The Origin and Organization of the Bee Colony *Apis mellifera L.*

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TABLE OF CONTENTS

INTRODUCTION

In the animal kingdom and in the insect class, the honey bee (*Apis mellifera L.*) is distinguished by the specificity of its lifestyle and the variety of its adaptations to a wide range of habitat conditions. Differentiation into subspecies and the evolutionary plasticity of the species is associated with the diversity of the climatic conditions of the habitation area. G.K. Gotze (1954) and Yu. A. Pesenko et al. (1989) distinguished eight subspecies of the honey bee: the Western Mediterranean (*A. m. intermissia* But.–Reep., 1906), the Euro-Siberian (*A. m. mellifera* L., 1761), the Middle Eastern (*A. m. meda* Skov., 1929), the Afro-Tropic *(A. m. adansonii* Latr., 1804), the Cape (*A. m. capensis* Esch, 1822), the East North African (*A. m. lamarckii* Cock, 1906), the Madagascan (*A. m. unicolor* Latr., 1804) and the Caucasian (*A. m. remipes* Gerstacker, 1862).

Their eurybionticity allowed the honey bee to occupy a wide area that extends to all inhabited continents. The progressive evolution of the species is associated with the development of sociality and the transformation of the colony into an evolving biological unit. On this basis, the reproduction and resettlement of bee colonies have developed through sociotomy, which has some distant resemblance to asexual reproduction in protozoa.

Human interest in bees goes back to antiquity. Settlements of bees attracted people with an abundance of carbohydrate (honey) and protein (pollen and brood) food reserves contained in them. However, in order to use them, it was required to obtain such necessary skills as detecting bee colonies and extracting bee products from their dwellings, which is life-threatening because bees have an effective means of protection – a poisonous sting.

Initially, the extraction of bee products by man was one of the forms of hunting for bees, as well as for many wild animals. As the methods of hunting improved, the bee trade began to appear. Its improvement was stimulated to a large extent by the difficulties associated with the detection of bee colonies, and intense competition between hunters. Also, animals were competitors for hunters, since they were attracted by honey or the bees themselves.

Bee trading in various forms existed and progressed for several thousand years. Honey hunting (honey harvesting) is one of its forms. At the initial stages of its development, it already included elements of bees' care, which was expressed in the preparation of places for the settlement of swarms. For these purposes, trees were hollowed out with special cavities.

The use of smoke is one of the earliest methods mastered by man for controlling the behavior of bees. According to the cave paintings of the Mesolithic era, preserved in the caves of Eastern Spain, people started to use smoke at least 7–9 thousand years ago to suppress the aggressiveness of bees. Even nowadays this instrument is used by beekeepers. But bees associate the smoke not with a beekeeper but with fires that induce bees to fill their honey crops. This prevents the bees from bending their abdomen, which is necessary to sting the beekeeper.

A significant contribution to the improvement of beekeeping technology was made by the invention of the artificial wax foundation for the construction of honeycombs (honeycomb base) by G. Kretchmer in the first half of the nineteenth century. The use of a perforated artificial wax foundation made it possible to control the construction of honeycombs with given cell sizes. As a result, the bees were able to reduce energy costs for the construction of cells.

Despite the use of bees in the household, the honey bee did not acquire the typical traits of a pet. Their domestication effected a change in their morphophysiological features and the development of specific forms of behavior that are controlled by a person when their normal existence is strongly dependent on the human. In contrast, different technologies for keeping and breeding bees did not affect the modification of the genetically programmed behavior of bees.

The preservation of the typical honey bee's species characteristics that have not changed in the process of long-term domestication does not allow one to consider it as a typical pet. The honey bee kept in the household remains a wild animal, capable of independent existence regardless of a person's influence. In the process of sociotomy, bee colonies leaving their hives successfully master new dwellings and continue their independent existence regardless of humans. An increase in the number of bee colonies and their expansion through the development of new zones with temperate and cold climates occurred in the evolution of a species in this way. Natural selection favored the honey bee's development of instincts for reproduction and settlement.

CHAPTER ONE

THE ORIGIN OF COLONIES OF APIDAE

In the group of aculeate Hymenoptera (Aculeata), bees represent one of the largest superfamilies of Hymenoptera formed in the process of coupled evolution with flowering plants. Since the flourishing of angiosperms occurred in the Late Cretaceous, the appearance of bees probably dates to this epoch (Michener, 1965, 1975; Rasnicin, 1980a, 1980b; Brothers, 1975; Dietz, 1986).

The number of bee species increased progressively at the end of the Oligocene and the beginning of the Miocene (Rasnicin, 1980a; Michener, 1975, 1979). The superfamily includes 11 families, uniting 520 genera. Nowadays, the greatest taxonomic diversity is in the Neotropical, Neo- and Palearctic realms, where 315, 260 and 243 genera of bees are known respectively. Their lowest representation is in the Australian region, where only 18 genera are found (Radchenko & Pesenko, 1994).

Bees have developed care for their offspring. The expression of this instinct depends on their way of life. Bees are divided into solitary, social and parasitic living by this feature. Most species of the modern superfamily of bees are represented by solitary living insects. Various forms of social organization are found in representatives of the Apidae, Bombidae, Halictidae, Anthophoraidae, and Euglossiedae families.

In the order of the Hymenoptera, social insects are found not only among bees. Fully social species are represented by the superfamily of Formicoidea (ants). Among the other 35 orders of insects, only the representatives of Isoptera (termites) lead a social way of life. Unlike the Hymenoptera, this order is completely represented by socially living species.

The presence among bees of a variety of transitional forms from typical solitary-living to highly organized socials allows us to trace their general patterns of origin and sociality development. The main developing directions can be traced by comparing the advantages in the struggle for existence and the social relations of modern species of bees that differ in their way of life.

It is possible to distinguish several levels of social organization. Eusociality is considered to be the rudimentary (initial) form of social organization. This is expressed by the fact that the female offspring of the female-foundress can provide her with some assistance in life support in the temporary colony. When it breaks up the generation of females flies away and establishes its own nests. Temporary colonies also form subsocial species. A similar organization is characteristic of eusocial species. Highly organized eusocial species are those that constantly live in colonies or where at least two generations of the female-foundress live with her in one nest. Adult individuals participate in the construction and protection of the nest, the delivery of food and the feeding of the female-foundress' offspring. Along with the female-foundress, her daughters can also participate in the reproduction of offspring.

Nest Constructions and Trophic Provision of Offspring

Solitary bees. The nest construction of solitary bees depends on the place of settlement. Most often they use different cavities in plants, rocks or the ground. Bees subject these cavities, used for sheltering offspring, to some processing (deepening, expansion, cleaning). Many species settling in the ground dig out passages and cavities by themselves, while some build nests in open spaces (stones, tree trunks, soil surfaces, etc.). The construction of nests is carried out by females (female-foundresses) that are ready to perform reproductive functions. The choice of the place of settlement, materials for the construction of shelters and ways to process them belong to species-specific features.

Among a wide range of nest structures, the most primitive ones are those where food stocks and developing individuals are in one common cavity. That is typical of the bee *Metallinella atrocaerulea* (Fig. 1A). It settles in a ready shallow cavity in wood that has one inlet. The female fills the nest cavity with food (pollen mixed with nectar), ovipositions 4–12 eggs in it and then seals the entrance with a plug of crushed leaves. The emergence of larvae and their development does not occur simultaneously. The first to complete the larval stages and turn into pupae are individuals emerging from the eggs ovipositioned at the base of the nest; at the entrance of the nest settle the latter – at the upper part from the facing side of the plug (Radchenko, 1979). There is competition between the larvae due to the localization of all of them in the same trophic substrate, whose intensity of consumption depends on their age. This prevents the appearance of consolidation among developing individuals.

However, in the superfamily of bees, the use of a common nesting chamber by developing individuals has a limited occurrence. Along with *M. atrocaerulea*, this form of offspring reproduction was found in the family of Anthophoridae in representatives of the genus *Allodapini* (Radchenko, Pesenko, 1994). The insignificant representation of species with this form of nesting in the rapidly progressing superfamily of bees is evidently associated with the incipience of rather perfect instincts of caring for offspring, based on the use of the individual isolation of developing offspring.

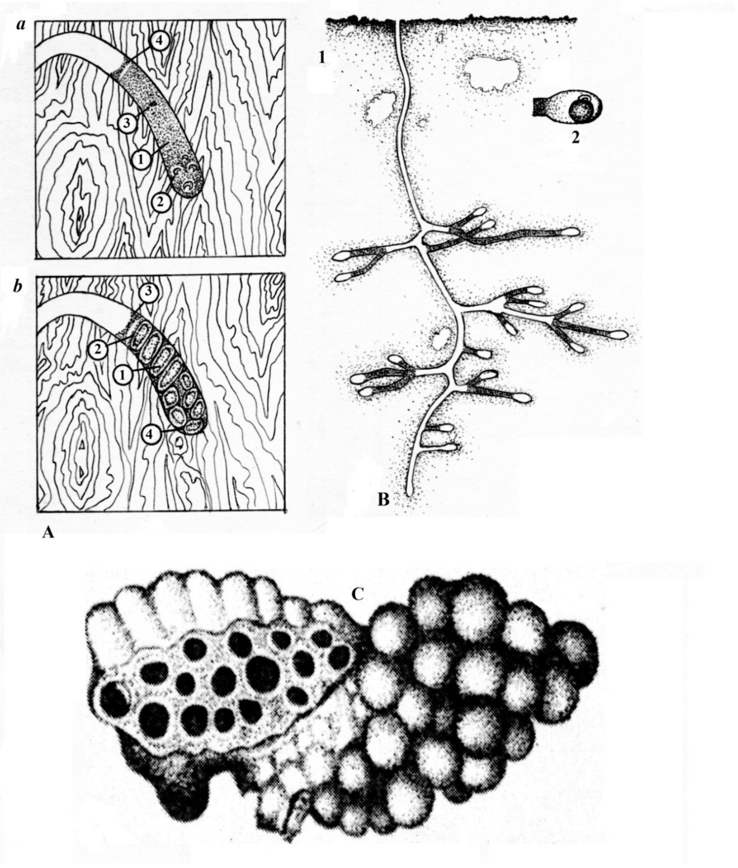

Fig. 1. Nest structures of solitary living bees: A – a nest of *Metallinella atrocaerulea* with developing bees: a-bees at the egg stage and larvae (1-pollen; 2-larva; 3-egg; 4-plug); b-stage of pupae (1-cocoon, 2-excrement, 3-plug, 4-formed cocoon) (by: Radchenko, 1978); B – *Nomioidea minutissimus* (1) and one of the sealed cells with food and eggs (2) (by: Radchenko, 1979); C – ground honeycomb of the bee *Halictus quadricinctus* (by: Blagoveshchenskaya, 1983)

Natural selection in bees favored the acquisition of instincts responsible for behavior providing individual isolation to the developing offspring. This was fully satisfied with the construction of cells where only one individual could develop. It was also specially supplied with food once or periodically during its development. In such situations, the cell turned into an elementary unit of nesting construction (Fig. 1B, C).

The choice of the settlement's location and the materials used for the construction of the cells differ in diverse species of bees with a wide variety. Many types of Megachilidae construct cells of a cylindrical shape (or close to such a form) from pieces of leaves or petals of flowers. Species' differences determine the size of the body of insects, which affects the size of the cells. The discrepancy between the large diameter of the nest cavity and the biological needs of the individuals developing in them is corrected by an increase of the walls' thickness. However, the reduction in the diameter of the cells constructed in narrow nest cavities is reflected in the decrease in size of the developing bees. Therefore, improving the nest behavior of Megachilidae was accompanied by the acquisition of the ability to control the size of the cavity chosen for settlement. Its successful choice is achieved by reducing the energy costs for the construction of cells by reducing the walls' thickness under optimal development conditions. Thus, with the possibility of choice, leafcutter bees (*Megachile rotundata*) prefer a diameter of tunnels limited to 6–6.5 mm for settling (Pesenko, 1982).

The number of cells constructed in the nest cavity depends on its depth and is limited by the reproductive potential of the female-foundresses. The reproduction of the leafcutter bee is limited to about 40 offspring. Within a day the female can oviposition no more than two eggs. This limits the breeding rate of offspring (Stephen et al.*,* 1969).

The leafcutter bee fills each cell with the pollen mass, lays an egg on it, and then closes (seals) it with the cover. Especially for this, the bee spends up to 6 pieces of leaves of the same plants from which the cell is built. The constructed nest can contain 1–20 cells and is completed with the construction of the plug. The bee spends 8–50 pieces of leaves on it. A small cavity usually remains unoccupied between the plug and the closest cell cover (Stephen, Torchio, 1961). The plug performs a protective role, reducing the negative impact of external environmental factors and prevents penetration into the nest by other insects (Stephen et al., 1969).

The ratio between females and males that develop in the same nest depends on the size of the cells, their localization in the nest cavity and the food supply. In addition, the female-foundress ovipositions the fertilized eggs from which the females develop into the cells that appeared at the beginning of the nest's construction, and the unfertilized ones closer to the exit (which were constructed later). Developing females are supplied more abundantly with food than males, who leave the nest before females (Stephen et al., 1969; Pesenko, 1982). For females, it takes a longer time to develop from egg to adult stage than for males.

The use of plant leaves by Megachilidae and other species of solitary bees for nesting is conditioned by their easy accessibility, but is limited by their low strength and high moisture permeability. This is due to the acquisition by the bees of the tools that contributed to increasing the protection of developing offspring from the adverse effects of the physical and biotic factors of the environment. On this path, instincts and morphophysiological adaptations have been developed that ensure the expansion of the diversity of settlement places. Thus bees of the genera *Heriades (Osmiini)* and *Megachile* cover the inner surfaces of the cells with resinous substances. This results in an increase in the waterproofing of the cells and protection from the penetration of parasites in it (Tsuneki, 1970; Maciel, 1976).

There are objects used by some bees that, without additional processing, meet the needs of developing individuals in the natural environment. For example, *Osmia rufonirta* and *O. bicolor* (Megachilidae) settle in the empty shells of snails in order to use each of them for one developing individual. To do this, the bee firstly cleans the shell, then brings the food into it, and after ovipositioning the bee seals the egg with the paste made from chewed leaves. Further care for the offspring is expressed in the sheltering of shells from competitors and enemies as well as from overheating by the sun's rays. *O. rufonirta* usually roll the shell from an open surface into a thicket of grassy vegetation and *O. bicolor* dig it into the soil (Grozdanic, 1971).

The strengthening of competition for suitable ground nesting places could affect the acquisition of instincts and morphophysiological adaptations for settlement in the ground. First of all, bees could be attracted by cavities in the dead parts of the root system that emerged on the surface as well as tunnels and depressions left by soil invertebrates in the ground. So, *Megachile albocincta* adapted to use earthworms' tunnels on the surface for nesting. As material for cell building, the bee uses pieces of leaves. The construction of the first cell begins at the depth of the tunnel and the last one at its exit. This behavior is similar to the leafcutter bee that settles in terrestrial cavities (Fabre, 1963).

The increase in the adaptability of bees to settlement in the ground developed in the direction of growing independence from the availability of suitable cavities and environmental factors that threaten the developing offspring. In this way, bees have acquired devices for building passages and cavities in the ground. The form of settlement when the female-foundress digs out a small hole in the ground where it is possible to build at least one cell belongs to the simplest one. Such nest behavior is characteristic of one species of Colletidae – *Colletes daviesanus* – settling on sandy, forest or limestone unshaded hillsides with southern exposures. In the excavated holes, the bee constructs up to four cells singly or in small rows (Scheloske, 1974). The representative of another Megachilidae family – *Megachile japonica* – constructs up to eight nests containing only 1–2 cells (Maeta, 1979). Each of them is dug out with a cavity about 2 cm in depth.

The complication of the nest behavior of bees settling in the ground was expressed in the acquisition of instincts for the construction of tunnels, labyrinths and brood chambers. Relatively simple nests of this type are built by the bee *Cantridini aethyctera* (Anthophoridae). It settles in dry forest soil and digs an almost vertical tunnel with a depth of 8–14 cm, to which 3–6 cells are adjoined (Vilson, Frankie, 1977). Side branches from the entrance tunnel to horizontally located brood cells are constructed by the bees *Panurginus atriceps*, *P. occidentalis* (Andrenidae) (Rust, 1976) and *Nomioides minutissimus* (Halictidae) (Radchenko, 1979). In *Augochlorella dentata* (Halictidae), a bunch-like cluster of cells strengthened on ground supports have a remote resemblance to honeycomb (Eickwort G., Eickwort K., 1973). The ground nest of the Halictus bee (*Halictus guadricinctus*) is closer to them. This bee has a nest with a convex or spiral curved structure measuring approximately 6x12 cm that is formed by several tens of closely spaced cells (Blagoveshchenskava, 1983).

A threat to the developing offspring of bees is represented by a hydro factor in many environmental situations. The development of protection means against it involves the acquisition of waterproofing instincts of the cells' contents. Bees use plant extracts or their own secretions as moisture-proof substances. Using the pitch of woody plants, the bee *Melipona tourea* (Anthophoridae) veneer the walls of brood cells. The surface of the cells is covered with an oral secretion of the *Nomia melanderi* (Halictidae) settling in alkaline soil (Batra, 1970). The secretion of the Dufurov gland, which is a complex mixture of liquid triglycerides, is used to cover the cells of the Anthophora bee *Anthophora antiope* (Batra, 1980) and *A. abrupta* (Norden et al., 1980).

The high reliability of a cell's contents in isolation is provided by wax. It is produced in bees by the glands of the body's integument. The use of wax or wax-like substances has been found in solitary living Andrenes *Andrena ovatula* (Wafa et al., 1972), Anthophoras *Anthophora urbana*

(Mayer, Johansen, 1976), Ptilothrix *Ptilothrix bombiformis* (Rust, 1980), etc. These substances usually cover only cell walls, and the plug is usually constructed from the nest substrate. For example, *Andrena urbana* seals the cell with a soil plug (Mayer, Johansen, 1976).

Nesting in open surfaces is the result of the absence of suitable cavities, morphological devices for processing natural substrates or their physical properties (high strength, humidity, etc.). A widespread use of such building materials as small stones fastened with dust and moistened by oral secretions was seen in the bees *Chalicodoma pyrenaica* (Fabre, 1963), *Hoplitis anthocopoides* (Eickwort G., Eickwort K., 1973), *Osmia anthocopoides* (Radchenko, Pesenko, 1994), etc. The female firstly supplies each of the alternately constructed cells with food, then ovipositions an egg in and seals it. The material used to seal the cell does not contain small stones, as they could prevent the release of individuals reaching the imago stage. The construction of such nests containing a little more than ten cells is completed by the building of an additional shelter above them.

Eu- and subsocial species. Primitive social insects include bumblebees (*Bombus*), represented in the insects' fauna by about 250 species. In bumblebees living in the Palearctic, the overwintered female-foundress during the spring-summer season creates a colony that breaks down in late summer or early fall. Burrows of rodents, tree hollows, and crevices of rocks are used as places for bumblebees to settle. The bumblebee nest is covered with various heat-insulating materials found nearby such as dry moss, straw, leaves, etc. A wax-like shell can be used for the waterproofing of the nest (Eskov, 1992; Eskov, Dolgov, 1986). Species living in the tropics use the live or dead leaves of plants to shelter the nests (Janzen, 1971) when they settle on trees.

The seasonal cycle of the development of the bumblebee colony begins with the search for a suitable nesting place for the fertilized female, where she constructs a cell for feed and a brood chamber for her offspring (Fig. 2). Wax is used as a building material by bumblebees and is usually mixed with pollen. This building material is used many times in their nests and when they settle in the abandoned nests of other colonies (Alford, 1971). It is also possible to use other wax-like substances as a building material, for example, plasticine has been found in nest cavities. If there are small containers resembling feed cells, bumblebees can finish building them and store their food reserves there (Dolgov, 1982).

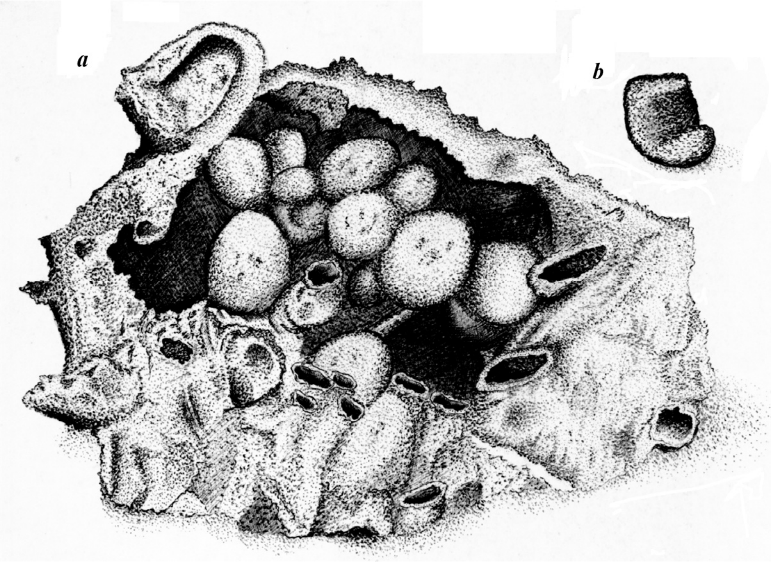

Fig. 2. Dissected nest of the bumblebee *Bombus terrestris* (a) and an enlarged cell with sealed eggs (b).

The construction of the brood cell by the female-foundress is preceded by the detachment of the wax base. The female forms a pollen ball moistened with nectar and rings it with a small wax roller on it (Dolgov, 1982). The females of *B. pratorum*, *B. humilis*, *B. pascuorum* and others make holes in the pollen ball where one egg is ovipositioned (Alford, 1975). The female *B. hortorum* ovipositions eggs at different levels of the pollen ball (Alford, 1971). Females of *B. balteatus* and *B. polaris* oviposition eggs in pollen balls, fill them with a pollen mixture and then cover them with a waxy membrane (Alford, 1971, 1975; Richards, 1973). The construction of separate brood cells where the female ovipositions one single egg is characteristic of *B. rufocinctus* (Hoobs, 1965).

Different types of bumblebees oviposition 8–16 eggs in the first brood cell. Their number also varies among females of the same species. A different time is required for the female-foundress to complete the first ovipositioning cycle. Under favorable weather conditions, *B. agrorum* spends about three days ovipositioning eggs (Free, Butler, 1959; Alford, 1971, 1975; Dolgov, 1982).

The emerging larva systematically receives food (nectar and pollen). It is brought into the cell through the pollen pocket or temporary holes made in the cell (Sakagami, Zucchi, 1965; Alford, 1971; Sakagami, 1976). As the larva grows, the female repeatedly rebuilds the brood cell, completing the waxy membrane. Subsequent brood cells are usually placed randomly on a common base constructed at the initial stages of the nest's construction. With the emergence of working individuals, the colony's protection from the adverse effects of biotic and abiotic environmental factors and the reproduction of offspring increases.

Eusocial species. In highly organized social types of bees, nest structures mainly differ in the use of building materials, the orientation of honeycombs and the location of fodder stocks. According to these species' features, the greatest differences are found between stingless bees and representatives of the genus *Apis*.

Stingless bees. A large group of stingless bees (Meliponinae) permanently live in colonies where structural organization and size can vary significantly. For the place of settlement, stingless bees usually use various natural shelters such as trees or ground cavities and also inhabited or abandoned termite mounds (Wille, Michener, 1973). Some species settle in trees (Darchen, 1969).

Regardless of the settlement place, bees isolate the nest from the outside environment with a multi-layered shell using wax, pitch, clay, wood and other materials (Koeniger, 1976). The entrance to the nest is in the form of a slit or tunnel that in *Meliponen* is made of clay, and in *Trigona* – of resin (Brian, 1986). In order to protect against the penetration of robbers and parasites into the nest, the bees guard the entrance during the day, and at night close it with a cork constructed from the material used for the building of the tunnel entrance. Some species protect the entrance from ants with sticky substances (Ihering, 1903; Rooley, Michener, 1969). The drainage pipe can be constructed to remove water in the lower part of the nest (Brian, 1986; Michener, 1974). Some wax balls may be used in the nest as a reserve building material (Brian, 1986).

The cells for brood and food, as a rule, differ in shape and location in the nest. The largest cells are constructed to store the reserves of honey and pollen. They are placed on the periphery of the nest. In *Melipona beecheii*, their diameter reaches 2–3 cm (Darchen, Delage-Darchen, 1975). The main part of the nest cavity is occupied by relatively small cells for the brood. They are strengthened by supports. The nest material is used for these constructions. In some species the brood cells are arranged in groups forming bunches. For most species it is characteristic to have a horizontal distribution of brood cells, forming one-sided honeycombs (Fig. 3). The construction of vertical two-sided honeycombs was found in *Dactylurina staudingeri*. Working individuals and drones are developed in the cells of honeycombs. Cells for the reproduction of large females (queens) are located at the bottom of the honeycomb or in the inner surface of the shell of the nest (Michener, 1974).

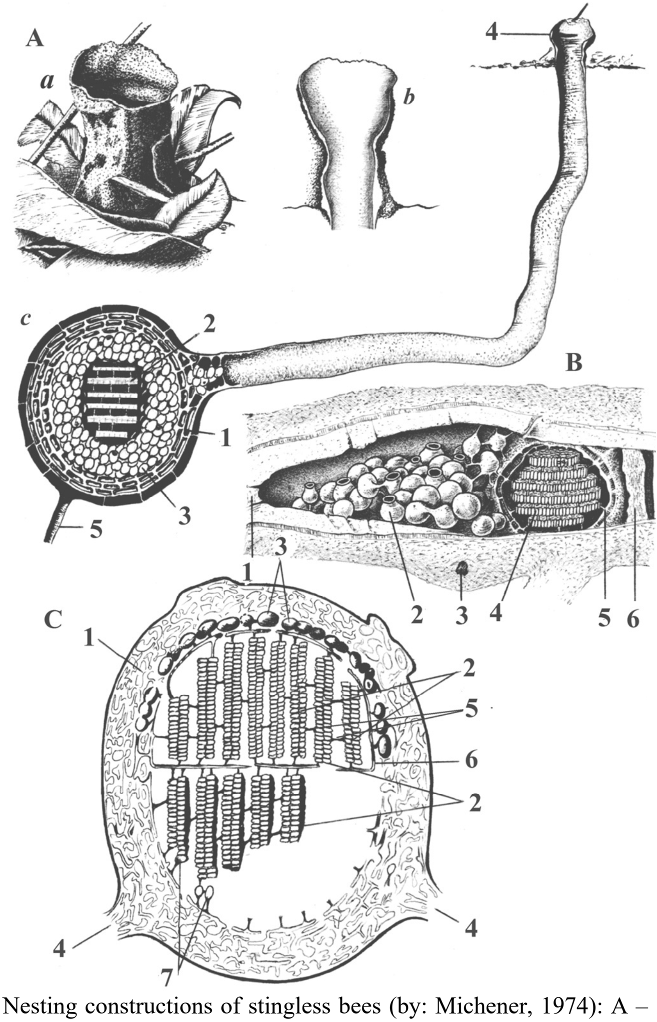

Fig. 3. Nesting constructions of stingless bees (by: Michener, 1974): A – *Trigona recursa* nest in the ground: a – the appearance of the entrance; b – entry section; c – longitudinal section of the nest located in the ground (1 – layered shell, 2 – honeycombs, 3 – fodder reserves, 4 – entrance, 5 – drainage tube); B – nest in the hollow of a tree (1 – wall that limits nesting space, 2 – fodder reserves, 3 – entrance, 4 – brood honeycombs, 5 – protective shell, 6 – wood); C – section of the nest of *Dactylurina staudingeri* (1 – nest shelter, 2 – brood cells, 3 – fodder reserves, 4 – entrance to the nest, 5 – supporting partitions, 6 – drainage tubes).

Working individuals are engaged in the construction of the nest cavity and cells. They also fill the cells with food (a mixture of pollen and nectar), adding to it the secretion of hypo- or propharyngeal glands. Firstly the queen consumes part of this food and then ovipositions an egg. After that, bees seal the cell, not worrying about the trophic supply of the developing individual (Darchen, Delage-Darchen, 1975; Sommeijer et al., 1982).

Bees of the genus Apis. The genus Apis includes three subgenera, each of which unites two species that have similarities in their lifestyle in the specificity of settlement places and the design of nesting structures. The most evolutionarily advanced subgenus combines *A. mellifera* and *A. cerana*. The intermediate position is taken by the species *A. dorsata* and *A. laboriosa* (subgenus *Megapis*). The most primitive species are *A. florea* and *A. andreniformis*, which form a subgenus (*Micrapis*). The most widespread is *A. mellifera*. Other species mainly live in the tropical forests of Southeast Asia. Only *A. cerana* inhabit the Palearctic (in Northeast China, Japan, and Southern Primorye) and *A. laboriosa* live in the Himalayas, settling at an altitude of 3–4 km above sea level.

Representatives of *Megapis* and *Micrapis* construct only one honeycomb attached to a tree branch, the bottom surface of a rock or other aboveground objects. When choosing a settlement place, *Microapis* bees must see at least a small part of the sky from a honeycomb. By its polarization, bees determine the position of the sun; this is used in the system of spatial orientation. This is not required for the other four species of bees of the genus *Apis* (Lindauer, 1971; Eskov, 1979, 1992).

Bees start the construction of honeycombs at the place where it is attached and complete it later in the process of mastering the new settlement place. *A. florea* usually settles on the side of rocks facing to the south in the summer and to the east in winter (Dutton, Simpson, 1977). Its honeycombs usually have a shape close to a semicircle or an ellipse with one side having an area of about 500 cm². The dimensions of the cells differ depending on their purpose. Relatively small cells with a diameter of about 2.5 mm occupying approximately 80% of the honeycomb's surface are used for the development of working individuals. Larger cells are used for the development of drones. In the upper part of the honeycomb, there are large cells that are used for storing honey and flower pollen. In the lower part of the honeycomb, bees build several cells of an acorn-form shape where queens develop. When settling on tree branches, the nest's protection from ants is achieved by constructing rings made of sticky resinous plant extracts (Butler, 1969).

When settling on trees, bees of the subgenus *Megapis* build honeycombs at a height of up to 20 m, and less often of up to 40–80 m above the surface of the soil. The honeycomb can hang under the weight of honey close to the ground but usually does not come into contact with it. The clustering of nests in one place is characteristic of these bees. More than 150 colonies can settle on one large tree (Butani, 1950), although there are also single nests. The minimum diameter of the branches used to build the honeycombs is 12 cm. However, most often, bees prefer branches with a diameter of about 30 cm (Morse, Laigo, 1969). When the construction is completed, the honeycomb becomes a truncated ellipse where one side's area can reach 0.5–1.5 cm^2 (Kaiser, 1976).

The largest cells (their depth can exceed 8 cm) localized at the top of the honeycomb are used as food stocks (Singh, 1962; Morse, Laigo, 1969). Cells used for the development of working individuals and drones come under the food tier. In this part, the thickness of the honeycombs decreases to 35-40 mm. Ellipsoidal queen cells are located in the lowest part of the honeycombs (Morse, Laigo, 1969).

Honeycombs' protection from the direct influence of biotic and abiotic factors is provided by bees forming a multilayer covering with their bodies. This is mainly formed by young bees hanging upside down, clinging to each other with their legs (Roepke, 1930). The size of such a nest shelter, which usually hangs over the lower border of the honeycomb, depends on the number of bees in the colony that reaches its maximum before the sociotomy (Morse, Laigo, 1969).

The bees *A. mellifera* and *A. cerana* differ from the bees *Micrapis* and *Megapis* in their adaptation to sheltered settlements (hollows of trees, clefts of rocks and other cavities). Such shelters protect them from the influence of unfavorable physical and biotic factors. When it is possible to choose a place of settlement, the honey bee prefers cavities in wood with a volume of 70 ± 103 cm^3 located at an altitude of 8–19 m (Petrov, 1983). This indicates that they have instincts of evaluating the suitability of a potential dwelling with the biological needs of the colony.

The nests of Indian honey bees form vertical two-sided honeycombs, the number and shape of which depend on the configuration of the nest cavity. One large honeycomb can be enough for a nest of honey bees that has settled in a narrow cavity. In representatives of this species, as well as other bees of the genus *Apis*, the upper part of the honeycomb is usually used for food stocks. The brood cells are placed below, and the acorn-form queen cells – on the periphery. At different times, all honeycomb cells can be used to store food except for the queen cells.

The diameter of the cells (the distance between opposite angles) in a honey bee nest varies from 4.1 to 7.7 mm (Fig. 4). The cells with a diameter of 5.1-5.4 and 6.5-7.0 mm have the largest frequency of occurrence (about 60%). The first of them are used for the reproduction of working individuals, the others – for drones. The tendency to cell enlargement can be traced at the initial stages of honeycomb construction during the period of mastering a new dwelling (Eskov, Eskova, 2001, 2012).

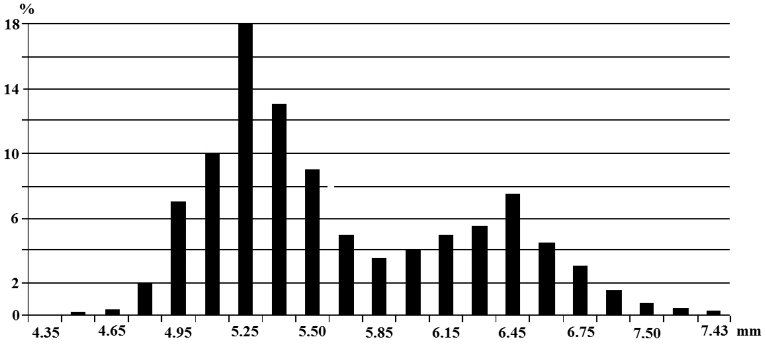

Fig. 4. Percentage distribution of 43,279 cells (y-axis), differing in the distance between their opposite angles (x-axis); honeycombs are built up by bees in free nesting spaces.

Preserving the building material and maximizing the use of the nest structure in bees of the genus *Apis* favored the closeness of cells and the honeycomb formation. The bees built bunch-shaped clusters of cells in the initial phases of the development of this building instinct that is typical for some Halictus and relatively low-ordered stingless bees. One-sided honeycombs are distinguished by higher ordering. They are widespread in stingless bees and are also found in some social types of Halictus. At the same time, the needs of relatively small Halictus colonies for the reproduction of offspring are satisfied by the presence of only one honeycomb. However, this is not enough for large colonies of stingless bees. Therefore, they had a need for constructing a multi-tiered nesting structure containing several honeycombs connected by a plurality of supports and bridges. They provide an increase in the strength of the brood nest zone, but this is associated with additional costs to building materials and the restriction of the useful volume of the nest cavity. Cells of one-sided honeycombs of stingless bees are unsuitable for food stocks. For these purposes, large cells that are tuned outside the brood zone are used.

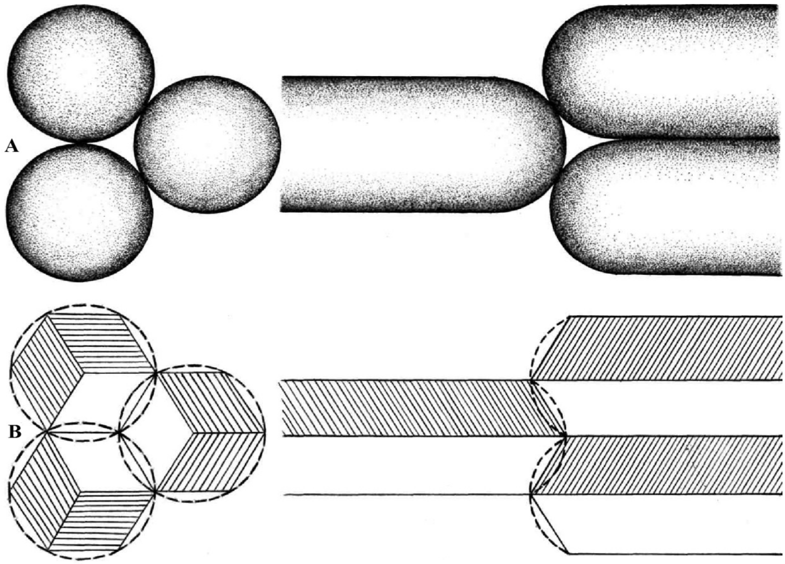

Fig. 5. Schematic representation of the transformation of rounded cells into hexahedral cells due to their compaction (A), and the resulting transformation of oval bottoms into trapezoidal ones (B).

The transition from a horizontal to a vertical placement of cells is associated with a modification of building instincts, which could be motivated by the adaptation to shelter life. With the development of the instinct for two-sided honeycomb cells' construction, the selection favored the convergence of the separated common adjacent walls. The partial overlapping of their bases on opposite sides of the cells is associated with the convergence of cells. Each of the three converging cells on one side of the honeycomb forms a concave base for the cell on its opposite side. The maximum convergence of cells led to the transformation of their originally rounded shape into a hexagonal one, and the combined parts of the bases transformed into trapezoids. Each of the three rhombs forming the base of the cell began to be included in three adjacent cells on the opposite side, thus maximizing the convergence of the cells of bilateral honeycombs, saving building material (wax) and providing a relatively high amount of strength (Fig. 5).

Morphofunctional Differentiation of the Bee Colony

The size and the members of the colony. Colonies of eu- and subsocial species include a small number of adults and developing individuals. In the nests of *Losioglossum sp*. (Halictidae), during the intensive development of the colony, there may be 20–25 adult females, approximately the same number of developing individuals at the larval and pupal stages, and about 10 males (Houston, 1970). *Exoneura eremophila* and *E. setosa* (Anthophoridae) constantly reproduce males during the period of the colony's existence, but they do not stay in the nest for a long time. The maximum number of adult females in the nests of these species can reach 20 individuals, and the brood – a little more than 40 cells (Houston, 1977).

The number of bumblebee colonies has a pronounced tendency to increase with the migration of various species from zones of cold and temperate climates to subtropical and tropical ones. Short summers in the upper latitudes limit or completely prevent the raising of workers. Therefore, with a move to cold climate zones, bumblebees come closer to the way of life of typical solitary living insects (Malyshev, 1928; Richards, 1955a). In contrast, in the tropics, the raising of working individuals, mature females, and males is possible throughout the year (Michener, Amir, 1977).

In seasonal colonies of species inhabiting temperate climates, by the time of maximum development, the number of adults is usually limited to a few tens, and in the tropics – by hundreds. Among adults in tropical species, the ratio between mature females and working individuals is maintained at about 1:10 (Ihering, 1903). In seasonal colonies, females are generally reproduced more than males. For example, during years with warm weather, by the end of summer in *B. agrorum* colonies the ratio of the reproduction of females and males corresponds to about 0.6:1, and at the early onset of cold weather this changes to 1:1.6 (Brian, 1951, 1952). The number of males also increases in cases of the loss of the female-foundress. In *B. terricola* and *B. melanopygus*, the ratio between females and males can be as high as 1:6 in size, and 1:2.9 in biomass (Owen et al., 1980). The quantity of males in the colony increases correspondingly to the increase of the period between the onset of ovipositioning by the female-foundress and the working individuals of haploid eggs (Duchateau et al., 2004).

Interspecific (interspecies) differences in stingless bees are characterized by high variability. The smallest number of them is several hundred individuals. This is characteristic for colonies of *Melipona quadrifasciata*, *M. scutellaris*, and *Trigona silvestris*. One to several thousand is characteristic for colonies of *T. capitata*, *T. mombuca*, *T. testaceicornis*, *T. droryana*, and *T. Postica*. 50–180 thousand adults can be contained in colonies of *T. rufrus* (Lindauer, Kerr, 1960). The ratio between the number of queens and working individuals in them is usually in the range of 1:3–1:4 and can exceed these limits depending on the availability of food for colonies (Darchen, Delage-Darchen, 1975). When there is a lack of food in *M. beichei* colonies, this ratio increases up to 1:9, and with an abundant food supply it can reach 1.3:1 (Darchen, 1973).

In the colonies of the honey bee, the workers usually have the largest representation. Their quantity is subject to pronounced seasonal variability depending on the external temperature and productivity of the forage place. In zones with a temperate and cold climate, the maximum numbers of worker bees reach 30-70 thousand individuals in the summertime, and the minimum – at the end of wintering and the resumption of flying activity. Drones are temporary members of the bee colony. They emerge in April-June and are expelled from colonies in late summer or early fall. Drones remain in the nests for the winter only in queenless colonies.

The honey bee is characterized by a monogynous organization of the colony. The presence of two or more adult queens is possible only during the period of sociotomy when the separation of the new colony resulting in swarming is delayed due to unfavorable weather. The participation of two queens in carrying out the reproductive function is possible in colonies that replace the queens. However, their life together is usually not long.

Life expectancy and the reproductive potential of females. In social insects, females (female-foundresses) performing reproductive functions usually differ from their female offspring that appear in the initial phases of the development of the new colony. These females in social insects most often perform auxiliary functions and do not directly contribute to the reproduction of their species. This is most often associated with their sexual underdevelopment.

Female-foundresses. The lifespan of female-foundresses and their female offspring varies and depends on the level of the social organization of the bees. Female-foundresses of eu- and subsocial bees have a relatively low life expectancy. In species that have the lowest level of social organization, the female-foundress may not survive until her offspring reach the adult stage. Unequal trophic support at the larvae stage is the cause of differences in the development of reproductive organs. As a result, sexually mature females are engaged in the reproduction of offspring, and underdeveloped females perform subsidiary functions. This form of communality is known in the bees *Exoneura eremophila* and *E.*

setosa (Anthophoridae) settling in the core of the stems of herbaceous plants. Female-foundresses in these bees do not always survive until the appearance of the first underdeveloped females. When they reach the imago they remain in the nest, and after the emergence of mature females they participate in the protection of the nest and the trophic support of the generation of their sisters (Houston, 1977).

In higher-organized social species of *Ceratina*, for example, in *Ceratina japonica*, *C. flavipes* and *C. iwatai*, the female-foundress' care of developing offspring helps to reduce mortality from approximately 50% to 3-19% (developing individuals can exist without female-foundresses in the event of their death). The strengthening of the relationship between female-foundresses and the offspring of Ceratina is sometimes expressed (in about 10% of cases) in joint overwintering, and afterward the female-foundresses start to perform reproductive functions (Sakagami, Maeta, 1977). The increase in the life expectancy of female-foundresses related to the increased interrelation with their offspring is even more pronounced in some species of the Halictus bee. For *Lasioglossum* (*Dialictus*) *umbripenne*, the female-foundress lives for about a year, with the first generation of her offspring performing the function of working individuals. During this time, she is not replaced by her daughters (Wille, Orozco, 1970).

In one-year-old colonies of bumblebees, working individuals always develop in the first brood cell constructed by the female-foundress; their number in *B. agrorum* and *B. humilis* reaches eight (Alford, 1970), and in *B. hortorum* – 16 (Alford, 1971). In the next generations, mature females develop. The reproduction of males takes place at the end of the development season of bumblebee colonies. The lifespan of female-foundresses is limited to one year; workers and males die when the cold comes. Female-foundresses live much longer in perennial colonies inhabiting the tropics. However, in these colonies, several females of different ages may simultaneously oviposition fertilized eggs (Sakagami, Zuchi, 1965; Michener, Amir, 1977).

The activity of the reproductive function in bumblebee female-foundresses increases in the process of the development of their colonies. In the first brood cell, the female *B. agrorum* usually ovipositions eight eggs within three days. This is followed by a reproductive pause that ends after the emergence of the first working individuals, and after that new brood cells are built in the nest (Alford, 1970). With the increase of the number of adults, the reproductive activity of the female can reach 12 eggs per day (Brian, 1951, 1952). The reproductive potential of perennial tropical colonies is much higher than that of annuals. Within a day, the female *B. transversalis* can oviposition up to 300 eggs (Michener, 1979).

The female (queen) bees of the genus *Apis* are distinguished by their high fertility and lifespan. In different races of the honey bee, the queen can oviposition from a few hundred to three thousand eggs during the day, which, along with genetic differences, depends on the ecological situation and the number of working individuals in the colonies (Taber, 1980; Eskov, 1995a). The reproductive activity of the queens decreases with their age. The life expectancy of queens is generally limited to 4–6 years, but the maximum, according to the observations of A.D. Betts (Eskov, 2013), can be eight years. The death of the queens most often happens during the wintering period. The probability of death increases with age.

Worker individuals. Regardless of the level of social organization in bees, the underdeveloped females as a rule act as workers. They appear in seasonal colonies at the initial stages of their development. In social Halictus types, workers live for about 30 days (Wille, Orazco, 1979). In some types of Halictus, small underdeveloped females appear along with large, mature females in the first reproduction. They replace the female-foundress in the case of her death. In the colonies of *Exoneurella eremophia* and *E. setosa*, the representation of mature females can reach 75%. They perform a reproductive function with the female-foundress in the colony (Houston, 1977).

Males are usually developed from eggs ovipositioned by unfertilized worker bees. In some species, the contribution of working individuals to the reproduction of males is of crucial importance. Thus, in the colonies of bumblebees, the proportion of males developing from eggs ovipositioned by working individuals can reach 90%, and in the *Trigona* – 95% (Lin, Michener, 1972). The behavior of working individuals ovipositioning eggs differs from the behavior of female-foundresses. Workers are characterized by randomly ovipositioning several eggs in one brood cell. In this process, workers often occupy other cells, eat eggs and replace them with their own (Katayama, 1973). Females are obligatorily similarly related to brood cells constructed and occupied with eggs ovipositioned by working individuals (Garofalo, 1978).

The life expectancy of bumblebee workers depends on the forms of participation in the life of the colony. The bumblebees engaged in food delivery usually do not live as long as workers performing intra-nest work. In colonies of species inhabiting temperate climates, the average life expectancy of workers is limited to about 25 days, and the maximum lifespan reaches 69 days (Brian, 1952). This is similar to tropical species of *B. morio*, where foragers live on average for 36 days, but individuals who specialize in performing intra-nest work live twice as long – 73 days (Garofalo, 1978).

Among the bees of the genus *Apis*, working individuals begin to perform reproductive functions in the absence of the queen. In a queenless colony of a honey bee, up to 25% of bees can be found ovulating (Perepelova, 1928), while representatives of *Megapis* have only one (Velthuis et al., 1971). The number of eggs ovipositioned by the ovulating working individual in *A. mellifera* varies from 19 to 32 (Perepelova, 1928). The working bee spends 17–251 sec/s (Gaydak, 1969) ovipositioning eggs, and the queen spends about 10 sec. Convergent similarities of working bees and bumblebees engaged in ovipositioning eggs are expressed in disordered (chaotic) behavior.

The lifespan of honey bee workers is subject to seasonal variability. Bees actively participating in the replenishment of food reserves of spring-summer generations live for 30–40 days, and in wintering ones – up to 6–7 months (Eskov, 1995a). The maximum life expectancy of bees of spring-summer generations can reach 89 days, and for wintering – 304 days. Some bees can survive for up to 307–396 days in queenless colonies (Maurizio, 1958). The concentration of carbohydrate food consumed by worker bees has a significant effect on their life expectancy. An increase in water content leads to a reduction in life expectancy (Eskov, 1992, 1995a).

Determination of gender. Bees' gender differentiation is mainly associated with a cyclic replacement of haploidy and diploidy. Females in most known species of bees develop from fertilized eggs and males from unfertilized eggs. If you do not take into account the mutation process, then the kinship coefficient between the female-foundress and her daughters in a case of single pairing approaches 1:4, and in the case of a pairing with two males (polyandry), it increases up to 1:2; with a triple pairing – up to 5:12; and with a tenfold pairing – up to 3:10.

The probability of females mating with one or more males is related to species-specific features but may depend on the environmental situation. Polyandry is not widely spread among bumblebees. In most of their species, females mate with males at the end of summer and the beginning of fall. However, *B. hypnorum* females may have a 2-3-fold pairing (Roseler, 1978). The honey bee is characterized by polyandry. Queens of these species can mate during the mating season with 17 drones under favorable weather conditions, otherwise they remain unfertilized.

In the case of arrhenotoky, common in groups of honey bees living on the Eurasian continent, colonies with unfertilized queens are eliminated. The greatest probability of survival without fertilized queens is in the colonies of species characterized by thelytoky. This was first discovered in the bees of *A. mellifera capensis* inhabiting the Cape region of South

Africa (Onions, 1912). The colonies of these bees usually contain about 20% of individuals with enlarged ovarioles. Among these initially working bees, there are individuals that for 28–42 days oviposition unfertilized eggs, from which females hatch and develop. In Cape bees, the thelytoky is stimulated by the loss of the ovulating female. If there is a thelytoky in the colony, the drones will develop from eggs ovipositioned by working individuals. These bees are freely interbred with European bee races. When crossing *A. mellifera capensis* with *A. m. carnica*, the thelytoky dominates in metis, and in the case of crossing with *A. m. ligustica* this feature turns into a recessive state (Ruttner, 1977).

The development of drones from fertilized eggs has been discovered in honey and Indian bees. Bees usually destroy such drones in the early stages of ontogeny. However, sometimes they develop up to the imago stage and can occupy up to 30% of the places in the cells used for working individuals' reproduction (Woyke, 1980). Adult diploid drones differ in appearance from haploid ones, having similarities with females and males at the same time (mosaic gynandromorphism). The increase in the size of certain parts of the body can be due to polyploidy (Woyke, 1980). Gynandromorphism in diploid Melipona drones is expressed by the presence of similarities with females in the structure of their exoskeleton, wings, and eyes (Kerr, 1974).

The seasonal sequence of the reproduction of sexually mature females and males. In one-year-old bee colonies, the sequence of the reproduction of mature females and males, their time of flight from the nest and mating is determined by the hereditary program acquired in the process of adaptation to typical living conditions. For example, *Osmia lignaria* females complete development and leave the nest before males, whose size decreases from the first to the last generation. This is caused by a deterioration in trophic support (Torchio, Tepedino, 1980). In bees of *Lasioglossum (Dialictus) umbripenne*, reproductive periods of sexually mature offspring are associated with cycles of drought, but the seasonal cycle of the development of colonies is completed by the reproduction of drones (Wille, Orozco, 1970). During the second half of the summer, the reproduction of sexually mature offspring takes place in colonies of bumblebees living in temperate climate zones. In colonies of tropical species, the reproduction of males and females continues uninterrupted throughout the year. The female can live for more than one year. Nevertheless, new colonies are always based on the same female (Michener, Amir, 1977).

In colonies of the subsocial species where the females are completely incapable of independent existence, the cyclicity of the rearing of sexually