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Gallberry *(Ilex glabra)* is a very important source of honey in Georgia and Florida. It occurs as far north as Nova Scotia, and along the Atlantic coast from Massachusetts to Virginia and west to Louisiana. It is a small evergreen shrub with white flowers and dark leaves. In the southeast it begins to bloom at the start of May and continues for 24-28 days.

The honey is light amber in colour, heavy in body, granulates very slowly and has a very mild but distinctive flavour. Most gallberry honey is blended with better known honeys: the name gallberry does not lend itself to promoting the honey under its own name, for the black berries on the bush are renowned for their bitterness, but this does not alter the fact that the honey is of very high quality. GDM

Genetic problems of inbreeding Heredity of the honey bee can be viewed as having two aspects: one involves study of what is inherited, how it is inherited, and the relationship of the hereditary material to the expressed character, or trait, of the bee. The other consists of changing the bees more nearly to conform to what is considered desirable. The first can be thought of as genetics, and the second as breeding.

Breeding better bees has long been a popular intention among beekeepers but a serious obstacle prevented realization of this aim. Queens mate only in free flight, and control of the mates of such queens by humans is extremely difficult, if not impossible, when queens mate naturally. Instrumental insemination is therefore essential to any bee breeding or bee genetic programme.

Soon after the instrumental insemination of virgin queen bees became practical, bee scientists noticed that the brood patterns of some of their stocks were no longer solid, but that many empty cells, or cells with young larvae, were among the sealed cells of brood. Dr Otto Mackensen suspected this was caused by a method of sex determination that had been demonstrated in a distant relative of the honey bee. He showed that sex in the honey bee is determined by a series of sex alleles, now thought to number as many as 17. Alleles are variations of a particular hereditary element. Normal males develop from unfertilized eggs and have any one of the sex alleles. Females develop from fertilized eggs and have any two sex alleles that are unlike. An egg that is fertilized by a sperm carrying a sex allele like that of the mature egg will develop into a male, or drone, larva, and this is eaten by the nurse bees to leave empty cells among the brood (see SEX DETERMINATION).

Bee breeders attempted to circumvent the consequences of this by producing inbred lines and crossing those having different alleles. It was intended also to take advantage of increased vigour that had been demonstrated in some plants when inbred lines are crossed to produce hybrids. The results in some cases were excellent, but the difficulty and cost of producing and maintaining highly inbred lines has caused a lessening of interest in this method of breeding.

A concept of closed population bee breeding, originally advanced by H.H. Laidlaw, and augmented by R.E. Page and by K.J. Kubasek, appears to be a viable method of retaining the sex alleles in the population, and a practical alternative to hybrid bee breeding. Virgin queens from a group of selected mothers are instrumentally inseminated with a thorough mixture of semen of many drones taken from the entire group of selected mothers, so each queen has all of the sex alleles of the population in her spermatheca.

Bee breeding presents an unusual array of complexities. The necessity to instrumentally inseminate the queens, determination of sex, multiplicity of mates, and colony structure of sub-families and two generations, as well as sensitivity to environmental differences, are factors to be considered. Finally, the evaluation of colonies must be recorded so the data can be readily analyzed. HHL

See also CASTE DETERMINATION; GENETICS OF THE HONEY BEE; INSTRUMENTAL INSEMINATION.

Genetics of the honey bee The general principles of genetics, such as the chemical nature of genes, Mendelian principles and meiosis, that are emphasized in basic textbook discussions of genetics hold true for honey bees just as they do for other organisms. However, honey bees conform to these general principles in certain ways that make them unique among the plants and animals that man cultures for food, feed and fibre.

As with all organisms, honey bees have chromosomes that carry genes. Female honey bees (both queens and workers) develop from fertilized eggs that have 32 chromosomes; one set of sixteen (i.e. haploid) from their mother, and a second haploid set of sixteen from their father (i.e. they are diploid, see CASTE DETERMINATION). Drones, on the other hand, develop from unfertilized eggs (see SEX DETERMINATION) which contain only one set of sixteen chromosomes, supplied by the queen that produced the egg (i.e. they are haploid).

The difference between the chromosome numbers of queens and drones leads to a different meiosis pattern in the two castes. Queens have a meiosis quite similar to what is described in textbooks for diploid organisms. Generally, meiosis in queens produces a gamete (egg) which has a single functional set of sixteen chromosomes (an egg also contains three other sets of sixteen chromosomes that normally disintegrate). Thus, the typical reduction in chromosome number, independent assortment of genes, crossing over, etc., that occur in normal meiosis all occur in queen honey bee meiosis. Drones, however, start with only sixteen chromosomes in the cells that will undergo meiosis and eventually produce sperm. Consequently, meiosis in drones is modified. The final sperm cell produced has sixteen chromosomes that are identical to the sixteen chromosomes in the egg that originally gave rise to the drone. Thus, there is no genetic variation among the millions of sperm cells produced by a single drone. This fact is a central theme in bee genetics which must be considered in nearly every genetic experiment and breeding programme.

One result of haploid drones producing genetically identical sperm can be seen in the family structure of a honey bee colony. As a family, a bee colony is composed of a mother-queen, her daughter-workers, her daughter-queens and her son-drones. The father-drones (approximately ten), which died upon mating with the mother-queen, provided the sperm which is still present in the colony, carried in the spermatheca of the mother-queen. A bee colony is also a super-family composed of a number of sub-families. Each father-drone is the father of one sub-family, while the mother-queen is the mother of all sub-families. Two worker bees in a single sub-family are closely related to each other, since each worker received an identical sperm from the father-drone. These, called super-sister bees, have three-quarters of their genes in common because of their parentage. One half of the genes in common are from the father-drone, and one quarter are from the mother-queen. This genetic relationship is halfway between that of typical sisters and monozygotic (identical) twin sisters in a human family. Between sub-families, worker bees are half-sisters and have one quarter of their genes in common, because the queen is the mother of all sub-families. Since drones develop from unfertilized eggs (see PARTHENOGENESIS) the son-drones are related to the family only through the mother-queen.

This super-family is rather complicated because of the varied genetic relationships. Also, not every sub-family is equally represented in the colony at any specific time, since sperm from drones is not randomly distributed in a queen's spermatheca. Thus, a colony of bees is a continually changing super-family with a complicated genetic nature.

The family structure of a bee colony makes the study of bee genetics and bee breeding a difficult task. Many bee characteristics of interest to both geneticists and bee breeders are behavioural characteristics of whole colonies, such as honey-production, pollination activity, overwintering ability, etc. To study or breed for change in these characteristics, the whole colony has to be considered a genetic unit or genetic individual, when clearly it is not.

Fortunately, queen bees can be instrumentally inseminated. Instrumental insemination techniques help overcome many of the problems resulting from identical sperms from a drone and the super-family structure of a bee colony. One solution to the problem of genetic evaluation is the inbred queen/single drone mating, using instrumental insemination. Such matings produce a colony with worker bees that are all very similar genetically, and thus the performance of whole colonies of bees can be judged in genetic terms.

Using the inbred queen/single drone technique, honey bee geneticists have made major contributions to the science of genetics. For example, Walter Rothenbuhler, from Ohio State University, used the technique to study the genetics of nest-cleaning behaviour in bees. He found that one gene with two alleles controlled whether or not bees would uncap cells containing dead larvae and pupae. A second independently assorting gene, also with two alleles, controlled whether or not bees would remove dead larvae and pupae once the cells were uncapped. This discovery is one of the clearest examples of genes controlling complex behaviour.

Not only does the genetic study of bees contribute to the greater understanding of general genetic principles, it also provides the foundation for modern bee breeding. By studying aspects of practical breeding, bee geneticists have made several important discoveries. For example, geneticists have shown that the variability both among and between stocks of bees is extremely large, and provides an excellent basis for stock improvement programmes. Also, bees generally respond to genetic selection breeding programmes with very strong rates of improvement. At the same time, bees seem especially likely to suffer inbreeding depression.

By considering these and other factors, bee geneticists can design breeding programmes tailored to both the needs of bee breeders and the special features of honey bee genetics. TER

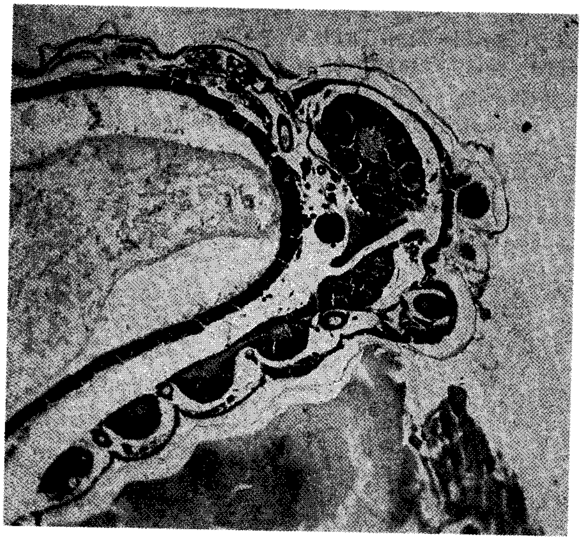
See also BREEDING HONEY BEES; GENETIC PROBLEMS OF INBREEDING.

Glands, endocrine and exocrine see **Glandular system of the honey bee**

Glandular system of the honey bee can be divided into two natural groups: the endocrine and the exocrine glands. The former secrete hormones inside the body, and the latter secrete various substances, including pheromones, to the outside. The position and structure of these glands are shown in the illustrations below.

Endocrine glands There are three major endocrine glands in the honey bee larva: the prothoracic gland, the corpora cardiaca and the corpora allata. The prothoracic gland is a very small leaf-like structure situated between the pro- and meso-thoracic segments of the larva, just behind the first spiracle on each side of the body. The gland produces ecdysone, the hormone involved in MOULTING, and is not present in the adult.

Section of honey bee larva head, showing the small round corpus allatum just behind the sub-esophageal ganglion below the brain.



The corpora allata, the corpora cardiaca and the neuro-secretory cells in the brain are all connected together by nerve fibres. The neuro-secretory cells are situated on either side of the centre line at the top of the brain, in the intercerebrales (see NERVOUS SYSTEM), which are connected to the corpus cardiacum on each side. Each corpus cardiacum is a loose body of cells attached to the wall of the aorta. The neuro-secretory cells do not, as far as is known, secrete hormones into the blood, but produce substances which pass down the nerves to the corpora cardiaca, where they are stored. The corpora cardiaca are known to secrete hormones into the blood in some insects, but little is known of their activities in the honey bee.

Each corpus cardiacum is connected to a small solid spherical body of cells, the corpus allatum, which lies on the stomodeum just behind the brain. In the larva the corpora allata produce JUVENILE HORMONE, which controls the retention of the larval type of body organization during the early period of development, and is involved in the differentiation of the female castes (see CASTE DETERMINATION). In the adult bee the corpora cardiaca and allata are present and situated on the esophagus just at the end of the pharynx. The function of the glands in the adult is not certain, but by analogy with other insects they may be involved in egg production and water control.

Exocrine glands and their products have been studied in much more detail than the endocrine glands, probably because they are larger and more easily seen, and partly because, to the beekeeper, their secretions are so obviously important to the life of the colony.

Labial glands Each lobule of the head sections (post-cerebral) has its own reservoir. Each thoracic section has a single large reservoir in its outlet duct. Secretion from all the glands is discharged by the pump at the base of the tongue. The pump cavity or lumen is enlarged by muscles that pull out its anterior wall, and collapsed by the stiffness of its posterior wall; positive pumping is ensured by a valve at the outlet and the friction of the long ducts from the glands; the walls of the ducts have circular thickenings which keep them from collapsing during suction. Secretion from the outlet is slightly alkaline water, and is used to dissolve and dilute sugary foods and wash surfaces free from them, and to moisten substances being chewed. Discharge can occcur with the tongue folded or extended. For washing, the tongue is used like a sponge, by raising and lowering