

An Introduction To
The Genetics Of
Habrobracon Juglandis Ashmead

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TO MY WIFE





FOREWORD

This summary is designed for students of Habrobraconology. Although written primarily for use in course work, it is hoped that it may serve as a reference for those engaged in experimental genetics. The aim of the work has been to present a clear and readable account of the results of investigations made thus far in the genetics of *Habrobracon juglandis* (Ashmead).

The insect is described, and its method of culture as well as that of its host is outlined in detail. A complete list of extant and discarded mutant types is included. The statistical formulas utilized in determining crossover values and other linkage problems are presented. Tables in the appendix summarize present linkage information and effects of X-radiation. A glossary and a complete bibliography of Habrobraconology accompany the summary.

I am deeply indebted to Professor P. W. Whiting, of the University of Pennsylvania, for reading the manuscript and for making valuable suggestions, and to Dr. G. M. McKinley, of the University of Pittsburgh, for his encouragement. Special thanks are given to my wife, Dr. Phyllis C. Martin, of the Pennsylvania College

for Women, who read the text at several stages in its preparation, and assisted in the clarification of the language.

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HABROBRACON JUGLANDIS ASHMEAD

Chapter I

INTRODUCTION

For the purpose of studying inheritance, the insects have been of primary importance, chiefly because their life cycle is short, and because they produce large numbers of progeny. The fruit-fly, *Drosophila melanogaster*, and the bee, *Apis mellifica*, have been studied intensively by a number of workers; but the parasitic wasp, *Habrobracon juglandis* (Ashmead), has been given special study by P. W. Whiting and his co-workers during the past thirty years.

Habrobracon is a parasitic hymenopteran of the superfamily Ichneumonoidea, family Braconidae, subfamily Vipiinae, genus *Microbracon*, species *hebetor* (Say) (Muesebeck, 1925). The species *M. hebetor*, was first described in 1836 by Say who, however, called it *Bracon hebetor*. Later that same year he described another species, which he called *B. dorsator*. The species, *B. hebetor* and *B. dorsator*, are now known to be the same. Many other names have been applied to this insect since the original ones proposed by Say: *B. brevicornis* (Kirby, 1884; Marshall, 1885), *B. juglandis* (Ashmead, 1889), *Habrobracon hebetor* (Johnson, 1895), *Bracon (Habrobracon) honestor* (Riley, 1895; Howard, 1895), *Habrobracon beneficentior* (Viereck, 1911), *H. brevicornis* (Cushman, 1914; P. W.

Whiting, 1918, 1921e), and *H. juglandis* (Cushman, 1922).

The type specimens of *Bracon hebetor* (Say) and of *B. dorsator* (Say) have been lost, but those of *B. juglandis* (Ashmead), and *Habrobracon beneficentior* (Viereck) are in the United States National Museum, Washington, D. C., the former bearing type catalogue number 2913, the latter, number 13494.

The species, *Microbracon hebetor* (Say), is exceedingly close to *M. brevicornis* (Wesmael), and the two have been much confused in literature. In early papers on the genetics of *Habrobracon juglandis*, the name, *H. brevicornis* (Wesmael) was used. Cushman (1922) cleared up this matter, calling attention to the difference in habit between the two species, and pointing out some morphological differences. *Habrobracon brevicornis* is known to parasitize the European corn-borer, *Pyrausta nubilalis*, while *Habrobracon juglandis* parasitizes the Mediterranean flour moth, *Ephestia kuehniella* (Zeller). The females of *Microbracon hebetor* are readily distinguished from those of *M. brevicornis* by the antennae, which consist of 13-15 segments in the former, and 17-19 segments in the latter. At this time, however, Cushman did not regard *Bracon juglandis* (Ashmead) as identical with *B. hebetor* (Say). It appears, after a careful consideration of Say's description of *B. hebetor*, that there can be no reasonable doubt that Say and Ashmead were dealing with the same species (Muesebeck, 1925). The name *Hadrobracon brevicornis* (Wesmael) was used by Doten (1911) in describing the relation of food to reproduction and longevity in cer-

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tain hymenopterous parasites, and by Cushman (1914), and P. W. Whiting (1918, 1921e) in their work with *Habrobracon juglandis*. This use of *Hadrobracon* is clearly a misspelling since no such generic name is recognized in scientific literature (Neave, 1939). There have been some genetic studies reported on *Microbracon brevicornis* (Wesmael) (Speicher and Speicher, 1940) and *M. pectinophorae* (Watanabe) (Inaba, 1939, 1940) under the generic name, *Habrobracon*. The present account, however, deals mainly with the work done on the genetics of *Microbracon hebetor* (Say), but since the name *Habrobracon juglandis* (Ashmead) has been used as a synonym for *Microbracon hebetor* (Say) and is so well entrenched in genetic literature, it is preferable to use it in a work of this kind.

At present five wild-type stocks of *Habrobracon juglandis* are being reared by Whiting for genetic studies. These stocks have been named for the geographic locality in which they were found, and have been arbitrarily numbered to differentiate one from the other in genetic crosses. Thus wild-type stock number one (1) is from Lancaster, Pennsylvania, stock number eleven (11) from Iowa City, Iowa, stocks number thirty-two (32) and thirty-three (33) from California, and stock number twenty-five (25) from New York City, New York.

Habrobracon juglandis is ecto-parasitic on various cereal-infesting caterpillars. References in literature to *Bracon* or *Habrobracon brevicornis*, *Microbracon hebetor*, or *Habrobracon juglandis* as parasites of the Mediterranean flour moth, *Ephestia kuehniella* (Zeller) (Washburn, 1904), of the meal moth, *Plodia inter-*

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punctella (Grandi, 1931), the fig moth, *Ephestia cautella* (Walker) (Simmons and Reed, 1929) and of the bee moth, *Galleria mellonella*, concern this species. *Habrobracon* is distributed throughout the world wherever its hosts, particularly the flour and meal moths, are present (Fahringer, 1928; Goidanich, 1934; Muesebeck, 1925; Watanabe, 1935). It does especially well in laboratory cultures if raised on the caterpillars (larvae) of *Ephestia kuehniella*. The original Lancaster (1) stock was derived from seven females bred from a single infested *Ephestia* caterpillar and mated to their sons in June, 1919.

Genetic research with *Habrobracon* was begun at the University of Pennsylvania in the fall of 1916 by P. W. Whiting. The first mutant type, a recessive orange eye color, appeared March 27, 1920 (P. W. Whiting, 1921c). Tests made with this first mutant indicated that three types of individuals occur regularly in the species where the parents are related. Males arise from unfertilized eggs, and are, therefore, haploid and display only maternal traits; females develop from fertilized eggs, and, therefore, may show both maternal and paternal characters. In a few cases diploid males have appeared (P. W. Whiting, 1921e). These may be recognized because they show paternal characteristics. *Habrobracon* is, therefore, typical of the order, in that it reproduces both gamically and parthenogenetically.

Habrobracon illustrates complete metamorphosis and furnishes rich material for experimentation because of the striking effect of temperature on its body color, its habit of parasit-

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ism, its parthenogenetic method of producing haploid males, the occurrence of gynanders and other genetic mosaics, its impaternal or parthenogenetically produced females, and its inheritance of easily distinguished mutant traits.



Chapter II

DESCRIPTION

Habrobracon juglandis in the adult stage is approximately three millimeters in length. Variations in size are directly related to the quantity of food available to the larvae. General body coloration varies from honey-yellow to jet black, depending largely upon the temperature during development. Females are, in general, less deeply pigmented than males in any given strain. Body colors are similar on dorsal and ventral sides of head and thorax. The distribution and quantity of integumental pigmentation are exceedingly variable, but normally produced individuals are bilaterally symmetrical. The color pattern of the praescutum, scutum, mesoscutellum, and the dorsal plate of the mesophragma is used in classifying degrees of pigmentation since it is consistently related to muscle areas and is not complicated by other factors. There is a high degree of asymmetry of pigmentation in specimens mosaic for mutant factors and for sex. As compared with females (Fig. 1), males (Fig. 2) have longer antennae. The antennae consist of a scape, and a pedicel, in the males a flagellum of 20 to 22 segments, and in the females a flagellum of 13 to 15 segments. The males have larger ocelli, smaller wings and legs, and larger compound

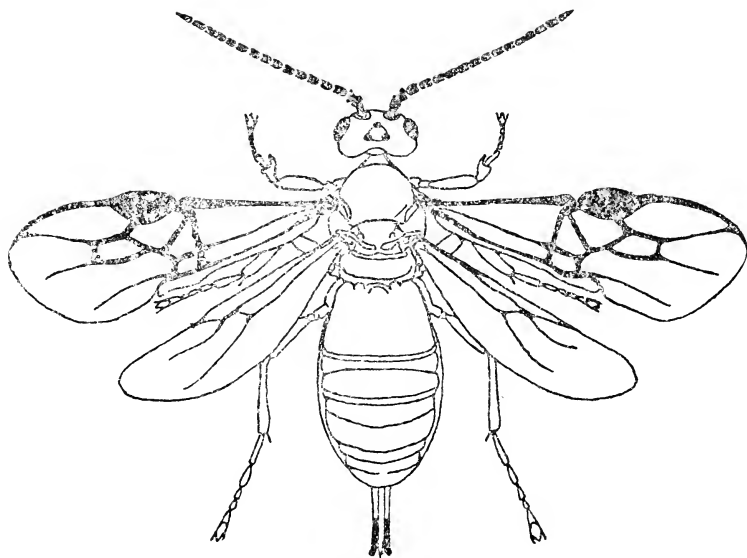


Fig. 1. Dorsal view of Habrobracon female.

X 18.

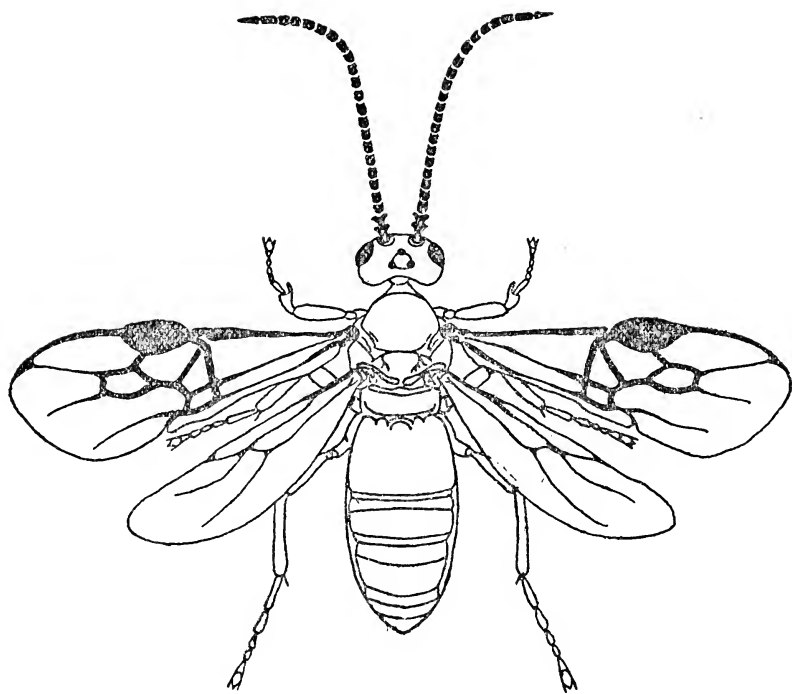


Fig. 2. Dorsal view of Habrobracon male.

X 18.

DESCRIPTION

eyes, although the facets of the ommatidia closely approach those of the females. The wing size of a normal specimen varies considerably along with differences in general body size. Measurements from tip of sclerite at base of costa to end of radius vein on the costal margin vary from 2.04 to 2.35 millimeters for female wings and from 1.89 to 2.30 for male wings. These figures make it clear that, while males have slightly smaller wings than females, variations which normally occur within each sex are such that measurements are ordinarily of no avail for sex identification. The microchaetae, however, may be used to differentiate diploid males from haploid males and diploid females, since each bristle on the wing corresponds to and gives indication of the presence of a wing surface cell which is larger in diploid males than in haploid males or diploid females (Speicher, 1935; Grosch, 1945). Males also have smaller abdomens with abdominal sternites smaller and thinner than those of females. Abdominal tergites, especially the first and second, are thinner in the males. A transverse sub-basal depression is evident especially on the fourth and fifth tergites of the males. In all types the abdomen is covered, ventrally and laterally, by a cuticle which is thin and transparent except for small sclerotized regions at the lateral ends of the abdominal sternites.

Female genitalia consist of a pair of elongate sensory gonapophyses blackened distally, a brownish sting, and a vagina anterior and ventral to the gonapophyses. The paired gonads of *Habrobracon* females each consist of two ovarioles morphologically composed of three regions:

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(1) dorsal, apical end-chamber with oögonia, followed by (2) masses of nurse cells alternating with (3) developing oöcytes each of which is surrounded by follicle cells. In mature females which have fed upon host caterpillars the lower end of each ovariole is expanded into a storage chamber (uterus) in which there are from two to five eggs with chorion and yolk fully developed and with follicle cells still present but with nurse cells gone. In females about to emerge from the cocoon the uteri are small and empty. The first maturation division is initiated before oviposition. Speicher (1936) showed that when the egg reaches the uterus, acquires a chorion, and loses its nurse cells, its nucleus increases in size, and the chromatin elements appear. They quickly shorten and with the disintegration of the nuclear membrane move to the center of the nuclear area and become arranged on a flat metaphase plate. A spindle forms at the same time. The chromosomes continue to late metaphase stage, and here maturation is stopped until after oviposition. Oviposition will not occur unless the female has fed upon the host caterpillar. Within the nuclei of the younger oöcytes the earlier processes of the meiotic prophase are going forward.

The genitalia of the male consist of an outer and an inner pair of claspers and a penis. In normal haploid males the paired, rounded, yellowish testes (about one-fourth millimeter in diameter) are fused and lie dorsally to the intestine in the posterior part of the body. Each gives off a lateral duct which passes around the intestine and unites with the acces-

DESCRIPTION

sory gland to form a common duct which connects with the penis. Internally the testes are subdivided into a number of cysts. Scattered throughout the testes of immature individuals are spermatogonial cells many of which are in compact rosettes. Some are in larger, looser rosettes. In the gonads of late pupae maturation division figures and even some spermatids may be observed, but gonads of freshly eclosed males show the highest percentage of cells in active division and have, therefore, been studied most intensively.

Definite types of reactions characteristic of sex are found in *Habrobracon*. The females sting the host caterpillars on which they subsequently feed and lay their eggs. The males are entirely indifferent to caterpillars, but they show characteristic reactions towards female wasps, such as flipping wings, mounting, and beating with wings and antennae in the process of mating.

Chapter III

CULTURE

Habrobracon juglandis has proved to be excellent material for laboratory study and research investigations because of the ease with which it can be handled, the low cost of feeding the stocks, and its brief ten-day generation period. These factors together with its fecundity make possible the accumulation of large numbers of progeny in a short time.

Habrobracon is cultured in shell vials, twenty millimeters by seventy millimeters, plugged with cotton covered with fine mesh cheese-cloth through which neither caterpillars nor wasps will burrow. When the wasps are cultured in this manner it is possible to observe the mating procedure and the complete life cycle. After mating, the female is given one caterpillar of the host, *Ephestia kuehniella*, and incubated at 30° C. After stinging the caterpillar the female sucks juice from the puncture but deposits no eggs until her victim has become torpid. Young females are given only one caterpillar at first because they do not always sting immediately, and the caterpillars, if not stung, start to spin webs upon exposure to incubator temperatures. The caterpillars may in this way escape being stung by the wasp, or the wasp may become trapped in the web and be killed by the

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caterpillar. After a wasp has once stung caterpillars and oviposited, she usually stings as soon as she is confronted with fresh caterpillars, and as many as five can be given at once. Female wasps feed on the juice which is essential to reproduction. This is borne out by the fact that females will not lay eggs until they have fed upon a stung caterpillar, although they may be kept alive for weeks on diluted honey. On the other hand, *Habrobracon* males subsist on a diluted honey diet entirely and will not feed on caterpillar juice even when it is available. Both the males and the females may be kept alive in shell vials for extended periods by feeding on a mixture of honey and water. It is convenient to keep the honey and water in separate small containers, for if the two are mixed, fermentation occurs. A metal rod such as a dissecting needle or a dental probe is dipped into the honey, then into the water and touched to the inside of the vial where the drop will adhere. At ordinary room temperature it is necessary to feed the wasps every other day, but if it is desired to keep any individuals isolated for an extended period it is better to feed them once and set them in the ice chest at approximately 10° C.

Following the stinging of the caterpillar, the female, if mated, deposits both fertilized and unfertilized eggs on top of or on the under side of the caterpillar; if a virgin, only unfertilized eggs will be laid. These eggs may be easily observed. If it is desired to study the ovipositing wasps or to count their eggs the paralyzed caterpillars are placed upon a piece of glass which is set about three-fourths

of an inch above a mirror. Then by focusing either upon the insect directly or upon the image, upper or lower sides may be observed. There is no danger of contamination from the food even if wasps have infested the caterpillar culture for eggs are never laid except upon torpid and flaccid hosts. Such should, of course, be discarded in selecting caterpillars for the culture vials.

An occasional female lays many sterile ova. Data on eggs of such exceptional females are not included in general summaries. There is likewise a tendency on the part of many females to lay "shells," apparently filled only with fluid. This soon evaporates, and the egg becomes brittle. In one series (A. R. Whiting, 1940a) the percentage of such "shells" was 2.26 for the first ten days of life of the females and 12.06 for the second ten days. Some females produced no "shells," although all were from the same inbred line. Those "shells" are likewise omitted in computing hatchability ratios. It has been thought that the "shells" might be the result of the females stinging their eggs. It has been concluded that females sting eggs very rarely if at all, and that stung eggs can continue development after such injury. In order to determine the time of death of eggs which, for various reasons, do not hatch, the eggs may be collected at intervals and placed in the mineral oil, "Nujol," where development proceeds normally and conditions can be clearly observed.

The developmental limits for the egg have been found to be 12-38° C. at a relative humidity of 76-98 per cent (Maercks, 1933). The

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life cycle is completed in the shortest time at 33.5° C. and a relative humidity of 32-98 per cent. The optimum temperature is, however, 29-30° C. with a relative humidity of 80 per cent. The temperature optimum is considered to be the temperature at which there is 0 per cent mortality and the smallest variation in the effect of various percentages of relative humidity. The relative humidity optimum is found on the humidity scale at the point where there is the greatest range of temperature with the same mortality. The duration of development is influenced especially by temperature and only slightly by relative humidity. At the temperature optimum the mortality is not influenced by slight deviations from optimum humidity, but at non-optimal temperatures, either high or low, there is an increase in mortality the farther the temperature and humidity are removed from the optimum. The mortality at non-optimal temperatures is influenced considerably by humidity; however, the duration of development of the survivors is less affected.

At optimum or near optimum conditions, the deposited eggs hatch into larvae in two or three days. The larvae feed on the juice of the host caterpillar and grow to the size of two to five millimeters depending upon how much food is available. These maggot-like larvae upon emergence cling to the integument of their host.

About three days after setting, or when larvae are present on the caterpillars, the female should be transferred to a new vial and given fresh caterpillars. A small camel's hair brush is useful in making such transfers, as the wasps

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tend to cling to the sides of the vial and must be brushed off into the new vial. Transfer at three day intervals is continued until the female dies.

The larval stage lasts about two days, at the end of which time the larvae spin cocoons with silk from the salivary glands. The cocoon entirely surrounds the larva, but only a very thin layer of threads is laid down where it adheres to the inner surface of the vial; thus it is possible to watch the development of the pupa from this side. The caterpillars by this time are reduced to shrivelled remnants which may be removed from the vials.

In the higher hymenopterans the end of the stomach is closed during larval life. The fecal matter is, therefore, retained in the stomach until pupation and then discharged into the end of the pupal case. This discharge appears as a dark brown mass and marks the posterior end of the developing pupa.

After two days, the pupa changes externally from the worm form of the larva into approximately adult insect form. Legs and wings are not fully formed until the third day of pupal existence when pigmentation and sclerotization take place rapidly. Compound eyes are formed externally by the end of the second day, but the internal tissues are not completely developed until the third day, and facets are not apparent until the wasp is almost ready to hatch. Near the end of pupal life the thorax and antennae become deeply pigmented. The time of pupal life varies somewhat, but most wasps average about four days.

In three day pupae, the ventral side lies

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squarely under the thin attached layer of the cocoon. Antennae are folded down the ventral side, and in females they reach to about the posterior end of the thorax; in males, they extend to about the second sternite of the abdomen. The sexes may be readily separated by observing the long antennae of the males and the prominent sting and sensory gonapophyses of the females.

At eclosion both males and females are either mature sexually or almost so; consequently females are certainly virgin only if males are not present. In obtaining virgin females, pupae should be isolated, or great care should be taken to see that no mature wasps are present in the culture. These insects have the habit of crawling back into the cocoons after eclosion. For this reason it is important to see that cocoons are either empty or intact.

Since virgin females are often necessary in experimental work, methods have been devised for obtaining them in numbers and with a minimum of attention. The method that has proved most successful is also the simplest. Caterpillars are stung by females of any kind. The females are removed before any eggs are laid. Then about five stung caterpillars are spread out along one side of a shell vial, and the mated female that is to be the mother of the desired virgins is placed in the vial with them. The vial is laid on its side and kept in that position. The female then lays her eggs on the caterpillars, the larvae hatch from them and feed, and when they are ready to pupate, they crawl off the host caterpillars and spin their cocoons on the side of the vial instead of pil-

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ing up on each other as they would if the vial were kept upright. As they develop into mature wasps, they can be observed through the vial by means of a hand lens or a binocular dissecting microscope, and as the sex becomes evident, the males or any questionable pupae may be killed with a needle, thereby insuring the eclosion of virgin females only.

If it is necessary to rear all the progeny but still to retain the females as virgins, another method is effective. This consists of placing the caterpillars and wasp larvae on cellophane discs placed in petri dishes. When the larvae have pupated, the sex of the pupae may be determined by viewing them from the under side of the cellophane by means of a hand lens or a microscope. The sexes may be separated by cutting the cellophane surrounding them, and the males and females may be placed in separate vials to await eclosion.

Various non-genetic influences affect the ratio of offspring. Sperm supply in the seminal receptacles influences the female ratio. Production of females tends to be somewhat reduced in later culture vials preceding their total absence after exhaustion of sperm supply. Matings with old males result in lower female ratios than matings with young males, probably because of lowered sperm supply. In much of the earlier work, entire fraternities were summarized including the haploid males produced after depletion of sperm. Ratios thus obtained are subject to great variation. They depend in large measure on the length of life of the mothers, who may die before they have exhausted

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their supply of sperm received from the initial mating, or who live for many days afterward.

The average size of fraternities varies according to length of life of the mother and the technique of the investigator, being reduced by poor cultural conditions such as small size, scarcity, or disease of the host caterpillars, overcrowding and presence of recessive lethals or semilethals, as well as by crossing between related stocks (close-crossing). Average offspring per day or per vial may be determined for individual females or for groups of females. The average number of fertilized eggs and hence females per vial or per fraternity may be twice as high in crosses between unrelated stocks (outcrosses) as in close-crosses. The number of eggs remaining unfertilized and hence the average number of haploid males will be unaffected, except for crowding in the larger, out-cross fraternities.

To facilitate the counting of *Habrobracon* progeny, it is necessary to etherize and to examine the anaesthetized individuals under a binocular dissecting microscope at about twenty diameters magnification. Since *Habrobracon* is much more resistant to ether than is *Drosophila*, it is usually safe to allow one group of wasps to remain in the etherizing bottle while another group is being counted. For anaesthesia two wide mouthed bottles are used. A cork with cotton suspended on a wire and saturated with ether may be transferred from one bottle to the other. One group of wasps is placed in one of these wide mouthed bottles and etherized while those from the other bottle are being counted and examined. After examination the wasps may

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be returned to their shell vial, destroyed by dropping them into a jar of mineral oil, or preserved for future use.

Preserving fluid is nine parts of 95 per cent alcohol to one part of glycerine. The glycerine prevents drying out. In this medium the colors are retained, and the specimens remain opaque as is desired for observation by reflected light. A binocular dissecting microscope is best for observing preserved material. The insects, well-covered with fluid, should be placed in a Syracuse dish and are best seen against a white background. For detailed study low magnification with a compound microscope is desirable (A. R. Whiting, 1933a). A few specimens may be placed in a drop of glycerine on a slide covered with a small cover glass. Although the glycerine clears eventually, opacity will be retained long enough for careful study and drawing during a laboratory exercise. Reimmersion in alcohol will restore opacity, and the same specimens may be used several times. A pipette is useful for returning the alcohol to the vials, and the insects may be picked up with a camel's hair brush.

The rearing of *Habrobracon* as an experimental animal is dependent upon many factors, the most important of which is the culturing of its host, *Ephestia kuhniella*. These insects show a complete metamorphosis, and it is the larval stage that is utilized in rearing *Habrobracon*. The *Ephestia* larvae are about five-eighths of an inch in length when full grown. Success in rearing the moths is attained with rolled wheat (Pettijohn's Breakfast Food) or untreated yellow corn meal. These cereals appear to furnish

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the optimum stimulation for oviposition, and the larvae feed well upon them and grow large and fat if ample floor space is provided in breeding boxes. The moths scatter their eggs over the cereal and these hatch in approximately a week, the time varying according to the temperature. The young larvae spin webs attaching particles of cereal together. After two or three weeks, an inspection should reveal webbiness of the cereal, denoting successful pairing and fertility. If temperature is high the larvae will attain full size in four weeks from time of isolating the parental moths. A warm temperature 27-30° C. gives best results, but humidity must be fairly high, 80-90 per cent, or the young larvae will not develop. Pupae are formed in silken cocoons. The entire period from egg to eclosion may be reduced to five weeks, but usually six weeks are required for a generation in summer weather. Eclosion begins at the end of this time, and moths will continue to emerge for three or four weeks or longer.

Moths rest on the cover, sides of box, or on the cereal, and may be conveniently collected in a shell vial. A vial is placed over each one, and at the same time the culture box or cover is tipped in such a way that the insect will fall down into the vial when touched by it. If many moths have emerged and are inconveniently active, the box may be cooled slightly to quiet them. Several individuals, approximately twenty, are collected in the vial which is then inverted into new culture medium. The development of *Ephestia* larvae may be arrested for prolonged use by placing the culture in a cold place.

Chapter IV

GENE MUTATIONS

Habrobracon juglandis has proved to be excellent material for the study of gene mutations which produce visible effects, since the haploid nature of the males prevents recessives from being carried over more than one generation before the mutant individuals appear. Most mutations occurring in the germ tract of a normal wild-type female will appear in her mutant sons if her eggs are not fertilized. Should her mutant eggs be fertilized, her daughters that develop from these eggs will produce sons, fifty per cent of which will show the new trait. Recessive mutations occurring in the germ tract of a normal wild-type male will become evident in certain of his grandsons; that is, in half the sons of those daughters which developed from eggs fertilized by sperm bearing the mutant gene. Of course, this ratio may be disturbed by the lowered viability of the mutant. Several mutations have occurred spontaneously in wild-type stocks. These have involved eye color, shape, and size; body color, shape, and size; wing pattern, shape, size, venation, and position; antennal length, structure, and position; leg length and structure; foot structure; varying degrees of lethality; and sex. Muta-

GENE MUTATIONS

tions have also been induced through X-radiation and temperature variation.

Variations in eye color were among the first mutations to be observed. A quadruple allelic series of factors affecting eye color was reported (A. R. Whiting and Burton, 1926).

ORANGE, o (eyes). The normal wild-type, jet black eyes and dark brown ocelli, mutated to orange, in which the ocelli have but a slight trace of pigment while the eyes are orange varying to pink and red. The first appearance of orange (P. W. Whiting, 1921c) was in a single male found March 27, 1920. Crosses between orange and wild-type gave the first definite genetic check on the supposition that males, being haploid and from unfertilized eggs, inherit only from the mother. They also gave the first indication that related parents occasionally produce a few sons from fertilized eggs which are diploid and like their sisters in appearance.

IVORY, oi (eyes). On June 24, 1924, there appeared in a fraternity of orange stock, four ivory-eyed males. Ivory has colorless ocelli and compound eyes of a greenish white with occasionally a trace of pink. This mutation has proved to be recessive to both wild-type and to orange, forming the third in an allelic series.

LIGHT-OCELLI, ol (eyes). In January, 1925, there appeared from a cross of ivory female by wild-type male a single female with light ocelli but with the compound eyes black as in wild-type. This mutant proved to be an allele of

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ivory, and hence the mutation took place in spermatogenesis involving at least one sperm. Light-ocelli has black eyes but ocelli are very light in compound with ivory or with orange. In pure light stock the ocelli may be characterized as light brown, somewhat darker in the males. It was found to be recessive to type and, as regards compound eyes, dominant to orange and to ivory. In combination with orange or ivory the ocelli were lighter than in the homozygous condition. Light-ocelli was lost before the appearance of a fifth allele, dahlia, and, therefore, was never tested with that or with any eye colors found later.

DAHLIA, o^d (eyes). The fifth allele in the orange locus appeared December 1, 1929, from a cross of an ivory female by a wild-type male. A single female with light ocelli and eyes very dark reddish-brown appeared. This mutant, called dahlia, proved to be dominant to orange and to ivory although somewhat lightened in combination with either. In view of decreasing dominance associated with decreasing pigmentation in this series, it is probable that light-ocelli would have come between wild-type and dahlia, could it have been tested.

The locus, orange, appears to be especially unstable, but there is certainly no striking increase of mutability correlated with X-ray treatment (P. W. Whiting, 1932a). P. W. Whiting (1928b) reported a very high correlation between mosaicism and apparent mutation for this locus. The orange series is female fertile with good viability of both males and females. These stocks, except for light-ocelli, are be-

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ing carried in the homozygous state in the laboratory for genetic studies.

CANTALOUP, c (eyes). The first eye mutation not in the orange locus was cantaloup, recessive to wild-type. A female from orange stock was treated by P. W. Whiting in March, 1928, with X-rays (dosage about 1100 R units). One male with eyes resembling ivory was produced, and subsequent tests proved it to be a new mutation. At the time of emergence cantaloup eyes appear white with a slight greenish tinge. They quickly change to a light pink and frequently darken so as to resemble orange or carrot, which will be described later. After death they usually become black, differing in this respect from orange and carrot, which show no corresponding change in color. Ocelli are colorless. No other allele has been found at this locus. In a mixed culture it may be confused with ivory or with orange. Both males and females are fertile, and this type may be kept in a homozygous condition.

MAROON, ma (eyes). Another locus has become marked by maroon, a form resembling dahlia. This mutant was found in January, 1931. Maroon has light ocelli with the compound eyes a very dark red, so dark that it is often necessary to use the light ocelli as an aid in separating it from wild-type. This stock is male and female fertile and can be kept homozygous.

WHITE, wh (eyes). Another allelic series involves white and carrot. White first appeared in June, 1931, and resembles ivory in color

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with colorless ocelli. White is of normal viability and fertility. In combination with shot-veins, to be described later, white consistently shows small red flecks scattered in the posterior and ventral part of the eyes. White shot-veins is, therefore, known as variegated (Fig. 3).

CARROT, wh³ (eyes). In March, 1932, mutant males with carrot eyes appeared. This eye color closely resembles orange. White is almost dominant to carrot. The white-carrot heterozygote has a yellowish cast by which it can be accurately separated from white. Both of these alleles are of normal viability and fertility.

SPECKLED, Sk (eyes). This factor is due to a dominant gene and results in numerous small, bright red flecks of pigment in a white eye. Preliminary work indicates that the specks are not on the cornea but lie in the soft tissue beneath. They do not appear in the pupal eye until about the third day of pupal life. Speckled varies in its expression in the two sexes and is sensitive to temperature. At 30° C., a few specks are visible in the eyes of the females, which vary among themselves in the degree of speckling. At room temperature, specks are usually lacking in female eyes. In males at 30° C., the degree of speckling is very pronounced both as to depth of coloration and number of specks. Although specks are scattered at random throughout the compound eye, there is a denser speckling in the ventral half of the eye. Males, too, vary among themselves in the intensity and the number of specks. At room

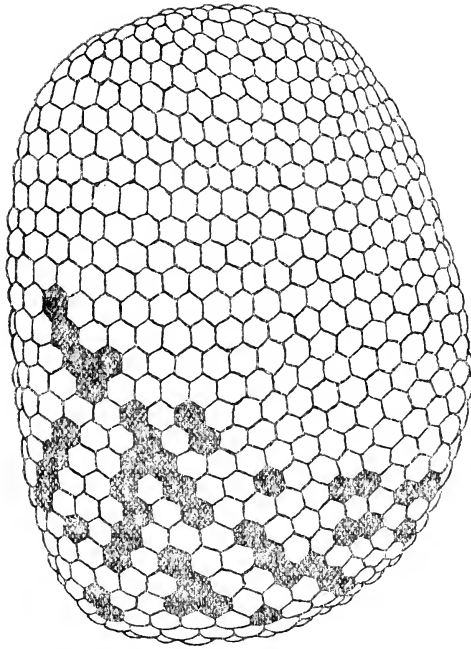


Fig. 3. Right compound eye showing effect of the mutant, shot-veins, in a white eye. The darkened areas are red in the living animal. X 160

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temperature, if the lighting is good, a few specks can usually be distinguished in males. So far, white is the only underlying eye color that will differentiate speckled. This mutant is of normal viability and fertility.

RED, rd (eyes). Red is a recessive factor for eye color which is not allelic to orange. It varies considerably in intensity, depending on the temperature, from a light red to a dark red almost black. The ocelli are a light pink and can be used as an aid for distinguishing the very dark red eyes from wild-type. This mutant is female fertile, and the males are of normal viability.

PELLUCID, pl (eyes). Pellucid is an eye mutant in which the compound eyes are semitransparent. It is female fertile, and the males are of normal viability.

PINK, pk (eyes). This is an eye mutation in which the compound eyes are pink. It appeared in the progeny of an X-rayed female in the summer of 1945. It is of normal viability and fertility. (Discarded)

TINTED, tn (eyes). This mutation can best be observed in combination with white. In this combination the compound eyes are not opaque but have a grayish cast with a semitransparent background. It is female fertile, and the males are of normal viability.

MOTTLED, mo (eyes). This is an eye mutation in which the compound eyes are not uniformly black

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but have purple splotches in the ventral portion, and the ocelli are light. It is female fertile, and the males are of normal viability.

GLASS, gl (eyes, antennae, and tarsi). In October, 1931, mutants having smaller eyes and slenderer antennae than normal were found in a fraternity from a female heterozygous for orange and maroon. Glass eyes lack facet outlines and resemble the shiny, immature eyes of developing pupae. Sections of glass eyes show incomplete tissue differentiation; hence, this mutation may result in arrested development of the eye. Ocelli apparently are not affected. Antennae are very slender and of uniform diameter. The tibial spurs of the prothoracic legs are small while those of the mesothoracic and metathoracic legs are lacking. The foot is much malformed and reduced in size with claws very small or lacking. Glass females are weak and of decreased fertility. Glass males are of good viability.

GLAZE, gz (eyes). This mutant appeared in the summer of 1934 in the offspring of an X-rayed female (dosage about 4000 R units). Glaze resembles glass, but antennae and tarsi are not affected. It is female fertile with males of normal viability.

SHINY, gz^S (eyes). Shiny is an eye mutation where the compound eyes are of the wild-type black but show a very enamel-like gloss on their surface. In various tests it has been found to be allelic to glaze. Both sexes are fertile with normal viability. (Discarded)

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TRANSPARENT, tp (eyes). This is an eye mutation in which the compound eyes have a transparent appearance. It shows up only with light eye colors. It is female fertile, and the males are of normal viability. Several recurrences of this mutation occurred in the summer of 1945.

LIGHT-OCELLI, lo (eyes). This mutant appeared in the summer of 1934 in the offspring of an X-rayed female (dosage about 5000 R units). Here normal wild-type black compound eyes are accompanied by light ocelli. This mutant was not allelic with orange, and both sexes were found to be fertile. (Discarded)

PORT, pt (eyes). This mutant appeared in the summer of 1934 in the offspring of an X-rayed female (dosage about 4500 R units). Here compound eyes are of a dark red color with light ocelli. In this mutant the males appeared to be sterile, and it was lost immediately after appearance.

The several cases of eye-color "mimics" are of some interest. White and ivory are indistinguishable except under a high magnification, when it can be observed that white is more translucent than ivory. Both have a slight greenish tinge. Carrot is somewhat more pink than orange although very similar to it, while dahlia and maroon resemble each other with dahlia tending on the average to be lighter. Any two of these "mimics" crossed together reconstitute the dominant in the F1 females.

Multiple recessives are as light as or lighter than any single mutant type entering into their genetic constitution. In the major-

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ity of cases they lack pigment. Dahlia and maroon form a double recessive which is but slightly different from either single type. The lightening influence of one mutant on another is not necessarily correlated with intensity of its color. For example, maroon is darker than dahlia, but when combined with carrot it gives white, whereas dahlia-carrot is a somewhat lightened carrot (A. R. Whiting, 1934).

Mutations for eye size and shape have not been as numerous as have those for eye color.

KIDNEY, k (eyes). A mutation to kidney eye shape was found on August 18, 1930, and was described by P. W. Whiting (1932a). The mutant appeared in a male with compound eyes lacking with the exception of a very minute one on the right side. Ocelli were of approximately normal size. The mother had been X-rayed with a dosage of 2600 R units. When the wasps are bred at 30° C., compound eyes and ocelli are reduced in size and elongated dorso-ventrally, some of them kidney shaped. The majority of specimens are inviable, many dying in cocoons as elongate pupae often with small heads. At lower temperature, 25° C., for example, they are of excellent viability and both sexes are fertile.

W. F. Dunning (1931) obtained two mutant types, "small" and its allele "extreme small." These have proved allelic with kidney.

SMALL-EYES, k^s (eyes), and EXTREME-SMALL, k^e (eyes). These alleles are of normal viability and fertility. A study has been made of dominance in the kidney-extreme-small compound fe-

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males as affected by temperature differences (Speicher, 1932b, 1933a,b, 1934a,b). The eye size of mutant-type wasps showing this character is extremely variable, ranging from a total lack of eyes to those which, though approaching, never reach the normal size (Fig. 4). The individual facets, when present, are of normal shape and size, the variation occurring as a decrease in the total number. The sizes of right and left eyes vary somewhat independently of each other. The ocelli are likewise affected and are also extremely variable, ranging from none at all to those apparently normal in size. Although no actual measurements have been made, it has been noted that the ocelli of any one individual tend to be of the same size. Aside from the modification of compound and simple eyes no other external effect is manifest. (Discarded)

SMALL, sm (eyes). This mutant appeared in the summer of 1934 in the offspring of an X-rayed female (dosage about 4500 R units). This mutant, in which the compound eyes are much reduced in size, closely resembles small-eyes. It was discarded soon after its appearance.

EYELESS, el (eyes). W. F. Dunning (1931) reported a mutation which she called eyeless, a recessive mutant type in which the heads are much malformed when the wasps are bred at 30° C. with large lobes on either side. At lower temperatures these lobes fail to appear. Rudiments of compound eyes may be present, and the wings tend to be somewhat wrinkled. Both sexes are fertile, but females are somewhat weak.

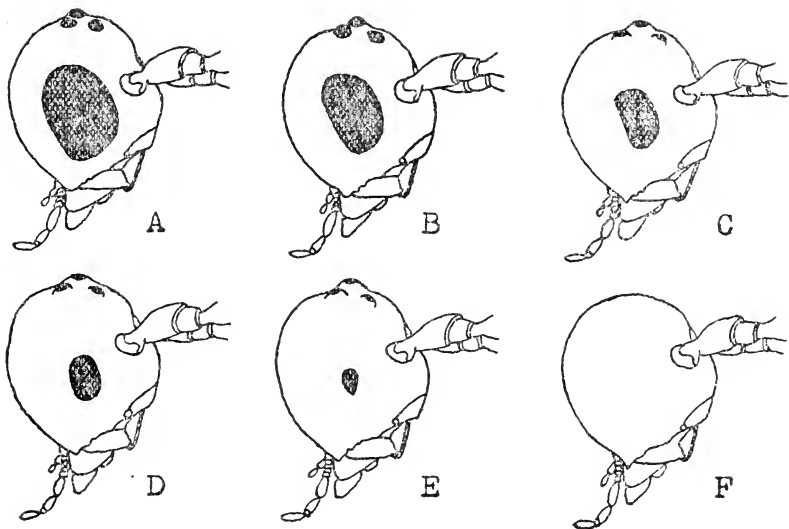


Fig. 4. Eyes of wild-type (A) and mutant type (B - F) wasps. From a study of the kidney-extreme-small alleles. B. R. Speicher, 1932b.

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Viability of males is about fifty per cent that of their wild-type sibs. (Discarded)

BAR-EYES, be (eyes). W. F. Dunning (1931) reported on another eye mutation, which she called bar-eyes, a recessive mutant type. Males are fertile, but 121 tested females proved sterile. (Discarded)

CRESCENT, cr (eyes). In August, 1931, an eye mutation affecting both ocelli and compound eyes appeared in a fraternity of 35 males. The compound eyes are slightly smaller than normal, and the ocelli are crescent-shaped. Crescent is of normal viability and fertility in the male, but fertility seems slightly reduced in females.

PEBBLED, pb (eyes). In March, 1932, five males of a fraternity had a new eye character, pebbled, with facets irregularly arranged and eyes somewhat smaller than normal. Pebbled males are rather small and they mate with difficulty. The females are weak or sterile. Viability of males is normal. (Discarded)

BULGE, bu (eyes). In this mutant type the compound eyes are abnormally bulged transversely. Both sexes are fully fertile with normal viability.

Mutations for body color have not been as numerous as have those for eye color. The wild-type individuals vary in color from honey-yellow to almost black, depending upon the temperature at which they are reared; the higher the temperature, the lighter the color. During

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the time in which *Habrobracon* has been reared in the laboratory, six mutations in body color have come to light. Three of these mutants, black, honey, and lemon, are fully fertile and can be kept as homozygous stocks with each color separate or in any desired combination. The remaining three mutants, cheese, silver, and sooty, have been discarded. Breeding tests have shown that the genes for the first three mutant body colors are linked and are, therefore, on the same chromosome.

BLACK, *bl* (body). The recessive mutant black was found among descendants of X-rayed material. Later a recurrence of the same gene appeared among the progeny of another X-rayed mated female (A. R. Whiting, 1939b). The factor blackens the animal to an extreme degree, even at higher temperatures. The black pattern is similar to that of wild-type reared at 21-22° C., but yellow areas are considerably lighter, almost cream in fact. The stematicum remains very black while the praescutum differs from that of wild-type at a lower temperature in the shadowy continuation of the median patch to the posterior edge. Dissection shows this pattern to be entirely within the cuticle. Legs are completely black and wings and antennae darkened. The whole animal presents a glistening jet-like appearance which becomes even more striking at 19° C. Dissection reveals in the praescutum a ghost pattern corresponding to the light areas of higher temperatures, but no trace of the light spots characteristic of the mesoscutellum. Mandibular teeth are black. No difficulties are encountered in

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separating black from wild-type whatever the conditions of rearing, for the final check is always extent and intensity of yellow regions on head and legs. They remain more extensive and a deeper yellow in wild-type.

HONEY, ho (body). In 1932 a type female produced eight daughters and six sons. One of these males lacked black pigment entirely. This trait was found to be hereditary and recessive, and it was called honey. Black pigment is everywhere absent, even in animals reared at low temperatures. A praescutal pattern similar to wild-type may be observed, but this is represented in darker yellow or red instead of black. This pattern is in the cuticle and not in the structures beneath it. At 30° C., honey has the same color as wild-type raised at a temperature high enough to prevent the formation of black in the body. This trait is associated with good viability, but females are of reduced fertility.

LEMON, le (body). In September, 1933, one male with lemon body color appeared in a fraternity of 124 males bred from a virgin female (P. W. Whitings, 1934b). A wild-type female had been crossed with a gynoid (to be described later) male which had been X-rayed (dosage about 3500 R units). The trait is very striking, the ground color being pale lemon-yellow, rather than honey-yellow as in wild-type and honey. The black pigmentation of the feet, female gonapophyses, and wings appears perfectly normal while the antennae are black except for the two basal segments which are lemon-yellow.

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Lemon thus shows a striking contrast to honey, and is partially dominant to wild-type. Pale basal segments and characteristic lemon praescutal pattern are dominant whereas general body color of the heterozygote resembles wild-type. There are present on the praescutum two distinct anterior bands sharply divided by a light line, and below these, irregular spots, often asymmetrical. Study of the cuticle of the lemon thorax by means of sections and removal from tissue underneath shows that the black pattern is in the cuticle itself. The spotted effect results from internal structures showing through the transparent portions which correspond to the yellow regions in the wild-type and other mutant forms. The two praescutal bands, characteristic of lemon, outline more accurately the muscle masses beneath than does the solid patch of non-lemon forms, for dissection reveals a definite longitudinal division in the muscle masses of this region in all color types. This dividing line in the praescutal pattern is mentioned by Schlottko (1926) as appearing in some wild-type individuals at high temperature, and it sometimes shows in honey as a darker line in the center of the median praescutal patch. In lemon, however, it is consistently present and more extreme. Lower temperatures change the black pigment of the lemon mutant less strikingly than that of wild-type or black. The black areas never become as intense or widespread, but in spite of this there is a striking lightening of yellow. The females of this mutant are fully fertile, and the males are of normal viability (A. R. Whiting, 1939b).

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CHEESE, ch (body). This mutant appeared in the summer of 1934 in the offspring of an X-rayed female (dosage about 4500 R units) (P. W. Whiting, 1935b). Cheese is a pale, opaque, greenish-yellow, and the color is especially noticeable in the head. It was discarded soon after its occurrence.

SILVER, si (body). This mutant appeared in the summer of 1934 in the offspring of an X-rayed female (dosage about 4500 R units). In this mutant type pigmentation is apparently arrested since the body fails to darken. This mutant has been discarded.

Variation in general body pigmentation is controlled largely by temperature, but influence of hereditary factors is also obvious. When reared at 30° C., the wasps show differences in color of the mesosternum.

SOOTY, s (mesosternum). A factor for sooty mesosternum was shown (P. W. Whiting, 1926a) to be linked with defective (see wing mutations). This mutant has been discarded.

A few mutations affecting body size and shape have occurred.

MINIATURE, m (body). One mutation for body size occurred in March, 1928. Six sons from a female mated to an X-rayed male (dosage about 2950 R units) appeared with body size much reduced. The primary wing is less rounded on the costal margin. The antennae are shortened, both by shortening of the segments and by reduction of their number. There is also some irregularity in the way the segments are set

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together. No marked disproportion appears in the reduction of the size of the legs. Miniature is a semilethal. Many die as pupae. Adult males are of good fertility, but adult females are almost sterile. (Discarded)

BROAD, br (thorax). In August, 1930, a number of males were found with thorax abnormally broadened. There is some tendency toward reduplication in the wings. The mutant type was first noticed in about 50 per cent of the sons of two different sisters. The character is somewhat irregular, and it cannot be stated with certainty that this represents the first appearance of the mutation (P. W. Whiting, 1932a). Broad may be called an irregular recessive, but about 50 per cent of the heterozygous females show the trait to a slight extent. Broad has good fertility and viability. (Discarded)

SMALL-HEAD, sh (head). This appeared in the progeny of a mated female that had been X-rayed (P. W. Whiting, 1929b). Wasps exhibiting this mutation have very small heads. The mutant type is much more distinct in the homozygous females and shows considerable overlapping in the males. It is of good fertility and viability. (Discarded)

EXTENDED-HEAD, Eh (prothorax). In July, 1931, an X-rayed mated wild-type female (dosage about 3840 R units) produced in her progeny one male with an extended head, which proved to be a dominant mutation (N. C. Bostian, 1931). In this mutant type, the membrane dorsal to the

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prosternum is much expanded so that the head is thrust forward. When dead and dried, the mutant type cannot be distinguished from normal. Heterozygous females have fertility somewhat reduced. Extended-head males have their viability reduced somewhat less than fifty per cent as compared with their wild-type sibs. (Discarded)

By far the most numerous mutations in *Habrobracon*, are those affecting the wings. Shape, size, position, and venation may be affected singly or in combination. The normal wild-type wing is fairly regular in outline with a few definite veins (Fig. 5). The wing mutations, like all others, have been named from the effect most obvious to the discoverer.

DEFECTIVE, d (veins). Defective is one of the most common of the wing variations occurring in nature. This mutation involves a break in the fourth branch of the radius vein (R4). Multiple genetic factors are involved, and temperature influences the trait, the greater defect being correlated with higher temperature (P. W. Whiting, 1932a). A single gene occurring early in breeding experiments, possibly derived from wild-type stock (P. W. Whiting, 1924b), was isolated and found to give about 95 per cent phenotypically defective under standard conditions, 30° C. Defective is of normal viability and fertility. (Discarded)

WRINKLED, w (wings). Wrinkled occurred in a female, and is the result of a mutant factor causing difficulty in shedding pupal integument (P. W. Whiting, 1926b). As a consequence ir-

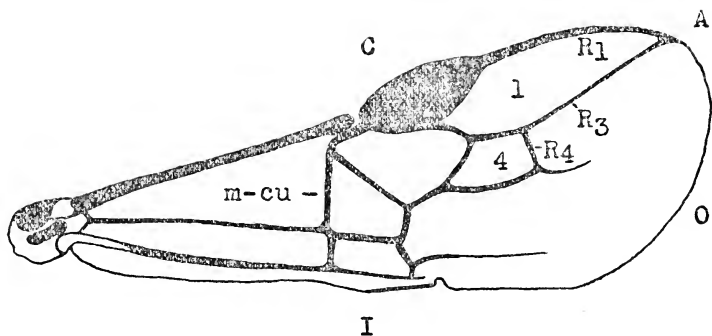


Fig. 5. Right primary wing. C. Costal margin. O. Outer margin. I. Inner margin. A. Apex. R₁, R₃, R₄. First, third and fourth branches of radius vein. m-cu. Medio-cubital cross-vein. 1, 4. First and fourth radial cells. P. W. Whiting, 1932c.

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regular wrinkling of the wings results, and portions of the integument are found adhering to the antennae which show a tendency to fragment. Wrinkled is fertile in both sexes but is mechanically hampered in eclosion and in other activities. (Discarded).

REDUCED, r (wing size). This mutation occurred in March, 1925 (P. W. Whiting, 1926b) in a single male which had small wings and irregular reduced venation (Fig. 7). The trait is variable but always distinct from type. Reduced affects chiefly the middle area of the wings and usually causes disappearance of vein m-cu. It is of good viability and fertility in both sexes.

SHORT, sh (wings). This mutation was first observed in cultures derived from some of the sibs of the miniature mutants (P. W. Whiting, 1932a). It is uncertain whether short occurred as a mutation at approximately the time of the mutation to miniature or whether it had been carried in the stock. Short is very susceptible to temperature, overlapping with normal to a considerable extent. It is impossible to distinguish a culture of short from type when reared at room temperature. Under standard conditions, 30° C., wings of short average much smaller, but even in this case there is more or less overlapping. Females are fully fertile, and males are of normal viability. (Discarded)

NARROW, n (wings). Narrow was first observed in April, 1930. Fourteen males appeared from a cross between a type female and a type male

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that had been X-rayed (dosage about 2100 R units). Narrow cuts off irregular slices of both wings on costal and inner margins. It is somewhat variable but does not overlap with type. It is of good viability and fertility in the male, but females are apparently sterile. (Discarded)

WAVY, wa (wings). Wavy appeared in June, 1930, from a wild-type female that had been mated to an X-rayed wild-type male (dosage about 2740 R units). Wings of wavy are shortened, showing transverse waves which are especially noticeable near the distal part of the costal margin. Antennae are usually normal, but in many cases one or both become markedly depigmented distally, the segments tending to drop off. Fertility and viability of males are good, but females are somewhat weak.

VESTIGIAL, v (wings). Vestigial is a wing mutation found in August, 1930. A virgin mother produced a number of vestigial winged males. Vestigial is semilethal, many wasps dying before eclosion. Fertility in the males that eclose is good, and many of them live a normal length of time. (Discarded)

SPREAD, sp (wings). This mutation appeared in May, 1930, from a male fraternity of orange stock. Eight males with wings spread out to the sides were observed. Further examination showed that these males had light areas on the mesopleura in the position of insertion of the directive wing muscles. The wings themselves are normal, and the defect is probably muscu-

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lar. The trait grades into type. It was impossible to obtain offspring from female spread. Males are of normal fertility. (Discarded)

NOTCH, No (wings). Notch is a mutation affecting the outline of the wing. It appeared in April, 1930, in the progeny of a type female by a tapering male (see antennal mutations). Notch exerts its effect on the margin of either primary or secondary wings; the notches may be terminal or lateral. The first branch of the radius vein is shortened, causing the usual rounded lobe of the wing to be notched; however, there is much irregularity and asymmetry in the expression of this factor. Notch does not breed true, and it is very likely that there are more factors than one involved. In many cases the trait acts like a dominant lethal. (Discarded)

SHOT-VEINS, sv (veins). Shot-veins is a semi-dominant factor that arose simultaneously in three different lines after extreme heat treatment of larvae. It causes veins of the wings to be broken and distorted (Fig. 7). This mutant was found in August, 1930. Shot-vein stock has proved to be fully fertile and stable. In connection with studies of linkage made in 1931, shot-veins was crossed to white eyes, and the F₁ females bred as virgins. The double recessive, shot-veins and white eyes, showed a mottling of red spots in the posterior ventral region of the compound eye. It has since been observed from very large numbers that these spots are present in both eyes of all white-eyed individuals with shot-veins. Their dis-

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tribution and intensity show some variation, but they can never be seen from the dorsal view. A homozygous, white shot-veins stock was derived and called variegated. This variegated stock has been found to breed true and to be of normal viability and fertility (A. R. Whiting, 1933f, 1934).

BENT-WINGS, bw (wings). In June, 1932, a virgin female produced a fraternity of eighteen males, five of which had bent-wings. In this mutation the wings are quite narrow and are bent anteriorly along the costal margin. The females are apparently unable to sting active caterpillars. However, when placed with paralyzed caterpillars a few may sting, feed, and lay eggs, but the eggs fail to hatch. The males are of normal viability. (Discarded)

GABLED, gb (wings). In March, 1932, an orange defective female (which had been mated with an X-rayed male) produced wild-type females. Seven of the azygous males obtained from them had wings which sloped when folded like gables of a roof. The mutant type is thus easily recognized in the vials. The wings have venation more reduced than in any other mutant type except veinless. The factor causes very poor viability; gabled males are less than ten per cent as frequent as their normal wild-type sibs from heterozygous mothers. Gabled females have not been produced (P. W. Whiting, 1934b). (Discarded)

FLARE, fl (wings). In February, 1932, a wild-type virgin female produced eleven males two of

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which had wings in which the costal margin flared forward distally. Flare overlaps with wild-type so that classification is uncertain. Flare females produce among their offspring some which are phenotypically normal. Both sexes are fertile and of normal viability. (Discarded)

INDENTED, in (wings). In December, 1931, an orange defective female, X-rayed (dosage about 1500 R units) as a five-day larva, was subsequently mated to a wild-type male. An F1 female produced eighteen males of which five had the primary wings somewhat indented toward the tip. Indented frequently shows irregular thinning of the radius veins beyond the stigma in primaries and irregular narrowing of the secondaries. Viability is normal and females are fertile. (Discarded)

CUT, ct (wings). In February, 1931, six azygous males with cut wings appeared in a fraternity. The outer margin of the wing is greatly indented or straightened giving a cut appearance (Fig. 6). The trait is very variable but may be readily recognized. Viability and fertility are normal.

STRAP, sr (wings). In January, 1932, three males with strap wings appeared in wild-type stock. The first and third radius veins are greatly shortened and the outer margin of the wing is, therefore, given a lobed appearance. The trait is very pronounced and of equal viability with wild-type. (Discarded)

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CONFLUENT, cf (wings). This is a mutation affecting wing veins and antennal segments. It was found on August 2, 1930, in a male with shortened wings showing fusion between first and third branches of radius veins at their extremities. There is more or less fusion and deficiency of segments distally in the antennae. Degree of abnormality in wings is correlated with that of antennae. At slightly increased temperature many confluent die in cocoons, and at lower temperature confluent overlaps with wild-type. Females are fully fertile and males are of normal viability. (Discarded)

TRUNCATE, tr (wings). This mutation was found on August 7, 1930, in the offspring of an X-rayed female (dosage about 2600 R units). One of the male progeny had primary wings much shortened distally tending to cause coalescence of the first and third radius veins. Truncate is very irregular in appearance, apparently having a considerable overlap into type. Terminal antennal segments are very likely to be more or less fused, and wings are often but slightly affected. The variation suggests confluent in certain respects, but in combination with reduced it is more easily recognized. Both sexes are fertile with normal viability. (Discarded)

UNEXPANDED, un (wings). This first appeared in the progeny of a type female by a wild-type male in August, 1930. Wasps with this mutant trait have primary and secondary wings unexpanded. This character was carried for several generations, but the wasps were highly invia-

GENE MUTATIONS

ble, the majority dying in cocoons. Females were obtained, but were inviable and the stock was discarded.

POINTED, p (wings). In July, 1931, N. C. Bostian (1931) X-rayed (dosage about 3200 R units) a wild-type mated female. One of the daughters produced among her progeny twelve males with pointed wings. The tips of the wings of this mutant type, both primaries and secondaries, are narrowed and wrinkled, the narrowing being especially noticeable in the radial cell. Females are sterile: they sting caterpillars, feed and lay eggs, living for several days, but the eggs fail to hatch. Pointed males appear in normal numbers from heterozygous mothers. (Discarded)

TRUNCATED, td (wings). In December, 1931, an orange defective female, X-rayed (dosage about 2000 R units) as a five-day larva, was subsequently mated to a wild-type male. An F₁ female produced among her progeny five males with truncated wings. The first radial cell in the primary wings of this mutant type is greatly reduced, the wing is narrowed slightly, and the outer margin assumes a squared appearance. The trait is variable but easily recognized and does not overlap with wild-type as does truncate, previously described (P. W. Whiting, 1932a). Truncated females are weak, failing to sting caterpillars or to oviposit. Truncated males appear in normal numbers from heterozygous mothers. (Discarded)

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SMALL-WINGS, sw (wings). In March, 1933, six males appeared showing a mutant trait, small-wings. These were among the progeny of an F1 female from a cross between a heterozygous orange female by a narrow winged male. In this mutant type venation appears perfectly normal but wing size is greatly reduced, and there is no overlapping with wild-type (Fig. 6). Small-wings is of good fertility and viability.

CREPE-WINGS, cw (wings). In April, 1932, a heterozygous female produced a fraternity of seven males including two with wings irregularly wrinkled. The outer margin of the primary and secondary wings is very irregular, and the surface of the wings resembles crepe paper. The trait is variable but easily recognized. The mutant type is somewhat over fifty per cent viable as compared with wild-type sibs. Females are of decreased fertility. (Discarded)

DROOPY, dr (wings). In March, 1933, a mutant type with wings held out and sloping downward appeared. Droopy males occur in good numbers but are likely to die in cocoons. They are less viable when reared at 23° C. than at 30° C. Droopy females try to sting the caterpillars but have produced no offspring except in one case when droopy males only appeared. (Discarded)

EXTENDED-WINGS, ew (wings). In July, 1932, five males with extended wings were found. This mutant type is easily distinguished when the wasps are active, but if they are etherized there seems to be no observable difference from wild-type. They must, therefore, be separated

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in the active condition, which makes counting tedious. The secondaries are extended laterally at an angle of 45 to 60 degrees from the midline, and they also droop somewhat. Both deviations from the normal are apparently the result of deformation at the axilla. The primaries may be held almost normally, or they may be extended laterally at an angle approaching or equal to that of the secondaries. The primaries are not held downward like the secondaries, but in the normal plane as though the axilla of the primary is normal, and their position is simply the result of a defect in the secondaries. The abdomen is slightly elevated as if for balance, especially in cases where both pairs of wings are widely spread. The females are sterile but the males seem to be of normal viability. (Discarded)

BROKEN, bk (wings). In 1934 a male with mutant wings appeared in the progeny of an X-rayed wild-type female (dosage about 4500 R units). In this mutation the outer margin of the primary wings is broken and the wings are very fragile. The veins in the primary wings often resemble those of shot-veins. Broken and shot-veins have been tested together and found to segregate independently (Fig. 7). Both sexes are fertile and of normal viability.

AEROPLANE, ae (wings and tarsi). This mutation appeared in the progeny of an X-rayed female (dosage about 3500 R units) in 1934. The wings are stiffly outstretched, and the tarsi are black and brittle. The males are unable to

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mate, and the mutant was lost immediately after appearance.

EXTENDED, ex (wings). In 1934 in the progeny of a wild-type female, X-rayed (dosage about 4000 R units), a male appeared with wings held back but failing to fold over the body. This mutant does not show when the wasps are bred at room temperature. This mutant was not tested with others and was discarded soon after its appearance. This mutation recurred in the summer of 1945 in the progeny of an X-rayed wild-type female. Both sexes are fertile and of normal viability.

PINCHED, pd (wings). In 1934 this mutant appeared in a single male among the offspring of an X-rayed wild-type female (dosage about 4000 R units). The fourth radius vein is very short so that the longitudinal veins are drawn together giving the wing a pinched appearance. Both sexes are fully fertile and of normal viability. (Discarded)

REDUPLICATED, re (wings). In 1934 there appeared among the progeny of an X-rayed wild-type female (dosage about 4500 R units) a number of males with the primary wings more or less doubled. The mutant is variable, sometimes being indistinguishable from type. The males usually have drooping antennae, but the heterozygous females have normal antennae. This mutant seems to be semi-dominant since the heterozygous females usually have wings reduplicated. The females are fully fertile and the males are of normal viability. (Discarded)

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ROUGH, ro (wings). This mutant appeared in the summer of 1934 in the progeny of a wild-type female that had been X-rayed (dosage about 3500 R units). In this mutant type the fourth radius vein is absent and the adjacent veins are roughened (Fig. 6). It is female fertile with males of normal viability.

VEINLESS, vl (wings). The veins of the wing are partially or wholly missing in this mutant, so that the major portion of the wing appears as an unbroken translucent structure. There is some variation in this mutant, but it is always distinguishable from wild-type (Fig. 7). Both sexes are fertile and of normal viability.

ELONGATE, eg (wings). In this mutant the first radial cell of the primary wings is elongated, and the outer margin of the wing is indented at the juncture of the third radius vein and the outer margin of the wing (Fig. 6). Both sexes are fully fertile and viable.

CRUMPLED, cp (wings). In this mutation the inner margin of the primary wings is not rigid and the entire wing surface is folded in a wave-like pattern giving the appearance of being crumpled (Fig. 6). The females are fully fertile, and the males are of normal viability. (Discarded)

CLIPPED, cd (wings). Here the primary wings are mere stubs with venation completely broken up. There is no wing pattern or variation in the mutant as the wing is so reduced that it completely obscures any classification of the

WING TYPES

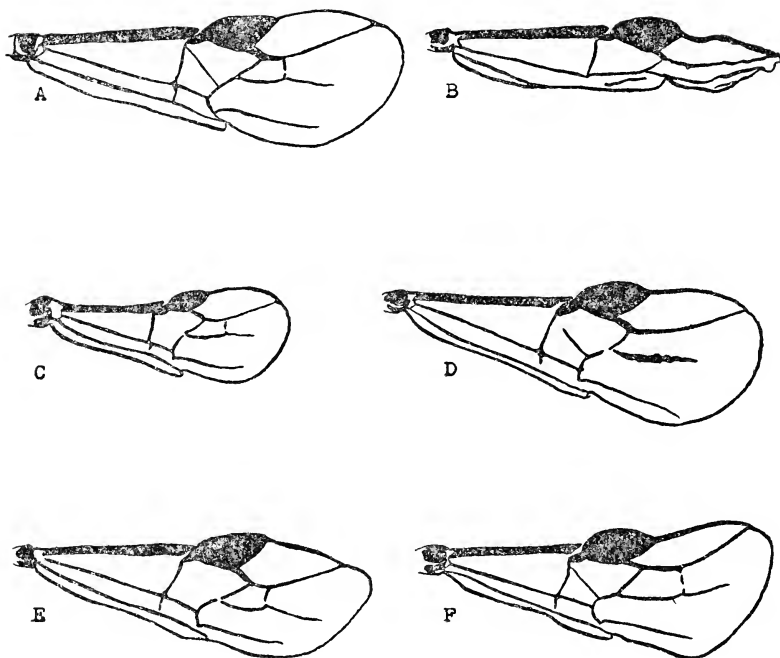


Fig. 6. Right primary wings of wild-type and certain mutants. A. Wild-type. B. Crumpled. C. Small-wings. D. Rough. E. Cut. F. Elongate.

X 22.

WING TYPES

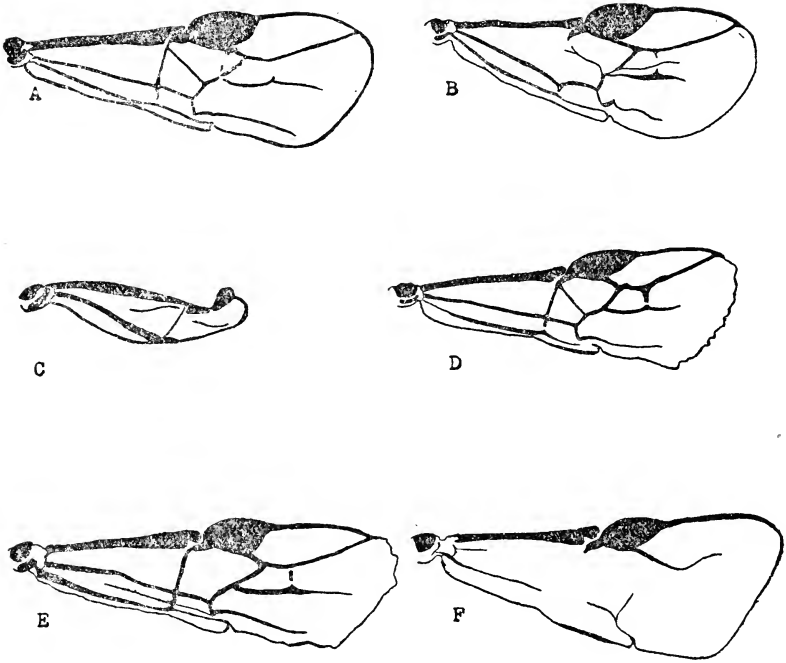


Fig. 7. Right primary wings of certain mutants. A. Shot-veins. B. Reduced. C. Clipped. D. Broken. E. Fused. F. Veinless.

X 22.

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wings. The wasps are easily distinguishable. The clipped females are sterile and the mutant must be introduced through the males which are of normal viability (Fig. 7). (Discarded)

WET, wt (wings). This mutation occurred in the summer of 1945 in the progeny of an X-rayed female. In this mutation the microchaetae of the primary wings are irregular in length, giving the wings a wet appearance. The females are fully fertile, and the males are of normal viability.

Mutations for antennal length, structure, and carriage have occurred in *Habrobracon*. These factors may be found singly or in combination. Many of the genes cited in the present work cause greater or less tendency toward antennal deficiency; however, only those that show marked deviations in antennal form are listed as antennal mutants.

DEFICIENCY, de (antennae and posterior extremity). In this mutant type the antennal segments may be irregularly fused. Failure of normal development of structures at anterior or at posterior extremities sometimes occurs. External genitalia may be small or lacking, and the digestive tract may fail to open posteriorly. No definite factors have been isolated for these deficiencies; however, they have been shown to be partially controlled by heredity and to be highly correlated with age of mothers (P. W. Whiting, 1926c). (Discarded)

MINNESOTA YELLOW, My (base of antennae). In August, 1929, wild-type stock from Minneapolis,;

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Minnesota, included wasps with three or four basal segments of antennae decidedly yellow when reared at 30° C. The difference evidently depends upon one gene with various modifiers, determining the extent of the trait which may be increased by selection. Minnesota yellow is of normal viability and may be regarded as dominant since heterozygous females show the trait under standard conditions. (Discarded)

YELLOW, Y (base of antennae). In February, 1929, two mutant males were found in the offspring of a female that had been treated with X-rays (dosage about 1460 R units) as a four day larva. The mutants had the three basal segments of the antennae strikingly yellow. The yellow color is more definitely confined to the three basal segments in this type than is the case in Minnesota yellow, but lowering of temperature during development induces melanogenesis in both cases. Since heterozygous females show the trait, it may be called dominant. Yellow is fertile in both sexes but of lower viability than wild-type. Distal segments of antennae often appear pale and if temperature is but slightly increased over standard, yellow wasps become deformed and often die in cocoons. This is not the case with Minnesota yellow in which viability is normal (P. W. Whiting, 1932a). (Discarded)

FUSED, fu (antennae and tarsi). A single male was found in February, 1929, with antennal segments fused together and with tarsal segments lacking or fused together (Fig. 8). The wing of fused (Fig. 7) has a very characteristic and

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constant indentation on the costal margin at the apex. The female cannot reproduce because of inability to feed from caterpillars. The fused males, however, are fertile to varying degrees, but they have some trouble in mating because of the defective tarsi (Fig. 9). Fused appears to be doubly effective in the duplex state since fused diploid males have antennae as short as those of the homozygous fused females; while in the haploid males with fused antennae, the antennae are approximately the same length as the antennae of normal females. Two other occurrences of fused appeared in February, 1931. These two recurrences of fused in the same month are noteworthy as no fused was being bred at the time. The two recurrences were moreover entirely independent (P. W. Whiting, 1932a).

LONG, l (antennae and wings). In June, 1929, a number of males appeared with antennal segments elongated and distal portion of wings shortened and curved ventrally (Fig. 8). Segments of the legs are somewhat longer and thinner than in wild-type. Males with the mutant long are of good viability and fertility but females are rather weak.

SEMILONG, sl (antennae and wings). A wild-type male was treated in June, 1930, with X-rays (dosage about 2280 R units) and then mated to three females. One of the daughters produced in her progeny six mutant males which have been called semilong because of their similarity to long. Semilong males are of good fertility and viability. Females are also viable and fertile

GENE MUTATIONS

but rather weak. Antennal segments are lengthened but are not as attenuated as are those of long (Fig. 8). Leg segments are also somewhat lengthened but heavier than corresponding segments of long. Distinction of semilong as of long from wild-type is clear in antennae and to a great extent in legs, but overlapping between long and semilong apparently takes place especially in legs. The wing of semilong is quite flat. Distal shortening, however, takes place as is evidenced by the form of the outer margin and especially by the abbreviation of the first radial cell. A slight indentation is present at the apex of the wing, not however, as pronounced as in fused. It was first thought that semilong might be allelic to long, but this proves not to be the case.

TAPERING, ta (antennae). In May, 1930, nine males with tapering antennae were found in a wild-type culture. The antennae are very deficient with much fusion and irregularity of segments distally (Fig. 8). Tapering does not overlap with type, but reverse mutations have occurred (P. W. Whiting, 1932a). Both sexes are fully fertile and of normal viability.

ANTENNAPEDIA, ap (antennae). In the course of genetic work involving tapering, wasps were observed with tarsal-like claws on the terminal segments of the antennae. A more or less well-formed foot may be present (P. W. Whiting, 1934b). The distal segments may be modified to resemble a tarsus with the terminal segment provided with claws, arolium, and calcanea as in the normal case. The foot may be present on

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one or both antennae and is often imperfectly developed. The trait occurs in a large but variable proportion of the individuals of a selected strain. (Discarded)

LEGLIKE, lg (antennae). In April, 1933, males with leglike antennae were found in the progeny of a heterozygous female. Leglike is a much more extreme deviation than antennapedia. The entire antenna, except for the two basal segments, has been changed so that the grooves for the sensillae are absent and yellow color similar to that of the legs has replaced the black. Fusion of several segments distal to the two basal segments and swellings on the resulting mass suggest the malformed tibiae of certain types of inviable pupae (to be described later). The foot is provided with tarsal claws, arolium, and calcanea similar to a foot from the normal position. Leglike could not be reproduced because the males would not mate, and no sisters were produced. (Discarded)

ACIFORM, ac (antennae and female genitalia). In December, 1932, two sons of a wild-type female were observed to possess antennae with segments of the terminal half much reduced in diameter (Fig. 8). The mutant type males are of normal viability. Gonapophyses of females are much shortened, and the sting is usually defective; so that the females are sterile, failing to sting and feed on active caterpillars. The antennal character is easily distinguished, since the basal nine or ten segments are normal, but the terminal segments are much

GENE MUTATIONS

narrower with more or less fusion and deletion in both sexes.

DWINDLING, dw (antennae). In July, 1931, a mated wild-type female was X-rayed (dosage about 3200 R units). Among her offspring was one male with dwindling antennae. This mutant type shows much irregularity and fusion of antennal segments in the male, but the proximal half of the antenna is not affected. Females of dwindling cannot be distinguished from wild-type phenotypically. Dwindling males are numerically equal to somewhat over two-thirds of their normal brothers. (Discarded)

ATTENUATED, at (antennae and genitalia). In May, 1932, a fraternity was bred consisting of males, fifty per cent of which had antennae with much malformation and fusion terminally. Genitalia were also abnormal, and the type could, therefore, not be perpetuated. The mutation has been reported, and the mutant type figured (P. W. Whiting, and A. R. Whiting, 1934). The antennae are similar in appearance to those of dwindling. (Discarded)

GYNOID, gy (antennae and abdominal sclerites). In April, 1932, among the offspring of a heterozygous female, a male appeared having short antennae resembling those of a female. This mutant type, gynoid, the gene for which causes haploid males to be weakly intersexual was later described by P. W. Whiting, Greb, and Speicher (1934). Gynoid males are similar to normal males in internal structure and in external genitalia. Their ocelli are large re-

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sembling those of normal males. Sclerotization of the abdomen is progressively heavier anteriorly, approximating the condition found in the female. Gynoid females are indistinguishable from wild-type. The trait acts as a recessive in heterozygous diploid males (P. W. Whiting, 1943b). This mutant is highly fertile and viable in both sexes.

SHORT, sh (antennae). In the summer of 1934, in the offspring of an X-rayed wild-type female (dosage about 4500 R units), a male was found with reduced antennal length. The mutant short resembles tapering, but the antennae are very much smaller. Both sexes are fertile and of normal viability. (Discarded)

STUBBY, sb (antennae). Males with antennae seven to nine segments long were observed in the offspring of an X-rayed wild-type female (dosage about 3500 R units). This mutant first appeared in the summer of 1934. The homozygous females for the mutant have antennae with five to seven segments. These few segments may be fused together giving the appearance of one or two large segments forming the antennae (Fig. 8). Both sexes are fertile with males of normal viability.

STUBBY-ABNORMAL, sb^a (antennae). Males with abnormally long stubby antennae were observed in a homozygous stubby stock. Breeding tests have shown that stubby and stubby-abnormal are allelic. Both males and females are fully fertile with normal viability.

ANTENNAL TYPES

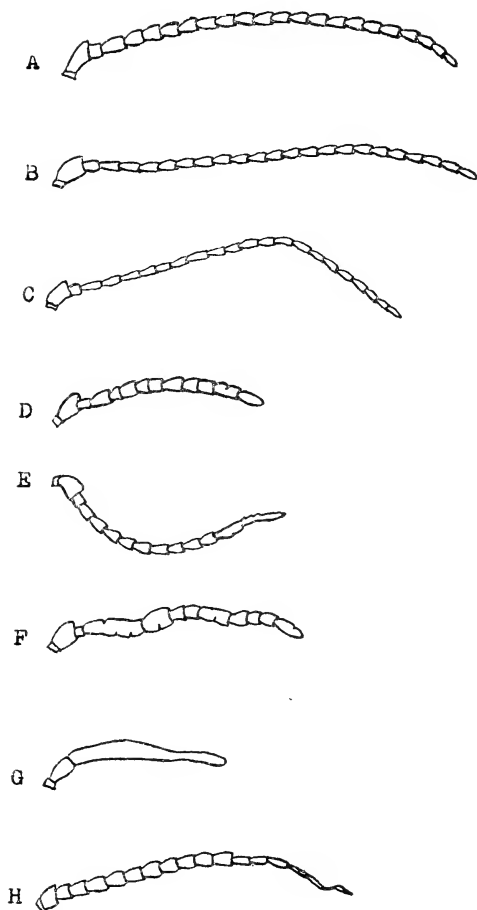


Fig. 8. Right antennae of wild-type and certain mutant type males. A. Wild-type. B. Long. C. Semilong. D. Stubby. E. Tapering. F. Coalescent. G. Fused. H. Aciform.

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COALESCENT, co (antennae). In a fraternity of wild-type stock several males were observed with antennae of approximately normal length but with the segments coalescent. The females are fully fertile with males of normal viability.

A few mutations involving leg length and structure and foot structure have occurred in *Habrobracon*. These factors, like those for eye, wing, body, and antennal mutants, may be found singly or in combination. However, leg and foot mutants seem to cause reduced viability. This may be the result of a semilethal or their inability to mate properly.

BEADED, b (legs). In August, 1929, a fraternity of males was observed containing a number of mutants with beaded legs. The proportions of the various parts of the wing of beaded are very aberrant, and wings often fail to expand. Antennae are very likely to show fusion of segments and often more or less distal deficiency. Beaded is semi-lethal. The mutant types survive much better at 23° C. than at 30° C. Even at higher temperature the majority may attain the pupal stage, but few emerge from the cocoons. Tibiae and femora are much shortened and swollen, the swelling of the tibiae being confined to the distal half (P. W. Whiting, 1934b). Males of beaded are fertile, but viable females have not been found (P. W. Whiting, 1932a). (Discarded)

STUMPY, st (legs). In September, 1930, a single male with stumpy legs was found among the offspring of an X-rayed female (dosage about 3250 R units). The most striking characteris-

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tic of stumpy is the extreme reduction of tarsal segments (Fig. 9). The appendages appear otherwise normal. Stumpy may be called a recessive, but a large proportion of heterozygous females bear a spur at the tip of their prothoracic metatarsi. More or less irregularity occurs in tarsal segments of all legs so that heterozygotes are not as sure footed as pure wild-type. No metatarsal spur has ever been found on middle or hind legs of heterozygotes nor has a prothoracic metatarsal spur ever been found in wild-type females. This spur closely resembles the spur normally occurring at the end of the prothoracic tibia. It may be present on either or both front legs, but many heterozygotes fail to show it. Even in its absence it is usually possible to identify heterozygotes by tarsal irregularity. Stumpy is of normal viability and fertility except that females have difficulty in feeding from caterpillars and consequently may die without producing eggs. Apparently they cannot brace themselves well enough to insert their stings for puncturing in order to feed.

TWISTED, tw (legs). A male of wild-type stock was X-rayed in January, 1930 (dosage about 3560 R units), and then mated to four females. In the offspring of one of these females there appeared fourteen males with twisted legs. Legs of twisted show much malformation and irregular bending. Many individuals fail to eclose, probably on account of mechanical difficulties. Males are of normal fertility, but females are almost sterile (P. W. Whiting, 1934b). (Discarded)

LEG TYPES

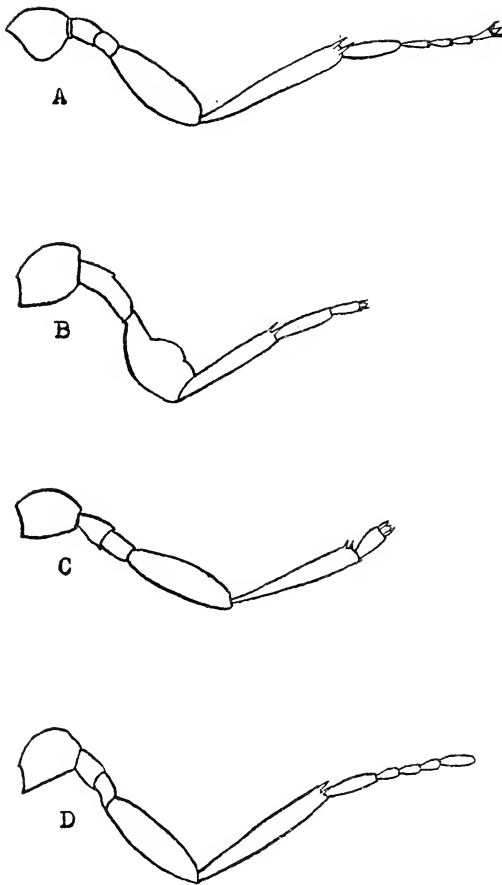


Fig. 9. Right metathoracic legs of wild-type and certain mutants. A. Wild-type. B. Fused. C. Stumpy. D. Footless.

X 26.

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CONSTRUCTED, Cs (femora). In August, 1930, a single female was observed with constricted femora. This mutant type is dominant and apparently lethal in the male. It is difficult to obtain offspring from constricted females, and fraternities are small. The difficulty is probably mechanical and concerned with feeding from the caterpillars. The trait appears in all three pairs of legs but is most obvious in the metathoracic pair (P. W. Whiting, 1932a). (Discarded)

CLUB, cl (tarsi and wings). In July, 1931, a mated wild-type female X-rayed (dosage about 3270 R units) produced among her offspring eight males with club feet. The terminal segments of the tarsi are much malformed, fused, and swollen. The wings show more or less abnormality with a tendency to form extra veins in the radial cell. Club males are about fifty per cent as frequent as their normal sibs. Females fail to oviposit even when caterpillars have been stung by another wasp. A recurrence of club appeared in the offspring of an X-rayed female (dosage about 3500 R units) in the summer of 1934 (P. W. Whiting, 1935b). The hind feet of the club males are flattened and curved down. The antennae droop terminally with deformation of three or four segments. There is a high percentage of pupal inviability, but the males proved fertile. (Discarded)

FOOTLESS, fo (feet). In March, 1933, fifty-two males appeared in the offspring of a heterozygous virgin female which were footless. This mutant type is characterized through a defect

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at the end of the fifth tarsal segment involving lack of claws (Fig. 9). Wings of footless tend to be more or less wrinkled. Footless males appear in good numbers from heterozygous mothers. The females drink honey, but cannot feed on caterpillars or lay eggs. The males mate readily but experience much difficulty in walking and are unable to climb. A recurrence of this mutant is described by P. W. Whiting (1935b). This mutation again appeared in the summer of 1945 in the progeny of an X-rayed female.

LUMPY, lp (legs). In the summer of 1934 a single male, with legs resembling beaded, appeared in the offspring of a wild-type female that had been X-rayed (dosage about 4000 R units). The mutant was discarded soon after its appearance.

WOOZY, wz (legs). A wild-type female X-rayed (dosage about 4500 R units) in the summer of 1934 produced in her offspring several males with leg segments abnormally dark. Some of the male offspring on the other hand were noticed to have leg segments practically without pigment. The wings in most cases were cupped over the body. This mutant type was found to be inviable at 30° C. and to overlap with normal wild-type at room temperature. Both sexes were fertile and of normal viability. (Discarded)

Many of the foregoing mutations, such as fused, are semi-lethal and would be lethal except for laboratory care in feeding and mating. However, a number of mutations have occurred which have their effect at a time or to such a degree that their possessor cannot eclose or

GENE MUTATIONS

live as adults. The effects of such factors are visible but completely lethal.

LETHAL NAKED PUPAE, np (pupae). A single female in a pure culture proved heterozygous for this factor. It caused metamorphosis of larvae into undersized naked pupae which attained approximately normal coloration, but died before reaching maturity. This factor (P. W. Whiting, 1921f) proved to be linked with orange (P. W. Whiting, 1932a).

INVIABLE PUPAE, ip (pupae). The following examples will serve to illustrate some of the types of pupae differing in size and bodily proportions and dying on account of lethal or semi-lethal genetic factors (P. W. Whiting, 1934b).

Records of mutant type males segregating from heterozygous mothers not infrequently show more or less numerical deficiency either of wild-type or of the mutant type. When this is statistically significant it is taken to indicate the presence of a linked lethal. Usually no record is made of inviable eggs or larvae, but in some cases dead pupae are recorded. The first case of linkage in *Habrobracon* was found (P. W. Whiting, 1921f) between orange eyes and a factor, lethal naked pupae, having a lethal effect during the pupal stage. Crossovers were 19.5 per cent and there were 142 pupae to 160 adults indicating that relatively few of the inviabilities died before pupation. No record was kept of eggs or larvae. The inviable pupae were of approximately normal proportions, perhaps slightly more slender, but they failed to

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spin cocoons and ranged in length up to 2.3 millimeters as compared with 2.9 millimeters for the normal wild-type wasp. A recurrence of this mutation occurred in the summer of 1934 (P. W. Whiting, 1935b) in the offspring of a mated wild-type X-rayed female (dosage about 4000 R units).

LETHAL, L (pupae). A locus of three allelic factors for lethal effects, wild-type, La, and Lb has been determined by Schaeffer (1945). The lethal effect is regarded as complementary and probably lies to the right of stubby.

In September, 1943, P. W. Whiting (1943a) described a series of multiple alleles which seem to determine sex in *Habrobracon*.

SEX GENE OR CHROMOSOME SEGMENT, x (sex). Nine factors are thus far known in the series, and they are designated by the symbols, xa, xb, xc, xd, xe, xf, xg, xh, xi. The tester stocks are designated as xa/xb, xc/xd, xe/xf, xg/xh, and xa/xi. Evidence of allelism of these sex factors is furnished by the fact that they are all closely linked with the gene, fused. The multiple alleles are regarded as differential chromosome segments which have been built up in the early evolution of the Hymenoptera. They may each consist of many genes, which determine the numerous sex differences, structural, functional, and behavioristic, which characterize the Hymenoptera. These genes have the effect that all haploids or homozygous diploids are similar and male, and that heterozygous diploids or combinations of any two different alleles result in females.

Chapter V

RECORDING OF DATA

In recording genetic data in *Habrobracon juglandis*, P. W. Whiting has simplified the conventional methods. Mutants are symbolized by the first letter or certain letters of the name given the mutant; for example, gl stands for glass, r for reduced, and gz for glaze. If the mutant is recessive to its normal wild-type allele, lower case letters are used; however, in a few cases, the mutant is dominant to its normal allele, and it is then written with the first letter of the symbol capitalized; for example, Y stands for yellow, and Sk for speckled. Normal or the usual wild-type alleles are symbolized by the plus (+) sign. The plus sign is used at all times to indicate the dominant allele of any recessive character, but is omitted from the male and female formulas wherever possible.

The following example will more clearly indicate the method of writing genetic formulas in *Habrobracon* studies. Let us, for example, cross a homozygous mottled female by a reduced male. The female would be indicated thus, +.mo/+.mo. She is type for reduced and therefore the + sign need not be written in the formula. She is also homozygous for mottled so it would be permissible to merely write mo for her

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genetic composition. The male would be indicated thus, $r.+$. He is type for mottled, therefore, the + sign may be omitted from his formula leaving only the r to indicate that he is both phenotypically and genotypically a mutant with reduced wings. We may, therefore, indicate this cross by the formula $mo \times r$. The F1 heterozygous females produced from this mating would be phenotypically type but carry in their genotype the recessive r and mo . Their formula would then be $+.mo/r.+$ which may be written mo/r indicating that the mo gene was received from their mother and the r gene from their father. This again eliminates the + sign and simplifies the formula. The F1 males produced would, of course, all be mo . The F1 females, if set as virgins, will produce four classes of sons in gametic ratios, +, mo , r , $mo.r$. For clarity a period is used to separate the symbols of the double mutant. Since four classes of sons are produced by the F1 virgin females we may be certain that the mutants involved are not allelic. On the other hand if only two classes appeared as in some eye color crosses it would indicate that the mutants involved were allelic, each affecting the same character.

In recording the F2 progeny of the F1 females, it is advisable to assign each female involved a number--1, 2, 3, etc., and to letter each successive vial through which they are transferred--a, b, c, etc. Thus we have 1a, 1b, 1c, etc., for the first F1 female of the original $mo \times r$ cross. The progeny of each female and for each vial through which she passes may then be tabulated as in Fig. 10. The entire progeny from each female in the experiment is

EXPERIMENT 3646

mo X r

No. 1 mo/r F₁ Virgin Set for F₂ Sons
 Progeny

Vial	+	mo	r	mo.r	Total
1a	3	2	2	0	7
1b	4	3	5	2	14
1c	5	8	6	4	23
1d	8	4	7	5	24
1e	0	3	4	2	9
1f	2	5	0	3	10
1g	5	6	3	1	15
1h	3	4	2	6	15
1i	3	0	2	5	10
Total	33	35	31	28	127

Fig. 10. Individual F₁ female chart showing F₂ male progeny produced per vial and the total F₁ female progeny.

EXPERIMENT 3646

To Test for Linkage of *mo* and *r*

mo X *r*

F_1 *mo/r* Virgins Set for F_2 Sons

Progeny

Fraternities	+	<i>mo</i>	<i>r</i>	<i>mo.r</i>	Total
3646.1	35	35	31	28	127
3646.2	39	26	32	28	125
3646.3	29	26	20	32	107
3646.4	26	29	27	33	115
3646.5	35	26	37	37	135
3646.6	42	37	47	27	153
3646.7	29	28	35	26	118
3646.8	34	24	41	31	130
	<u>267</u>	<u>231</u>	<u>270</u>	<u>242</u>	<u>1010</u>

Conclusion: *mo* and *r* segregate independently.

Fig. 11. Master sheet of F_1 females showing the total progeny in the experiment and conclusions.

RECORDING OF DATA

then tabulated on a master sheet (Fig. 11). Each female carries her own number and to it is added the number of the experiment and the year in which it was performed. Thus in the number 3646.8 the 36 represents the experiment, the 46 the year in which the experiment was performed, and the .8 the eighth F1 female set in the experiment.

This method of recording data is suggested by the writer as it offers the most convenient and accurate way of keeping track at all times of each F1 female and her progeny involved in any experiment.

Chapter VI

SEX CONDITIONS

Like other hymenopterans, *Habrobracon juglandis* is parthenogenetic in that males are produced from unfertilized eggs, so that the males possess only a single set of chromosomes. Females which normally develop only from fertilized eggs have a double set of chromosomes and are diploid. The haploid males are extremely useful in genetic studies, since their appearance indicates their exact genetic composition. The females, being diploid, may bear more factors than they show, since the effects of certain genes may mask those of others, which are recessive. In order to bring recessive alleles to light, females are set unmated on *Ephestia* caterpillars and allowed to lay eggs. The resulting sons exhibit the effects of all the genes carried by their mothers, since during egg maturation the paired chromosomes of the females separate giving dominant genes to some eggs and their recessive alleles to others. For this reason, the wasp is an especially advantageous animal for genetic studies, since in one generation only, all of the genic characters possessed by the stock are brought to light.

Occasionally females from unfertilized eggs (thelytoky) are found in fraternities which normally produce males from unfertilized eggs

SEX CONDITIONS

(arrhenotoky). These males and females from unfertilized eggs have been termed "impaternate" by Ray Lankaster (1919) to differentiate them from the parthenogenetic virgin mother. Breeding tests show that impaternate females are normal diploids. P. W. Whiting (1924a) has explained their production from unfertilized eggs by the assumption that the second maturation division of the oöcyte is suppressed. If this assumption is true and the impaternate females occur among the F₂ from a cross involving mutant characters, their genotypes, as indicated by their appearance and that of their offspring, are of interest in ascertaining whether the first division of the oöcyte from which they were formed was equational or reductional for the locus or loci involved (K. G. Speicher, 1934). If the F₁ female producing an impaternate daughter is heterozygous for a recessive factor and the first oöcyte division is reductional for the locus of that factor, the impaternate daughter will be homozygous for either the recessive or its type allele. If the first oöcyte division is equational, the impaternate daughter will be phenotypically wild-type. Breeding tests are necessary to distinguish impaternate females resulting from an equational division from those receiving the type allele from a reductional division.

Diploid males of biparental inheritance regularly occur in related stocks. These sterile (or near-sterile) males are diploid, developing like females from fertilized eggs. The haploid males have been called uniparental and azygous in contrast to the biparental zygyous males and females. The offspring of these diploid males

crossed with recessive females are triploid females showing the dominant traits of their diploid fathers. There is no evidence of intersexuality in diploid males or in triploid females unless the reduced size of ovaries and near sterility of the latter indicate this. Moreover their reproductive reactions are entirely normal, the diploid males mating readily and the triploid females stinging caterpillars and feeding and ovipositing upon them.

Unmated females produce azygous sons only. Mated females produce azygous sons from unfertilized eggs but in smaller numbers than do unmated females. They also produce zygyous biparental offspring from fertilized eggs. Whether the biparental offspring shall be daughters only or both sons and daughters depends upon the relationship of the male and female used in the mating. If the male is from a stock unrelated to the female all the biparental offspring are daughters, but if the male comes from a related stock, biparental sons as well as daughters are produced.

In general the azygous and biparental offspring from a mated female occur in the same ratio from the different vials through which the female is transferred (a, b, c, d, etc.) until her supply of sperm is exhausted. In subsequent vials (e, f, g, etc.), azygous sons only appear.

Biparental males cannot conveniently be separated from their azygous brothers unless the mother has a recessive trait and the father has the allelic dominant. Orange-eyed females crossed with wild-type (black-eyed) males produce black-eyed daughters and orange-eyed azy-

SEX CONDITIONS

gous sons. If biparental sons are produced they may be readily separated from their azygous brothers by their black eyes.

Fertilized eggs may be "female-producing" or "male-producing," the latter occurring only if parents are related. "Male-producing" fertilized eggs are less likely to hatch than "female-producing." Consequently there are more "bad eggs" and fewer biparental offspring if the mating has been with a related male, since the percentage of eggs fertilized is the same whether the male is related or unrelated. Biparental male larvae are also less likely to mature than female larvae. This further reduces offspring from related parents.

Two types of male sterility may be distinguished in *Habrobracon*. If the eggs are not fertilized, the mated female breeds like an unmated female, producing a large number of azygous sons. This occurs in the case of matings with biparental males which produce diploid sperm rarely capable of fertilizing eggs. There are also males with abortive sperm ducts or testes which may readily be mated but transmit no sperm. Recent evidence indicates that sperm may to some extent be inactivated by high dosages of X-rays, so that they are unable to penetrate the eggs.

Cytological studies indicate that there are ten chromosomes in the normal haploid male (Fig. 12) and twenty in the biparental diploid male (Fig. 12). The normal female has twenty chromosomes (Fig. 12), while the daughters of normal mothers and biparental fathers have an as yet undetermined but considerably larger number, in all probability thirty. A spermatogonial study

CHROMOSOMES OF HABROBRACON

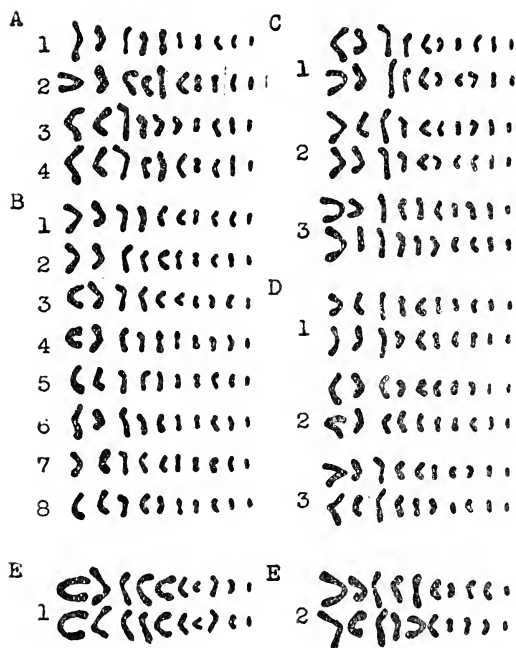


Fig. 12. Metaphase chromosome complexes. From left to right there are shown in decreasing order of magnitude: one V, one L, one J, one L, three V's, one J, one which is often rod-like but may be a V, and one rod. M. Torvik-Greb, 1935.

- A, 1-4. Spermatogonial complexes of haploid males.
- B, 1-8. Second spermatocyte complexes of haploid males.
- C, 1-3. Spermatogonial complexes of diploid males.
- D, 1-3. Second spermatocyte complexes of diploid males.
- E, 1-2. Oögonial complexes of diploid females.

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has been made in both the normal and biparental males. Following the spermatogonial divisions, both kinds of males show an abortive first maturation division--a small bit of the cytoplasm being pinched off at the narrow end of a pear-shaped cell. This division of the sperm cell in the male is comparable to the reduction or meiotic division of the egg, at which time the paired chromosomes separate, forming abortive polar bodies and one haploid egg nucleus. Eggs if unfertilized by sperm will hatch into normal haploid males. If fertilized, they will produce normal diploid females; and in abnormal cases, diploid biparental males.

It has been shown (Speicher, 1935; Risman, 1941) that diploid males have much larger cells than diploid females, while haploid males have cells approaching the diploid female size. It seems possible that large cell size might be responsible for the high diploid male mortality and that a demonstrable difference in cell size might appear between diploid males differing in mortality.

In developing *Habrobracon* it is observed that each bristle on a wing surface corresponds to and gives indication of the presence of a wing surface cell (Speicher, 1935). Since each cell of the single layer forming the upper surface of the wing bears a single bristle (microchaeta), variations in cell size produce proportional variation in dispersal of bristles. Thus, if fewer microchaetae are noted per unit area larger cells are present in the wing surface. A tendency toward larger cell size in diploid male material with higher mortality is indicated in microchaetal evidence. The tendency is

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not extreme in the adult animals studied presumably because extreme types did not survive to the adult stage. Evidence of selective action of mortality is shown by differences between frequency distribution curves of diploid males and the curves of more viable types.

In all material investigated (Grosch, 1945) diploid male cell size was significantly larger than female cell size. This is shown by the number of microchaetae per unit area of wing surface and by measurements of eye facets. To explain diploid male mortality it is suggested that doubled gene situations in the diploid male, homozygous for a sex allele, might function poorly under the surface-volume relationship of the large diploid male cell. The large size of diploid male cells may itself be the result of gene duplication. The system which raises haploid male cells to a size comparable with diploid female cells may be increased in activity when its determiners are doubled in the homozygous sex allele condition of the diploid male.

No statistically significant differences are shown in body length between diploid males and females, and observations indicate that diploid males do not exhibit gigantism. Haploid male mean body length is shown to be consistently less than that of diploid wasps, and this is taken as indication of the tendency toward dwarfism of the haploid male. Wing length corresponds to body length in all classes.

Larger eyes of the male are a secondary sex character not affected by cell size differences. This sex character is not as clear cut as antennal length. Long antennae of the male are a

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secondary sex character. In no diploid males has there been a significant shortening of antennae which would be considered a tendency toward intersexuality. Such stability of secondary sex characters is discussed on the basis of the sex allele being a differential chromosome segment. Female antennae are shorter chiefly because of fewer segments. Diploid males have a tendency toward fewer and longer antennal segments than haploid males. Fewer antennal segments in the diploid male are not regarded as the result of intersexuality but as an indirect effect of chromosome number.

Definite types of reactions characteristic of sex are found in *Habrobracon*. The females sting caterpillars on which they subsequently feed and lay their eggs. The males are entirely indifferent to caterpillars, but they show characteristic reactions towards females, such as flipping wings, mounting, and beating with wings and antennae in the process of mating.

Gynanders (sex-mosaic individuals) occasionally appear in bisexual fraternities. Gynandromorphic offspring from a recessive female by a dominant male show the maternal trait in the male (haploid) parts, the paternal trait in the female (diploid) parts. This evidence is consistent with the theory of egg binuclearity. Fertilization of one nucleus results in the female parts; development of the other without fertilization results in the male parts. Gynanders may have male heads, female abdomens, or the reverse; one side may be male, the other female; anterior left and posterior right may be of one sex, the remainder of the other sex; male islands may occur in female regions or female

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islands in male regions. When genitalia are mixed in sex, there may be a full set of male structures and a half set of female structures. Two of these cases have been published (P. W. Whiting and A. R. Whiting, 1927). Gynanders indicate that the various sexual reactions are determined by the head rather than by the reproductive organs of the animal. Those with male heads and female abdomens react towards females but are indifferent to caterpillars; while those with female heads and male abdomens pay no attention to females but respond to caterpillars. Gynanders with mixed heads act in general either like males or like females. Gynandromorphic behavior is not all as clear-cut as the head and abdomen variations described above. Some show momentary sex-reversal for one or more brief periods of time, and therefore, behave sometimes like females and sometimes like males. There is also a bisexual type of individual which attempts to sting caterpillars as well as to mate with females; and there is also a type which has been termed "wires crossed." These individuals attempt to mate with caterpillars and to sting females. All these various irregularities of behavior are thought to be caused by the mosaic character of the sensory and nervous systems rather than to any hormonal action.

Very little evidence of intersexuality has been found in *Habrobracon* so far. One mutant type, gynoid, has been found, the gene for which causes haploid males to be weakly intersexual. Gynoid females are indistinguishable from wild-type. The trait acts as a recessive in heterozygous diploid males. Gynoid males are similar to normal males in internal structure and in

SEX CONDITIONS

external genitalia. Their ocelli are large resembling those of normal males. Their normal male instincts indicate that the brain is structurally as in the male, since mating reactions in *Habrobracon* are determined by the brain. Sclerotization of the abdomen is progressively heavier anteriorly, approximating the condition found in the female. Antennae of normal males have about twenty-one segments in the flagellum, those of females usually not more than fourteen. In gynoid males the segments are reduced in number to that of the female, although they are not quite as short and thick. Superficially a gynoid male suggests a sex-mosaic or gynander with female head and male abdomen. Certain structures intergrade, the body is approximately symmetrical with all parts presumably of the same genetic constitution, and the type is perpetuated as a pure-breeding form.

Nine intersexual females have recently occurred among the offspring of a single female. Superficially these appear to be the reverse of the gynoid males, being more masculine anteriorly and more feminine posteriorly. The heads are characteristically male having large ocelli and long antennae, the segments ranging from eighteen to twenty-one with twenty as the mode. Tests made on five of the nine showed indifference to caterpillars and vigorous attempts to mate with females, indicating the brain to be structurally male. Abdominal sclerotization is male-like anteriorly. The first and second tergites are thin and the anterior sternal thickenings small. Sclerotization is progressively heavier posteriorly and sternal thickenings become elongate, approximating the condition of

the female. Like gynoid, these intersexes differ from sex mosaics in being approximately symmetrical and similar to each other. They possess intermediate sex characters and occur in a group in one fraternity as if caused by a single hereditary factor.

The existing data must be regarded as inadequate to prove whether these intersexes are the result of a modification of the normal sex-differentiating factor or whether, like gynoid, they are the result of an independent change. It is questionable whether the diverse effects of gynoid antennae and abdominal sclerotization should be regarded as multiple effects of a single gene. Gynoid may possibly be a translocation from the differential segment determining sex. In a male with the sex allele in the normal position this might give a complementary feminizing effect causing intersexuality.

Mosaics also occur which apparently possess either one sex or the other; however, these too exhibit interesting peculiarities. Genetic evidence indicates that mosaics, with but few exceptions, arise from binucleate eggs. The two nuclei are assumed to be the products of the second oöcyte division. In the case of gynanders one of the nuclei is fertilized and gives rise to the female parts while the unfertilized nucleus produces the male parts. Cell descendants of each of the two nuclei tend to be more or less segregated in different regions of the embryonic syncytium and consequently the genetically diverse regions may be roughly separated by a plane. This plane of division may apparently lie at any angle to the axis of the body and may separate proportions varying from ap-

SEX CONDITIONS

proximate equality to such decided inequality that tissues of either type may represent but a minute portion of the specimen. Furthermore, the region on either side of this plane may contain tissues of the opposite genetic constitution indicating more or less wandering of nuclei in the embryonic syncytium. Occasionally lack of segregation may be so extreme that the resulting mosaic is an irregular patchwork. Readjustments during later embryonic development may, moreover, cause intermingling of adjacent tissues differing genetically.

In certain normal wasps, there occur two non-allelic, recessive genes both of which cause the eyes to be whitened. For convenience, these genes are called white and ivory. One interesting combination of these colors occurs in the mosaic compound eye, one section of the eye being genetically white, the other genetically ivory. Such an eye might be expected to look uniformly white; however, such is not the case. The white, non-ivory region remains white and is sharply marked off from the ivory, non-white region by a black border which grades imperceptibly into the ivory (Fig. 13) (A. R. Whiting, 1933b). The double dominant character is reconstituted in the region where the two recessives are in contact even though there is no diploid tissue present there. This phenomenon is thought to be the result of the diffusion of some substance from the white region into the ivory. Another instance of the effect of one gene upon another is exhibited in the progeny of a female heterozygous for ivory and cantaloup eye colors. Such a female set as a virgin may produce, in addition to the four genotypes of sons regular-

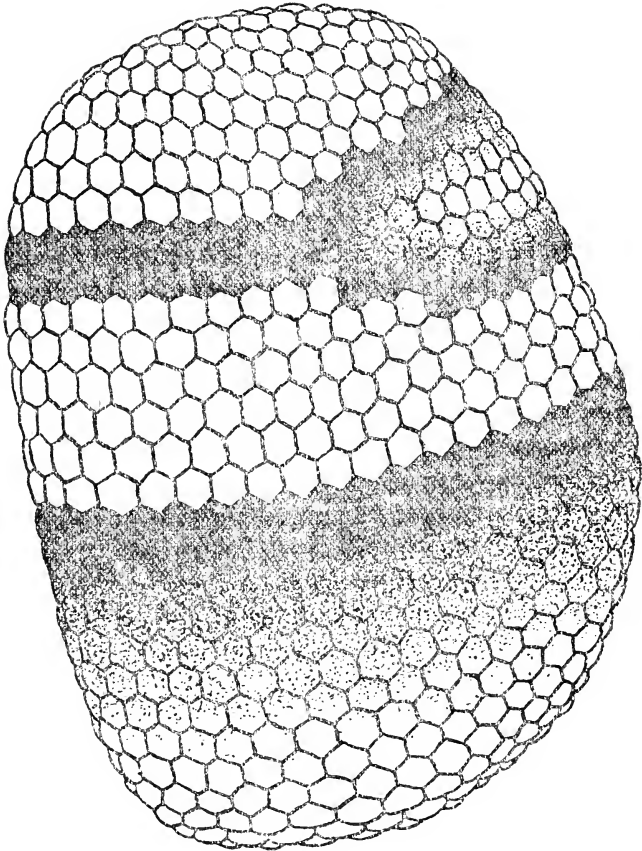


Fig. 13 . Right compound eye of male mosaic for white and ivory. The double dominant character is reconstituted in the region where the two recessives are in contact.

X 208.

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ly expected, a male with ivory, non-cantaloup and non-ivory, cantaloup regions in the same eye. In this case the genetically ivory region bordering the cantaloup changes to wild-type black, a phenotypic complementary effect the result of soaking through into the ivory region of some product dependent upon the dominant allele to ivory in the cantaloup region. Similarly, feminization occurs in the genitalia of a high proportion of haploid mosaic males, the result of a complementary effect, an interaction between sex factors, differing in the two regions, X and Y. These "gynandroid" males (P. W. Whiting, Greb, and Speicher, 1934) develop from unfertilized binucleate eggs in which the sex alleles have been segregated at maturation into the different nuclei. They are, therefore, haploid throughout. They suggest gynanders (haplodiploid male-female mosaics) which also arise from binucleate eggs, but in the formation of a gynander one of the nuclei must be fertilized to originate the female regions. Gynandroids are entirely male in appearance except for the relatively small feminized structures added to the male genitalia, usually on one side only (Fig. 14). The male genitalia may show reduplication of parts. Gynanders, on the other hand, have extensive female regions of the body, while the genitalia may be either male, female, or mixed. In the latter case there is usually a complete set of male parts but no reduplication. The female structures tend to be lateral on one side only and anterior to the male organs, with appendages of full length. Interpretation of gynandroidism as a complementary effect led to the conclusion that females are heterozygous and

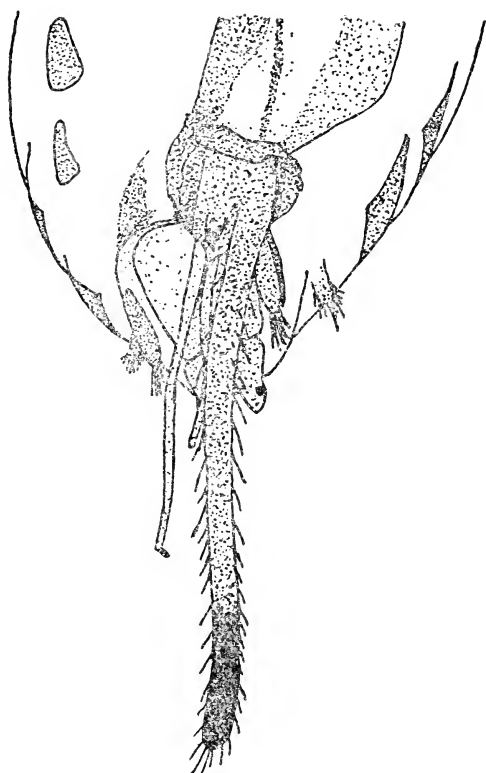


Fig. 14. Ventral view of the genitalia of a gynander, a male-female mosaic. A complete set of male genitalia is present. The left sensory gonapophysis of normal length, and two elements of the sting, are the female structures. X 120. P. W. Whiting, 1940a.

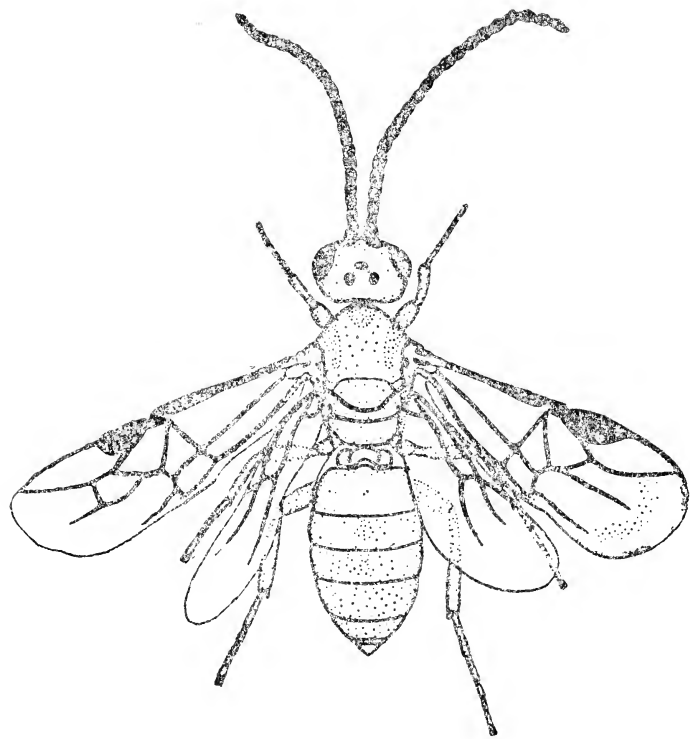


Fig. 15. Dorsal view of male, mosaic for long (antennae and wings), for narrow (wings), and for cantaloup (eyes). P. W. Whiting, 1934c.

X 20.

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that normal males are X and Y with equal frequency.

The feminized structures just mentioned do not appear on all mosaics, for in many the line of mosaicism does not pass through the genitalia. It has also been found, however, that these structures do not always occur in mosaics even when the line does bisect the body (Fig. 15). These facts have led to the supposition that in *Habrobracon* there are several kinds of males, genetically distinct for sex-determining factors but phenotypically similar. When tissues differing in sex-determining factors adjoin in a haploid mosaic male, one influences the other, and traits characteristic of diploid tissue are the result.

CHAPTER VII

SEX DETERMINATION

Genetic research with the wasp *Habrobracon juglandis* was begun at the University of Pennsylvania in 1916 by P. W. Whiting. Many phases of this work have been developed since that time but the central problem has always been that of sex determination.

In 1845 Dzierzon put forth the theory that in the honey bee, drones (males) develop from unfertilized eggs while workers and queens (females) come from fertilized eggs. This theory was based on the fact that unmated and old queens produce drone broods and that race-crossing results in drones like the maternal race while the daughters are hybrid. Dzierzon (1854) stated that the drones of the second generation from a cross resemble either the paternal or the maternal race and that those two types occur in equal numbers. He, therefore, glimpsed the fundamental gametic ratio twelve years before Mendel published his paper on peas. Dzierzon's Law applies to other insects of the order Hymenoptera, including wasps, ants, ichneumonflies, chalcis-flies, and saw-flies, but many exceptions occur. P. W. Whiting (1918) working with the ichneumonoid wasp, *Habrobracon*, found that in this form also haploid males are pro-

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duced from unfertilized eggs, and females from fertilized eggs.

Nachtsheim in 1913 had shown that somatic cells of the honey bee possess the haploid number of chromosomes in the case of the male, and the diploid number in the case of the female. Sex determination in the Hymenoptera was then assumed to rest upon the possession of one sex chromosome in the haploid male or two in the diploid female.

Bridges (1925), discussing sex determination in the bees and wasps stated that it was the outstanding unsolved puzzle, although before the genic balance theory it seemed one of the clearest and simplest of cases.

The explanation of sex determination in *Habrobracon* was further complicated when diploid males were found to occur occasionally. Tests made with the first mutant type, the recessive orange eye-color, demonstrated that three types of individuals, haploid males from unfertilized eggs and diploid males and females from fertilized eggs, occur regularly in the species when parents are related. When orange females were crossed with the wild-type black-eyed males, there appeared not only the expected black-eyed heterozygous females from fertilized eggs and orange haploid males from unfertilized eggs, but also a smaller group of "anomalous" sterile or almost sterile males which were black-eyed. Since males were then regarded as necessarily haploid, these "patroclinous" sons were thought to be either androgenetic or mosaic in origin, having arisen through failure of syngamy (P. W. Whiting, 1921a).

This view persisted until 1925 when it was

SEX DETERMINATION

shown (P. W. Whiting and A. R. Whiting, 1925; A. R. Whiting, 1926, 1927, 1928a) that "patroclinous" males were really of biparental inheritance, receiving dominant traits of both parents. Genetic search was then made for a gene that they might possess in the simplex condition, occupying an odd X chromosome or a differential X region in one of the pairs. No such gene was found. Later cytological work (Torvik-Greb, 1935) indicated no visible difference between the ten pairs of chromosomes of these biparental males and the ten pairs characteristic of females. According to the principle of genetic balance, if the genetic complex of the female were merely that of the male doubled, the ratio of male-producing to female-producing genes should remain the same. There should then be but one sex, the male, because any multiple of the haploid complex would make but a slight change in size or proportion of parts, not affecting such a radical transformation as is involved in sex difference.

In 1933 (P. W. Whiting, 1933e,f) the hypothesis of complementary factors was suggested and shortly thereafter proved true by sex-linkage. According to this hypothesis the female is heterozygous for a pair of sex factors, called X/Y at the time, and she produces two kinds of haploid males from unfertilized eggs, X and Y. Mating with a closely related X male gives diploid zygotes, male-producing X/X, female-producing X/Y, and male-producing Y/Y. The male-producing homozygotes are much less viable than the female-producing heterozygotes, accounting for the low frequency of diploid males.

A supplementary hypothesis of differential

maturation was proposed by P. W. Whiting (1933e) to explain the absence of diploid males in out-crosses. In these crosses, the egg, being in an indecisive stage of reduction division at the time of fertilization, would eliminate into the polar body the same sex factor that was being carried in by the sperm, and thus the fertilized egg would always be heterozygous for the sex factor, that is, female-producing. In close-crosses, however, some influence seemed to prevent this mechanism of differential maturation from affecting the disposal of the like sex factor; and so there were some diploids which, being homozygous for the sex factor, were males.

It had been noted previously (A. R. Whiting, 1925) that females mated to related males were less fecund than those mated to unrelated males. This appeared to be the result of excess bad eggs in close-cross fraternities. On the basis of the theory of complementary factors, these eggs are considered to be male-producing zygotes, and increased fecundity in out-crosses the result of a replacement of these by female-producing zygotes.

This hypothesis of complementary factors was suggested after study of complementary effects in eye-color and in genitalia of haploid mosaic males, which occur occasionally among the progeny of unmated females heterozygous for mutant traits (P. W. Whiting, Greb, and Speicher, 1934). Interpretation of gynandroidism as a complementary effect led to the conclusion that females are heterozygous and that normal males are X and Y with equal frequency. This hypothesis of complementary factors was proved true by sex-

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linkage of the recessive gene, fused (P. W. Whiting, 1935a,c).

Snell, in 1935, presented evidence based on Bostian's (1934) published data that would support a theory of independently segregating multiple sex factors. He suggested that heterozygosity of one or more of these factors results in a female, but homozygosity of all produces a diploid male (Snell, 1935).

In 1939 P. W. Whiting proposed a theory of sex determination in *Habrobracon* based on multiple alleles (P. W. Whiting, 1939). In this theory, the explanation of sex inheritance in close-crosses is essentially the same as that proposed by P. W. Whiting in 1933. The females are heterozygous for the sex factor, the haploid males are of different types as regards the sex factor, and the diploid males are homozygous for the two sex alleles involved. The importance of the multiple allele theory is the fact that it gives an explanation of sex determination in outcrosses, where no diploid males are produced. The upper case letters X and Y were then abandoned as sex symbols, and lower case x was taken to indicate the sex factor exclusively. The x accompanied by certain letters of the alphabet now designates the various alleles in the series--xa, xb, xc, etc. According to the multiple allele theory any heterozygote for two members of the series, xa, xb, xc, etc., is female, any homozygote or azygote (haploid) is male. Given n alleles in the series, there should be possible n different haploid males, n corresponding diploid males and $(n^2-n)/2$ females.

With respect to the three classes of offspring--females, diploid males, and haploid

males, different ratios have been considered in the publications. At first, ratio of females among total progeny was used, but this was soon given up in favor of ratio of total diploids. Ratio of males among diploids was also calculated. It was noted that these two ratios were negatively correlated and that outcrossed females had higher fecundity than close-crossed. The latter fact, checked later by egg counts, showed that low viability of diploid males, together with presence or absence of male-producing zygotes rather than difference in ratios of eggs fertilized, lies at the basis of the negative correlation. Since, according to the multiple allele theory, male-producing zygotes are formed in close-crosses with frequency equal to female-producing, the ratio of diploid males to females may be used to express the relative viability of the diploid males.

Bostian (1939) gave the first evidence supporting the multiple sex allele theory. He selected for independent segregation of fused and sex for twenty generations, while constantly inbreeding. He was unable to establish a line breeding true for independent segregation of sex and fused, although on the basis of Snell's hypothesis, the establishment of homozygous sex factors on the chromosome bearing fused would allow for such a condition. The results of this work indicate that there were triple sex alleles present. A review by P. W. Whiting (1940c) of the available data further supports and confirms the multiple allele theory of sex determination.

The multiple allele theory of sex determination in *Habrobracon* has been exhaustively tested

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(P. W. Whiting, 1940c, 1943a). Laboratory stocks have been analyzed for sex factors. Technique consisted in selecting one stock, designating its sex alleles as x_a/x_b , and introducing into it a recessive gene. If all significantly large fraternities from crosses of recessive females of this stock to dominant males of an unknown stock contained dominant males (diploid), as well as the recessive males (haploid) and dominant females (diploid), the P1 male stock was considered to have the same sex alleles, x_a/x_b . If no dominant males (diploid) appeared in any of the fraternities, the P1 male stock was regarded as having different alleles--for example, x_c/x_d . If only one-half the fraternities included dominant males, the P1 male stock was considered to have one allele in common with x_a/x_b --for example, x_a/x_i . Recessive genes were introduced into each new stock as it was analyzed for sex factors, and "tester" stocks were made up for future use.

Nine factors are thus far known in the series (x_a through x_i), and the tester stocks are designated x_a/x_b , x_c/x_d , x_e/x_f , x_g/x_h , and x_a/x_i . Evidence of allelism of these sex factors is furnished by the fact that they are all closely linked with the gene, fused. Lack of diploid sons and equality of fused and non-fused daughters from crosses of stocks tentatively designated as having different sex alleles in the x series proves the sex factors to be different, but their linkage with fused indicates their allelism.

The multiple alleles are regarded as differential chromosome segments which have been built up in the early evolution of the Hymenoptera.

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They are necessarily associated with haploid parthenogenesis, and consist of many genes determining the numerous sex differences, structural, functional, and behavioristic, characterizing Hymenoptera. These genes have, in the aggregate, duplicate effects such that all haploids or homozygous diploids are similar and male, but combinations of any two different alleles result in females (heterozygous dominants), likewise all similar.

This principle of sex determination may be illustrated by the following example. An x_a/x_b female homozygous for the autosomal recessive gene, veinless, but heterozygous for fused and having fused associated with x_b may be crossed with a non-veinless x_b fused male (Fig. 16A). The recessive veinless serves to mark the haploid sons which are fused and non-fused in equal numbers. The diploid offspring, whether males or females, will be non-veinless. Among the daughters, x_a/x_b , the non-crossovers will be wild-type, the crossovers fused, but among the diploid sons, x_b/x_b , the reverse condition exists. Since crossing over between x and fused is about ten per cent, fused will show great deficiency among the daughters, great excess among the diploid sons. If both parents have fused associated with x_a , the offspring occur in the same ratio (Fig. 16B), but if fused is associated with x_a in one parent and with x_b in the other, the ratios of fused among the two types of diploid offspring are reversed (Fig. 16C and D) giving an excess of fused among the daughters, deficiency among the sons. Thus there are four different arrangements possible

CROSSES INVOLVING SEX DETERMINATION

MOTHER	FATHER	HAPLOID SONS		DAUGHTERS		DIPLOID SONS AND EXCESS BAD EGGS	
				x_a/x_b or x_a/x_c and x_b/x_c		x_a/x_a or x_b/x_b	
				vl	vl.fu	+/fu	fu/fu
A $\frac{vl}{vl} \frac{xbfu}{xa+}$	$\frac{xbfu}{}$	5	5	9	1	1	9
B $\frac{vl}{vl} \frac{xafu}{xc+}$	$\frac{xafu}{}$	5	5	9	1	1	9
C $\frac{vl}{vl} \frac{xa+}{xbfu}$	$\frac{xafu}{}$	5	5	1	9	9	1
D $\frac{vl}{vl} \frac{xb+}{xafu}$	$\frac{xbfu}{}$	5	5	1	9	9	1
E $\frac{vl}{vl} \frac{xbfu}{xa+}$	$\frac{xcfu}{}$	5	5	10	10	0	0

Fig. 16. Ratios of offspring expected according to various arrangements of sex alleles in crosses of veinless females heterozygous for fused by fused males. P.W.Whiting, 1943a.

for x and fused but only two phenotypically separable ratios.

Fraternities of the close-cross type may now be called two-allele fraternities, those of the outcross type three or four-allele fraternities. A third allele brought into the cross by a fused male, xc.fu for example, always masks sex-linkage, since all diploid offspring are heterozygous for x and hence female, fused and non-fused in approximately equal numbers (Fig. 16E). Diploid males reappear with inbreeding, and their presence is always associated with obvious sex-linkage of fused as shown by Bostian (1939).

Sex determination, is in a sense, polygenic, but because of no crossing-over within the segment, the various groups of genes act as a single series of allelic factors. Just as the many sex-producing genes distributed among the X-chromosome of *Drosophila* segregate as a unit from the Y without crossing-over, so the dominant female-producing genes and the recessive male-producing genes of the x factor in *Habrobracon* segregate without crossing-over from their homologues. Males, as determined by the various alleles (whether azygous or homozygous), or females as determined by any of the heterozygous combinations, are always phenotypically similar (P. W. Whiting, 1945b).

Whether the sex alleles ever mutate has not been established with certainty. They appear to be very stable. Extensive breeding within a two-allele stock has resulted in two-allele fraternities almost exclusively, as evidenced by the presence of diploid males. With certain very rare exceptions, the fraternities lacking diploid males are small, so that the lack is

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evidently the result of error in sampling. The rare exceptions, which were not adequately tested, may have been the result of contamination, though this is unlikely, or to some combination of factors reducing diploid male viability, or to mutation in a sex allele itself.

The nature and evolution of the sex factor, x , the differential segment, may now be considered. Mutant genes are known to cross over both to the left and to the right of x , hence x is interstitial, but so far no crossing over within x has been noted. If, however, crossing over within x did occur, x would be inconstant, x_a would not remain distinct from x_b , or x_b from x_c , etc. The work of Horn (1943a,b) demonstrates that F_2 males segregating from crosses of x_a/x_b with x_e/x_f stocks are still x_a , x_b , x_e , or x_f , that they all sire diploid sons, and that those that were x_a or x_b sire diploid sons by x_a/x_b females and not by x_e/x_f females and the reverse (as shown by linkage with fused). It may be concluded, therefore, that there is no crossing over within x ; or perhaps the rare "mutations" of x , if such actually occur, may be crossovers.

Whether or not Whiting's multiple allele theory of sex determination is applicable to the Hymenoptera in general is as yet a question. Were it not for parthenogenesis, this complementary scheme might never have been proposed. Diploid males have been shown in two other species of *Habrobracon* (Speicher and Speicher, 1940; Inaba, 1939), but so far no one has applied breeding and observational tests that

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might reveal them elsewhere; and no evidence has yet appeared that prevents the extension of the multiple allele theory to the Hymenoptera in general.

Chapter VIII

LINKAGE

So far in *Habrobracon juglandis* there have occurred about one hundred known mutations each involving a different gene. Since the wasp has only ten pairs of chromosomes, it is apparent that each chromosome must bear a number of different genes. The position of each gene and its allele or alleles is definite; that is, each pair of alleles always occupies the same locus on the same pair of chromosomes in diploid wasps. Of course, in haploid males, only a single set of chromosomes is present. Crosses have been made involving these mutant types in various ways to test the principles of heredity. Linkage tests are made by crossing various mutant types and counting the F₂ haploid sons of the unmated F₁ heterozygous females. The azygotic ratios thus obtained approximate gametic ratios except as they may be affected by differential viability of the various haploid genotypes. Linkage tests thus made show that maps are very long in crossover units. On this account, despite much work extending over several years, there is as yet no approximation of linkage groups to the number ten, corresponding to the haploid set of chromosomes.

If certain gene mutations, such as speckled, reduced, and glass, occur more frequently in

combination than they do separately, the genes are said to be linked; and therefore, borne on the same chromosome. At the present time four linkage groups (Fig. 17) are recognizable. These groups may occupy four different chromosomes or they may be found to be linked and thus occupy fewer than four chromosomes. In 1933 fifty genes were known, and they comprised eight linkage groups. It was thought then that each group represented a different chromosome. However, since that time, new genes have come to light that have linked the second and fourth groups, others have linked the fourth and fifth, others have linked the fifth and eighth, and still others have linked the first and third. It is apparent, therefore, that while the number of known genes has increased, the number of linkage groups has decreased.

There is one unusually long sex chromosome known to be at least five hundred units in length. Starting at the left end of this sex chromosome, designated linkage group one (I), the genes are arranged in the order: speckled, reduced, glass, etc. Helsel (1943, 1944) conducted experiments in order to check recombination and interference in this region, and to compensate for any viability disturbance or position effects introduced the genes in all possible combinations. She reported 12.07 per cent crossing over between speckled and reduced, and 12.69 per cent crossing over between reduced and glass. Coincidence is 0.264, but varies markedly as the genes are introduced in different combinations. Linkage of these genes had been shown (P. W. Whiting, and Benkert, 1931) with about 13 per cent crossing over be-

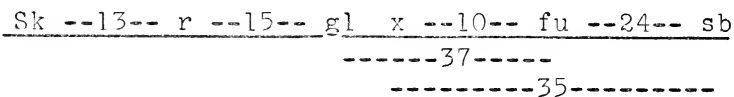
HABROBRACON LINKAGE GROUPS

Group I	Group II
Sk -- 13 -- r	k -- 28 -- m
r -- 15 -- gl	m -- 8 -- o
gl -- 37 -- fu	o
x -- 10 -- fu	
fu -- 24 -- sb	
sb -- 30 -- bl	
bl -- 14 -- le	
le -- 6 -- c	
c -- 15 -- l	
l -- 3 -- n	
n -- 9 -- ho	
ho -- 8 -- vl	
vl -- 12 -- cw	
cw -- 5 -- ro	
ro -- 12 -- bu	
bu -- 37 -- dr	
dr -- 17 -- cr	
cr -- 41 -- sl	
sl -- 0 -- co	
co -- 33 -- ct	
ct -- 22 -- rd	
rd -- 40 -- gy	
gy -- 4 -- ac	
ac -- 4 -- el	
el	
	Group III
	bk -- 25 -- st
	st -- 9 -- wh
	wh -- 10 -- at
	pl -- .3 -- wh
	at -- 22 -- st
	Group IV
	sv -- 12 -- td
	td -- 27 -- ma
	sw -- 24 -- sv
	ma

Fig. 17. Linear arrangement of genes with crossover percentages. For additional data see Table II.

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tween speckled and reduced, and about 15 per cent crossing over between reduced and glass. The sex gene lies to the right of glass and is followed by fused and stubby, which have been shown to be sex-linked. The strength of the sex linkage of fused has been shown to vary from 8.6 per cent to 17.6 per cent crossing over (P. W. Whiting, 1940e). Hager (1941) working with orange-eyed females heterozygous for stubby, showed crossing over to be 37.5 per cent between stubby and the sex gene, and 24.2 per cent between stubby and fused. Linkage across the sex gene indicates that speckled and stubby appear to segregate independently, and no linkage between speckled and fused is noted. Stubby shows very slight, if any, linkage with reduced or with glass. A study by P. W. Whiting and Benkert (1934) indicates linkage between reduced and fused with 45.5 per cent crossovers. Linkage between fused and glass, with 41.7 per cent recombinations, suggests that glass is nearer fused than is reduced. Recent experiments bear out this conclusion. No conclusive evidence is as yet available for the sex linkage of glass, which may be very loose or may be masked by a third allele and by viability differences. A linkage map of regions near the sex gene with approximate intervals may be constructed as follows:



Anderson and P. W. Whiting (1939) reported a "cantaloup" group of 14 loci with a map dis-

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tance of 187 units lying to the right of stubby. Klotz (1940) reported on linkage tests made with veinless, lying approximately in the center of this group. Veinless and honey are linked with a crossover value of approximately 7.5 per cent (Clark, 1942). Veinless and stubby show no crossing over and are, therefore, thought to be not linked. Veinless and lemon show a linkage value of approximately 32.3 per cent. Veinless and black show a linkage value of approximately 34.6 per cent. These data indicate that the factors, veinless, honey, lemon, and black, are located on the same chromosome. Crossover percentages are 14 between black and lemon, six between lemon and cantaloup, and 19 between cantaloup and honey (A. R. Whiting, 1939b). Black is linked to stubby with a crossover value of approximately 30 per cent. Veinless and cantaloup are linked with approximately 30.6 per cent crossing over. Long and veinless show a linkage value of approximately 17.0 per cent. Long and cantaloup show a linkage value of approximately 14.5 per cent. Interference is evident in the three point cross between cantaloup, long, and veinless, with the ratio of coincidence being 0.537. Clark (1942) reported data from six loci scattered along about 70 units of the "cantaloup" group thought to be near the center of the sex chromosome. These data indicate that the black to lemon region does not interfere with the lemon to cantaloup region, but the cantaloup to honey region does interfere with the lemon to cantaloup region. In testing the possibility that the length (23.0) of the black-lemon region might be responsible for the lack of interference,

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the region was compared with a region of similar length (22.3) to the right of lemon, namely, cantaloup to honey. Coincidence for black-lemon, and lemon-cantaloup, was found to be 1.07, while the lemon-cantaloup, and cantaloup-honey, was 0.28. Clark suggests that the reason for the lack of interference between the black-lemon, and the lemon-cantaloup, regions is that the spindle fiber attachment center is located near lemon. If such is the case, then the region of the sex gene is about 150 units away from the spindle fiber attachment region.

A third group of genes designated as the "red" group (Anderson and P. W. Whiting, 1939) consists of five loci with a map distance of 74 units. This group forms the right end of the sex chromosome. Twelve other genes are also located on this first chromosome. For their position and crossover value see Fig. 17 or Table II.

A second chromosome, or linkage group two (II) of three loci, 35 units in length, has been identified (P. W. Whiting and Benkert, 1934). This linkage group consists of three mutants, kidney, orange, and miniature. A three point experiment planned to determine the relative positions of kidney, orange, and miniature, gave 7.5 per cent crossing over between orange and miniature, and 27.5 per cent crossing over between miniature and kidney, with 2.8 per cent double crossing over. From these data it may be concluded only that miniature lies about one-fourth the distance from orange to kidney (Fig. 17).

The third chromosome, or linkage group three (III), of four loci is approximately 44 units

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in length. Carson (1941) introduced three genes, broken, white, and stumpy, in the four possible combinations. Linkage between broken and stumpy gave a crossover value of approximately 25 per cent. While the linkage between stumpy and white gave a crossover value of approximately nine per cent. From these and other data Carson concluded that broken, stumpy, and white, are arranged on the chromosome in that order. The gene, attenuated, since lost, showed linkage with white with 10 per cent crossing over, and with stumpy with 22 per cent crossing over. Its position, therefore, is to the right of white (Fig. 17). Recent work done by P. W. Whiting shows that white and pellucid are very closely linked, only a few recombinations occurring out of several hundred wasps counted. There is also suggestive evidence for linkage between red and white with 41.5 per cent recombination (Helsel, 1942). Further breeding tests will be required to substantiate the evidence. If found valid, the known linkage groups will be reduced to three.

The fourth chromosome, or linkage group four (IV), consists of four known loci and is approximately 63 units in length (P. W. Whiting and Benkert, 1934). The four mutants in this linkage group are shot-veins, small-wings, truncated, and maroon, arranged in this order on the chromosome. Shot-veins and small-wings are linked with a crossover value of approximately 24 per cent. Matings between shot-veins and truncated show linkage with a crossover value of approximately 12 per cent. Maroon and truncated are linked with crossing over approximately 27 per cent.

There are ten genes remaining to be located in the ten possible linkage groups, Table II. At present, breeding tests are being carried on in order to test the presence or absence of linkage among these unlocated genes. New genes are still coming to light. These may prove to be located on chromosomes as yet unmarked, or it may be that they will be found to be linked with known groups. The number of genes that may eventually show up through visible effects is incalculable. Table II shows which genes have been so far tested.

In linkage tests, the x-factor acts as a single gene, occupying a point on the linkage map. The method of making a linkage test with the sex-factor may be illustrated by a single example (P. W. Whiting, 1945b). The mutant gene, fused, lies about ten units to the right of x. An orange-eyed female heterozygous for fused, $o.xa.+/o.xb.fu$, is crossed with a black-eyed fused male, $+.xb.fu$. The orange-eyed sons are haploid from unfertilized eggs and are fused and non-fused in equal numbers. Sex-linkage is not determinable among these because xa males and xb males are similar. The black-eyed zygous diploid or biparental offspring $o/+$, are either fused or non-fused, and either males or females. From the ratio of the different combinations the percentage of crossovers may be determined. In the example given, the non-crossover offspring will be $xa.+/xb.fu$ or non-fused females, and $xb.fu/xb.fu$ or fused males; the crossovers, averaging in this case 10 per cent, will be $xb.+/xb.fu$ or non-fused males, and $xa.fu/ab.fu$ or fused females. This is called a two-allele cross.

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In crosses involving three sex-alleles, sex-linkage cannot be determined because all the zygous offspring are heterozygous for x and are, therefore, female; $x_a/x_b \times x_c$ gives x_a/x_c , x_b/x_c . Fecundity is higher here, and the ratio of females to haploid males is doubled because the poorly viable diploid males are replaced by females. In this case, if the cross is made between a female heterozygous for fused and a fused male, fused and non-fused females are produced in equal numbers.

Three kinds of fraternities from heterozygous females by fused males are therefore distinguishable as follows:

	Females	Diploid Males	Haploid Males
	Non-fused fused	Non-fused fused	Non-fused fused
(1) two-allele	9/1	1/9	1/1
(2) two-allele	1/9	9/1	1/1
(3) Three-allele	1/1	0	1/1

Linkage tests involving two or more mutant types fall into two general categories, (1) repulsion tests, ($a \times b$), and (2) coupling tests, ($a.b \times +$). The mutant factors may be introduced from different parents (repulsion tests) or the double mutant type may be crossed with wild-type (coupling tests). It is advisable to make these reverse crosses to check deviations that result from viability differences, but thus far most tests have been of the repulsion type as this is the more convenient way to test

new factors. No consistent differences have been found between F₂ fraternities resulting from reciprocal crosses (a female X b male and b female X a male in the case of repulsion tests or + female X a.b male and a.b female X + male in the case of coupling tests). When two mutant types are female sterile, the female heterozygous for one is crossed with the male of the other, in which case only those F₂ fraternities containing both mutants are of value.

Unmated females resulting from crosses involving various mutant genes produce males parthenogenetically. These segregate in gametic ratios. Thus a female, o/bl, from a cross of orange-eyed by black-bodied, shows independent segregation of these two differences. The four types of sons, wild-type, orange, black, and orange-black, occur in equal numbers. The same result is obtained from the reverse cross female, +/o.bl, resulting from a cross of wild-type, by orange-black. Lemon body color and cantaloup eyes are linked with about ten per cent crossovers. Thus le/c females produce males, +, le, c, le.c, in 1:9:9:1 ratio while +/le.c females give the same types of male offspring in reverse ratio, 9:1:1:9. A female may be heterozygous for several differences producing more complex ratios. Factor interaction is shown, as in lemon, honey, and black, body color, giving characteristic and clearly distinct double mutant types, le.ho, le.bl, ho.bl, and the triple mutant, le.ho.bl. Masking effects are illustrated, as when white eyes prevent other eye color differences from showing. Viability differences appear when some mutant types are less frequent than wild-type. Dif-

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ferent mutant combinations show different degrees of reduced viability which may be determined by relative numbers in counts of segregating fraternities.

Linkage estimates are ordinarily made from double backcross data. Breeding out virgin *Habrobracon* F1 females gives ratios of the type obtained from a double backcross. The formula for estimation of linkage is derived by using the method of Maximum Likelihood (Mather, 1938; Fisher, 1941). This method leads, in the theory of large samples, to an estimate having the smallest standard error which the data will allow. If P equals recombination fraction, r equals number of recombinations or crossovers, s equals number of straights or non-crossovers, then $P = r/(r + s)$. It must be remembered that each double recombination represents two cases of a single recombination and must be added to the single recombinations in each region to obtain the total amount of recombinations in that region. The recombination fraction can never exceed 50 per cent since of the four available chromatids only two can produce detectable recombinations. A higher recombination fraction indicates that the genes are relatively far apart; a low recombination fraction, that the genes are close.

A variation of the formula, $P = r/(r + s)$, was presented by P. W. Whiting and Benkert (1934). They let AB, aB, Ab, and ab represent the frequencies of the four phenotypes of offspring expected from heterozygous females $a.b/+$ (coupling test) or a/b (repulsion test). It may be supposed that wild-type, AB, is the most viable, but somatic overlapping may increase the

relative number of AB and of aB phenotypes at the expense of Ab and ab respectively, or the reverse may occur. It may also happen that AB will be increased at the expense of aB, while AB is not increased at the expense of ab. This may be the result of the influence of factor B versus b or to a modifier of trait A versus a linked with factor B or b. A factor preventing overlapping acts as a "differentiator" (Bridges, 1919).

AB may exceed aB as the result of differential viability in which case we might expect a comparable excess of Ab over ab. However, the ratio ab/AB cannot be predicted from (aB/AB) X (Ab/AB) since in some cases the double mutant type fails to be reduced proportionally to the single while in others the double may be highly lethal although one or both of the singles may show viability equal to that of wild-type under the conditions of culturing.

Linkage of one of the genes (A or a for example) with a lethal or semilethal may cause an excess or a deficiency of a mutant type of normal viability. Thus aB may surpass AB or the reverse. In this case we may expect a corresponding shift between ab and Ab, but such may not be obvious because of viability differences or somatic overlaps between the various combinations of A and a with B and b, or because of linkage of a second lethal or semilethal with B or b. While lethals are invisible in the material thus far presented on linkage, semilethals may be either visible or invisible. Complete lethals, dying as pupae, which may be identified as to a second trait (eye color for example), have been shown in *Habrobracon*. Degree

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of lethality of a semilethal factor differs widely under diverse environmental conditions and in different stocks. This has been shown in *Habrobracon* for a number of visible mutant types of low viability. The mutant genes are here semilethals which have a recognizable effect on the surviving individuals. Factors ordinarily designated as semilethals presumably differ from these only because of failure to find a conveniently visible trait difference (Schaeffer, 1945). In *Habrobracon*, with its haploid males, stocks very quickly become pure for modifying factors by lethal selection. It seems likely that a balance of factors should thus be readily attained tending toward greater viability. Relatively disharmonic combinations may be expected to enhance by their cumulative effect the influence of a semilethal among the progeny of hybrid females. A larger proportion of the La/Lb daughters than of the La/Lb sisters of the hybrid mother might then be inviable. In five tests involving reciprocal crosses of two orange-eyed stocks and in one test of one of these stocks having the loosely sex-linked gene stubby with a third stock, lethal effects were present associated with the dominant allele to stubby. The lethal effect is regarded as complementary. It is probable that this lethal factor lies to the right of stubby (Schaeffer, 1945). Another lethal factor (Helsel, 1942) showing 25 per cent recombination with white and pellucid has been detected.

In the case of linkage between a and b, $AB/(AB + aB)$ might be expected to equal $ab/(Ab + ab)$ were it not for one or more of the three disturbing factors--somatic overlapping, non-

proportionate differential viability, and linked lethals or semilethals.

It is obvious that what has been said as to the relations of a and b may also apply to the relations of either a or b with a third factor c, or a fourth factor, d. It is sometimes necessary to make comparisons of pairs of frequencies as regards a and b, separately for groups CD, cD, or Cd since either c or d may affect phenotypic ratios of a or b.

Table I has been prepared in order that the reader may readily estimate the statistical significance of various pairs of frequencies occurring in the summaries of linkage data in *Habrobracon* literature. By dividing the lower frequency by the sum (n) a percentage is obtained deviating more or less below 50 per cent. (P = .90) are those percentages at or below which 10 per cent of the samples of a given size (n) will be expected to fall, while (P = .99) are those percentages at or below which one per cent of the samples of corresponding size will fall. The reader may then be 90 per cent sure that there is a significant difference from equality between the two frequencies if the percentage is as low as or lower than (P = .90) and he may be 99 per cent sure if it is as low as or lower than (P = .99). Whether these statistically significant deviations indicate somatic overlapping, differential viability, linked lethals, linkage of the two genes under consideration, or some combination of these conditions must be judged in the individual case from the nature and variability of the traits and comparison of the different percentages

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with each other and with the relation of the factors in the F1 parent.

Whether there is linkage and what may be the best estimate of the percentage of crossovers cannot necessarily be determined from the ratio $(AB + ab)/(AB + aB + Ab + ab)$. Muller (1916) has shown a convenient method, The Square Root of the Product Method, for determining gametic ratio, recombinations (r) to straights (s), which compensates for viability differences. If viability is affected proportionally by two pairs of alleles, regardless of their combination, and if the numbers of the genotypes be AB , aB , Ab , and ab respectively, the gametic ratio, r/s equals $(\sqrt{AB \times ab} : \sqrt{aB \times Ab})$ for

the repulsion test and $(\sqrt{aB \times Ab} : \sqrt{AB \times ab})$

for the coupling test. If, however, the factors differ in their effects on viability according to their various combinations with each other and if genotypes from the repulsion cross be AB_1 , aB_1 , Ab_1 , ab_1 , and from the coupling cross AB_2 , aB_2 , Ab_2 , and ab_2 , then gametic ratio should be equal to any one of the four expressions:

$$\sqrt{\frac{AB_1 \times Ab_2}{AB_2 \times Ab_1}} \quad \sqrt{\frac{AB_1 \times aB_2}{AB_2 \times aB_1}} \quad \sqrt{\frac{ab_1 \times Ab_2}{ab_2 \times Ab_1}} \quad \sqrt{\frac{ab_1 \times aB_2}{ab_2 \times aB_1}}$$

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This second method, the method of reverse crosses, does not compensate for linked lethals, but comparison may be made of the six ratios obtainable (two by first method in case reverse crosses are made and four by second) and in case of differing results presence of linked lethals determined.

Muller's method does not compensate for somatic overlaps or for difficulty in determination of types, in which case phenotypic ratio involves not only deficiency of certain types below gametic ratio but also excess of other types. If viability difference be absent between A and a and if overlapping be from a to A in the same proportion whether B or b be present, then the phenotypic distribution AB, aB, Ab, ab, may be corrected as follows: Decrease AB by subtracting $((AB + Ab - aB - ab)/2(AB + Ab + aB + ab)) \times aB + ab$ and increase aB by the same amount. Also decrease Ab by subtracting $((AB + Ab - aB - ab)/2(AB + Ab + aB + ab)) \times ab + aB$ and increase ab by the same amount. In other words each of the two numerically deficient groups should be increased at the expense of its corresponding excess group by a proportion of itself equal to one-half the difference between the sum of the deficient groups and the sum of the excess groups to the total.

The gametic ratio calculated after this correction is made will in case of linkage always give fewer recombination types than the original data. If overlapping of one difference is always in the same direction and unaffected by the other difference or correlated differences, the gametic ratio obtained should be correct. Even if overlapping is in both directions (from

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A to a as well as from a to A), recombinations after correction should be fewer than before. True crossover value will not be greater than that indicated by ratio thus obtained, but it may be considerably less. The value of the method lies in the fact that it gives a maximum which is lower than may be calculated from the frequencies directly.

If the percentage of single recombinations is known for each of two regions, the probability of two recombinations occurring simultaneously, one in each region, is the product of the percentage of singles in each region. Theoretically, the percentage of double recombinations observed should equal the product of the percentages of singles but actually, in most cases, the observed double percentage is lower than that expected because of interference. Stevens (1936) has derived the following formula for measuring interference in terms of coincidence using the method of Maximum Likelihood:

$$c = wn/(w + x)(w + y)$$

where c equals coincidence, w equals number of double recombinations, n equals total number in cross, x equals region (1) recombinations, and y equals region (2) recombinations. This formula makes possible the estimation of coincidence directly from the raw data. A coincidence value of one (1) indicates no interference; a value of zero (0) indicates absolute interference.

There is no significant change in recombination percentage because of aging of the female. Coincidence values also show no significant

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change because of aging of the female; however, all crosses indicate that the variation of the coincidence value from one (1) is less in the later vials, but not significantly so.

Chapter IX

ENVIRONMENTAL EFFECTS

It has been found that in *Habrobracon juglandis*, as in other experimental animals, certain environmental factors have marked effects upon the appearance, fecundity, and behavior of the animal. The nature of mutations and the rate of their occurrence are also affected. Investigation of various factors and their effects is at present in progress. Temperature, humidity, and X-radiation, have been found to be important in developmental studies.

Ever since *Habrobracon* has been reared in the laboratory, the degree of temperature has been known to determine body color, to affect reproduction, to affect the production of mosaics, and to cause mutations. Wild-type individuals vary from honey-yellow to almost black, higher temperatures producing more yellow pigment, lower more black. Heredity plays some part, for races under constant temperature differ consistently in pigmentation.

Schlottke (1926) from a carefully planned and controlled study of temperature and pigment interrelationships in wild-type *Habrobracon* draws the following conclusions: (1) deposition of pigment (black) decreases linearly with rising temperature; males are on the average, darker than females, (2) pigment is deposited especial-

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ly at points of muscle attachment and the last parts to become light in higher temperatures are the regions where muscles attach vertically, (3) animals bred at lower temperatures are larger and darker than those at higher, but at a given temperature the smaller animals are the darker, and (4) changes in temperature at any time between egg stage, four days before laying, and prepupal stage, affect adult coloration. In a later study (1934) he shows that increase or decrease of oxygen content of the atmosphere increases pigmentation; and he concludes that variation of oxygen concentration influences the oxidations concerned with pigment formation indirectly as a non-specific stimulus on the organism as a whole. Kuhn (1927) has shown by selection and by crossing that heredity plays a considerable part in color determination. He argues for a hereditary cytoplasmic influence. P. W. Whiting (1926a) has demonstrated linkage of a gene affecting color of mesosternum with a gene determining defects in wing vein, R4. An extensive series of experiments indicates considerable genetic independence of various body regions as well as both linkage and physiological correlation with certain mutant genes.

Despite the great range of variability in diverse regions of the body, bilateral symmetry is the rule with very rare exceptions. An occasional defective specimen with asymmetrical morphological malformation is likely to show correlated changes in pigmentation. There have likewise occurred a few specimens with an irregular mottling of color, but this appears to be pathological. Instances in which specimens of normal form and non-mosaic for mutant traits

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have shown pigmental asymmetry are exceedingly rare. Observation of specimens mosaic for various mutant factors and for sex (gynanders), however, indicate greater or less asymmetry in body color. A certain quantity of black pigment in the given region is, of course, a prerequisite for visible asymmetry. Total absence of color resulting from high temperature during development or to other causes obviously renders a genetic difference incapable of expressing itself. Likewise, if environmental conditions are such that the parts are very black, a relatively slight difference determined genetically would not be apparent. Females are in general less deeply pigmented than males in any given strain, and consequently gynanders usually show striking asymmetry in color correlated with asymmetry in sex.

The pigments of the stemmaticum of *Habrobracon* are granular and present in hypodermal cells beneath clear cuticle. The other pigments, ranging from pale yellow through brown to black, are in the cuticle and appear to be non-granular. Both granular and diffuse pigments are similarly affected by temperature changes and undoubtedly belong to the melanins. The melanins are formed from colorless substances or chromogens with the aid of enzymes in the presence of oxygen. A. R. Whiting (1939b) points out that Wright's theory of pigment formation in mammalian hair is apparently applicable to the cuticular pigments of *Habrobracon*. According to Wright (1917) the colorless chromogen is formed in the cytoplasm, and two enzymes or their forerunners are formed in the nucleus. The union of these substances in the cytoplasm in differ-

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ing amounts and under different conditions gives rise to different colors and intensities of color. Chromogen and enzyme I (and O₂) are necessary for any color production; acting together they produce yellow. Enzyme II has no effect alone, but in combination with I oxidizes chromogen to black and is effective below the threshold of I alone. In the absence of I no color can be produced, in the absence of II, no black. Figure 18, is an attempt to express in simple form the maximum potentiality of each genetic type in respect to each enzyme. Wild-type is used as a standard. Quantity of enzyme I is represented on the left, of II on the right. Any environmental condition which lowers the expression of II increases the expression of I. Lower temperatures change the black pigment of the lemon mutant less strikingly than that of wild-type or black. The black areas never become as intense or widespread, but in spite of this there is a striking lightening of yellow. This fact taken together with the lighter general color at higher temperatures and the observed transparency of thoracic cuticle at both temperatures suggests a deficiency of enzyme I. There is too little of I to combine with II to form as much black as in wild-type and likewise too little to produce the full amount of yellow even at high temperatures (A. R. Whiting, 1939b).

The effect of temperature on the eye colors, carrot, maroon, and the combination, carrot-maroon, has been tested (David, 1938). Limited experiments have also been made with the eye color, cantaloup, and with the body color, lemon. The temperature ranged from 37° C. to 15° C. Except for cantaloup, which showed little

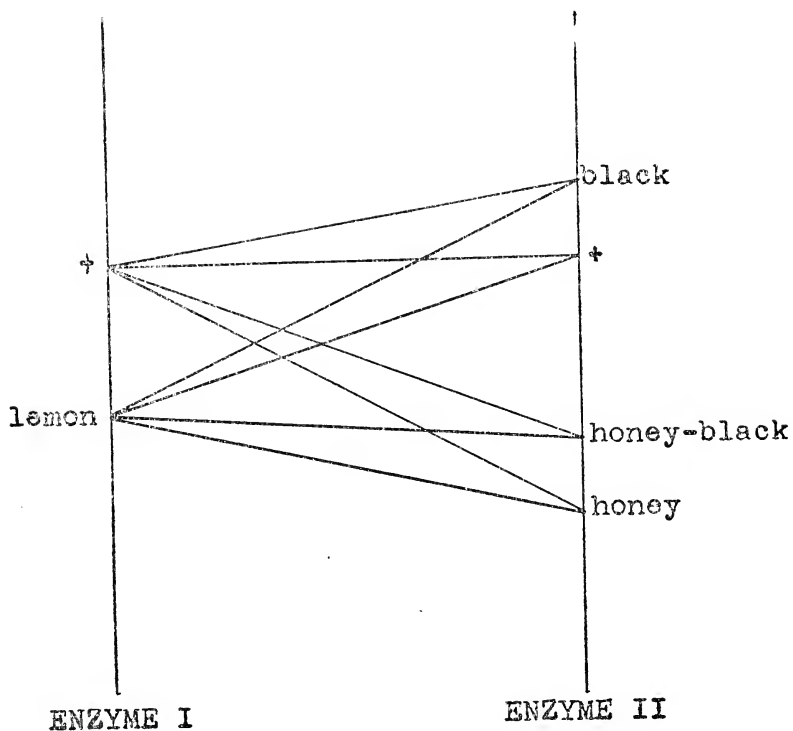


Fig. 18. Relative potencies of enzymes I and II in each genetic type. A. R. Whiting, 1939b.

if any change, the intensity of the eye colors varies inversely with the temperature, in contrast to that of body color (type and lemon) which varies directly with the temperature. Carrot showed wide variation from white at low temperature to a deep reddish carrot at high temperature, maroon showed less variation, from a bright red to a dark red or black, and the combination, carrot-maroon, showed still less variation from white to pale yellow. White-eyed carrot wasps were phenotypically like genetically white-eyed. The bright red of the maroon was similar to the deep reddish orange of the carrot. Body color is determined earlier in development than is eye color.

Temperature treatment affects fecundity although short time exposure to cold has only a slight effect. Constant high temperature decreases fecundity by a little less than a third and constant low temperature lowers it to less than half that of control wasps. Constant cold and extreme heat both have very significant effects on fecundity though they apparently act in different ways. Cold acts by slowing down all the activities of the adult wasps thereby decreasing the rate of egg production. Cold also keeps many of the eggs from hatching and kills many of the young larval wasps. Heat treatment apparently has little or no effect on rate of egg production. It affects the young, the consequences being especially noted in the pupal stage. There are many naked pupae and many dead in the cocoons.

Maercks (1933) investigated the influence of temperature and relative humidity on the eggs of *Habrobracon*. He found the optimal tempera-

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ture for hatching to be 29° C., the optimal relative humidity, 80 per cent. The time required for hatching is increased by lower temperatures but is not noticeably influenced by relative humidity except at 19° C. and below, when lower relative humidity slows up development. At optimal temperature egg mortality is not significantly influenced by relative humidity; at low or high temperature it is increased by low relative humidity; at optimal relative humidity it is low through a wide range of temperatures (16-35° C.) but rises quickly to 100 per cent near the lower and upper limits (12° C. and 38° C.).

Temperature treatment of mated females slightly affects the sex ratio of offspring, the most significant decrease in female ratio being observed at constant low or high temperatures. Short time exposure of heterozygous females to extreme cold does not significantly affect the rate of production of male mosaics and gynanders. However, when such females are placed at a constant low temperature, no mosaic offspring appear. On the other hand if females are kept at 35° C. to 37° C. a significantly greater number of mosaics appear (Greb, 1933c).

Experiments with crosses of closely related stocks show that the percentage of diploid males decreases as culture temperatures are increased (P. W. Whiting and Anderson, 1932). Females mated with related males produce fewer biparental offspring if kept at 30° C. than if kept at 20° C. However, at the higher temperature, the percentage of diploid males is greater. Transfer of young to other temperatures appears to have no effect on ratios except that the ratio of biparentals is increased if transfers are

made from 20° C. to 30° C. or 35° C. This is probably to be explained by a differential lethal effect on males in general. At all temperatures percentages of males among biparentals change significantly with increasing age of mothers. An experiment in which eggs were counted showed that at the higher temperature the percentage of eggs producing impaternal males was decreased. Among biparental offspring males were increased and females correspondingly decreased. The conclusion is drawn that increased temperature increases mortality of males and favors homeosyngamy (male-producing combinations) at the expense of heterosyngamy (female-producing) (Anderson, 1935, 1936). On the whole, however, sex ratio is less dependent upon temperature than is fecundity.

High temperature may cause or, at least, bring to light, various mutations. The mutant, shot-veins, a semidominant factor, appeared accidentally. It arose simultaneously in three different lines after extreme heat treatment of larvae. It causes veins of the wings to be broken up and distorted. The trait proved to be hereditary, and shot-veins is fully fertile and stable.

A number of mutations have occurred following X-radiation in *Habrobracon*. Treatment is given at various stages, to eggs in the mother before they are laid, to eggs after laying, to larvae, to pupae, and to sperms in the adult male before mating. The offspring of the treated wasps are examined, and the unusual individuals are allowed to produce progeny to show whether or not the questionable traits are hereditary.

Unlaid eggs of *Habrobracon* are most sensi-

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tive to irradiation in late metaphase I, almost equally so in latest prophase I (diakinesis) and least so in prophase stages before diakinesis. Adult (haploid male) survival from unfertilized eggs laid by treated females is used as the criterion (A. R. Whiting, 1939a, 1940a,c).

Hatchability percentages of unfertilized *Habrobracon* eggs X-rayed in late prophase I with doses up to 400 R units are significantly higher than those of controls, and the lethal dose is about 35,000 R units (A. R. Whiting, 1941). Eggs treated in late metaphase I are sensitive to 50 R units, and the lethal dose is about 1,250 R units. There is no evidence of recovery in this stage. The dose-hatchability curves of the two stages differ, that of metaphase I showing a linear relationship to dose. In 1942 (A. R. Whiting, 1942a) evidence against "physiological effect" as an important factor for metaphase I sensitivity was presented as well as preliminary cytological observations.

Two criteria for judging injury are used (A. R. Whiting, 1945a). One of these, hatchability, gives degree of lethal effect, both dominant and recessive, and is a very accurate measurement in *Habrobracon* where unfertilized haploid eggs are capable of development, where every egg can be accounted for, where the ideal environmental conditions are known and easily controlled, and where there is available a stable wild-type stock consistently giving 96 per cent hatchability or higher. The second criterion, chromosome changes in successive stages of the treated oöcytes, is less satisfactory because *Habrobracon* chromosomes are too small (1 μ in diameter) for very careful analysis. Giant salivary chromo-

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some are lacking. Enough has been learned from cytological observation, however, to make this method of some value in connection with hatchability data. The chromosome aberrations observed are necessarily gross ones and undoubtedly represent lethal effects in most cases.

Unmated mature *Habrobracon* females, when well-fed on host caterpillars and restrained from ovipositing for several hours by removal from host, store in each of their four egg sacs from two to five fully mature eggs which may be retained for at least thirty-six hours without injury. After a much longer period of storage they undergo resorption. They are all in late metaphase I with spindle attachment regions separated and about half way to the poles. The ends of the dyads are still in contact so that the chromosomes appear to be under tension. Occasionally, an egg in late diakinesis or in early metaphase I can be seen entering an egg sac. Successively younger prophase oöcytes occupy the ovarioles anteriorly. Synapsis occurs as soon as the youngest oöcytes can be distinguished from oögonia. An ovariole is represented semi-diagrammatically in Fig. 19.

Dominant lethal effects are induced in all eggs treated in metaphase I at about 1,000 R units, in spermatozoa at 10,000 R units, and in eggs treated in prophase I at 45,000 R units. Spermatozoa are not actually inactivated by doses much larger than 10,000 R units. Eggs are also not inactivated by doses much larger than lethal since they continue meiotic phenomena under such conditions. These facts strongly support the theory that the sex of the cell has nothing to do with its response to X-rays but

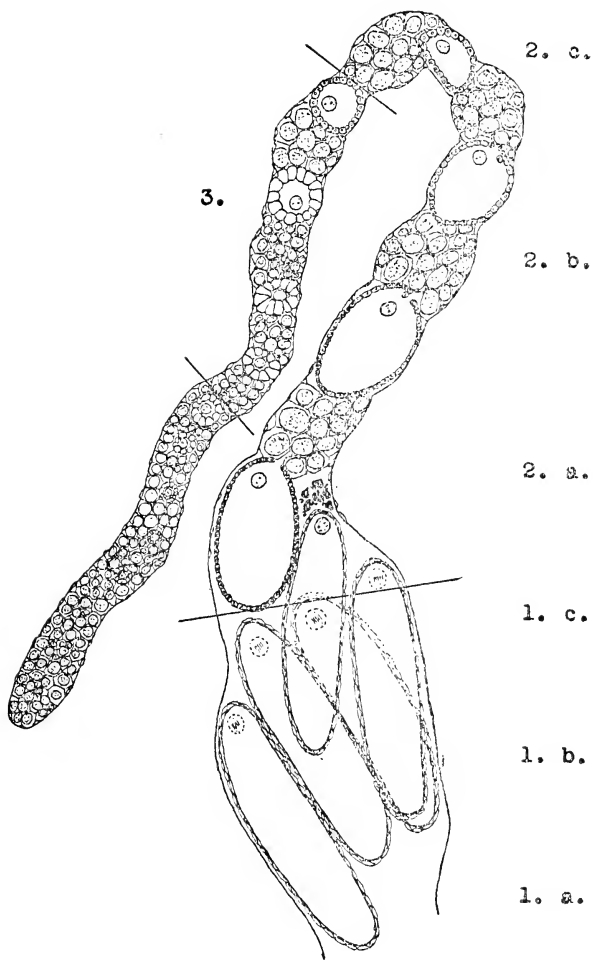


Fig. 19. A single ovariole (semidiagrammatic) showing regions used in classification of treated eggs; 1a, b and c include eggs in metaphase I stored in egg sac; 2a, b and c include eggs in metaphase I, late and mid prophase I; 3 includes eggs in early prophase I. All are post-synaptic.

A. R. Whiting, 1945b.

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rather than the condition of the chromatin determines cell sensitivity.

The extreme and unexpected sensitivity of metaphase I in *Habrobracon* oöcytes has caused some investigators to suggest that the effect is "physiological" and not the result of direct chromosome change. It has been found that haploid (male) larvae are more sensitive to irradiation than diploid (female) larvae of *Habrobracon*, as expected if chromosome change is responsible.

Eggs treated in metaphase I and in prophase I all have chromosomes and fragments, when present, distinct in outline in stages following oviposition and no fusion bridges have been seen. Absence of a low dose threshold for injury and absence of a high one for clumping and retardation of meiosis and early cleavage furnish additional evidence against any serious "physiological" effect in this stage. Since both metaphase I and prophase I eggs, after their respective lethal doses, present the same pattern in regard to degree of development before death, causes of death would appear to be of the same nature for each.

The linear proportionality between dose and hatchability as well as the other facts about metaphase I oöcytes outlined above can be explained by the following hypothesis (A. R. Whiting, 1945a). At the time of treatment, dyads are under tension since spindle fiber regions have started toward the poles while ends are still held in contact by chiasmata. When a hit breaks a pair of chromatids (a dyad) proximal to a chiasma the parts will separate, too far to rejoin but not far enough for the fracture to

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be seen. Subsequent complete terminalization and separation of dyads in anaphase I leaves fragments and there are no bridges. A broken dyad produces a bridge in division II in either spindle with equal frequency. If a single chromatid is broken the fragment remains attached to its uninjured partner and appears in division II. An egg with a single deletion will fail to hatch if unfertilized, and, even if fertilized, when the deletion is large. If two chromatids in a "lug" (distal to chiasma) were broken and the chromatids fused laterally, an occasional bridge in division I might be expected. Tension is much less in this region so that restitution usually occurs when a hit causes a break in this short length of chromosome. As explained above, an egg with one double fragment has one chance in two of hatching, an egg with two such fragments, one chance in four (if the possibility of two breaks in one dyad be left out of consideration).

In *Habrobracon*, bridges in division II following treatment in late metaphase I cannot be explained by chromosome splitting following breakage in view of the structure of the metaphase tetrad. It therefore seems probable that a single hit has broken two chromatids in late metaphase I. It is known that many deficiencies are viable in the heterozygous condition, lethality being dependent on gene content of the segment lost. Since diploid larvae are most resistant to irradiation than haploid, recessive deficiencies must be induced in somatic cells. It is surprising, in view of these facts, that all the lethal effects of irradiation appear to be dominant. If breaks proximal to the chias-

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mata are the ones which tend to be permanent, these would necessarily result in large (and therefore dominant) terminal deletions. Deletions small enough to act as recessives might not have a lethal effect on the haploid embryo until after hatching and therefore would not be detected with methods used in present work. In the limited tests made with fertilized eggs it is also possible that a few deficiency heterozygotes surviving would not noticeably affect hatchability ratios.

Genetic literature includes much discussion of lethal factors. In *Habrobracon* the occurrence of dominant lethals in the sperm can be readily distinguished from direct killing of the male gametes. The most striking result of X-radiation of males is, however, the production of sterility (or partial sterility) of a second type. In this case the sperm are not inactivated but are fully capable of fertilizing the eggs. Such fertilized eggs, however, do not hatch because the sperm have a dominant lethal effect. Females mated to males with this type of sterility produce azygous sons only and in numbers equal to those produced by females mated to normal males; in other words, although they produce no females, as the result of dominant lethal effects of the sperm which have entered the eggs, they behave like mated rather than unmated females in respect to number of azygous sons. *Habrobracon*, then, is especially well suited for separating dominant lethal male sterility from sterility resulting from inactivated sperm on the basis simply of numbers of azygous sons produced by females mated to the males to be tested (P. W. Whiting, 1938a,b).

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As to the nature of dominant lethals it is probable that they are the result of extensive chromosomal alterations rather than to changes in restricted regions or in single genes. A lethal effect from a single gamete may be called dominant in contrast to a condition which must be present in both gametes and hence recessive.

Since in *Habrobracon* an unfertilized egg provided with a single set of genes develops normally into a male and since the addition of a second complete set by fertilization likewise results in normal development into a female, it might be thought that the addition of a deficient set should not be lethal to the resulting zygote. In other words, if both $1n$ and $2n$ may develop normally, why should not $1n + (n-x)$ also develop normally? The explanation is doubtless to be found in genic balance. If $n-x$ is too small to act as a recessive, containing relatively extensive deletions for example, the balance should be so disturbed that development would be prevented. Theoretically the genic set in a sperm might become so extremely deleted by X-radiation that the fertilized egg would develop as an unfertilized egg into a male. No sex intergrades have ever been found in the treated material that might be interpreted as hyperploid males or hypoploid females. The sex types surviving after X-radiation have been fully as normal as in untreated stock.

Recessive lethal (or semilethal) factors may be a cause of "bad eggs" (P. W. Whiting, 1929a; Maxwell, 1935). Half of the unfertilized eggs of a female heterozygous for a recessive lethal do not hatch. Eggs may likewise be defective in their gross morphological or non-nuclear as-

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pects because of unfavorable cultural conditions (very low humidity) or inadequate nutriment of females (feeding with honey instead of caterpillar juice) while females of certain genetic types lay withered eggs of irregular form. Non-hatchability may then be the result of non-nuclear causes, recessive lethals, dominant lethals, or male-producing fertilization (P. W. Whiting, 1938a,b).

Dominant lethals may be induced in the sperm of *Habrobracon* by X-radiation of the males. At 10,000 to 20,000 R units all sperm have at least one lethal. With very high dosages, 41,000 to 142,000 R units, some sperm are directly inactivated while many still remain active and able to carry dominant lethals into the eggs (P. W. Whiting, 1937a,b). Neutrons have also been shown to produce dominant lethals (P. W. Whiting, 1936), being actually much more effective than X-rays. Ultra-short (1 meter) radio waves appear to be ineffective (P. W. Whiting, 1937a,b).

Biparental males have been obtained (Stancati, 1932; Bishop, 1937) after X-radiation of sperm from related males, but the data are not sufficient to indicate their decrease. X-radiation of sperm from unrelated males has never resulted in biparental males. Experiments from crosses with closely related males (treated and untreated) indicate that while the number of haploid males produced per day is not changed by X-radiation of sperm, both kinds of biparental offspring (males and females) are decreased with increasing dosages and that they are decreased at approximately the same rate. This indicates that X-radiation of sperm fails to modify the type of fertilization and that the changes in-

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duced in the sperm are just as lethal to the biparental males as to the females (P. W. Whiting, 1938a,b).

If females are treated and subsequently mated, there is no appreciable reduction in male ratio, indicating that few, if any recessive lethals are induced in the egg. While treatment of mated females causes a radical lowering of female ratio indicating that more dominant lethals are induced in the sperm than recessive lethals in the egg. It has also been noted (P. W. Whiting, 1929a; N. C. Bostian, 1931) that the percentage of female offspring from X-radiated mothers, mated previous to treatment, is markedly decreased (Greb, 1933).

P. W. Whiting (1937a) demonstrated that treatment of sperm with X-ray dosages of 20,000, 40,000, and 75,000 R units produces at least one dominant lethal in every sperm cell. No daughters occur in the progeny and the average number of males produced per day does not equal that to be expected from virgin females, indicating that many eggs are fertilized and die. Sperm treated with 75,000 R units fertilized almost as many eggs as untreated sperm; therefore, the treatment apparently did not cause inactivation. However, a slight increase in the average males per day from mates of males treated with 75,000 R units as compared with those from mates of untreated controls suggested the possibility that spermatogenesis might to some extent be stopped and sperm supply decreased.

Thus partial male sterility results from dominant lethals at relatively weak dosages, complete male sterility results from dominant le-

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thals at stronger dosages, and partial sperm inactivation at very high dosages.

Treatment of *Habrobracon* larvae with X-rays was begun in January 1929. Progeny from crosses of different stocks were used with pure stocks sometimes treated as checks. Treatments ranging from 730 to 4378 R units were given. No treatment had complete lethal or sterilizing effect, although the highest dosage approached this. Younger larvae were found to be more susceptible to X-radiation than older, and male larvae more susceptible than female larvae. Irradiation tended to kill the younger larvae immediately while the older ones continued development and often died after metamorphosis and before eclosion (A. R. Whiting and Bostian, 1931).

There have been some fifty mutant types derived from X-ray experiments on *Habrobracon*. Dosages of 2,000 to 5,000 R units have produced the majority of these mutations. After 10,000 R units there is a dominant lethal change of some sort produced in practically every sperm cell. Dosage for egg cells must be much higher for the chromosomes are not so closely packed together and apparently the closer the packing the better chance for irregular recombinations. Table III has been prepared to summarize the effect of various dosages of X-rays on eggs, sperm, and larvae. Considerable experimentation is still being carried on along this line, and various dosages of X-rays are now being combined with treatment at various degrees of temperature.

Chapter X

CONCLUSION

The body of information assembled thus far establishes *Habrobracon juglandis* as a genetic animal of unusual merit. In addition to its possession of all the prerequisites for a genetic form it has the advantages offered by parthenogenesis. Since the normal males are haploid, their genotypes are phenotypically expressed; thus the need for the traditional backcross is eliminated. While it has been shown that a considerable amount of information has been accumulated along various lines, in no case is the knowledge complete, and numerous avenues of research are open for investigation.

Habrobracon has ten pairs of chromosomes. Only four and perhaps fewer than four are as yet known; so that at least six await exploration and mapping. Many mutations have come to light, but unpredictable numbers await the chance to show their effects in haploid males. Numerous mutations have occurred whose effects are lethal to their owners; these when linked with non-lethals may disturb expected ratios in such a manner as to betray their presence. These may be located on given chromosomes.

Regarding the development of the mutants, very little is known. They are known in their final adult form, but exactly when and where

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deviation from normal development takes place is yet largely a mystery. In some mutants, there is a suggestion of accompanying differences in behavior. These remain to be studied.

Sex determination in *Habrobracon* has been shown to be complementary, but further experiment is necessary before this hypothesis can be shown to hold for the Hymenoptera in general. The effects of environmental changes, X-radiation, and neutron treatment are being tested, and these are bringing up new questions. All these problems await investigation, and their solution holds promise of interesting and significant contributions to the field of genetics.

APPENDIX

TABLE I

Percentages deviating below 50 per cent with probability equal to .90 or to .99 that true value is no lower in population from which sample of a given size, n , is taken. (Whiting and Benkert, 1934)

n	27	32	37	42	47	55	65
Per cent (P.90)	35	37	37	38	39	40	40
Per cent (P.99)	27	29	30	31	32	34	35
n	75	85	95	110	150	170	190
Per cent (P.90)	41	41	42	42	44	44	44
Per cent (P.99)	36	36	37	38	40	40	41
n	250	350	450	550	800	1500	2500
Per cent (P.90)	45	46	46	47	47	48	48
Per cent (P.99)	42	43	44	45	45	47	47

TABLE III

X-RAY RESPONSES OF HABROBRACON

Dosage	Sperm	Metaphase I Egg	Prophase I Egg	Larvae	Adult
50 R	Viable	Approx. 15% killed	Viable	Young killed	Viable mutations
1,400 R	Viable	Approx. lethal dose	Decline in hatchability	Old active	Viable mutations
2,500 R	Dominant lethals	Meiosis and cleavage	85% hatch	Old pupate	Viable mutations
4,050 R	Dominant lethals	Meiosis	78% hatch	Approx. lethal dose 4,378	Viable mutations
10,000 R	98% Dominant lethals		60% hatch		
20,000 R	100% Dominant lethals		20% hatch		
25,000 R	100% Dominant lethals		12% hatch		
35,000 R	100% Dominant lethals		Lethal dose 44,800 R		
200,000 R	Still active		All killed		
250,000 R					Still alive inactive
300,000 R					All killed

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GLOSSARY

GLOSSARY OF TERMS MOST COMMONLY USED IN HABROBRACONOLOGY

A

ALLELE, one of two or more alternative hereditary units or genes, or of the characters associated with the genes; for example, the gene responsible for orange eyes in *Habrobracon* is an allele of the alternative normal gene for black eyes (Synonymous with ALLELOMORPH).

ANDROGENESIS, development from a sperm.

AROLIUM, an appendage between the claws of insects.

ARRHENOTOKY, production of impaternate males.

AXILLA (AXILLARIES), the articular sclerites of insect wings (excepting the tegula, which is at the front edge of the wing-joint).

AZYGOUS MALE, male produced by haploid arrhenotoky in the regularly established parthenogenesis of Dzierzon's Law.

B

BACK-CROSS, the mating of a hybrid to one of the parental varieties or species which produced the hybrid.

THE GENETICS OF *HABROBRACON JUGLANDIS* ASHMEAD

C

- CALCANEA, largest segment of the insect foot, frequently designated the metatarsus.
- CENTROMERE, a definite region of a chromosome which takes the lead in activity during mitosis and meiosis. It is the point of spindle-fiber attachment.
- CHARACTER, a term used to designate any structure, function, or trait of an organism. A Mendelian character represents the end product of development, in which a particular gene has a specific effect.
- CHIASMA, cross-like figure formed by chromatids in meiosis.
- CHORION, tough shell or covering of the insect egg.
- CHROMATID, either one of the two identical strands into which a chromosome splits in anticipation of cell division.
- CHROMOGEN, a substance that under proper conditions may give rise to color.
- COINCIDENCE, the ratio of the actual number of double breaks to the expected number of double breaks which should occur if there were no interference.
- COSTA, the first principal insect wing vein. It constitutes the anterior edge of the wing.
- CROSSING-OVER, the interchange of blocks or chains of genes between two homologous chromatids; also applied to characters which show recombination as a result of such exchange.

GLOSSARY

CUTICLE (CUTICULA), firm layer outside the hypodermis which protects the insect body and serves as a support for the internal organs. Formed from chitin.

D

DELETION, the loss of a chromosomal segment.

DIAKINESIS, the final stages of meiotic prophase in which the homologous chromosomes are in intimate association.

DIFFERENTIATOR, a factor that prevents somatic overlapping of traits.

DIPLOID, referring to the double set of chromosomes, as found in the body cells of animals and the sporophyte generation of plants, as distinguished from the single (haploid) set, found in the mature reproductive cells.

DISPERMIC, an egg fertilized by two sperms.

DOMINANT, a character which appears as the result of the presence of either a single or a double dose of a particular gene, as contrasted with the recessive, which develops only when both members of a pair of genes are alike. Applied also to the genes.

DOUBLES, double breaks in chromatids that occur during diakinesis, and the resulting genotypes, and the individuals possessing them.

DYAD, each of the two chromatids formed from a single chromosome during meiosis.

E

ECLOSION, emergence of adult insect from the pupal case.

THE GENETICS OF *HABROBRACON JUGLANDIS* ASHMEAD

ECTOPARASITE, a parasitic animal infesting the outside of its host as opposed to endoparasite, which lives inside the host.

F

FACET, external face of an insect ommatidium.

FEMUR, the third part of the insect leg, following the coxa and trochanter, usually the largest part.

FIRST RADIAL CELL, region of the insect wing enclosed by radius veins one and three.

FLAGELLUM, the terminal part of an insect antenna.

FOLLICLE CELLS, cells surrounding the developing insect egg which are responsible for the formation of the chorion.

G

GAMETIC RATIO, the ratio of all types of eggs produced by a heterozygous female, expressed phenotypically in the male offspring of *Habrobracon*.

GONAPOPHYSES, the elements that constitute the insect ovipositor.

GYNANDER, an individual, mosaic for sex.

GYNANDROID, an entirely haploid individual which, however, exhibits characteristics of both sexes.

GYNOGENESIS, development from an unfertilized egg.

GLOSSARY

H

HAPLOID, referring to the reduced or single number of chromosomes, and to the structures and individuals that bear that number, such as eggs, sperms, and, in *Habrobracon*, azygous males.

HETEROSYNGAMY, union of dissimilar gametes, or gametes with unlike genotypes.

HOMEOSYNGAMY, union of similar gametes, or gametes with like genotypes.

HOST CATERPILLAR, in *Habrobraconology*, the larva of *Ephestia kuehniella*.

HYPERPLOID MALES, males bearing more than the normal haploid set of chromosomes.

HYPODERMAL CELLS, cells of the living layer of the insect body wall.

HYPOPLOID FEMALES, females bearing fewer than the normal diploid set of chromosomes.

I

IMMATERNATE, originating from a sperm and an egg whose nucleus has been destroyed.

IMPATERNATE, originating without involvement of male parent or sperm, as the normal males of *Habrobracon*.

INTERFERENCE, the inhibitory effect of one crossover upon the possibility of another.

INTERSEXUALITY, a condition in which individuals show characters intermediate between those of two sexes.

THE GENETICS OF *HABROBRACON JUGLANDIS* ASHMEAD

L

LINKAGE, the tendency of certain characters to remain together in heredity, since the genes responsible for their expression are located on the same chromosome.

LOCUS, the position of a given gene or any one of its alleles upon a chromosome.

LUG, either end of a chromosome.

M

MELANINS, black pigments.

MESOPHRAGMA, the transverse partition between the prothorax and the mesothorax in insects.

MESOPLEURON, the mid-region of an insect pleuron (see PLEURA).

MESOSCUTELLUM, the mid-region of an insect scutellum (see SCUTELLUM).

MESOSTERNUM, the mid-region of an insect sternum (see STERNUM).

METAMORPHOSIS, the series of marked changes through which an individual passes from the egg stage to the adult stage. In insects, complete metamorphosis includes egg, larva, pupa, and adult stages.

METATARSUS, the first segment of the insect foot.

MICROCHAETAE, minute bristles on an insect body. Those on the wings are of particular use in Habrobraconology.

MIMICS, individuals assuming the appearance of individuals with dissimilar genotypes, such as ivory and white eyes in Habrobracon.

GLOSSARY

- MOSAIC, an individual whose body indicates the possession of more than one genotype by the appearance of varying phenotypes in different regions; for example, in *Habrobracon*, individuals with one white and one black eye occur.
- MUTANT, an individual possessing or exhibiting the effect of a changed gene.
- MUTATION, a sudden change in a gene resulting in a new hereditary variation.
- MULTIPLE RECESSIVE, the genotype or phenotype of an individual possessing the recessive alleles of two or more different pairs of genes; or the individual itself.

N

- NURSE CELLS, cells that alternate in masses with the eggs in the ovarioles of *Habrobracon* and other insects.

O

- OCELLUS, a single eye of an insect borne separately from others.
- OMMATIDIUM, a single eye of the compound eye of an insect.
- OOGONIUM, a descendant of a primordial reproductive cell which will develop into an oöcyte.
- OVARIOLE, an egg tube in an insect.

P

- PARTHENOGENESIS, the development of an individual from an unfertilized egg.

THE GENETICS OF *HABROBRACON JUGLANDIS* ASHMEAD

PATROCLINOUS, having certain characteristics derived from the father, as diploid males in *Habrobracon*.

PEDICEL, the second segment of an insect antenna.

PLEURA, the lateral divisions of an insect segment.

PRAESCUTUM, the anterior chitinized line of an insect notum, or prothoracic sclerite (see SCLERITE).

PRIMARY WINGS, the anterior wings of an insect.

R

RADIUS VEIN, the vein that forms the distal costal margin in *Habrobracon* primary wings.

RADIUS VEINS, R1, R3, and R4, are branches of the radius vein.

RECOMBINATION, a new combination of linked characters in an individual resulting from crossing-over in one or both of the parents; also the individual possessing the new combination.

S

SCAPE, the first segment of an insect antenna.

SCLERITE, any definite area of chitinization in the cuticle of an insect.

SCUTELLUM, the posterior chitinized line of an insect notum or prothoracic sclerite (see SCLERITE).

SCUTUM, the central chitinized line of an insect notum or prothoracic sclerite (see SCLERITE).

SECONDARY WINGS, the posterior wings of an insect.

GLOSSARY

- SENSILLAE, the sense organs of touch in insects, particularly hairs and cones.
- SEX-MOSAIC, an individual that is part one sex and part the other. In *Habrobracon*, sex mosaics are part haploid and part diploid.
- SIBS, related individuals, particularly brothers and sisters.
- SINGLES, a term applied to genotypes resulting from one crossover, and to the individuals possessing them.
- SOMATIC OVERLAPPING, the intergrading of one phenotype into another so that neither are clearly distinguishable.
- STEMMATICUM, the triangular patch between the simple eyes or ocelli of an insect.
- STERNITE, an area of chitinization in an insect sternum.
- STERNUM, the ventral division of an insect segment.
- STIGMA, a thickened, opaque spot on the anterior margin of the primary wing of an insect.
- STING, a pointed, hollow, needle-like organ at the posterior end of the abdomen in certain female insects; for example, bees and wasps.
- STOCK, organisms reared and cared for for experimental purposes.
- STRAIGHTS, gametes containing genes in the same combinations that were present in the parents; the opposite of crossovers.
- SYNAPSIS, the conjugation of pairs of homologous chromosomes in meiosis.
- SYNCYTIUM, a mass of protoplasm in which the nuclei are free and not separated from each other by cell membranes or walls.
- SYNGAMY, the union of gametes.

T

TARSUS, the foot of an insect.

TERGITE, an area of chitinization in a tergum (see TERGUM).

TERGUM, the dorsal division of an insect segment.

THELYTOKY, production of impaternate females.

TIBIA, the fourth part of an insect leg, following the femur.

TYPE, the kind of a species most commonly found in nature in a given locality; also applied to the genes whose effects are exhibited by such an individual.

TYPE SPECIMEN, a specimen considered to possess the characters of a group. In order to be classified as belonging to that group, all other specimens must exhibit the same characters as the type specimen.

U

UTERUS, the lower expanded end of an insect egg-tube.

W

WILD-TYPE, the kind of species most commonly found in nature in a given locality.

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