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### Sex determination in honey bees (Apinae and Meliponinae) and its consequences

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#### ABSTRACT

The first experiments on sex determination in bees began with Dzierzon, Meves, Nachtshe Petrunkevitch, Manning. Whiting, (1943) found multiple alleles in *Bracon xo* that are the Rosetta determination in Hymenoptera. Whiting also discovered that some species of microhymenoptera do not have *xo* sex alleles. Therefore, Hymenoptera apparently presents two types of sex determination: haplodiploidy. In the panmictic groups hemizygous ( $xo^1, xo^2, \dots, xo^n$ ) and homozygous ( $xo^1xo^1, xo^2xo^2, \dots, xo^nxo^n$ ) are males while heterozygous ( $xo^1xo^2, \dots, xo^{n-1}xo^n$ ) are females. There is no such series of  $xo^n$  in Hymenoptera, since the constant elimination of diploid males would be damaging to the population. A mutation of  $xo$  to  $xo^n$  would be quickly eliminated. Besides the Whiting hypothesis, four others are discarded: a) new hypothesis of genomic imprinting, of Beukeboom, is eliminated since: a) spermatozoa that do not come from the egg produce male tissue; b) telitokous parthenogenesis due to the fusion of two haploid cells produces females; c) last instar larvae treated with juvenile hormone become queens. The Cunha and Kei (female determining genes are totally or partially additive and male determination is totally nonadditive) explains all known cases. The *xo* is a female determining gene. Sex determination in social bees is due to the gradual evolution of two systems of caste determination: one in which queens and workers and males are very different (Apinae), and another in which workers and males are very similar and very different from the queens (Meliponinae). This second system in stingless bees implies that many of the genes that improve worker capacities also affect the males that will carry out some activities that in Apinae are female ones. Ten of these activities are described.

#### INTRODUCTION

The first scientific studies of sex determination in the Hymenoptera were those of Johannes Dzi

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1854, 1898, 1899). He found that a virgin queen only laid eggs that developed into drones and correctly that males originate from unfertilized eggs and females from fertilized ones. Siebold (18 spermatozoa in 30 eggs (out of 52 analyzed) collected in worker cells and none in 27 taken from which confirmed the assertion of Dzierzon. Cytological evidence was provided by Meves (1907), chromosomes in spermatogonia, and Nachtsheim (1913) who found 32 chromosomes in fertilized (1951) and Imai *et al.* (1977) have shown that the presence in females of  $2n$  chromosomes and of general for all Hymenoptera, except for the thelytokous ones. The first cytological evidence for this provided by Paulcke (1899), Petrunkevitch (1901), Nachtsheim (1913) and Manning (1950), who each egg of *Apis mellifera* receives from 8 to 20 spermatozoa, of which only one joins with one of the nuclei of the egg and later on becomes either a worker or a queen; unfertilized eggs have no sperr develop into males that are true representatives of a queens gametes. Bridges (1925), working with *melanogaster*, demonstrated that its sex is determined by a balance between genes determining maleness on the autosomes (especially in chromosome II; Kerr, 1962), and genes determining femaleness, chromosome X. Dobzhansky (1930) demonstrated the importance of environment in the sex determination in *Drosophila melanogaster*.

## HYPOTHESES FOR SEX DETERMINATION

The statement that Hymenoptera females are diploid and males haploid is a cytological description not a detailed genetic explanation. Five genetic hypotheses of sex determination have been presented and summarized they are:

1) Involvement of a single series of multiple alleles (Whiting, 1943, 1945; Mackensen, 1951). Whiting from his studies of diploid males of *Bracon hebetor* (published as *Habrobracon juglandis*). From his work he concluded that sex in this Braconid is determined by a series of at least 8 heteroalleles that in homozygous ( $xo^1xo^1, xo^2xo^2... xo^8xo^8$ ) condition are males and in heterozygous ( $xo^7xo^8$ ) are females. This was the Rosetta stone of the studies of the sex determination in the Hymenoptera. Whiting himself found that some species of microhymenoptera do not produce diploid males. Mackensen, using inbred lines of *Apis mellifera*, suggested that the same multiple alleles occurred in *Apis mellifera* (1963, 1979, 1986) actually demonstrated that in *Apis mellifera* and *Apis cerana* the homozygous di-allelic conditions were males (Hoshiba *et al.*, 1981). All endogamous Hymenoptera that have been studied and genetically have not such series of multiple alleles (Kerr *et al.*, 1988).

Among the Hymenoptera there are two systems of sex determination: one is found in endogamic species where the  $xo$  allele is male and  $xo/xo$  is female. The mutation rate of  $xo$  to  $xo^1$ , or to  $xo^2$ , or ...  $xo^n$  has an average rate of  $1.6 \times 10^{-6}$  (Kerr *et al.* 1980; Chaud- Neto *et al.*, 1983; Kerr, 1986b). This means that for every 1,600,000 gametes of a hymenopterous species about one  $xo$  mutates to  $xo^n$ . However, in natural populations no new  $xo^n$  mutations (that are constantly being produced) will be established because of unfavorable conditions for its persistence (Kerr *et al.*, 1988), namely,  $xo/xo^n$  needs to have an adaptive value greater than that of  $xo/xo$  or the haploid  $xo$  must have an adaptive value of 0.50 or smaller (the new  $xo$  being equal to 1). In a panmictic population, however, the new  $xo^n$  mutation (the homozygote produced by  $xo^n/xo^n$  drones) will become automatically established provided those  $xo/xo^n$  females have a selective advantage greater than  $xo/xo$ . The large advantage of 1/3 is not required, as is necessary in an endogamous population.

Since this mutation will occur randomly in all panmictic species, and diploid males (that produce eggs with  $2n$  chromosomes) cause genetic problems if they mate, different species selected different ways to avoid the effects of having them, for example: sterility of the diploid males, higher mortality of male larvae being eaten by the workers (Woyke, 1986) or adult diploid males and their queen (Camargo 1977a, 1979, 1984; Kerr 1987c,d); Carvalho *et al.*, 1995). The sooner the bees get rid of diploid males, the greater will be the adaptive value of the species.

2) Goldschmidt (1958), being aware of the work of Whiting (1945) but not knowing the work of Cu (1957), hypothesized that sex in Hymenoptera may be reached by an equilibrium between male genes (M) and female determining genes (F) in the following way (page 475): "The M and F determ located in different chromosomes, but both within the X-chromosome; further, they are completely and the F/M balance is such that F has a high potency which is additive in compounds but not in h the M potency is such that it has no action in the heterozygous condition (recessiveness of m) bu one in hemizygotes and homozygotes, so that MM (= mo, or mm, or  $m^a m^a m^b m^b$ ) is epistatic o Goldschmidt tried to explain and generalize the *Bracon hebetor* case. But there is no eviden chromosome in bees and Camargo (1977a,b) demonstrated that the feminizing genes xa, xb, xo are

3) Crozier (1977) suggested the hypothesis of many series of multiple alleles. In a certain way the  $\Lambda$  fits in Crozier's idea since the triple heterozygotes are females ( $x^{n-1}/x^n$ ;  $xa^1/xa^2$ ;  $xb^1/xb^2$ ). However, negates such series in the sex determination of endogamous populations: a) The lack of diploid males that naturally reproduce by obligatory endogamy (e.g., Agaonidae, *Telenomus*, *Melittobia*, *Goniozus*). Lack of diploid males in experimentally inbred populations. No diploid males were detected in 11 endogamic populations (crossing brother x sister or mother x son) of *Melittobia hawaiiensis* (V: personal communication) and in 22 lines with three to 18 generations of mother x son and 11 of brother x sister of *Muscidifurax raptor* and *M. zaraptor* (Legner, 1979). c) Cook (1993) carried out experiments with *Goniozus nephantidis* and obtained diploid males in none of them.

4) Genomic imprinting model. Beukeboom (1995) developed a model based on genomic imprinting. It assumes: 1) sex-specific imprinting of a sex-determining locus (S) that binds a product (P) which is produced by the egg. 2) Females imprint the S locus during oogenesis in such a way that it cannot bind a product (P), therefore eggs carry it in the inactive state (Si). 3) Males do not imprint the S locus and transmit it in the active state Sa, in which it does bind P. 4) The model assumes that the imprint is erased during zygotic development. 5) Binding of P to S activates the genes that turn on the female pathway, where non-binding leads to male development. Unfertilized haploid eggs are always male (non-active S locus) and fertilized diploid eggs are always female (one Sa and one Si).

Three facts eliminate this model: 1) The experiments of Walter Rothenbuler *et al.* (1952) and Rother have shown that male sperm can develop into male tissues (n) and some (that join the female nucleus) into female tissues (2n) in the same fertilization event (same egg). 2) The telytokous parthenogen *mellifera* shows females being produced without males (Tucker, 1958) by fusion of two post-meiotic nuclei. 3) Sex determination in bees is accomplished in two steps: a) few hours after fertilization in the embryo, sex is determined and b) in the prepupa when the adult characters (head, thorax, wings, and integument) are fixed; artificial addition in Meliponinae larvae of juvenile hormone determines queen or worker (Cunha *et al.*, 1995), which shows that female-determining genes of the second step are put into action by juvenile hormone and not by imprinting genes.

5) Cunha and Kerr (1957) suggested that the genes involved in the determination of male sex in endogamous Hymenoptera are not additive (are compensated) while the genes involved in the determination of femaleness are additive (or non-compensated). Subsequent to the data of Chaud-Neto (1972, 1975) and Neto and Duarte (1975) the expression "not additive" was replaced by "not additive or slightly non-additive" for genes determining femaleness; for genes determining femaleness it became "additive or almost additive". The  $xo$  gene derived from mutations in the  $xo$  gene or from themselves ( $xo^3$  to  $xo^8$ , for instance)

The following experiments favor this genic balance hypothesis.

a) Devlin *et al.* (1985) studied trisomics for the autosomes 3L and 2R in *Drosophila melanogaster* and found that four out of six enzymes determining loci produce disomic levels of the genic product, while two are dosage dependent (trisomic). However, in the X-chromosome (that acts in a haplodiploid fashion) the genes studied compensate the enzymatic level in trisomics.

b) Oliveira (1992) and Oliveira *et al.* (1992) estimated the number of protein molecules in you

female (white eyed) pupae and in adults of both *Melittobia hawaiiensis* and *Scaptotrigona pos* Meliponinae). They found that 9.2% of protein products are compensated, and 8.2% partially compensated, in a sample of 101 genic products, 5.9% were compensated, and 5.9% were partially compensated. This is the first biochemical evidence for the existence of genes with properties equal to those we have to characterize sex determining genes in the Hymenoptera. The adjustment of the genes producing different proportions of the same proteins in males and females may be done by specific genes, like *dpy* genes of *Caenorhabditis elegans* (revision in Kelley and Kuroda, 1995). Gergen (1987) found that in *Drosophila* sex determination precedes the establishment of a segmental pattern in the embryo. The expression of the X-linked pair-rule gene *runt* is already dosage compensated. Parkhurst *et al.* (1999) found that *Sxl-n1* males are lethal because their inappropriate *Sxl* expression leads to a failure of dosage compensation (sex lethal gene); *Sxl* is transcribed in both sexes but translation is truncated in males, therefore not detectable in male embryos.

c) Campos (1975, 1978) and Campos *et al.* (1975) working with *Melipona quadrifasciata*, and Bon (1985) with *Melipona compressipes*, treated about 200 last stage larvae with juvenile hormone; these treated larvae were females, but several male larvae were also treated. Campos demonstrated the action of juvenile hormone in Trigonini. Juvenile hormone is very effective in feminizing genes. Using techniques of numerical taxonomy it was demonstrated that Meliponinae are closer to males than to functional females (queens), and that juvenile hormone-treated males are closer to queens than to the untreated ones.

d) Fascinating was the work of Conceição Camargo (1977a,b): in the offspring of a brother x sister mating in *Melipona quadrifasciata* a 1:1 female to diploid males was obtained. In a group of 83 pupae raised with larvae with  $10^{-6}$  mg of juvenile hormone III, both female and diploid male adults emerged. Camargo found adults of which 38 were female queens and 45 diploid males (1:1). But among the diploid offspring segregation of phenotypes was obtained, that is, 3/4 (38) were males maintaining their beautiful bands while 1/4 (12) were brown and had a queen like shape. This indicates that besides being 2n they were also double heterozygous for the caste factors (*xa* and *xb*).

e) Chaud-Neto (1975) inseminated *Apis mellifera* queens with sperm of several diploid drones; triploid workers and queens; estimating the generalized distance between them, Chaud-Neto and D demonstrated that female-determining genes are not completely additive and male-determining genes are not entirely compensated, which would allow other genes and the environment (temperature, pH, humidity, for instance) to have a role.

f) In some species, where the genic balance is very near to equilibrium, intersexes may appear frequently. This is the case for several species of *Megachile* (such as *vidua*, *parallela*, *gemula*, *intergradus*, etc.) (Mason 1941) of *Ooencyrtus* (Wilson and Woolcock, 1960) and of Mutillidae (Quintero and Cambra, 1994, in many cases of intersexed mutillids). This balance can also be broken by aneuploidy as in *Bombus atratus* (Mason 1973 and Garofalo and Kerr, 1975).

g) The balance theory also predicts the existence of specific sexual genes, different from *xo*; for example, mutation *i* (allele of the normal gene *I*) induces intersexuality in the haploids of *Bracon hebetor* (Smith 1960).

Velthuis and Sommeijer (1991) proposed a new model for the genetic determination of caste. It is a model and deals with phenotypes. However, genetically it is equal to the one here proposed (Kerr and Kerr, 1975; Campos *et al.*, 1979, Maciel-Silva and Kerr, 1991). Using the own words of Velthuis and Sommeijer (1991, pages 366 to 368) we have: "This alternative model includes the interaction of two independent factors with food conditions (Figure 1). In this model, the first factor concerns the genetic system that determines caste development in the young larva. This development could be related to the rate of food intake, which is high or low, for instance, as the result of differences in the quality or amount of an enzyme. The enzyme is less efficient if alleles are homozygous than if they are heterozygous. The heterozygous condition favors queen development; the homozygous condition, worker development. However, both queen and worker disposition are not irreversibly fixed. They can still be modified later in life. A second gene

independent of the first, operates at a later larval phase. It regulates the production of juvenile hormone at a high or a low level. This gene is again, in the same way, more effective in its heterozygous than in its homozygous constellation. Two alleles are envisaged. The physiological translation of this genetic variation can have various forms; one of them could be that the genes lead to the production of an enzyme such as juvenile hormone synthetase. A set of two genes operating in this way allows for the existence of four classes:  $A^+/B^+$ ,  $A^+/B^-$ ,  $A^-/B^-$ , and  $A^-/B^+$ . In connection with the further development of these four classes, a mechanism is assumed that measures the amount of food ingested in the course of larval development. For the purpose of our discussion we distinguish between large and small amounts, but probably a continuous distribution exists in the amount of food ingested.

The combination of two sets of genes and two classes of food amount leads to eight categories of development. For a *Melipona* queen is  $A^+/B^+/H$ , for a worker bee  $A^-/B^-/L$ . In the latter case a low level of juvenile hormone is considered to be an adaptation to inferior food conditions. If the hormone level were higher, a higher metabolic activity would result, which would in turn lead to reduced body size in the adult; this could be disadvantageous, if not fatal ( $A^-/B^+/L$ ). However, if food amounts were higher, a larger worker or a worker that had some reserves could develop. In this part of [Figure 1](#) the categories represent the larvae that are the nearest to queen development, although they will still develop as worker only.

In the upper part of [Figure 1](#),  $A^+$  animals are predestined to become queens but  $B^-$  levels preclude this. By consequence, all  $A^+/B^-$  animals become workers. The  $A^+/B^+/L$  will become workers, while the  $A^+/B^+/H$  type will develop into queens.

The action of  $B^+$  is designed to be the most influential, because the artificial application of juvenile hormone has stronger effects than those of increasing the amount of food. It is to be expected, however, that the categories respond differently to such experimental treatments, and in addition to inducing queen development, the effect of juvenile hormone application on mortality should be considered.

The model is consistent with the observations that under natural conditions the maximum production is about 25%. This occurs when food conditions are excellent and, as a consequence, no  $L$  categories are present. Frequently the percentages of queens under natural conditions are lower and correspond to the ratio  $A^+/B^+$  category".

The demonstration that this model is equal to the genetic model is:

### Velthuis and Sommeijer model

$$A^+ = xa^1/xa^2$$

$$A^- = xa^1/xa^1 \text{ or } xa^2/xa^2$$

$$B^+ = xb^1/xb^2$$

$$B^- = xb^1/xb^1 \text{ or } xb^2/xb^2$$

therefore, in genetic terms we have:

$$1 = A^+/B^+ = xa^1/xa^2; xb^1/xb^2$$

### Kerr model

$$2 = A^+/B^- = xa^1/xa^2; xb^1/xb^1 \text{ or } xa^1/xa^2; xb^2/xb^2$$

$$3 = A^-/B^- = xa^1/xa^1; xb^1/xb^1 \text{ or } xa^1/xa^1; xb^2/xb^2; \text{ or}$$

$$xa^2/xa^2; xb^1/xb^1 \text{ or } xa^2/xa^2; xb^2/xb^2$$

$$4 = A^-/B^+ = xa^1/xa^1; xb^1/xb^2 \text{ or } xa^2/xa^2; xb^1/xb^2$$

## TWO SYSTEMS OF CASTE DETERMINATION

Sex determination in bees occurs in two distinct phases: i) the first takes place in the early hour development (three to eight hours, according to the species).

In endogamic populations of Hymenoptera, sex is controlled by an interacting set of maleness- and determining genes. In panmictic populations one of the  $xo$  femaleness-determining gene mutated to  $xo^n$ , which in bees contains eight to about 34 hetero-alleles (Mackensen, 1955; Laidlaw *et al.*, 1955; *al.*, 1977; Kerr, 1987a,b) depending on the population size and species. This locus  $xo^n$  determines heterozygous, diploid males when homozygous and normal haploid males when hemizygous. The hetero-alleles originated by mutation of the primitive gene  $xo$  (Kerr *et al.*, 1988). ii) The second phase is under the control of genes that act in the last larval stage, that is, they determine the future of the head and of the majority of the imaginal discs, except those whose fate had been determined in an earlier stage, like the antennae and genitalia (Kerr, 1987a). In the stingless bees femaleness-determination is made functional mainly by juvenile hormone (Campos, 1975; Campos *et al.*, 1975; Kerr *et al.*, 1975; *al.*, 1983).

A direct consequence of this system of sex determination is the evolution of two types of caste determination: a) superior bees (Kerr *et al.*, 1978; Kerr, 1987a,b,c; Kerr and Cunha, 1990).

a) One, in which specialization of the queen and workers has not drastically affected the workers nor their female characters, that is, the workers are more similar to queens than both are to males (as in

b) Another in which juvenile hormone became, in many evolutionary steps, gradually more important. Femaleness genes into action determining modifications in the workers and in the queens and, as a result, workers become more similar to males at each step (as in Meliponinae and some *Bombus*) and queens gradually more different from workers.

## WORKERS SIMILAR TO MALES; MALES DOING FEMALE WORK

As a result of the Meliponinae system of caste determination, workers are similar to males (Kerr 1990) and many mutations that are selected for improving worker capacities (and consequently survival) may also affect the males.

The demonstration of this is found in males of Meliponinae and Bombinae (and also in some Halictinae and some wasps) that perform activities that in *Apis* are reserved to the workers, like:

1) Incubation. Males of all stingless bees so far studied remain in the comb of young brood in a position as do the workers (Kerr, 1987a; Cortopasi-Laurino, 1979). The incubation behavior of male *griseocollis* and *Bombus pennsylvanicus* has also been described (Cameron, 1985).

2) Trophallaxis. Males of *Plebeia droryana* perform trophallaxis with males and with workers for most within the hive (about 15 days) (Cortopasi-Laurino, 1979). Trophallaxis between males was observed in *Melipona quadrifasciata* (Silva, 1977), *Scaptotrigona postica* (Engels and Engels, 1988) and in *Melipona compressipes*.

3) Feeding the queen. Cortopasi-Laurino (1979) saw young males feeding the queen of *Plebeia Imperatriz-Fonseca* (1970) found frequent trophallaxis between males and a virgin queen of *subnuda*. I saw a male of *M. quadrifasciata* feeding the queen before mating, in a cage.

4) Self-cleaning. Males of *Plebeia droryana* (Cortopasi-Laurino, 1979) and of *Melipona*, *Scaptotrigona* and *Bombus* do self-grooming.

5) Secretion of wax. Drory (1874, 1877, 1883) was the first bee researcher to observe wax scale: *Melipona marginata* and *Melipona scutellaris*. Kerr (1951, p. 313) observed in colonies of *Melipona rufiventris* and *Plebeia droryana* hundreds of males producing wax abundantly. Cruz-Landim (1967) studied the histological glands in males. Nogueira Neto (1963) observed wax being produced by males of *Nannotrigona testaceicornis*. Males of *M. rufiventris* (Kerr, 1950), and *M. compressipes* (Kerr, 1987a) were seen producing wax. Males of *M. compressipes* behaving like workers, taking the wax scales from their tergites and putting the wax deposits around the brood nests.

6) Working with the wax. The most general task that every worker carries out is to work with the wax. Males of *Melipona rufiventris* and *Melipona compressipes* working with wax, building small wax columns and involucrum sheets. I never saw them building the cells in which queens are going to deposit eggs. This appears to be done exclusively by the selected group of female workers that provides cells for oviposition.

7) Receivers and dehydrators. Males normally receive nectar directly from field workers and dehydrate it within the hive in the same way as do workers. Imperatriz-Fonseca (1973) saw males of *Schwarziana quadrifasciata* and Cortopasi-Laurino (1979) saw males of *Plebeia droryana* dehydrating nectar; Ferreira (1979, communication) saw males of *Melipona marginata* doing this task within the hive. No males were seen concentrating nectar in the honey pots. Recently, I observed in my meliponid apiary males of *Melipona rufiventris* and *M. scutellaris* dehydrating nectar outside the hive (standing on the wall of the building) one to five meters from the nearest hive, or right on the front hive board 20 cm far from the entrance. Males of the species permanently leave the colony after they reach about one third of their adult life and search for new flowers by themselves. During the time a virgin queen normally goes on her nuptial flight (each species has its preferred hours) many males stop foraging and stay close to the hive; dehydration of a nectar with 20% sugar would make a 90-mg male 33% lighter, what could allow it to be "the" only male that is able to feed a meliponid virgin queen.

8) Foraging. Many researchers found either through direct observation, or by occasional collection in the field, that males of many species of meliponids on flowers. Males of *Scaptotrigona postica* were seen collecting pollen in *Senecio brasiliensis* and *Dombeya acutangula* (Kerr et al., 1962) and males of *Plebeia droryana* collected nectar in flowers of *Croton floribundus* (Nogueira-Neto, 1964). I observed males of *Melipona mombuca* visiting daisies (*Chrysanthemum leucanthemum*). Brenha (1986) found males of *Melipona compressipes* in flowers of *Cordia multispicata* and Gondin (1984) saw males of *M. seminigra* in flowers of *Paullinia cupana sorbilis*.

Males of Euglossinae and Bombinae are, in many cases, considered good pollinators. Therefore, the absence of males in *Melipona mellifera* in which males are worker dependent for their feeding may be a recent evolution.

9) Communication. Workers of *Melipona rufiventris*, *Melipona quadrifasciata*, *Melipona bicolor*, *Melipona compressipes* and *Melipona scutellaris* (Kerr and Rocha 1988; Kerr, 1994) were found to perform communication by a smell odor track made near to the food source and by sounds produced inside the hive whose frequency and sound duration, like in *Apis*, have a high correlation with the distance between the hive and the food source (Esch, 1965; Von Frisch, 1967; Kerr and Rocha, 1988). In January 1989, I saw males of *Melipona rufiventris* and on November 16, 1989 males of *M. scutellaris* on an artificial food source 12 m from the hive.

observed again many times. These facts indicate that those males are also able to understand all same communication signs used among their sisters or mothers (0 to 95% of males, according to are sons of the workers; Beig, 1968).

10) Guards. In most meliponid species males leave the colony after migration of spermatozoa from the seminal vesicles is completed. Then, gradually they increase the distance from the mother hive tendency to congregate near a queenless colony (Kerr *et al.*, 1962; Kerr, 1973). Three times I saw *Melipona scutellaris* that was watching the hive entrance when a common spider (Salticidae) was approaching the entrance in order to catch one of the leaving or entering workers. Suddenly, the male flew toward the spider, jumped and ran away, interrupting the hunting of the day. Therefore, these males can occasionally act as external guards of the colony. Drummond (in press) observed that males of the wasp species *Zethenia* (Eumenidae) have an important role in nest defense during periods when females are absent from the nest. Sphecid males are also commonly involved in nest guarding (reviewed in Drummond, in press).

All these "worker" tasks carried out by males of stingless bees indicate that many more observations on different meliponine and other Hymenoptera species should be made. The observations cited here support the idea that, since the method of worker determination is a lack of activating femaleness-determining gene (a small amount of juvenile hormone), workers gradually become very similar to males. Consequently, a mutation that would improve the fitness of the workers would also induce the males to carry out those same tasks. The main selective forces that would keep males from becoming true workers would need to be fit and to be in the right time and in the right place for reproduction (Kerr, 1990).

The Brazilian Indians are very good observers of nature, but they cannot distinguish workers from Meliponinae bees; they use the word "fathers" for both adult males and workers of stingless bees.

The first mention in the scientific literature that the males "are very similar in appearance to the workers" point that it is not known whether they were among the swarms"... is from Salt (1929, p. 435).

Workers and males of stingless bees have an external morphology very similar to each other as on the figure painted by Camargo of *Melipona quadrifasciata* (front cover of both the journal "Ciência e Natura", Kerr, 1973, and the book by Schmidt, 1974). Distinction of males and workers of *Tetragonisca angustula* of the greatest experts in bee taxonomy can only be precisely made with the help of a magnifying glass.

Kerr and Cunha (1990) studied, using various methods, the morphological differences and similarities between workers, males and queens. They made 3096 measurements in *Bombus atratus*, 1935 in *Scaptotrigona* using 43 characters for each bee; generalized distances of Mahalanobis were estimated for six species of Meliponinae and in *Bombus atratus* their final morphology indicates that workers of these species are much more similar to males than to queens, contrary to what happens in *Apis* species. The explanation rests in the action of juvenile hormone that, as demonstrated by Campos, Velthuis and Camargo, Cruz-Landim and Kerr, activates the genes that determine femaleness if applied near the end of the phase; lack of juvenile hormone, due to a small size of the worker *corpora allata* or a small number of *corpora allata*, caused by haploidy or by a smaller amount of food (Kerr *et al.*, 1966), makes both the worker and the organs derived from the imaginal discs acquire male forms. Larger titers of juvenile hormone activate a battery of genes that determine female characteristics.

Morphological variations are the product of two evolutionary forces: selective (Darwinian) or chance (Kimuran). For this case of morphological convergence between males and females, it is very difficult to see a Kimuran process, especially since it happens in a great number of species; therefore, it may be with a good degree of certainty that they were submitted to strong and permanent selective pressure. The consequences for the workers were: a) being masculine on the outside, they do not attract males; b) the glandular system is more similar to males than to queens (Mota, 1988; Kerr, 1987a,c,d); c) in many species workers do not lay eggs even when a colony is queenless for many days (Kerr, 1987a,b).

Hartfelder and Engels (1992) found that among four characters (their Figure 4) when analyzing logarithmic plots, in two of them (eye width and tergite 2 length) workers are nearer to males than



one (head length) the data are overlapping, and the only one that makes the workers closer to queen than males is the scape. It is not surprising that scape difference between males and females is one of the few that persist since, like distinctive genitalia, it is a very fundamental and evidently ancient sex-specific character. In Sphecoidea, Apoidea, Vespoidea and Scolioidea there are almost always 13 segments in the male and 12 in the female (Riek, 1970). Figure 5 of Hartfelder and Engels (1992) is very similar to the ones for other species of *Melipona*, but all of them are very different from *Apis mellifera* (Kerr and Cunha, 1990). However, Engels (1992) may have discovered that the development of males and workers follows an allometric pattern in order to attain a similar adult appearance, where selection acts.

In all social insects caste is determined by genes and environment. A very elegant work in *Apis mellifera* was carried out by Severson *et al.* (1989). They provided clear evidence that the worker and queen differences in patterns of transcriptional activity during the larval and prepupal stages of development. Northern blot electrophoresis shows that queens and workers exhibit caste-specific differences in levels of translation products at the 83rd h after hatching. These differences become more striking by 156 h, with an increase in 71 and 27-kDa translation products in queen prepupae, while worker exhibit an obvious increase in only one translation product. Since queen and worker pupae exhibit less defined caste-specific differences in translatable RNAs the conclusion is that the genic mechanisms of caste determination occur mainly during the larval stages and prepupae. These stages are the only ones found in female larvae of *Melipona* where Campos, Velthuis, Bonetti and Kerr to react with juvenile hormone, transforming 100% of them into queens when good techniques are used (Bonetti *et al.*, 1995).

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## RESUMO

São relatados os primeiros experimentos sobre determinação do sexo em abelhas, iniciando com os trabalhos de Meves, Nachtsheim, Paulcke, Petrunkevitch e Manning. Whiting descobriu em *Bracon* alelos múltiplos  $x^0$  a  $x^n$  são considerados a pedra Rosetta da determinação do sexo em himenópteros. O próprio Whiting encontrou em algumas espécies de micro-himenópteros não têm alelos múltiplos  $x^0$  a  $x^n$ . Logo, nos himenópteros aparentemente dois tipos de determinação do sexo superpostos a haplodiploidia. Nos panmíticos há genes  $x^0, x^1, x^2 \dots x^n$  para os quais os hemizigotos  $x^0$  a  $x^n$  e homozigotos,  $x^0x^0$  até  $x^nx^n$  são heterozigotos  $x^0x^1, x^0x^2, \dots, x^{n-1}x^n$  são fêmeas. Nos endogâmicos não há essa série de alelos múltiplos. A hipótese de Whiting de que a mutação de  $x^0$  para  $x^n$  é rapidamente eliminada, a não ser quando o heterozigoto for muito mais viável. A hipótese básica de Whiting, discutem-se outras 4 hipóteses que tentam explicar a genética da determinação do sexo nos Hymenoptera. A nova hipótese, da impressão genômica, de Beukeboom, é eliminada pelos fatos: a) espermatozoides que se desenvolvem em ovos dão origem a tecidos masculinos; b) a ovotelia produz fêmeas e c) as larvas em último estágio, tratadas adequadamente com hormônio juvenil desenvolvem-se em rainhas. A hipótese que explica todos os casos conhecidos ainda é a do balanço de Kerr e Cunha, com pequenas modificações. A determinação do sexo nas abelhas sociais implica a evolução de dois sistemas de determinação das castas. Um em que as rainhas e as operárias se desenvolvem a partir de machos é diferente (Apíneos), e outro em que as operárias e os machos se parecem e são diferentes (Meliponíneos). Neste segundo sistema (Meliponíneos), os machos passam a, gradualmente, assumir atividades que são normalmente de fêmeas. São apresentadas 10 dessas atividades.

## REFERENCES

- Adams, J., Rothman, E.D., Kerr, W.E. and Paulino, Z.L.** (1977). Estimation of the number of sex queen matings from diploid male frequencies in a population of *Apis mellifera*. *Genetics* 8 [ [Links](#) ]
- Beig, D.** (1968). Produção de machos e desenvolvimento embrionário em *Trigona (Scaptotrigona)* thesis, UNESP, Rio Claro, SP. [ [Links](#) ]
- Beukeboom, L.W.** (1995). Sex determination in Hymenoptera: a need for genetic and molec *BioEssays* 17: 813-816. [ [Links](#) ]
- Bonetti, A.M. and Kerr, W.E.** (1985). Sex determination in bees. XX. Estudo da ação gênica *marginata* e *Melipona compressipes* a partir de análise morfométrica. *Braz. J. Genet.* 8: 629-638.
- Bonetti, A.M, Kerr, W.E. and Matusita, S.H.** (1995). Effects of juvenile hormones I, II and III, fractionated dosage in *Melipona* bees. *Braz. J. Genet.* 55 (Suppl. I): 113-120. [ [Links](#) ]
- Borstel, R.C. Von and Smith, P.A.** (1960). Haploid intersexes in the wasp *Habrobracon*. *Heredit* [ [Links](#) ]
- Brenha, S.L.A.** (1986). Abelhas sociais (Apidae, Apoidea) e seus hospedeiros alimentares em S Brasil. Monography for obtaining the degree of BSc of Biology. Fed. Univ. Maranhão, São Luís [ [Links](#) ]
- Bridges, C.B.** (1925). Sex in relation to chromosomes and genes. *Am. Nat.* 59: 127-137. [ [Lin](#)
- Camargo, C.A.** (1977a). Properties of the xo gene, sex determi- nation in *Melipona quadri*. (Hymenoptera, Apidae). *VIII Congress Int. Union for the Study of Soc. Insects*, pp. 191-192. [ [Links](#) ]
- Camargo, C.A.** (1977b). Effect of juvenile hormone on diploid drones of *Melipona quadri* (Hymenoptera, Apidae). *VIIIth Int. Congress IUSSI*, pp. 193-194. [ [Links](#) ]
- Camargo, C.A.** (1979). Sex determination in bees. XI. Production of diploid males and sex dete *Melipona quadrifasciata*. *J. Apic. Res.* 18: 77-84. [ [Links](#) ]
- Camargo, C.A.** (1984). Spermatozoa numbers and migration to the seminal vesicles in haploid and of *Melipona quadrifasciata* Lep. *J. Apic. Res.* 23: 15-17. [ [Links](#) ]
- Cameron, S.A.** (1985). Brood care by male bumble bees. *Proc. Nat. Acad. Sci. USA* 82: [ [Links](#) ]
- Campos, L.A.O.** (1975). Determinação de castas do gênero *Melipona* (Hymenoptera, Apidae). Papel juvenil. Masters thesis, Dept. Genética, Fac. Medicina de Ribeirão Preto, USP, Ribeirão Preto [ [Links](#) ]
- Campos, L.A.O.** (1978). Sex determination in bees. VI. Effect of a juvenile hormone analogue i females of *Melipona quadrifasciata* (Apidae). *J. Kans. Entomol. Soc.* 51: 228-234. [ [Links](#) ]
- Campos, L.A., Velthuis, K.F. and Velthuis, H.H.** (1975). Sex determination in bees. VII. Effe hormone analogues in caste determination of *Melipona*. *Naturwissenschaften* 62: 98-99. [ [Links](#)

- Campos, L.A.O., Drummond, M.S. and Lacerda, L.M.** (1983). Determinação do sexo em abelhas do hormônio juvenil I, II, III, na diferenciação das castas de *Scaptotrigona xanthotricha* (Hymenoptera: *Ciênc. Cult.* 35: 209-211. [ [Links](#) ]
- Carvalho, G.A., Kerr, W.E. and Nascimento, V.A.** (1995). Sex determination in bees. XXXIII. De hetero-alleles in a finite population of *Melipona scutellaris* (Apidae, Meliponinae). *Braz. J. Genet.* [ [Links](#) ]
- Chaud-Neto, J.** (1972). Operárias triplóides em *Apis mellifera*. In: *Em homenagem a Warwick Esteves Claro*, Brasil, pp. 63-70. [ [Links](#) ]
- Chaud-Neto, J.** (1975). Sex determination in bees. II. Additivity of maleness genes in *Apis mellifera*. *Braz. J. Genet.* 79: 213-217. [ [Links](#) ]
- Chaud-Neto, J. and Duarte, F.M.** (1975). Sex determination in bees. V. The action of sexual genes in *Apis mellifera*. *Ciênc. Cult.* 27: 125-129. [ [Links](#) ]
- Chaud-Neto, J., Kerr, W.E. and Bezerra, M.A.F.** (1983). Mutation in honeybees. 2. Average rate based on seven genes for eye colour. *J. Apic. Res.* 22: 17- 21. [ [Links](#) ]
- Cook, J.M.** (1993). Experimental tests of sex determination in *Goniozus nephantidis* (Hymenoptera: *Heredity* 71: 130-137. [ [Links](#) ]
- Cortopasi-Laurino, M.** (1979). Observações sobre a atividade de machos de *Plebeia droryana* Fr (Meliponinae). *Rev. Bras. Ent.* 2: 177-191. [ [Links](#) ]
- Crozier, R.H.** (1977). Evolutionary genetics of the Hymenoptera. *Ann. Rev. Entomol.* 26: 1-22. [ [Links](#) ]
- Cruz-Landim, C.** (1967). Estudo comparativo de algumas glândulas de abelhas e respectivas funções evolutivas. *Arg. Zool. São Paulo*, 15: 177-290. [ [Links](#) ]
- Cunha, A.B. and Kerr, W.E.** (1957). A genetical theory to explain sex determination by a parthenogenesis. *Forma Functio* (4): 33-36. [ [Links](#) ]
- Devlin, R.H., Grigliatti, T.A. and Holm, D.G.** (1985). Gene dosage compensation in trisomics of *Drosophila melanogaster*. *Dev. Genet.* 64: 39-58. [ [Links](#) ]
- Dobzhansky, T.** (1930). Genetical and environmental factors influencing the type of intersexes in *Drosophila melanogaster*. *Am. Nat.* 64: 261-271. [ [Links](#) ]
- Drory, E.** (1874). Arbeit über Meliponen. *Bienenzeitung* 30: 281-286. [ [Links](#) ]
- Drory, E.** (1877). Les mélipones et les trigones. *Rucher J. d'Apic. Rationnelle* 5: 144-149. [ [Links](#) ]
- Drory, E.** (1883). Nouvelles observations sur les mélipone. *Le Rucher du Sud-Duest* 1: 59-61.
- Drummond, M.S.** (1997). A system of social interaction in *Zethus miniatus* based on the analysis of social viability: consideration on the evolution of eusociality in Hymenoptera. *Braz. J. Genetics* (in press).
- Dzierzon, J.** (1845). Gutachten über die von Herrn Direktor Stohr im ersten und zweiten Kapitel Gutachtens aufgestellten Fragen. *Bienenzeitung* 1: 109- 113, 119-121. [ [Links](#) ]

- Dzierzon, J.** (1854). Fernere Beobachtungen über Vermehrung und Reinerhaltung der italienischen Biene. *Bienenzeitung* 10: 251-254. [ [Links](#) ]
- Dzierzon, J.** (1898). Widerlegung der jüngst gegen meine Theorie der Fortpflanzung der Biene vorgebrachten Einwände. 43 Wanderversammlung. Salzburg. *Bienenzeitung* 54: 299-302. [ [Links](#) ]
- Dzierzon, J.** (1899). Grundlosigkeit und Haltlosigkeit der neuen Lehre. Erste Wanderversammlung.... in Köln a. Rh. *Bienenzeitung* 55: 318-320. [ [Links](#) ]
- Engels, E. and Engels, W.** (1988). Age-dependent queen attractiveness for drones and mating in honey bees, *Scaptotrigona postica*. *J. Apic. Res.* 27: 3-8. [ [Links](#) ]
- Garofalo, C.A.** (1973). Occurrence of diploid drones in a neotropical bumble bee. *Experientia* 29: 115-116. [ [Links](#) ]
- Garofalo, C. and Kerr, W.E.** (1975). Sex determination in bees. I. Balance between femaleness and maleness genes in *Bombus atratus*. *Genetica* 45: 203-209. [ [Links](#) ]
- Gergen, J.P.** (1987). Dosage compensation in *Drosophila*: evidence that daughterless and sex-lethal chromosome activity at the blastoderm stage of embryogenesis. *Genetics* 117: 477-485. [ [Link](#) ]
- Goldschmidt, R.B.** (1958). *Theoretical Genetics*. X. University of California Press, Berkeley, CA. [ [Links](#) ]
- Gondim, C.G.E.** (1984). Alguns aspectos da biologia reprodutiva do guaraná (*Paullinia cupana* Mart., Ducke). Masters thesis, Univ. Amazonas, Manaus, AM, Brasil. [ [Links](#) ]
- Hartfelder, K. and Engels, W.** (1992). Allometric and multivariate analysis of sex and caste polymorphism in the neotropical stingless bee *Scaptotrigona postica*. *Insectes Soc.* 39: 1-16. [ [Links](#) ]
- Hoshiba, H., Ichiji, O. and Kusanagi, A.** (1981). The diploid drone of *Apis cerana japonica* chromosomes. *J. Apic. Res.* 20: 143-147. [ [Links](#) ]
- Imai, H.T., Crozier, R.H. and Taylor, R.W.** (1977). Karyotype evolution in ants. *Chromosoma* 86: 1-12. [ [Links](#) ]
- Imperatriz-Fonseca, V.L.** (1970). Aspectos da biologia de *Paratrigona subnuda*. Masters thesis, Univ. de São Paulo, Brasil. [ [Links](#) ]
- Imperatriz-Fonseca, V.L.** (1973). Miscellaneous observations on the behavior of *Schwarziana quadrifasciata*. *Biol. Zool. Biol. Mar.* 30: 633-640. [ [Links](#) ]
- Kelley, R.L. and Kuroda, M.I.** (1995). Equality of X chromosomes. *Science* 270: 1607-1610. [ [Links](#) ]
- Kerr, W.E.** (1950). Estudos sobre a genética de populações de himenópteros em geral e dos apídeos em particular. "Livre Docência" thesis, ESALQ, USP. [ [Links](#) ]
- Kerr, W.E.** (1951). Bases para estudo da genética de populações dos Hymenoptera em geral e dos Apidae em particular. *Anais da ESALQ, USP, Piracicaba, SP, Brasil*, 8: 219-354. [ [Links](#) ]
- Kerr, W.E.** (1962). Genetics of sex determination. *An. Rev. Entomol.* 7: 157-176. [ [Links](#) ]
- Kerr, W.E.** (1973). Genética e Biologia de abelhas. *Ciênc. Cult.* 25: 927-934. [ [Links](#) ]

- Kerr, W.E.** (1986a). Determinação do sexo nas abelhas. XVI. Informações adicionais sobre alelos *Rev. Bras. Biol.* 47: 111-112. [ [Links](#) ]
- Kerr, W.E.** (1986b). Mutation in bees. 3. Application in bee populations of a mutation rate of  $m =$  *Braz. J. Genet.* 9: 1-10. [ [Links](#) ]
- Kerr, W.E.** (1987a). Biologia, manejo e genética de *Melipona compressipes fasciculata* Smith (Hymenoptera, Apidae). Thesis for Full Professor of Genetics, Univ. Federal do Maranhão, S. Luis, Brasil. [ [Link](#) ]
- Kerr, W.E.** (1987b). Sex determination in bees. XVII. Systems of caste determination in the Apinae and Bombinae and their phylogenetical implications. *Braz. J. Genet.* 10: 685-694. [ [Links](#) ]
- Kerr, W.E.** (1987c). Sex determination in bees. XXIV. Critical appraisal of sex determination in honeybees (Japanese). *Honeybee Sci.* 8: 176-182. [ [Links](#) ]
- Kerr, W.E.** (1987d). Sex determination in bees. XXI. Number of sex-heteroalleles in a natural population of *Melipona compressipes fasciculata* (Apidae). *Insectes Soc.* 34: 274- 279.
- Kerr, W.E.** (1990). Why are workers in social Hymenoptera not males? *Braz. J. Genet.* 13: 133-136. [ [Links](#) ]
- Kerr, W.E.** (1994). Communication among *Melipona* workers (Hymenoptera, Apidae). *J. Insect Behav.* 128. [ [Links](#) ]
- Kerr, W.E.** and **Cunha, R.** (1990). Sex determination in bees. XXVI. Masculinism of workers in the honeybee. *J. Genet.* 13: 479-489. [ [Links](#) ]
- Kerr, W.E.** and **Esch, H.** (1965). Comunicação entre as abelhas sociais brasileiras e sua contribuição ao entendimento de sua evolução. *Ciênc. Cult.* 17: 527-538. [ [Links](#) ]
- Kerr, W.E.** and **Rocha, R.** (1988). Comunicação em *Melipona rufiventris* e *M. compressipes*. *Ciência e Tecnologia* 1200-1202. [ [Links](#) ]
- Kerr, W.E., Zucchi, R., Nakadaira, I.T.** and **Butolo, J.E.** (1962). Reproduction in the social honeybee. *Entomol. Soc.* 70: 265-276. [ [Links](#) ]
- Kerr, W.E., Stort, C.G.** and **Montenegro, M.J.** (1966). Importância de alguns fatores ambientais na determinação de castas do gênero *Melipona*. *An. Acad. Bras. Ciênc.* 32: 149-168. [ [Links](#) ]
- Kerr, W.E., Akahira, Y.** and **Camargo M.A.** (1975). Sex determination in bees. IV. Genetic control of sex hormone production in *Melipona quadrifasciata*. *Genetics* 81: 749-759. [ [Links](#) ]
- Kerr, W.E., Cunha, R.** and **Pisani, I.F.** (1978). Genética da determinação do sexo. XII. Aplicação de testes numéricos para agrupar sexos e castas de *Melipona quadrifasciata anthidioides* Lep. (Apidae). *Rev. Bras. Zool.* 38: 319-324. [ [Links](#) ]
- Kerr, W.E., Chaud-Neto, J.** and **Silva, A.T.** (1980). Mutação em abelhas. I. Taxa de mutação de genes que afetam a cor dos olhos nas abelhas. *Braz. J. Genet.* 3: 275-284. [ [Links](#) ]
- Kerr, W.E., Monteiro, S.G.** and **Kerr, H.A.S.** (1988). Sex determination in bees. XXV. Adaptive value of the *sex* gene in its origin. *Braz. J. Genet.* 11: 469-473. [ [Links](#) ]
- Laidlaw, H.H., Gomes, F.P.** and **Kerr, W.E.** (1956). Estimation of the number of lethal alleles in honeybees. *Genetics* 41: 101-106. [ [Links](#) ]

population of *Apis mellifera*. *Genetics* 41: 179-188. [ [Links](#) ]

**Legner, E.F.** (1979). Prolonged culture and inbreeding effects on reproductive rates of two Pterom of muscoid flies. *Ann. Soc. Am.* 72: 114-118. [ [Links](#) ]

**Maciel-Silva, V.** and **Kerr, W.E.** (1991). Sex determination in bees. XXVII. Castes obtained from homogenized food in *Melipona compressipes* (Hymenoptera, Apidae). *Apidologie* 22: 15-19. [ [Links](#) ]

**Mackensen, O.** (1951). Viability and sex determination in the honey bee (*Apis mellifera*). *Genetics* . [ [Links](#) ]

**Mackensen, O.** (1955). Further studies on a lethal series in the honey bee. *J. Hered.* 46: 72-74.

**Makino, S.** (1951). *An Atlas of the Chromosome Numbers in Animals*. 2nd edn. (First American Edition) 290. The Iowa State College Press, Ames, Iowa, USA. [ [Links](#) ]

**Manning, F.J.** (1950). Sex determination in the honey bee. V. The sperm. *Microscope* 7: 303-305.

**Meves, F.** (1907). Die Spermatocytenteilung bei der Honigbiene (*Apis mellifica* L.), nebst Bemer Chromatinreduktion. *Arch. Mikr. Anat. Entw.* 70: 414-491 + 5 tables. [ [Links](#) ]

**Mitchell, T.B.** (1929). Sex anomalies in the genus *Megachile*, with descriptions of new species (Hymenoptera, Megachilidae). *Trans. Am. Entomol. Soc.* 54: 321-383. [ [Links](#) ]

**Mitchell, T.B.** (1941). Some additional intersexes in *Megachile* (Hymenoptera, Megachilidae). *Pan-t* 17: 165-168. [ [Links](#) ]

**Mota, M.H.V.B.** (1988). Estudo comparativo das glândulas epidérmicas do abdômen dos (Hymenoptera, Apidae, Meliponinae). Doctoral thesis. IBRC/ UNESP, Rio Claro, SP, Brasil. [ [Links](#) ]

**Nachtsheim, H.** (1913). Cytologische Studien über die Geschlechtsbestimmung bei der Honigbiene (*Apis mellifica* L.). *Arch. Zellforsch.* 11: 169-241. [ [Links](#) ]

**Nogueira-Neto, P.** (1963). Novas pesquisas sobre Meliponíneos. *Chácaras Quintas* 108: [ [Links](#) ]

**Nogueira-Neto, P.** (1964). Abelhas indígenas sem ferrão - algumas observações. *Chácaras Quintas* 692. [ [Links](#) ]

**Oliveira, D.A.G.** (1992). Compensação de dose em *Scaptotrigona postica* (Hymenoptera, Apidae) e *Melittobia hawaiiensis*. Masters thesis, UNESP, Rio Claro, SP. [ [Links](#) ]

**Oliveira, D.A.G., Kerr, W.E.** and **Palma, M.S.** (1992). Compensação de dose em *Scaptotrigona postica* (Hymenoptera, Apidae). Proceedings of the X Congresso Latino Americano e XXXVIII Congresso Genética. *Braz. J. Genet.* 15 (Suppl. 1): 256-260. [ [Links](#) ]

**Parkhurst, S.M., Bopp, D.** and **Horowicz, I.S.H.** (1990). X:A, The primary sex-determining gene in *Drosophila* is transduced by Helix-loop proteins. *Cell* 63: 1179-1191. [ [Links](#) ]

**Paulcke, W.** (1899). Zur Frage der parthenogenetischen Entstehung der Drohnen (*Apis mellifica*). *A* 185-187. [ [Links](#) ]

**Petrunkewitsch, A.** (1901). Die Richtungkörper und ihr Schicksal im befruchteten und unbefruchteten Honigbiene (*Apis mellifica* L.). *Zool. Anz.* 27: 1-10.

Bienenei. *Zool. Jahrb. Anat. u. Ont.* 14: 573-608. [ [Links](#) ]

**Quintero, D.A** and **Cambra, R.A.T.** (1994). Systematics of *Pseudomethoca areta* (Cameron): sex description of the male and a gynandromorph and a new synonymy (Hymenoptera, Mutillidae). *J. Apic. Res.* 2: 303-308. [ [Links](#) ]

**Riek, E.F.** (1970). Hymenoptera (wasps, bees, ants). In: *The Insects of Australia* (Michener, C.D., ed.), Australian Journal of Entomology, C.S.I.R. Org., Canberra, Austrália, pp. 867-983 (pages 943-951, on bees). [ [Links](#) ]

**Rothenbuler, W.** (1957). Diploid male tissue as new evidence on sex determination in honey bees. *J. Apic. Res.* 2: 160-168. [ [Links](#) ]

**Rothenbuler, W.C., Gowen, J.W.** and **Park, W.** (1952). Androgenesis and zygogenesis in gynodioecious honeybees (*Apis mellifera* L.). *Science* 115: 637-638. [ [Links](#) ]

**Salt, G.H.** (1929). A contribution to the ethology of the Meliponinae. *Trans. Ent. Soc. Lond.* 7: 1-10. [ [Links](#) ]

**Schmidt, G.H.** (1974). Sozialpolymorphismus bei Insekten. Wissenschaftliche Verlag. MBH Stuttgart. [ [Links](#) ]

**Severson, D.W., Williamson, J.L.** and **Aiken, J.M.** (1989). Caste-specific transcription in the honey bee. *Insect Biochem.* 19: 215-220. [ [Links](#) ]

**Siebold, C.TH.** (1856a). Wahre Parthenogenesis bei Schmetterlingen und Bienen. Engelmann. [ [Links](#) ]

**Siebold, C.TH.** (1856b). Die Drohneneier sind nicht befruchtet. *Bienenzeitung* 12: 181-184. [ [Links](#) ]

**Silva, D.L.N.** (1977). Estudos bionômicos em colônias mistas de Meliponinae (Hymenoptera, Apoidea). *Univ. S. Paulo* 2: 7-106. [ [Links](#) ]

**Tucker, K.W.** (1958). Automitotic parthenogenesis in the honey bee. *Genetics* 43: 299-316. [ [Links](#) ]

**Velthuis, H.H.W.** and **Sommeijer, M.J.** (1991). Roles of morphogenetic hormones in caste polyphenism in stingless bees. In: *Morphogenetic Hormones in Arthropods: Roles in Histogenesis, Organogenesis and Morphogenesis* (Gupta, A.P., ed.). Rutgers University Press, New Brunswick, New Jersey, USA, pp. 1-12. [ [Links](#) ]

**Von Frisch, K.** (1967). *The Dance Language and Orientation of Bees*. Belknap Press of Harvard University Press, Cambridge, MA, USA. [ [Links](#) ]

**Whiting, P.W.** (1943). Multiple alleles in complementary sex determination of *Habrobracon*. *Genetics* 32: 382. [ [Links](#) ]

**Whiting, P.W.** (1945). The evolution of male haploidy. *Quart. Rev. Biol.* 20: 231-260. [ [Links](#) ]

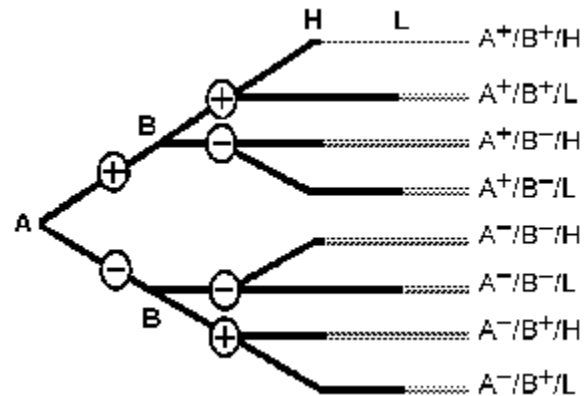
**Wilson, F.** and **Woolcock, L.T.** (1960). Temperature determination of sex in a parthenogenetic honeybee, *Ooencyrtus submetallicus* (Howard) (Hymenoptera: Ooencyrtidae). *Aust. J. Zool.* 8: 153-169. [ [Links](#) ]

**Woyke, J.** (1963). Drone larvae from fertilized eggs of the honeybee. *J. Apic. Res.* 2: 73-76. [ [Links](#) ]

**Woyke, J.** (1979). Sex determination in *Apis cerana indica*. *J. Apic. Res.* 118: 122-127. [ [Links](#) ]

**Woyke, J.** (1986). Sex determination. In: *Bee Genetics and Breeding* (Rinderer, T.E., ed.). Academ New York, pp. 91-119. [ [Links](#) ]

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**Figure 1** - Phenotypic representation of the model for caste determination in the genus *Melipona* Velthuis and Sommeijer (1991).

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