strain from Douala (Cameroun), Dr. F. Kuhlow with one from Ifakara (Tanzania) and Dr. J. Hammon with one from Bobo Dioulasso (Haute Volta). Fig. 1 shows the locations of origin of these strains. They are all within the range of the subspecies *Culex pipiens fatigans*.

These six African strains have been tested for compatibility or incompatibility in all possible combinations. Table 1 gives the numerical results (number of rafts; total number of eggs; number and percentage of hatched larvae; embryonated and nonembryonated eggs). In the last column the + or - sign indicates whether the cross is compatible or incompatible. In two cases only a single raft has been counted, but in general one single raft is sufficient for the decision whether a certain combination is compatible or not. If the first raft indicates incompatibility all further rafts will not hatch and vice versa

<sup>1</sup>In "cytoplasmic incompatibility," sperm from one strain are unable to function in the cytoplasm of another strain. An incompatible crossing is characterized by normal copulation and insemination; the penetration of the sperm stimulates the egg to meiosis and embryonic development which runs to an advanced stage; the sperm itself is blocked from karyogamy and does not contribute anything more; the organogenesis of embryos originating by induced parthenogenesis is irregular and distorted. High or low rates of "embryonation" do not reflect different mechanisms but are, rather, a characteristic of the strain used. We have some strains which will constantly show low rates, others high rates.

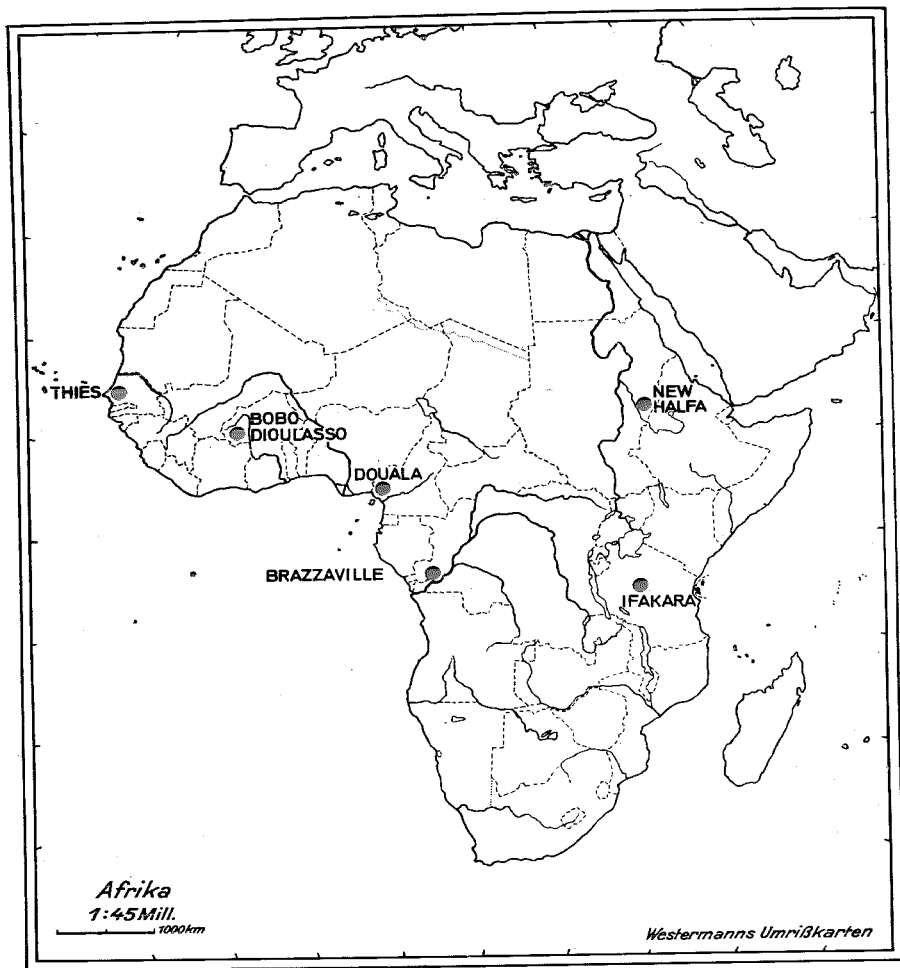


FIG. 1.—Localities and names of African populations of *Culex pipiens* in which the phenomenon of compatibility and incompatibility has been studied.

TABLE 1.—Results of crosses between six African strains of *Culex pipiens*. The + sign in the last column indicates compatibility (normal offspring), the sign —, incompatibility.

	Cross	No. of rafts	No. of eggs	hatched larvae		embryonated eggs		non-embryonated eggs		result
				No.	%	No.	%	No.	%	
1	Bobo x Thiès	8	1108	901	81,32	48	4,33	159	14,35	+
2	Bobo x Douala	2	262	261	99,62	0	0	1	0,38	+
3	Bobo x Brazzaville	3	465	461	99,14	4	0,86	0	0	+
4	Bobo x Ifakara	8	1298	1079	83,13	45	3,47	174	13,40	+
5	Bobo x New Halfa	2	146	0	0	96	65,75	50	34,25	-
6	Thiès x Bobo	6	866	853	98,50	3	0,35	10	1,15	+
7	Thiès x Douala	16	1279	2	0,15	1132	88,51	145	11,34	-
8	Thiès x Brazzaville	32	4218	5	0,12	2934	69,56	1279	30,32	-
9	Thiès x Ifakara	9	1439	950	66,02	5	0,35	484	33,63	+
10	Thiès x New Halfa	4	471	448	95,12	4	0,85	19	4,03	+
11	Douala x Bobo	3	322	310	96,28	8	2,48	4	1,24	+
12	Douala x Thiès	17	2232	1210	54,21	182	8,15	840	37,64	+
13	Douala x Brazzaville	13	1995	1761	88,27	40	2,00	194	9,73	+
14	Douala x Ifakara	5	704	690	98,01	9	1,28	5	0,71	+
15	Douala x New Halfa	14	1389	0	0	1233	88,55	159	11,45	-
16	Brazzaville x Bobo	4	764	734	96,07	7	0,92	23	3,01	+
17	Brazzaville x Thiès	10	1545	1087	70,36	137	8,87	321	20,77	+
18	Brazzaville x Douala	8	627	615	98,01	4	0,64	8	1,35	+
19	Brazzaville x Ifakara	1	147	147	100,00	0	0	0	0	+
20	Brazzav. x New Halfa	5	823	610	74,12	28	3,40	185	22,48	+
21	Ifakara x Bobo	5	782	726	92,84	5	0,64	51	6,52	+
22	Ifakara x Thiès	4	542	499	92,07	4	0,74	39	7,19	+
23	Ifakara x Douala	2	194	192	98,97	0	0	2	1,03	+
24	Ifakara x Brazzaville	1	176	173	98,30	1	0,57	2	1,13	+
25	Ifakara x New Halfa	5	862	3	0,41	255	29,58	604	70,01	-
26	New Halfa x Bobo	7	932	770	82,62	51	5,47	111	11,91	+
27	New Halfa x Thiès	18	3432	1471	42,86	426	12,41	1535	44,73	+
28	New Halfa x Douala	8	1001	932	93,11	7	0,70	62	6,19	+
29	New Halfa x Brazzav.	4	538	525	97,58	1	0,19	12	2,23	+
30	New Halfa x Ifakara	4	546	544	99,63	0	0	2	0,37	+

♀	♂ BOBO DIOU- LAS- SO	THIÈS	DOU- ALA	BRAZ- ZA- VILLE	IFAKA- RA	NEW HALFA
BOBO DIOLASSO	▨	+	+	+	+	—
THIÈS	+	▨	—	—	+	+
DOUALA	+	+	▨	+	+	—
BRAZZAVILLE	+	+	+	▨	+	+
IFAKARA	+	+	+	+	▨	—
NEW HALFA	+	+	+	+	+	▨

FIG. 2.—Crossing relationships of six African populations of *Culex pipiens*. + = compatible cross; — = incompatible cross.

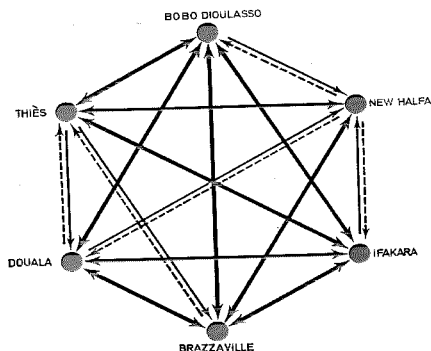


FIG. 3.—Crossing relations between African strains of *Culex pipiens*. Heavy lines with arrowheads in both directions indicate compatibility in both crossing directions. Double lines indicate unidirectional incompatibility, the full line indicates the compatible cross, the broken line the incompatible one. The arrowheads point to the female partner of the cross, indicating in this way the origin of the sperm and its entrance into the egg.

with compatibility. Line 8 with the combination ♀ Thiès x ♂ Brazzaville illustrates this. All 32 rafts were incompatible. Only five larvae (0.12 percent) did hatch. It is known that these larvae will mature into females. These come about by parthenogenetic development of single eggs, induced by the entering sperm.

As may be seen from Table 1 and from Fig. 2 and 3, most of the crosses were compatible (+). However, 5 out of the total of 30 were incompatible (—): ♀ Bobo Dioulasso had no offspring with ♂ New Halfa, ♀ Thiès no offspring with ♂ Douala and with ♂ Brazzaville, ♀ Douala with ♂ New Halfa and ♀ Ifakara with ♂ New Halfa. In all these cases the incompatibility was unidirectional, i.e., in the opposite direction the crosses are normal. The strain New Halfa is outstanding in so far as it is incompatible when used as the paternal strain with three

other strains, but can be successfully crossed, as females, with all five other strains. From the viewpoint of practical application for the control of *Culex* by means of cytoplasmic incompatibility, the New Halfa strain would be the most useful.

#### References

DOBROTORSKY, N. V. 1955. The *Culex pipiens* group in south-eastern Australia. IV. Cross-breeding experiments within the *Culex pipiens* group. Proc. Linn. Soc. New South Wales. 80:33-43.

KRISHNAMURTHY, B. S. 1962. Report to WHO (unpublished).

LAVEN, H. 1957. Vererbung durch Kerngene und das Problem der ausserkaryotischen Vererbung bei *Culex pipiens*. II. Ausserkaryotische Vererbung. Z. Vererbungslehre, 88:478-516.

———. 1959. Speciation by cytoplasmic isolation in the *Culex pipiens*-complex. Cold Spr. Harb. Symp. quant. Biol., 24, 166-173.

———. 1967a. Eradication of *Culex pipiens fatigans* through cytoplasmic incompatibility. Nature 216, 383-384.

———. 1967b. Speciation and evolution in *Culex pipiens*. In: Wright, J. W., & Pal, R., ed., *Genetics of Insect Vectors of Disease*, p. 251-274, Amsterdam Elsevier Publ. Co.

ROUBAUD, E. 1956. Phénomènes d'amixie dans les intercroisements de souches géographiques, indifférenciées extérieurement, du Moustique commun tropical *Culex fatigans* Wied. C. R. Acad. Sci. (Paris), 242:1557-1559.

ROZEBOOM, L. E. 1958. Hybridization of *Culex pipiens fatigans* Wiedemann from the Philippine Islands with American strains of the *Culex pipiens* group (Diptera:Culicidae). Amer. J. trop. Med. Hyg., 7:526-530.

SERVICE, M. W. 1956. Crossing of two allopatric populations of *Culex fatigans* Wiedemann. Nature, 178:1065.

## PART II. EGYPTIAN STRAINS.

Probably more than 400 different crosses between populations of the *Culex pipiens* complex have been made so far (Laven 1967). In the majority of these cases European strains were used. A good number of crosses have also been made in the United States, India, Russia, Australia and Africa. The greatest part of the crosses were made between populations of different countries of one continent, less numerous have been crosses between populations of different continents. The results produce an irregular and puzzling pattern of the distribution of compatibility and incompatibility.

In Europe and North Africa five different crossing types can be distinguished: a North German, a South German, a West European and an Italian and a Tunisian type. In the map (Fig. 1) the five types are separated by tentative border lines. However, it is not yet known where these types actually meet, whether they come in contact with each other nor what happens in these contact areas. The shortest distance between two different crossing types observed in Europe is about 320 kilometers (North German type: Hamburg, West

European type: Elberfeld). It has been suggested several times and by various authors that a survey of the populations between two crossing types would be highly desirable. By testing as many populations as possible on a line between the two points from which two different types are known, it would be possible to decide whether they are linked by transitional types or whether they meet somewhere in between without such intermediate populations.

A first attempt of such a survey has now been made. Although it does not fulfill the desired dense spacing of collecting points, the results are of such a kind that they are worth reporting.

A recent visit to Egypt (1964) gave me the opportunity to collect living material from local *Culex pipiens* populations from Assuan in the south to Alexandria in the north. All in all 13 populations were collected and bred for the first generation in the laboratory in Cairo. After that they were transferred to Mainz for the test crosses. The cooperation in collecting, raising and shipment of the material by Dr. Zein-el-Dine, Dr. Shawarby and Dr.

Mamud is acknowledged with heartiest thanks.

The collecting places from north to south (Fig. 2) and their distances were as follows: *Rashid (Ra)*, northwest of Alexandria; *Tanta (Ta)*, 82 km southeast of Rashid and about 80 km north of Cairo; *Nuba (Nu)*, south of Zagazig, about 55 km northeast of Cairo, 62 km from Tanta; *Salhiya (Sl)*, northwest of Ismailia, 55 km from Nuba; *Maadi (Md)*, 6 km south of Cairo; *Wasta (Wa)*, 75 km south of

Maadi; *Minya (Mi)*, 140 km south of Wasta; *Sohag (So)*, 190 km south of Minya; *Abydos (Ab)*, 45 km south of Sohag; *Qena (Qe)*, 80 km east of Abydos; *Luxor (Lx)*, 50 km south of Qena; *Edfu (Ed)*, 80 km south of Luxor; *Assuan (As)*, 95 km south of Edfu. All distances given are approximate straight-line distances. In all places fed females were caught in houses or huts.

The results of 113 of the 156 possible crosses between these 13 populations are

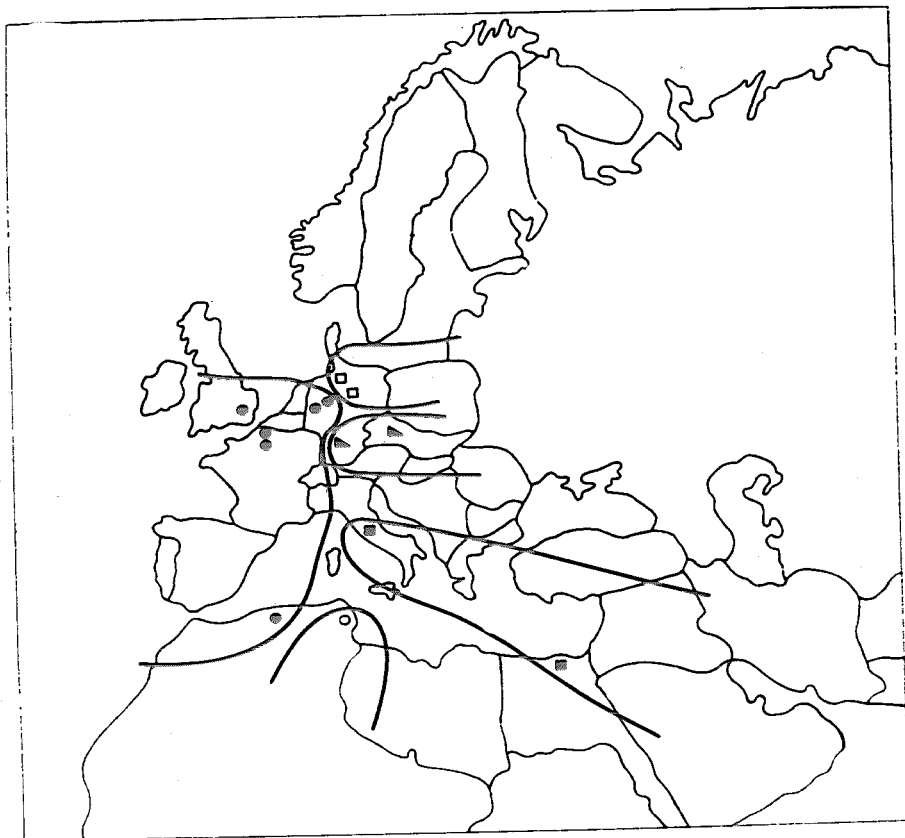


FIG. 1.—Distribution of "crossing type" of *Culex pipiens* in Europe and North Africa, (after Laven 1959).

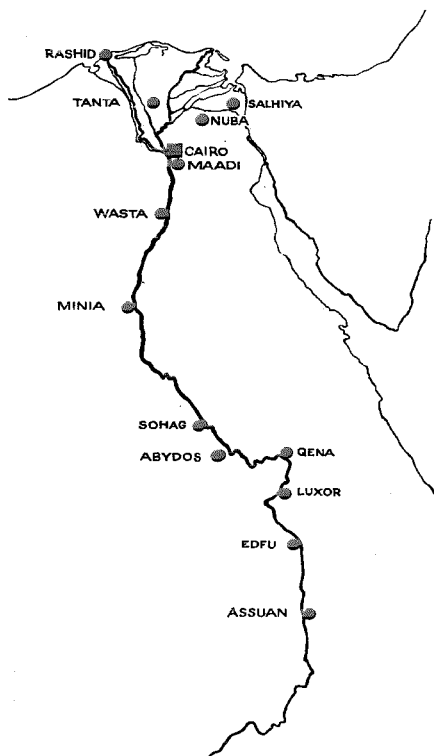


FIG. 2.—Map of Egypt with localities from which *Culex pipiens* populations have been tested for incompatibility.

shown in Fig. 3. The numerical results are given in Table 1. Not all crosses could be made because some strains died out before crossings were effected. Incompatibility, indicated by the minus sign in Fig. 3, has been observed in 7 cases out of the 113 crosses. These 7 cases involve crosses between females from Rashid (Ra) or Tanta (Ta) and males from various other strains and one case between females from Edfu (Ed) and males from Maadi (Md). The concentration of incompatibility in the north of the Delta region is very striking and needs a closer inspection.

		♂												
		Ra	Ta	Nu	Sl	Md	Wa	Mi	So	Ab	Qe	Lx	Ed	As
♀	Ra	-	/	+	+	+	+	+	-	-	-	-	-	+
	Ta	+	+	+	+	+	+	+	+	+	+	+	+	+
	Nu	+	+	+	+	/	+	+	+	+	+	/	+	+
	Sl	+	+	+	+	+	+	+	+	+	/	+	+	+
	Md	+	+	+	+	+	+	+	+	+	+	+	+	+
	Wa	+	+	+	+	+	+	+	+	+	/	/	+	+
	Mi	+	+	+	+	+	+	+	+	+	/	/	+	+
	So	+	+	+	+	+	+	+	+	+	/	/	+	+
	Ab	+	+	+	+	+	+	+	+	+	/	/	+	+
	Qe	+	/	+	/	/	/	/	/	/	/	/	/	/
	Lx	+	+	/	+	+	+	/	/	/	/	/	/	/
	Ed	+	+	+	+	-	+	+	/	+	/	+	+	/
	As	+	+	+	+	+	+	+	+	+	/	/	+	+

FIG. 3.—Results of crosses between 13 *Culex pipiens* populations from Egypt. + = normal offspring, compatible cross; - = no offspring, incompatible cross; / = cross not made. For abbreviation of names of localities see text.

The two strains Rashid (Ra) and Tanta (Ta) are not alike regarding incompatibility. First, they are different *inter se*, i.e. they show unidirectional incompatibility: Ra x Ta : -; Ta x Ra : +. Second, they have different crossing relationships with the other strains, as may be seen at once by comparing the first two horizontal rows in Fig. 3. The following strain Nuba (Nu) is again different from the first two. It shows no incompatibility at all, not as female and not as male. The strain Salhiya (Sl) behaves in all crosses like Nuba (Nu), but the strain Maadi (Md) males are incompatible with females from Tanta (Ta). Unfortunately the cross ♀ Nuba x ♂ Maadi has not been. This is a serious gap for the following considerations.

The crossing relations of the five populations sampled in the Delta regions are plotted in Fig. 4 in a geographical arrangement with indication of distances between the localities. If we suppose that the populations from Rashid (Ra) and Tanta (Ta) come in contact somewhere in between these localities, then we should find happening the following: The strain Tanta (Ta) will reduce the strain Rashid





TABLE I.—(Continued).

Crossing	No. of rafts	No. of eggs	hatched larvae		embryonated eggs		non-embryonated eggs		Result
			No.	%	No.	%	No.	%	
Salhiya x Rashid	2	177	154	87,0	-	-	23	13,0	+
Salhiya x Tanta	2	82	68	82,9	3	3,7	11	13,4	+
Salhiya x Nuba	1	92	73	79,3	8	8,7	11	12,0	+
Salhiya x Maadi	3	189	131	69,3	6	3,2	52	27,5	+
Salhiya x Wasta	2	217	183	84,3	1	0,5	33	15,2	+
Salhiya x Minia	3	237	197	83,1	9	3,8	31	13,1	+
Salhiya x Sohag	2	122	106	86,9	7	5,7	9	7,4	+
Salhiya x Abydos	2	111	78	70,3	4	3,6	29	26,1	+
Salhiya x Qena									
Salhiya x Luxor	1	56	50	89,2	4	7,1	2	3,7	+
Salhiya x Edfu	1	58	50	86,2	-	-	8	13,8	+
Salhiya x Assuan	2	194	190	97,9	1	0,5	3	1,6	+
Maadi x Rashid	1	64	56	87,5	-	-	8	12,5	+
Maadi x Tanta	4	266	263	98,9	3	1,1	-	-	+
Maadi x Nuba	2	96	88	91,7	-	-	8	8,3	+
Maadi x Salhiya	5	380	376	99,0	2	0,5	2	0,5	+
Maadi x Wasta	5	279	269	96,4	-	-	10	3,6	+
Maadi x Minia	5	301	245	81,4	19	6,3	37	12,3	+
Maadi x Sohag	1	67	64	95,5	1	1,5	2	3,0	+
Maadi x Abydos	4	299	297	99,4	1	0,3	1	0,3	+
Maadi x Qena	3	162	140	86,4	5	3,1	17	10,5	+
Maadi x Luxor	3	233	229	98,2	-	-	4	1,8	+
Maadi x Edfu	6	393	358	91,1	4	1,0	31	7,9	+
Maadi x Assuan	1	70	68	97,2	1	1,4	1	1,4	+
Wasta x Rashid	1	16	13	81,3	3	18,7	-	-	+
Wasta x Tanta	1	28	27	96,4	-	-	1	3,6	+
Wasta x Nuba	1	80	77	96,3	1	1,2	2	2,5	+
Wasta x Salhiya	2	172	165	95,9	3	1,8	4	2,3	+
Wasta x Naadi	2	183	173	94,5	1	0,5	9	5,0	+
Wasta x Minia	7	718	706	98,4	6	0,8	6	0,8	+
Wasta x Sohag									
Wasta x Abydos	4	277	275	99,3	-	-	2	0,7	+
Wasta x Qena									
Wasta x Luxor									
Wasta x Edfu	1	56	40	71,4	14	25,0	2	3,6	+
Wasta x Assuan	4	209	157	75,1	10	4,8	42	20,1	+

TABLE I.—(Continued).

Crossing	No. of rafts	No. of eggs	hatched		embryonated		non-embryonated		Result
			larvae		eggs		eggs		
			No.	%	No.	%	No.	%	
Minia x Rashid	1	47	8	17,0	-	-	39	83,0	+
Minia x Tanta	7	351	341	97,2	1	0,3	9	2,5	+
Minia x Nuba									
Minia x Salhiya	5	328	322	98,2	1	-	6	1,8	+
Minia x Maadi	2	144	138	95,8	2	1,4	4	2,8	+
Minia x Wasta	12	1230	930	75,6	223	18,1	77	6,3	+
Minia x Sohag	1	63	57	90,5	1	1,6	5	7,9	+
Minia x Abydos	1	53	51	96,2	-	-	2	3,8	+
Minia x Qena									
Minia x Luxor									
Minia x Edfu									
Minia x Assuan	3	142	141	99,3	-	-	1	0,7	+
Sohag x Rashid	2	93	73	78,5	4	4,3	16	17,2	+
Sohag x Tanta	2	135	117	86,7	4	3,0	14	10,3	+
Sohag x Nuba	1	34	18	52,9	2	5,9	14	41,2	+
Sohag x Salhiya	3	146	132	90,4	7	4,8	7	4,8	+
Sohag x Maadi	2	62	61	98,4	-	-	1	1,6	+
Sohag x Wasta									
Sohag x Minia	4	218	191	87,6	11	5,0	16	7,4	+
Sohag x Abydos	2	58	42	72,4	2	3,4	14	24,2	+
Sohag x Qena									
Sohag x Luxor									
Sohag x Edfu	2	102	81	79,4	3	2,9	18	17,7	+
Sohag x Assuan									
Abydos x Rashid	1	77	60	77,9	4	5,2	13	16,9	+
Abydos x Tanta	2	134	130	97,0	1	0,8	3	2,2	+
Abydos x Nuba	1	85	85	100,0	-	-	-	-	+
Abydos x Salhiya	2	196	123	62,7	72	36,7	1	0,6	+
Abydos x Maadi	3	205	201	98,0	-	-	4	2,0	+
Abydos x Wasta	2	195	190	97,4	-	-	5	2,6	+
Abydos x Minia	1	125	121	96,8	2	1,6	2	1,6	+
Abydos x Sohag									
Abydos x Qena									
Abydos x Luxor	2	181	180	99,4	-	-	1	0,6	+
Abydos x Edfu	1	119	118	99,2	-	-	1	0,8	+
Abydos x Assuan	1	63	43	68,3	11	17,5	9	14,2	+



TABLE I.—(Continued).

Crossing	No. of rafts	No. of eggs	hatched larvae		embryonated eggs		non-embryonated eggs		Result
			No.	%	No.	%	No.	%	
Assuan x Rashid	2	95	93	97,9	-	-	2	2,1	+
Assuan x Tanta	4	184	151	82,1	9	4,9	24	13,0	+
Assuan x Nuba	1	103	87	84,5	-	-	16	15,5	+
Assuan x Salhiya	3	234	211	90,2	16	6,8	7	3,0	+
Assuan x Maadi	2	93	88	94,6	2	2,2	3	3,2	+
Assuan x Wasta	2	165	58	35,2	86	52,1	21	12,7	+
Assuan x Minia	4	349	314	90,0	2	0,6	33	9,4	+
Assuan x Sohag	1	24	23	95,8	-	-	1	4,2	+
Assuan x Abydos	2	180	171	95,0	-	-	9	5,0	+
Assuan x Qena									
Assuan x Luxor									
Assuan x Edfu	1	51	37	72,5	5	9,8	9	17,7	+

(Ra) through crosses ♀ Ra x ♂ Ta, which are incompatible. The strain Tanta (Ta) will not suffer by this contact because the crossing ♀ Ta x ♂ Ra is compatible. If such a contact of two unidirectional incompatible strains is stationary in space and time we should find a belt between Rashid and Tanta where a certain number of rafts laid by the local females will not

hatch. The width of such a belt would be determined in the first place by the flight range of the mosquitoes, of the females as well as of the males.

There is no reason to suppose that such a contact belt must be stationary. To the contrary, the diminishing of the Rashid population through the incompatible cross ♀ Ra x ♂ Ta will allow the Tanta population to occupy gradually the habitat of the Rashid population under the premises that the habitat can support only a certain number of mosquitoes. As a consequence of such a situation it can be expected that the Tanta strain will replace, step by step, the Rashid strain until the latter has entirely disappeared. This will only happen, however, when the ecological requirements of both strains are alike. If for example the Rashid strain would be better adapted to the ecological conditions in the coastal area, it would lead to an equilibrium between the strains and to a standstill of the contact belt.

The same considerations as outlined here for the relationship between the Rashid and Tanta populations apply in exactly the same way for the correlation between the populations Tanta (Ta) and Maadi (Md). As mentioned before the position of the

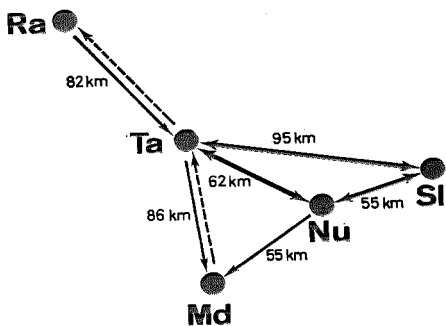


FIG. 4.—Crossing relations between the populations in the Nile Delta area of Egypt. Heavy line with arrow heads in both ends = reciprocal crosses compatible; single line with one arrowhead = compatible cross; broken line = incompatible cross (compare with Fig. 3).

population of Nuba to Maadi is not clear, because the decisive cross ♀ Nuba x ♂ Maadi has not been made. The picture would become very complicated, if this cross would turn out to be compatible.

The other cases of incompatibility indicated in Fig. 3 are between geographically distant populations: ♀ Rashid x ♂ Sohag, ♀ Rashid x ♂ Oena, ♀ Tanta x ♂ Abydos, ♀ Tanta x ♂ Luxor and ♀ Edfu x ♂ Maadi. It is interesting to note that the females from Rashid have a different incompatibility pattern compared with the females from Tanta, again an indication that these two strains are different. Furthermore these incompatibilities show that the populations in the middle part of Egypt (Sohag, Abydos, Qena and Luxor) are not identical in spite of the lack of incompatibility between these neighbouring populations in this part of Egypt. The last mentioned case of incompatibility, ♀ Edfu x ♂ Maadi, is somewhat exceptional, because it is the only one where females from the south show incompatibility with males from the north. But it should be taken in consideration that many of the crosses with the southern strains have not been made. A completion of these lacunae would perhaps reveal more and other incompatibilities. Nevertheless, the region from Sohag to Luxor and perhaps to Edfu seems to be populated by a group of strains with "cryptic differentiation" (Laven 1959).

All in all it is obvious that Egypt from the Mediterranean coast to Assuan in the south harbours at least six different crossing types of *Culex pipiens*, perhaps even more. The three different types Rashid, Tanta and Maadi are in very close proximity and they perhaps come in contact with each other with the consequences outlined before. The distances found here between these types are the shortest yet observed.

Although the observations reported here are far from complete, they lead to certain further problems and consequences. The first problem which turns up in connection with the strains in the Nile delta region is the problem of their origin. There can

be no doubt that the multiplicity of crossing types in the *Culex pipiens* complex as such must originate by some kind of "mutation" in the extrachromosomal genetic system responsible for incompatibility (Laven 1957, 1959). Three types, Rashid, Tanta and Maadi could have arisen by independent "mutation." But there is also another possibility, namely, introduction of a foreign crossing type. Mattingly (1957) has pointed out that in many areas in the world, especially in ports on the West African coast and in the Pacific, foreign populations of *Culex pipiens* have probably been introduced in recent times. Such an event could also have happened in Egypt. But at first sight the situation observed in Egypt seems to contradict the introduction hypothesis. We would in such a case suppose that the coastal area with ports like Alexandria and perhaps also Rashid would be the most likely place of introduction. But a new population, most likely consisting of only a few specimens in the beginning, could get a foothold only when the introduced females and their female offspring are compatible with the local population. What we observe in Egypt is just the opposite situation. If we suppose the Rashid population is the introduced one and Tanta the indigenous, the few Rashid females supposedly introduced or their offspring would have been wiped out at once at the start. The same applies to the strain Tanta in comparison to strain Maadi. But if we would suppose introduction into Cairo of at least two or probably three different strains in succession the situation as it is now could have arisen. Without any evidence for introduction we can only speculate about it and we will not stress it more at the moment. Investigations on introduced populations will be highly desirable and would perhaps give a clue for the explanation of the Egyptian situation.

In view of the use of incompatibility as a control measure against *Culex* populations (genetic control) the Egyptian situation is very instructive for any planning of such experiments. First of all it reveals that the crossing type in a country can

change over relative short distances. This possibility should and must be considered in any proposal for control of *Culex* by incompatibility over larger areas. Testing of many adjacent populations on a transect line through the area is a prerequisite for any practical work. If it would not be done, control work could fail or could lead to disastrous consequences. This can be illustrated with the Egyptian situation in the Delta.

Suppose we would try to control the population in Tanta with incompatible males either from Abydos (Ab) or Luxor (Lx). As far as the type Tanta goes we would get incompatible matings, dying embryos in the rafts and therefore a depression in the population and probably eradication. But as soon as we reach the point where the type Tanta changes to the type Nuba, we would have no influence on the *Culex* population; to the contrary, by introducing "new blood" into the Nuba type we would get very probably heterotic animals which have in general an advantage over the nonheterotic animals from the pure stock of Nuba. It could be expected that the heterotic animals would expand very rapidly. And if we would have created a vacuum in Tanta by killing part of the local population by incompatibility, the non-incompatible and heterotic population from Nuba and its cross with Abydos or Luxor would easily move into that vacuum. The whole work would

be a waste of time, labor and money. We would have accomplished nothing.

The experiments reported here need further amplification and corroboration. Many of the possible crosses between the southern populations have not been made and the most crucial cross in the Delta area, ♀ x ♂ Maadi, is urgently needed before the consideration brought forward above gets a sound basis. Nevertheless, the observations as far as they stand now, clearly indicate that much work and especially a much denser sampling and testing of local population needs to be done in Egypt and also in other places before the correlations between local populations are definitely known. The final picture will have profound significance for any proposal for genetical control. There is also a possibility that the different crossing types found in Egypt could have a correlation with the occurrence of filariasis in that country.

#### References

- LAVEN, H. 1957. Vererbung durch Kerngene und das Problem der auBerkaryotischen Vererbung bei *Culex pipiens*. II. AuBerkaryotische Vererbung. Z.f.Vererbungsl. 88:478-516.
- . 1959. Speciation by cytoplasmic isolation in the *Culex pipiens* complex. Cold Spring Harbor Symp. Quant. Biol. 24:166-178.
- . 1967. Speciation and Evolution in *Culex pipiens*. S. 251-275, in: J. W. Wright & R. Pal: Genetics of Insect Vectors of Disease. Amsterdam (Elsevier) 1967.
- MATTINGLY, P. F. 1957. Notes on the taxonomy and bionomics of certain filariasis vectors. Bull. Wild. Hlth. Org. 16:686-696.