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Biology of the honeybee

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Introduction

The ancient fascination exerted by insect societies, due to their perfect organisation (especially the division of labour), has been a source of analogies with human society. These are represented in "The wasps" of Aristophane, and Mandeville used them for his philosophic "Fables of bees". More recently, modern biologists identified the obvious adaptative advantage of the organisation of insect societies into a "super organism". For example, in terms of biomass, the social insects of the Amazonian forest represent 75% of the total weight of all insects globally and their mass is certainly 4 to 8 fold higher than the terrestrial vertebrates. By contrast, the number of species is very low: of the 750,000 insect species, 1300 (about 2%) are social insects of the two groups Isoptera and Hymenoptera.

The study of the social insects recently gave rise to a new discipline: sociobiology, which introduced the notion of "eusociality" for species showing the following characteristics: (i) superposition of many adult generations in the same social group; (ii) cohesion between the members of the same group; (iii) division of labour with a specialisation of a restricted number of reproductive individuals, all the other individuals being sterile and devoted to "altruist" tasks; and (iv) rearing of young in cooperation.

These characters are a product of biological evolution which is demonstrated by the ecological success of species organised in a social "super organism". Beyond the fundamental interest in social insects, ancient peoples exploited honeybees for hive products, mainly for food.

For successful modern beekeeping, veterinarians should have detailed knowledge of: (i) beekeeping practices, particularly management methods and apicultural techniques; and (ii) honeybee diseases and the anomalies of the beehive.

To understand these two important aspects, it is essential to begin by the study of honeybee biology in natural conditions.

Composition of a bee hive in natural conditions

The honeybee, *Apis mellifera*, is a social insect living in a colony or a hive comprising 50,000 to 80,000 individuals, in a small volume (some dm^3). Feral bee colonies are often established in hollow trees or other suitable cavities. The roof of the cavity forms the support for the construction of vertical, parallel wax combs.

A transverse section of comb shows a row of cells either side of a median thin plate. Each hexagonal cell is slightly oblique with the aperture directed upwards, the bottom of the cell being rounded (Fig. 1). There are approximately 750 cells per dm^2. In the upper part of the comb, provisions of two types are stored: cells which always remain open contain pollen, and other cells, which are later sealed with a cap of wax, contain honey. They are never mixed. The cells in the remaining part of the comb are devoted to the rearing of the immature stages of the bee, called the brood.

The brood is composed of eggs, larvae and nymphs (Fig. 2): (i) in the largest central zone are the worker brood cells; (ii) in the edge zone are larger cells with a convex cap, for the drone brood; and (iii) in the lowest zone, at certain periods of the colony's development, very large and prominent cells with an irregular shape may appear, for the rearing of new queens.

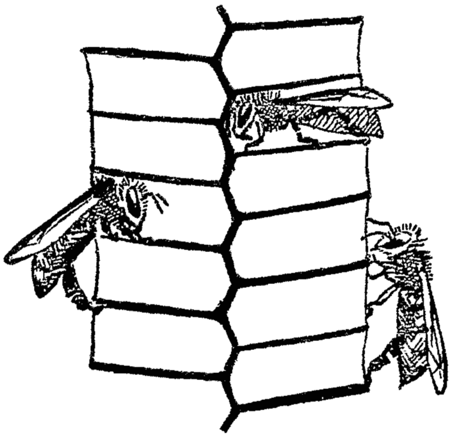

Fig. 1. Section through a comb.

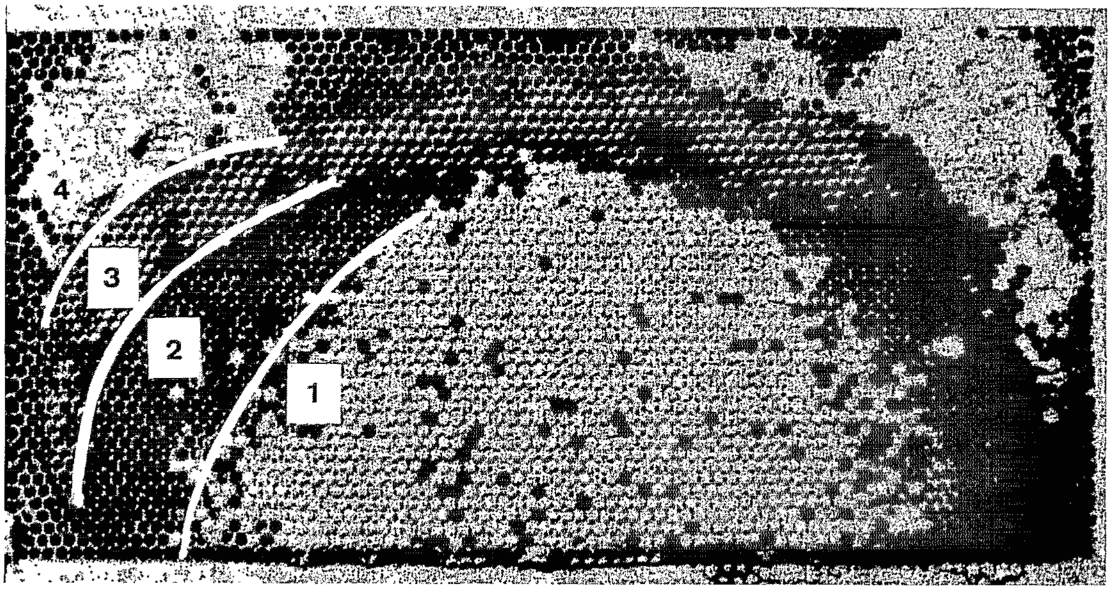

Fig. 2. A comb containing different areas: 1 capped worker brood; 2 open worker brood; 3 pollen cells; 4 honey cells.

General morphology of inhabitants

The population of the bee colony is composed of three different types of individuals, the castes: (i) the fertile female; (ii) the sterile females; and (iii) the males (Fig. 3).

(i) The fertile female, named the queen, is unique. Its length (around 20 mm) is due partly to an elongated body, but mainly to a large abdomen, so the wings appear shorter than the body. The head is small, with eyes moderately developed. The three pairs of legs are similar. The reproductive system is functional and the abdomen is armed with a curved smooth sting.

(ii) The sterile females, the workers, constitute the primary and essential elements of the colony population. Smaller than the queen, they are 15 mm in length. The wings are well developed and extend the length of the body. They are distinguished from the queen by some anatomical and physiological features:

- Well developed and long proboscis for nectar gathering, wax and brood food producing glands, hind legs modified for pollen collection.
- Well developed sting apparatus with a curved denticulated barb.
- Incomplete and normally non-functional reproductive system.

(iii) The males (drones) are produced only at certain times of the year. The body is stocky, 19 mm in length, the wings are as long as the body. The eyes are well developed, extremely large and join behind the occiput. Their well developed reproductive tract is functional. Drones do not possess structures for pollen or nectar collection, or stings.

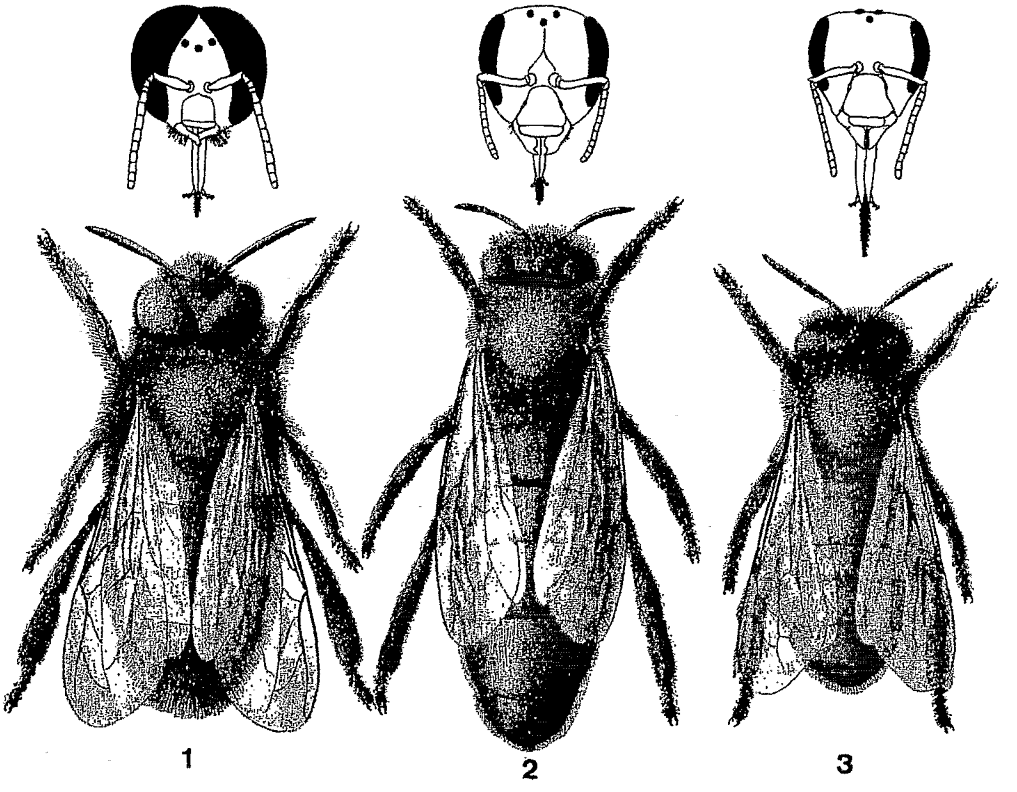

Fig. 3. External anatomy of: 1 drone; 2 queen; 3 worker.

Reproduction, development, longevity

Anatomy of the genital tract

The queen (Fig. 4)

The genital apparatus is very well developed and comprises two piriform ovaries, composed of: (i) clusters of numerous ovarioles; (ii) two lateral oviducts which join in a median one opening into a large vagina; and (iii) a spermatheca and two spermathecal glands above the vagina. Inside the vagina is a valve fold which presses the egg against the duct opening to the spermatheca, permitting fertilisation.

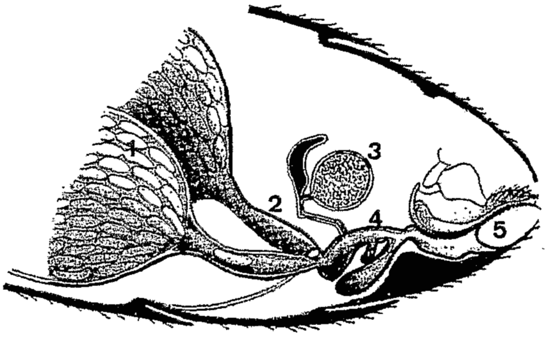

Fig. 4. Genital apparatus of the queen: 1 ovary; 2 oviduct; 3 spermatheca; 4 median oviduct; 5 sting chamber.

The drones (Fig. 5)

These also have a normally developed reproductive tract with two testes, two extensive mucous glands and a large and evaginable endophallus.

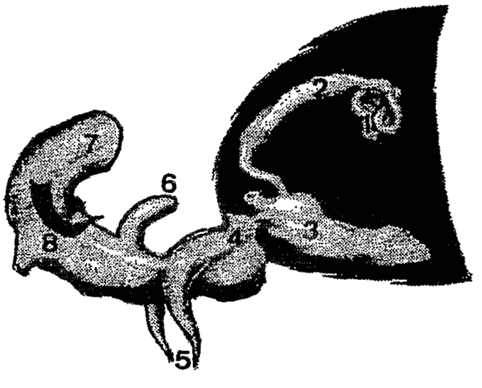

Fig. 5. Genital apparatus of the drone, with everted penis: 1 vasa deferentia; 2 vesiculae seminales; 3 mucus glands; 4 ductus ejaculatorius; 5 cornua; 6 fimbriated lobe; 7 bulb; 8 dorsal plate of bulb.

The workers

The genital tract is atrophied, with filiform ovaries.

Mating and fertilisation of the queen

After several short orientation flights during the first week or so after emergence the virgin queen leaves the hive to find a drone congregation area. These places are often the same year after year, with many thousands of drones coming from different areas. The queen is able to fly distances of 10 to 12 km, sometimes crossing geographical barriers up to altitudes of 1000 m. As the queen reaches the congregation area, the "nuptial flight" begins. The drones fly slowly in a circular formation; the queen flies over the males, and slowly descends. Some tens of males are attracted by both visual cues and the queen's pheromones. Increasing their flight speed, the group of drones form a "comet-tail". Copulation occurs in flight, at a height of about 10 m and in few seconds (Fig. 6). After evagination of its endophallus in the queen's vagina and the transfer of sperm, the copulatory apparatus is torn from the body of the male, becoming the "mating sign" attached to the extremity of the queen's abdomen. The male then dies. The queen removes the "mating sign" with her legs and is then able to copulate afresh. Over a few days, the queen may accomplish many nuptial flights; there may be no copulation at the time of the first nuptial flight. Usually, 8 to 10 copulations are needed to ensure life long fertility. Finally, the queen returns to the colony, often retaining the last "mating sign", which soon shrivels up and drops off. The sperm is stored in the queen's spermatheca, which contains a liquid for the first 20 days. After 20 days, if no spermatozoids are stored, the liquid in the spermatheca solidifies. Thus, if a young queen is not mated during the first 3 weeks of her life, she is unable to be fertilised. This is considered a major difficulty for apiculture in cold countries, where the climatic conditions may prevent nuptial flights within the required time. A normally mated queen stores enough spermatozoids for 2 to 3 years of continuous egg laying.

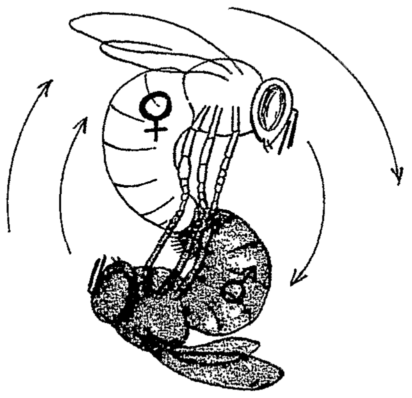

Fig. 6. Mating of the queen.

Oviposition

As the queen is mated in only one period during her whole life, she must retain the living sperm in her seminal receptacle. The duct of the seminal vesicle is supplied with a muscular sphincter and by relaxing or contracting the sphincter, the queen may or may not fertilise the eggs before laying:

(i) Fertilised eggs give rise to females (diploid individuals with 32 chromosomes).

(ii) Unfertilised eggs give rise only to males, which are haploid (n = 16), which means the multiplication of sexual cells without meiosis. It is the phenomenon of "parthenogenesis arrhenotoky". Egg laying may start approximately 2 days after mating, and proceeds regularly and continuously, except during periods of cold weather. The queen deposits one egg per cell, usually starting in the centre of the comb and continuing in an outward spiral pattern.

The liberation of spermatozoids is dependent on the opening of the muscular sphincter of the spermatheca, itself controlled by a reflex triggered by the size of the aperture of the cell opening detected by the queen's first pair of legs. Fertilised eggs are deposited in the cells of workers or queens, and the non-fertilised ones in the drone cells.

Development of the brood

The brood is defined as the whole pre-imaginal period (eggs, larvae and pupae) (Fig. 7).

The eggs

These are whitish and elongated, measuring 1 to 1.5 x 0.5 mm. At deposition they are vertical on the cell bottom, attached by one end, then oblique, and finally become horizontal on the third day. The duration of egg incubation is three days.

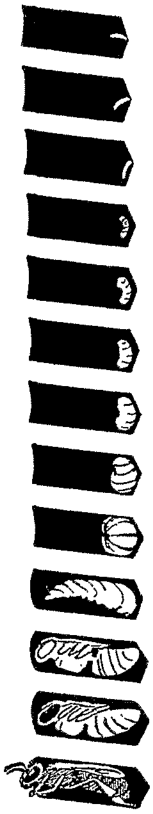

Fig. 7. Section through a brood comb showing eggs and different immature stages.

The larvae and the five larval instars

During the first three days after hatching, all the larvae are fed only with royal jelly (secretions of the pharyngeal glands of the nurse bees). Within three days, the weight of the larvae increases from 0.1 to 5 mg; i.e. by a factor of 50. Larvae that will become the future queens are fed ten times more often for the duration of their development, than are the larvae reared as workers. In addition, royal jelly contains secretions of the mandibular glands and more sugars, which enhances the quantity of food absorbed, by stimulating the appetite. The function of the corpora allata is also stimulated, particularly enhancing the secretion of juvenile hormone, responsible of the growth of the larva. After two and a half to three days, a worker larva is no longer capable of being reared as queen, even if it receives the same provisions as a queen. After the third day, the queen larvae still receive royal jelly exclusively, but of slightly different composition. The other larvae receive a mixture of nurse bee secretions, pollen and honey.

Metamorphosis

After the workers have covered the cells with a convex cap of wax (more convex for the male brood), the larvae cannot receive further food. Within 36 hours after cell capping, the larva spins a cocoon and defaecates. The last larval stage ends when the larva stops moving and stretches out on its back in the cell. After metamorphosis, the young adult emerges by chewing away the cell cap. The cell is then rapidly cleaned and reused.

Finally, there are two types of brood: (i) open brood = eggs and larvae; and (ii) capped brood = last instar larvae, prepupae and pupae.

If the regular spiral pattern of egg laying is followed, the open and capped brood is regularly distributed in concentric rings. When an irregular pattern is observed, interspersed with empty cells, it indicates an active destruction of eggs, larvae or pupae by the workers because of: (i) abnormalities of eggs or young larvae; (ii) the presence of diploid males; and (iii) the removal of stored provisions when the queen needs additional cells in which to lay eggs.

In addition, a pronounced irregularity of the brood pattern ("dispersed"; "in mosaics") may indicate the presence of a disease or toxic chemicals.

Longevity

(i) The queen: 3 to 5 years.

(ii) The workers: 4 to 6 weeks during summer time. Worker bees reared at the end of autumn can live until the following spring.

(iii) The males: 1.5 to 2 months. They appear in spring, their numbers diminish during summer time and they disappear in the autumn.

Functioning of the hive

The members of the casts and the general division of labour

The queen

The queen is the only female of the colony able to lay fertilised eggs. In temperate regions egg laying is minimal and intermittent during winter, it increases during spring, is maximal in early summer and declines during autumn. Egg laying is prolific during the summer months; the queen can produce one egg every 30 seconds, that means more than 2000 eggs per day which is equivalent to her weight. Sometimes, when an aged queen has no more sperm, only males are produced. The same is true for a young, inadequately fertilised queen.

The second function of the queen is the secretion of pheromones. Insect pheromones are analogous to hormones, but secreted externally and act upon other individuals of the same species, sometimes at great distance. They are secreted by the mandibular glands of the queen, which are large sac-like structures with their ducts opening at the base of mandibles. The secretion, called "queen substance", covers the whole external body surface of the queen. There are at least two characterised compounds: (i) 9-keto-(E)-2-decenoic acid; and (ii) 9-hydroxy-(E)-2-decenoic acid. The action of these compounds may include:

(i) An attractive effect on workers, bringing them close to the queen and, through contact, distributing the pheromone throughout the colony.

(ii) An inhibition of the worker's ovarian development. After the death of the queen, some workers may develop the ability to lay unfertilised eggs.

(iii) An inhibition of the building of queen cells by the workers.

(iv) An attractive effect on males during the nuptial flight.

The males

Drones contribute little to life inside the colony. Their primary and almost sole function is to fertilise the queen. Supplied by the workers in spring, when virgin queens are produced, tolerated during the summer, they are expelled or massacred in autumn. They may have a role in ventilation of the colony during hot days.

The workers

General division of labour

The workers undertake all the essential tasks in the hive. Their numerous duties are very precisely organised. Rösch (1927) observed that the division of labour was largely dependent on age.

(i) First two days: After emergence, the adult bees become cleaners, removing the remains of larvae and pupae and other debris from the cells. Next, they may become concerned with hive ventilation, collecting in rows at the hive entrance. Firmly clinging to the floor, they raise their abdomen and rapidly beat their wings. This activity serves to eliminate excess water vapour and regulate the hive temperature.

(ii) From the third to the fifth day: They become nurse bees, feeding worker larvae and drone larvae with honey, pollen and glandular secretions.

(iii) From the 6th to the 10th day: They feed worker larvae and drone larvae less than 2 days old and also queen larvae. They provision the cells with royal jelly secreted by the hypopharyngeal glands.

(iv) From the 10th to the 15th day: The bees become stockers, collecting nectar and pollen from foragers as provisions are brought in the hive, and storing them.

(v) From the15th to the 17th day: They are comb-makers, undertaking the task of constructing and repairing combs.

(vi) From the 18th to the 20th day: They become guards, defending the hive against other insects and especially against workers from other hives which are attracted by the stored honey. The drones of other colonies are, by contrast, tolerated.

(vii) Near the 21st day: The bees become foragers, leaving the colony to harvest pollen and nectar from flowers and secondarily, some other substances, such as propolis. It is remarkable that, for three weeks, the bees remain inside the hive. After this period of life, they go out, until their death, which can occur at their fourth week of life if foraging activity is intense.

In fact, the division of labour in bees appears less well defined, as was subsequently shown by Lindauer (1952) and Seeley (1983): (i) until day 2: cleaners; (ii) from day 2 to 11: care of brood; (iii) from day 11 to 20: storing provisions; and (iv) after day 20: foraging.

Moreover, considerable flexibility is possible: for example, at the end of winter, a lot of workers are old, nevertheless some of them revert to being cleaners, or nurse bees, etc. Also it has been observed that some workers of the same age do not undertake the same activity. In contrast, some individuals retain the same specialisation of activity throughout their life. The individuals concerned with the tasks of nourishment of very young larvae and queen larvae, of comb building, of guarding and of foraging, display some interesting biological adaptations.

Nurse bees

Only bees 6 to 10 days old are specialised in rearing brood less than 3 days old, because at this age they possess a pair of well developed hypopharyngeal glands, situated in an anterior position in the head (Fig. 8). The glands comprise a long sinuous tube, to which are attached solid and rounded lobes. Two distinct canals open separately at the base of the hypopharynx. During the first 3 days, all larvae receive royal jelly, secreted by the hypopharyngeal glands. However, Gontarski (1949), found that this initial secretion in the three kinds of cells (worker larvae, drone larvae and queen larvae) had a different composition, each of them being supplied by specialised nurse bees. Royal jelly is extremely nutritious, as demonstrated by the rapid growth of the larvae. After the first 3 days, the worker larvae and the drone larvae receive only a mixture with honey and pollen. By contrast, the queen cells are supplied with royal jelly for 5 days. Before the fourth day, both female casts are not differentiated: the larva will give rise to a worker or a queen, partially depending on the duration of feeding with royal jelly.

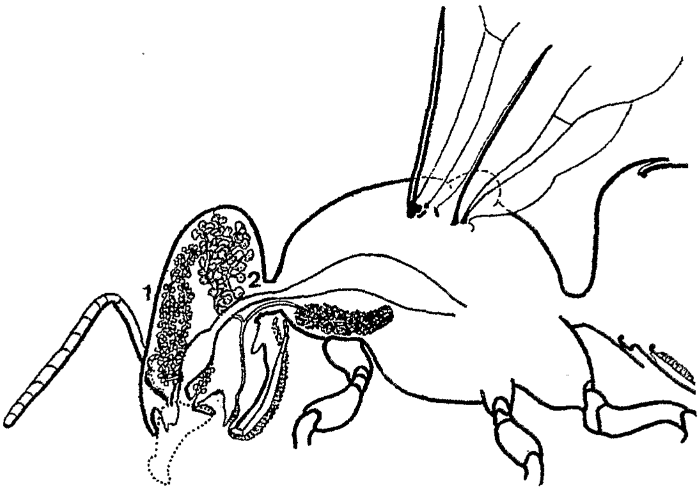

Fig. 8. Food (1) and hypopharyngeal (2) glands of a nurse bee.

Comb builders

Wax is produced by four ventral hypodermal glands, situated at the anterior of the fourth to seventh abdominal segments. It emerges as little wax scale, which the workers grasp with their posterior metatarsal clamp. After production, the scales are masticated by the mandibles, then deposited in areas of the comb where cells are under construction, generally mixed with other materials (Fig. 9). The secretion of wax is maximal in bees two weeks old, but younger individuals may contribute to comb building if necessary. A recently hived swarm produces as much wax during the first 15 days as during the remainder of the year. It has been estimated that 1 kg of wax is the product of the work of 150,000 bees. The construction of the combs is fast and starts just after the swarm's installation. When the first vertical comb is complete, others are built in parallel and these may be further strengthened by the construction of cross links. This activity requires considerable social coordination.

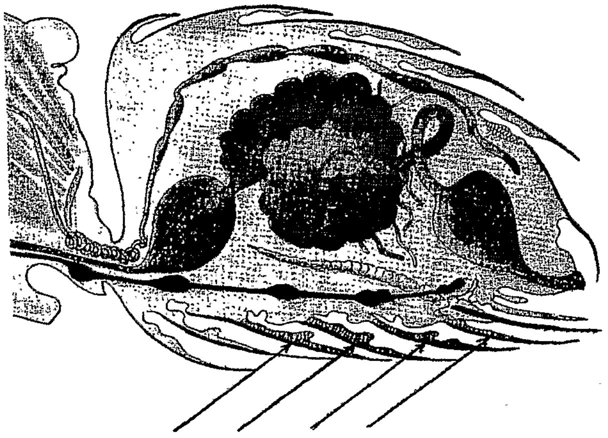

Fig. 9. Wax glands (see arrows).

The bottom of individual cells is always composed of three equal lozenge shapes, joined side by side and forming angles of 110° and 70° (Fig. 10). The cells of one side of a comb alternate with the cells of the other side, so that the three lozenges of one cell correspond to three distinct cells on the opposite side. De Réaumur (1740), and later other authors, demonstrated that this type of cell shape is the most economical use of space and resources. It allows the bees to accommodate the maximum number of larvae with the minimum of wax secretion.

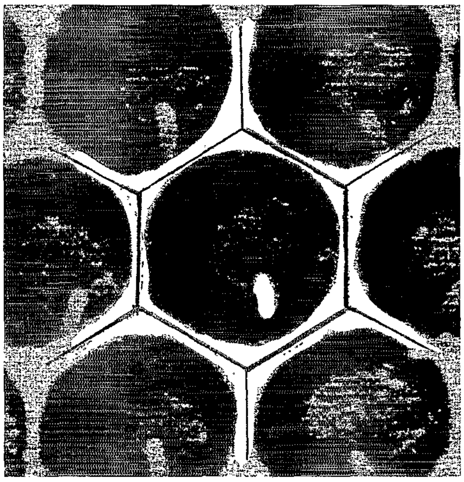

Fig. 10. Cell design in a comb.

Wax is a complex lipid comprising primarily hydrocarbons, monoesters, diesters, hydroxy polyesters and free acids. Since it is a poor heat conductor, it plays an essential role in the thermal insulation of the nest and allows the honeybee, an insect of tropical origin, to regulate the nest temperate in cold countries.

In an old hive, the wax loses its whiteness and the frames become covered more or less by another product, propolis, which is brownish or black colour. It is a resinous substance, collected from various trees and modified by the bees by adding wax and enzymes. It is collected in the same way as pollen. It makes a kind of protective cover serving to weatherproof the hive, to reduce the entrance and to seal any gaps. Workers construct columns of propolis at the entrance to prevent access to the hive by mammals and moths. Bees also use propolis to cover the dead bodies of animals which entered the hive. A strong colony produces approximately 400 g of propolis a year.

Guards

Only females (workers and the queen) possess a sting. Part of the female genital apparatus is transformed into a sting, connected to two poison glands (Fig. 11). The sting is composed of:

(i) A stylet resulting from the fusion of the genital pieces of the 9th segment, enlarged at the base and possessing two grooves internally.

(ii) 2 lancets: genital pieces of the 8th segment; rectilinear and denticulate in workers, they slide on the stylet rails. The venom canal is situated between the 2 lancets. The sting of the queen is curved and smooth.

(iii) 2 poison glands:

- The dorsal acid gland, "y" shaped, is the only one really venomous. It is linked to a bulky reservoir by a long canal.
- An alkaline gland with a non-toxic secretion, which serves to lubricate the lancets and to increase the pH of the venom, enhancing its toxicity.

The guard bees and also foragers use their sting to defend the colony against other invading and robbing insects. At the instant of stinging, the abdomen curves at 90°, which exposes the stylet and the lancets penetrate the body through the thin membraneous areas of the exoskeleton. When the bee stings an arthropod, it retracts the sting without any difficulty. By contrast when it attacks mammals (dogs, horses, or humans), the denticulate lancets of the worker remain fixed in the elastic skin, causing evisceration when the bee tries to fly off.

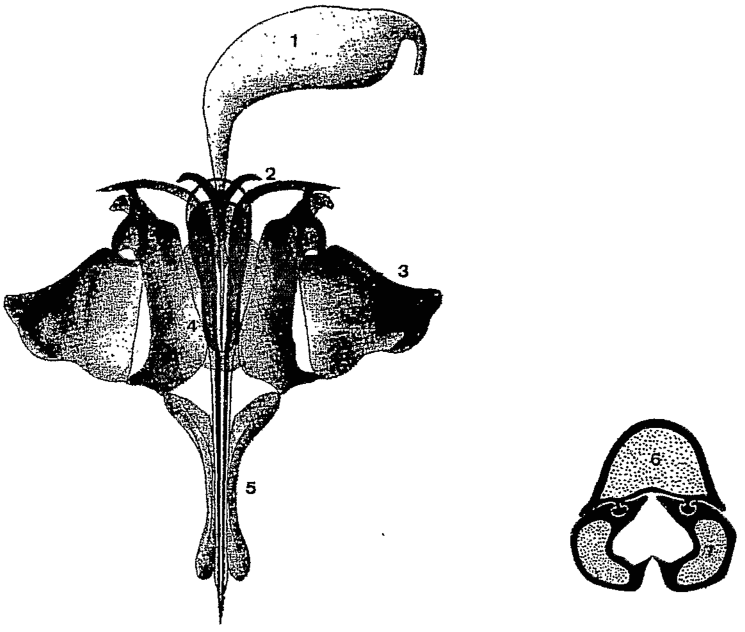

Fig. 11. Sting apparatus of the worker bee and cross section of sting shaft: 1 poison sac; 2 ramus; 3 quadrate plate; 4 oblong plate; 5 sheath, cross section of sting shaft; 6 stylet; 7 lancets.

Foragers

Morphology of the pollen collecting apparatus (Fig. 12): Essentially situated on legs III:

(i) Tibia:

- External side: "basket", bordered by rigid, curved bristles which constitute "the rake".
- Internal side: a "comb" formed by rigid bristles, on the distal part of the tibia.
- The tibia-tarsial articulation forms a pincer.

(ii) Tarsus: There is a brush on the internal side of the first hypertrophied article of the tarsus.

Legs I and II, bear only a brush, which is less well developed than on the III legs.

The mode of harvesting pollen: The bee scrapes together the pollen from the flower stamens with its mandibles and anterior legs. At the same time, it moistens the pollen grains with gland secretions and regurgitated nectar from its crop. When pollen is very abundant, the hairy body of the bee is covered in grains and it is collected by cleaning the body with the legs. When the bee flies between two flowers, the pollen is passed diagonally from brush to brush from legs I and II to legs III, by moving the legs alternately up and down. On leg III, the pollen is gathered with the comb of the opposite leg, then pushed with the pincer into the basket on the external side. Sometimes, legs II compress the wad of pollen inside the basket. On each homing flight, the foraging bee carries around 15 mg of pollen, which is deposited in different cells from those in which nectar is stored (Fig. 13). Pollen cells remain open. Pollen is a protein-rich food essential for the nutrition of brood and young bees.

Morphology of the nectar collecting apparatus (Fig. 14) and the digestive tract (Fig. 15): The nectar collecting apparatus comprises a well developed proboscis, formed by a labium, labial palps and two maxillae. The distal extremity of the labium is enlarged and spoon-like; the proboscis is folded when inactive, but it may be projected forward to reach to the bottom of the flower corolla. The proboscis may be 6 to 7 mm in length.

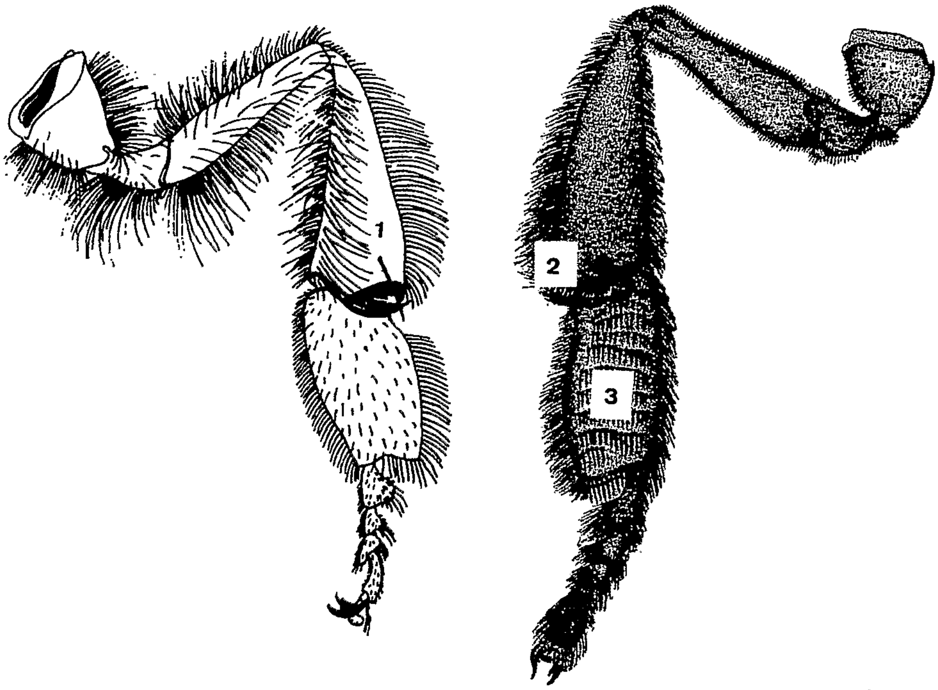

Fig. 12. Hind leg of a worker bee: outer surface: 1 pollen basket; inner surface: 2 pollen press; 3 pollen brushes.

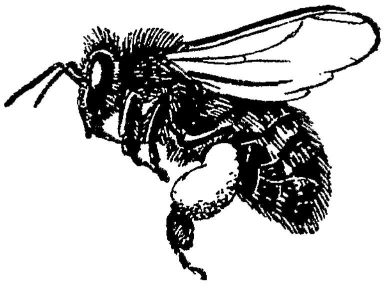

Fig. 13. Pollen carrying honey bee.

Harvesting of nectar and manufacture of honey: Flower nectar is composed of water (60-70%) and sugars (glucose, fructose, sucrose). It is sucked up by the bee and transported to the crop where it collects and undergoes the cleavage of the disaccharide sucrose into simple sugars under the action of the enzyme invertase, produced by the labial glands. These glands are situated in the head and the thorax and open at the base of the alimentary canal. The transformation of nectar into honey begins during the flight back to the colony and continues after regurgitation and storage in the cells (approximately 40 mg on each trip). In the cell, the reduction of the water content and the enzymic inversion of sucrose continues until the water content is below 20%. The cell is then sealed with a white wax capping. For the colony, honey represents a food reserve for winter time; it is the energy source. A colony harvests an average of 240 kg of nectar annually, equivalent to 60 kg of honey. The honeybee not only collects floral nectar, but also honeydew, which is the sticky exudate of aphids and other sap feeding insects, from trees and other plants. It is harvested and used by bees in the same way as nectar. Water is also brought to the hive to maintain a high humidity in the brood area.

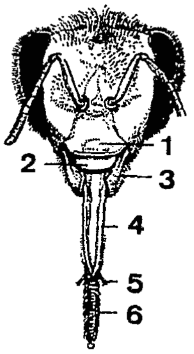

Fig. 14. The mouth parts of the worker bee: 1 clypeus; 2 labrum; 3 mandible; 4 maxilla; 5 labial palpus; 6 glossa.

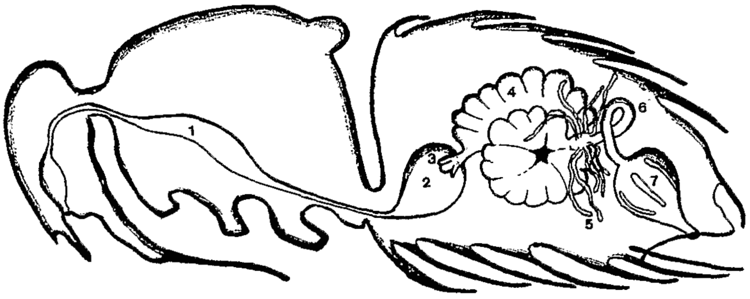

Fig. 15. The alimentary canal: 1 oesophagus; 2 crop; 3 proventriculus; 4 ventriculus; 5 Malpighian tubules; 6 small intestine; 7 rectum.

Foraging organisation

Innate orientation sense and ability to communicate information

Bees have an innate orientation sense and the ability to communicate information. These observations were described by Von Frisch as the "bee language". When a scout bee discovers a new and rich source of nectar, it comes back to the hive and gives some of it to other foragers for tasting. Then it performs a dance on the surface of the vertical comb, the dance movements indicating the direction and the distance of the source of nectar (Fig. 16). Two sorts of dance can be performed depending on the distance of the nectar source:

(i) The round dance indicates that the nectar source is situated in close proximity to the hive. The bees repeatedly make small circles, reversing direction every few revolutions. The profitability of food rewards is communicated by more vigorous dancing.

(ii) The waggle dance indicates food resources at a greater distance (over about 100 m) from the colony. Furthermore, detailed aspects of this dance allow other bees to learn the direction and distance of the source of nectar. The direction is indicated by the angle of inclination of the straight part of the figure eight in relation to the vertical.

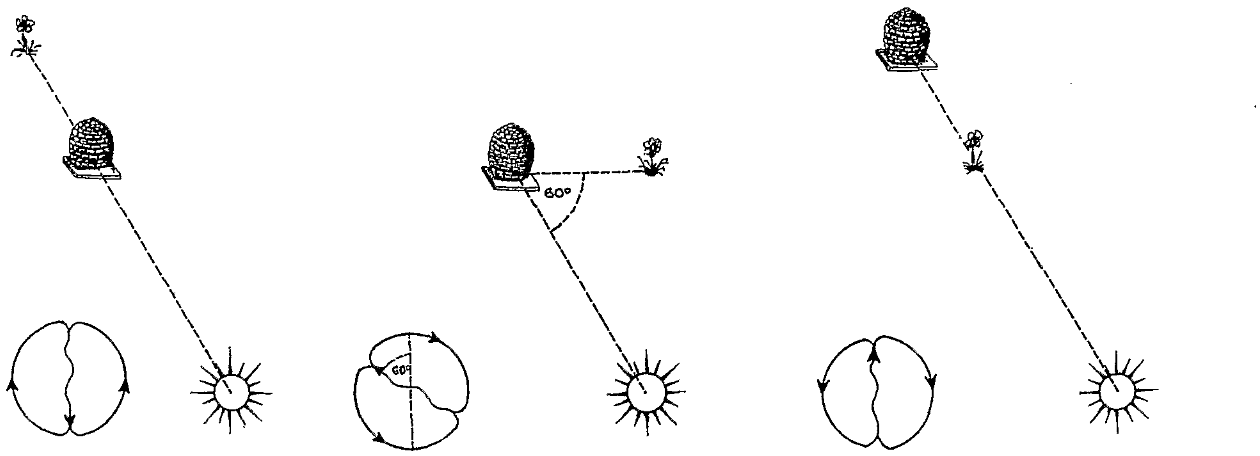

Fig. 16. Figure-of-eight dances indicating the direction of the food source in relation to the position of the sun.

When the bee is dancing straight up it indicates that the source of nectar is in the same direction as the sun. A dance downwards is indicating a direction opposite to the sun.

When the straight part of the "8" forms an angle towards the right or left of the vertical line, the bees take their direction towards the source of nectar by flying at the same angle from the sun.

The distance to the nectar source is indicated by the vigour of the waggling of the abdomen during the straight part of the "8" dance and also by the rhythm of vibrations emitted by the bee; a fast rhythm signifying that nectar is close to the hive. The relative precision of the response of bees to the dance message is very high. It is within 2° to 5° for the angle of direction and roughly 20 m for each km of distance. The sun is necessary for bee orientation, although when the sky is overcast, bees can use ultraviolet light for discerning the direction. If the clouds are too dense, dances are stopped.

Foraging specialisation

For many days, the same forager bee may specialise in the collection of either nectar or pollen and often visits only one species of flower. The work of the bee becomes more efficient and more profitable as it becomes familiar with a single flower type, which it recognises by colour and odour. Some bees also specialise in exploration and the location of food sources. These are the foragers that perform the communication dances most frequently.

How do foragers return to the hive?

At the time of their first flights, bees make short tours around the hive to familiarise themselves with their environment and landscape. They learn to recognise very precisely the position of the hive. For instance, it is easy to replace an old hive body by transferring the frames to a new hive in the same place because the bees will return to the same site. In contrast, foragers may be unable to locate their colony if it is moved some distance away. The visual memory of bees is very sensitive to certain colours. In practice, beekeepers paint their hives with different colours or patterns to aid foragers in the location of the correct hive entrance.

The dissemination of the species: Swarming

The secretion of pheromones by the queen has the effect of inhibiting the construction of queen cells by the workers. In certain circumstances, for example, when a queen is growing old or when the colony becomes overcrowded, the workers build queen cells and begin to rear queen larvae. As the development of the royal brood proceeds, the queen ceases her egg laying, ventilation and foraging activities are stopped and the colony is in a heightened state of excitement. Finally, the day comes when the old queen flies out, accompanied by some thousands of bees, who have previously filled up their crop with honey, and also by some tens of drones. This group constitutes the swarm, composed of 10,000 to 20,000 individuals, weighing 1 to 2 kg. After leaving the hive, it soon settles on the branch of a tree, or other suitable collecting site, near the hive. The search for a favourable place for the establishment of the colony is undertaken by scout bees, who fly off in all directions. On returning to the cluster they dance, to indicate the direction of their chosen site (in general, others will follow the more vigorous dancer). In the queenless colony, abandoned by the swarm, one can hear the buzzing of the future queens inside their cells, which is called "the queen's song". The first emerging queen hastens to kill all the other queens with her sting, after biting through the cap of the cells. If two queens emerge at the same time, they will fight until only one survives. It may sometimes happen that a new queen doesn't kill the others and will leave the colony accompanied by another group of worker bees. This secondary swarm usually flies off about nine days after the first one. It may have to travel further to find a suitable nest site and is generally less successful in establishing a new colony. Occasionally a tertiary swarm may be formed. Primary swarms are a favourable event in the life of the hive, whereas secondary swarms may be detrimental. For managed honeybee colonies there is selection for strains of bees which do not have a pronounced tendency to swarm.

Remark: Swarming must be distinguished from "false-swarming" or "absconding" which is a total abandonment of the hive in warm countries, occurring spontaneously or after manipulation.

The loss of the queen

It may happen that the queen dies after an accident or from old age, in a colony where no queen cells have been built. This event immediately induces unrest in the colony signalled by uncharacteristic sounds. Calm returns in few hours when the worker bees begin to build up the walls of 5 to 15 cells containing fertilised eggs or very young larvae less than two days old, to form queen cells. Later, they may destroy some of these larvae and tear down the walls of surrounding cells to retain only a few cells, of which they lengthen the walls and direct the opening downwards (Fig. 17). The remaining larvae will be fed with royal jelly for five days, which leads to the birth of a new queen.

Fig. 17. Queen cell and section through a queen cell showing a royal pupa.

Thermoregulation

The temperature in the brood area is maintained at 35° to 36°C. When it is warm, ventilation of the hive effectively regulates the temperature, but when it becomes excessively hot, the workers hang in a cluster outside the hive. During the winter, the bees gather together inside the hive and cease their outside activities. They form a tight cluster at the centre of the colony from which they move from time to time to feed on stored honey.

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