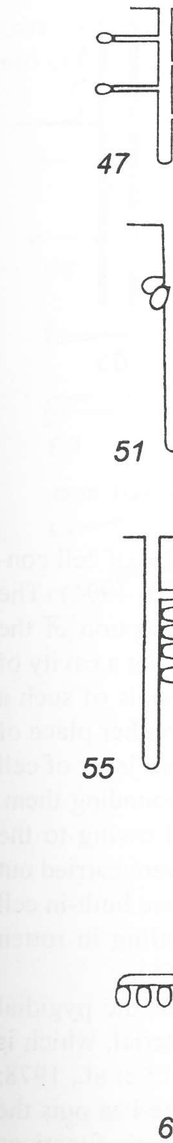
pical), *Eupetersia* BLÜTHGEN (Palaeotropical, with three subgenera), *Microsphecodes* EICKWORT et STAGE (Neotropical), *Ptilocleptis* MICHENER (Neotropical), and *Sphecodes* LATREILLE (nearly cosmopolitan but absent in South America, with two subgenera).

The following genera of the Halictinae inhabit the Palaearctic region: *Ceylalictus, Nomioides, Halictus, Pachyhalictus, Seladonia, Thrincohalictus, Vestitohalictus, Evylaeus, Lasioglossum, Ctenonomia, Lucasiellus, Sphecodes*. In Europe, 268 species of almost all the genera listed above occur (except for large Palaeotropic genera *Pachyhalictus* and *Ctenonomia*; each of which is represented in the Palaearctic region by few species). Only six genera (including *Sphecodes*) are represented in Poland where 92 species of the Halictinae are recorded.

Subfamily Halictinae: bionomics

Main kinds of nest patterns. The nest architecture of the Halictinae was studied in detail by SAKAGAMI & MICHENER (1962), with taking into account the most of data existent by that time. These authors have distinguished 8 types and 11 subtypes of halictine nests. In those groups one finds almost all known nest types proper to burrowing bees (Figs. 47-62). The most species build their nests in soil, although some of them sporadically or constantly settle in rotten wood, e.g. some Augochlorini. Some species exhibit a great plasticity in the choice of place for nest construction. For example, nests of *Halictus rubicundus* were registered both in ground (BONELLI, 1967b; BATRA, 1968; and some others), and in rotten wood (MICHENER & WILLE, 1961).

Halictine nests are as a rule characterised by the presence of nest turrets, which are formed in result of cementation of soil particles on the walls of the entrance passing through a conical tumulus. Due to that, after the tumulus gets washed away by rains there remains a vertical turret on the surface (Figs. 63-65). The most species make the lower blind burrow constituting one of the most salient peculiarities of halictine nests. For the brood rearing the bees construct cells usually ellipsoid in their form and bilaterally symmetrical. In most species the cells are oriented horizontally, and their lower part is always flatter than the rest of the walls. Halictines, which build inclined or vertically oriented cells, make one of the cell walls flatter than others. At this wall the pollen ball is usually placed, being sometimes attached to it. Considering such a peculiarity of the cell structure, MICHENER (1964) has come to a conclusion about primary nature of horizontally oriented cells. In each species the form and the size of cells are constant, with the exception of some differences in size that are closely associated with sexual dimorphism. At the same time in species leading advanced social mode of life and having female castes, cells that produce workers are of smaller average size than those producing queens. Even to a greater degree such distinctions are exhibited in the size of pollen balls prepared for the brood rearing by different castes.



47. Simple branc
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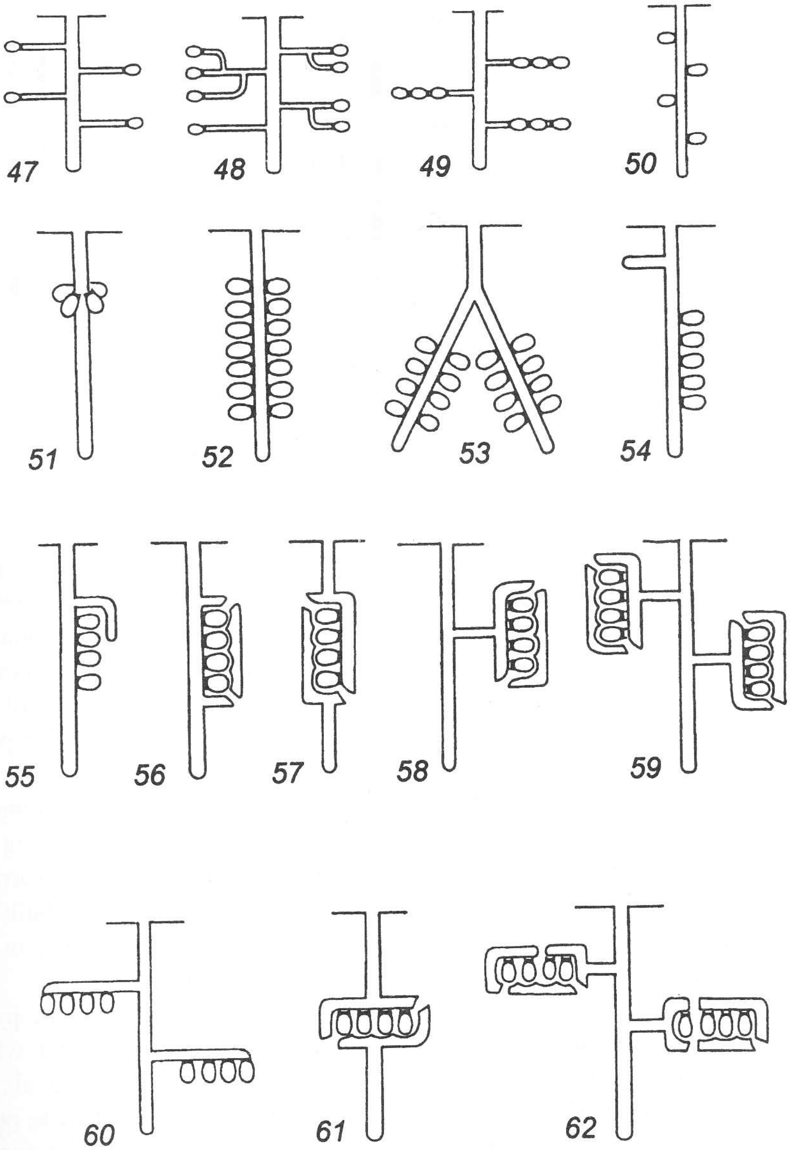
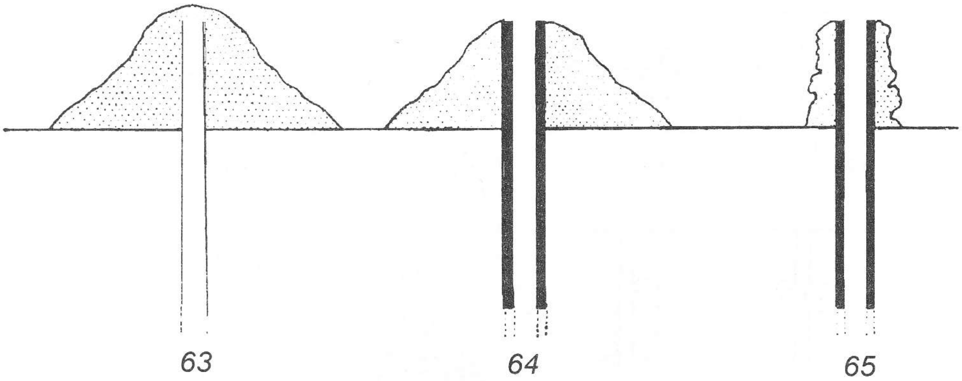


Figs. 47-62. Main kinds of nest patterns.

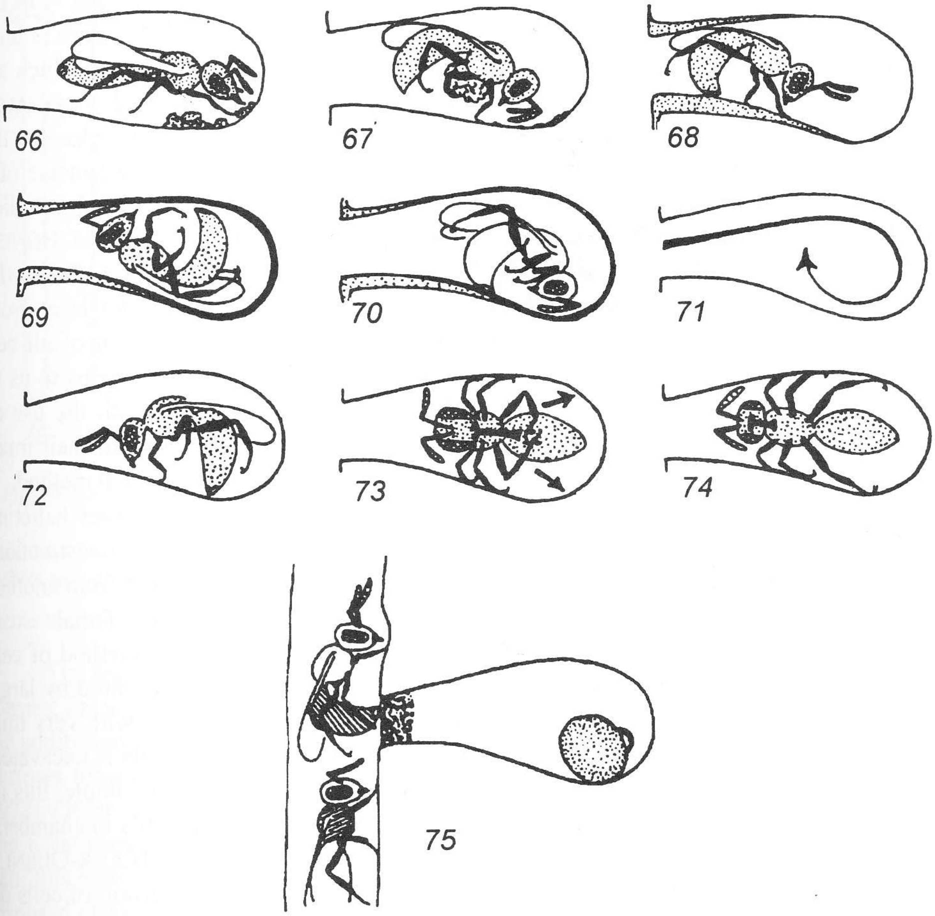
47. Simple branched nest. *48.* Twice-branched nest. *49.* Linear-branched nest. *50.* Nest with sessile cells dispersally deposited along the main burrow. *51.* Nest with sessile cells deposited along the main burrow. *52.* Nest with sessile cells forming clusters. *53.* Branched nest with sessile cells forming clusters. *54.* Nest with lateral blind burrow and sessile cells deposited at one side of the main burrow. *55.* Nest with partly formed chamber. *56.* Nest with complete chamber deposited near the main burrow. *57.* Nest with complete chamber deposited within the main burrow. *58.* Nest with complete chamber deposited at the end of the main burrow. *59.* Brunched nest with chambers. *60.* Brunched nest with vertically oriented cells. *61.* Chamber nest with vertically oriented cells. *62.* Chamber branched nest with vertically oriented cells.



Figs.63-65. Nest tumuli and turret of *Evylaeus marginatus* (from Plateaux-Quénu, 1960b: Fig. 5a-c).
63. Tumulus around the entrance of the nest. *64.* Tumulus with forced walls. *65.* Nest turret.

Stages of nest construction. All halictines apply pygidial method of cell construction (after the nomenclature adopted in Radchenko & Pesenko, 1994). The representatives of the tribes Augochlorini and Halictini, with the exception of the species of *Agapostemon* (Roberts, 1969) during the cell construction dig a cavity of a size larger than the final size of the cell. The bees coat the inner walls of such a cavity with thin layers (up to 1-2 mm thick) of sift soil obtained in another place of the nest; usually it is taken from blind burrows. As a result the thin inner layer of cell walls differs in structure, and sometimes in colour from the soil surrounding them. The picture of such cells construction was clarified in every detail owing to the results of observations of artificial nests of *Evylaeus zephyrus* which were carried out by Batra (1964, 1966b) (Figs. 66-75). Similarly to the species that have built-in cell walls of transported soil, some representatives of Augochlorini settling in rotten wood cover the cell walls with layers of sawdust (Stockhammer, 1966).

Females smooth and ram the inner cell walls with the help of the pygidial plate and then cover it with water-proof lining made of secreted material, which is produced by Dufour's gland (Bergström, 1974; May, 1974; Hefetz et al., 1978; Cane, 1981, 1983; Duffield et al., 1981, 1982; Hefetz, 1987). The bee puts the lining on the wall with a brush on the top of its metabasitarsus. The main functions of the cell lining are seen in the maintaining the optimum humidity and in the additional fixation of the cell walls. As well, the lining has fungicide and bactericide properties (May, 1974). The burrowing bees never destroy the cells with the growing brood, although their burrows frequently pass very close to cells, especially in dense nest aggregations. The safety of cells is also ensured by secreted lining. At the same time abandoned cells, from which bees are emerged, can be destroyed by the digging bees. In difference from most bees, some species of Halictinae, in particular *Evylaeus seabrai* (SAKAGAMI & MOURE, 1967), occasionally re-use the old cells after their preliminary re-lining.

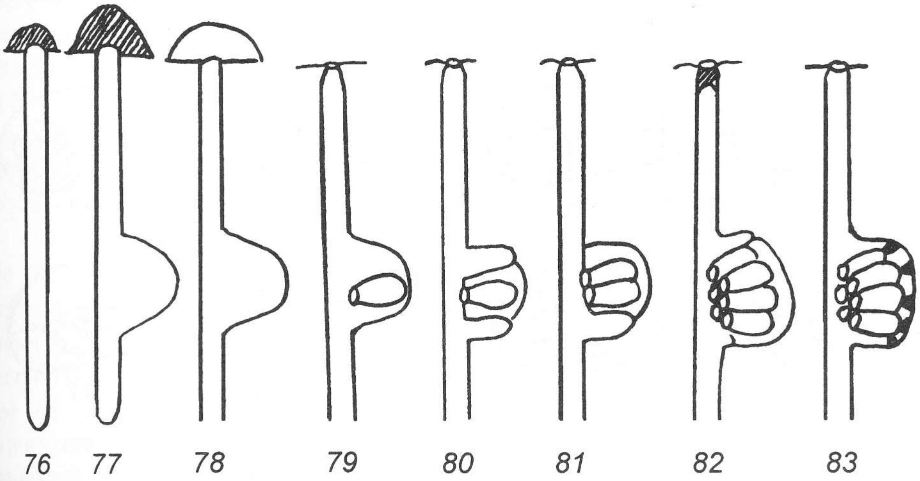


Figs. 66-75. Sketches showing methods of cell construction by *Evylaeus zephyrus*. Different individuals are indicated by different patterns of shading (from BATRA, 1964: Figs. 15a-i, 17f). *66*. Cell excavation. *67*, *68*. Excavated soil is carried back and used to form the narrow neck of the cell. *69*, *70*. Soil taken from burrows is used to line cell - here it is being packed down with the pygidial plate. *71*. Diagram of route commonly taken by bees while working in cell. *72*. Bee rubbing with apex of abdomen, presumably depositing secretion of Dufour's gland. *73*, *74*. Sequence in use of tongue and penicilli in spreading waxlike cell lining, at least part of which probably comes from Dufour's gland. *75*. Egg-layer plugs cell with soil.

Many of halictines characteristically construct nest chambers inside of which the cells are placed. The ways of the chambered nest construction are essentially different in different species. Thus, females of *Evylaeus linearis* at first build all the group of cells, and then dig it around with numerous burrows forming the chamber. Females of *Halictus quadricinctus* begin to form the nest chamber earlier – in the course of the building of cells. The uppermost cells, which are built first, are at once separated from the surrounding soil, whereas new cells of a given group, which are built later, remain tightly imbedded into the substrate (KNERER & PLATEAUX-QUÉNU, 1970). BONELLI (1965a, 1968) has informed that in *Evylaeus* calceatus the cell clusters are most probably formed not by excavation, being erected inside of a spacious chamber previously constructed by the bee, because in the nests he studied the females constructed chambers before the beginning of cell construction. BONELLI's supposition has been supported by MICHENER (1974) and PACKER (1983), who do not see an essential difference between the construction of an inner layer from substrate material inside of an excavated cell and independent erection of all cell walls inside the free space of a large nest chamber. Still this opinion seems to us to be erroneous. Such a method of construction can be realised only with the use of mandibles. In fact, the halictines construct cells (including embedding of their inner walls and cap) in chambers filled with soil, and applying only the pygidial method.

So, females of *Evylaeus calceatus, E. malachurus* and some other halictine species can excavate the nest chamber before the beginning of cell construction, however after this they re-fill such a chamber with sift soil transported from another place of the nest, usually from the blind burrows. Only afterwards the female excavates a cell inside the brought soil (Figs. 76-83). Such an unusual method of cell construction permits to avoid possible obstacles (which can be presented by large stones and other soil inclusions) to forming a dense cluster of cells with very thin built-in walls. In distinction from the nests, in which the group of cells is excavated in intact soil and usually increases progressively downwards (for example, this is the case with *Halictus quadricinctus*), in species which build the cells in chambers filled with soil (for example, *Evylaeus nigripes*; KNERER & PLATEAUX-QUÉNU, 1970), the group of cells can grow only upwards and asides. The group of cells in such nests is almost always surrounded by chambers, which grow as the size of the group grows. The inner walls of a chamber are as a rule rough and not submitted to any special treatment, being the exception of *Evylaeus duplex* (SAKAGAMI & HAYASHIDA, 1960) and *Megommation insigne* (MICHENER & LANGE, 1958c), in which they are smoothed.

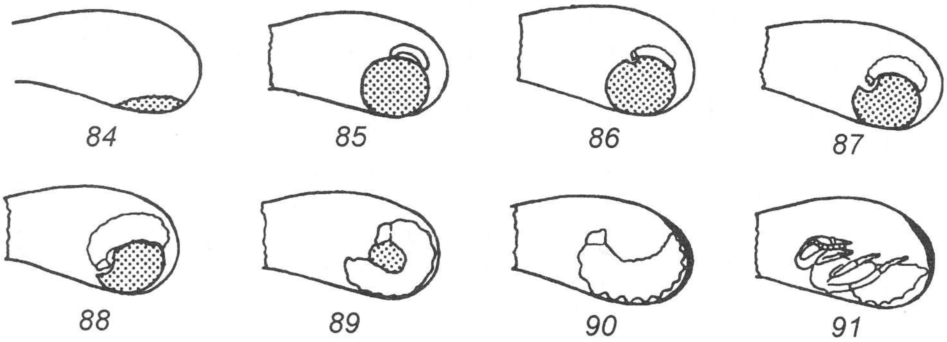
Evylaeus malachurus usually builds a chamber around the cells only for rearing the first brood of workers. SAKAGAMI & HAYASHIDA (1968) suppose that this is due to difficulties presented by construction of a chamber around immense cell cluster with reproductive offspring, and by holding it on thin soil columns. Construction of chambers is possibly a mode of adaptation to nesting in slowly drying soil (Knerer, 1980b; Packer, 1983). However it is unlikely that there exists distinct correlation between the soil characteristics of the substrate and the appearance of chambers among various groups of Halictinae (Sakagami & Michener, 1962).



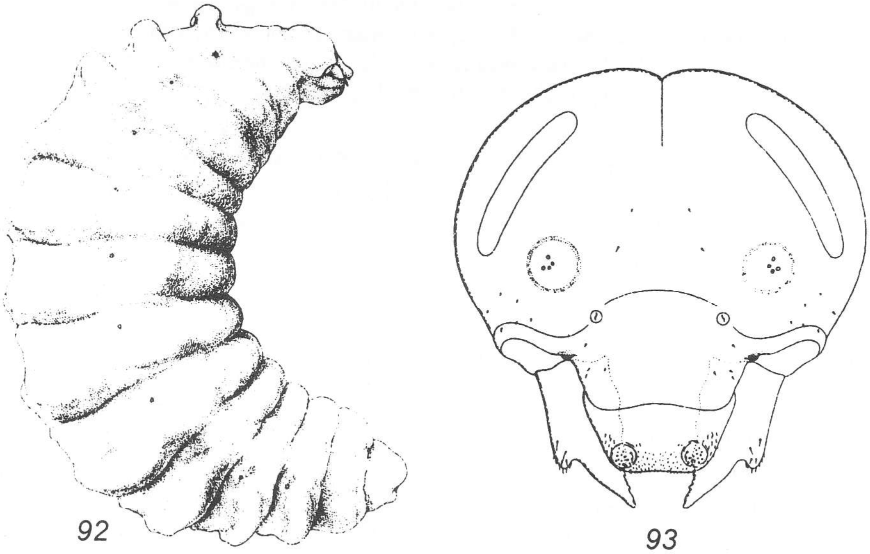
Figs. 76-83. Sequence of cell construction and forming of nest chamber by *Evylaeus malachurus* (from Knerer & Plateaux- Quénu, 1967b: Figs. 1-7, 9).
76. New nest with alone main burrow. *77.* Nest with empty chamber. *78.* Nest with chamber that filled with a fine soil. *79, 80, 81, 82.* Construction of the cells in the chamber with filled soil. *83.* Cells cluster surrounded by air space.

The ways of constructing chambers vary among different species. Thus, some species, for instance *Evylaeus calceatus*, build a cluster of several cells at the end of the additional (secondary) burrow. In the sequel this cluster gets dug around with burrows forming a chamber (Plateaux-Quénu, 1964; Sakagami & Munakata, 1972). Other species, e.g. *Evylaeus nigripes* (Knerer & Plateaux-Quénu, 1970) and E. laticeps (Packer, 1983), construct a chamber at once after building the first cell; this chamber grows as the number of cells increases. In clusters the cells are disposed close to each other, so that the distance between them usually amounts to several millimetres and occasionally, e.g. in *Evylaeus duplex*, to merely 1 mm (Sakagami & Hayashida, 1960).

The forage usually is deposited at the bottom of the cell and usually has a form of small spherical loaf more or less flattened at the poles (Figs. 84, 85). The egg lies on the top of the forage. In most species of halictines (except for some eusocial species, see below) cells are plugged with a cover. Larvae feed on the top of the pollen ball, without moving around it (Figs. 86-89). Having concluded its feeding, the larva lies on its back at the bottom of the cell and throws out excrement, which is put on the upper distal part of the cell (Figs. 90-91). Adult larvae of halictines have a thick worm-like body (Fig. 92) with a small rounded head possessing chitinised mandibles (Fig. 93). Larvae do not spin cocoons. Larvae pupate and transform into imagoes within one season. All the species except Nomioidini hibernate in the imago phase, having the imagoes already emerged and copulated.



Figs. 84-91. Growth of immature *Evylaeus imitatus* (from MICHENER & WILLE, 1961). *84*. Cell being provisioned. *85*. Complete pollen ball with egg. *86-89*. Stages in larval feeding and growth. *90*. Prepupa. *91*. Pupa.



Figs. 92, 93. Mature larva (*92*) and its head (*93*) of *Halictus scabiosae* (from GRANDI, 1961: Figs. 355, 356).

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The discovery and study of social life in halictines. The existence of eusociality in halictines was supposed by many authors as early as in the XIX century. However, colonies of halictines were regarded then rather as communities where every individual was able to produce offspring, even if some division of labour between them was not totally excluded. The proof that in halictine colonies there is authentic non-reproductive caste of working individuals appeared only in the works of NOLL (1931), who was the first to undertake artificial management of halictine bees (in particular, *Evylaeus malachurus*), and in his investigation of ovaries of different females from the same nest discovered sharp differences between the degree of their development in the queen and the workers.

Large-scale investigations of eusocial colonies of halictines were launched in the late 50's of the XX century by PLATEAUX-QUÉNU in France, MICHENER with his colleagues and students in America, and SAKAGAMI with his fellows in Japan. The majority of numerous studies on nesting in halictines issued after the simplified method of their artificial rearing in observational nest constructions, which permits to see the internal world of underground nest, was introduced (MICHENER & BROTHERS, 1971; BELL et al., 1974). Regrettably, these investigations concerned the artificially created so called 'semisocial' colonies, where one of the workers functioned as the queen. Such a female is considerably different from a true queen in many of its behavioural, physiological, and often also morphological traits. Apart from that, in a large part of relevant experiments artificial colonies composed of unrelated individuals were unintentionally used, which unfortunately often fails to be clearly stated in the publications. Another source of confusion is the extended use of the term 'queen' for the egg-laying female dominating over its sisters and contemporaries in 'semisocial' groups. Thus conclusions obtained due to experiments carried out in artificial colonies partly call for supporting evidence to be provided by investigations of natural halictine colonies.

In 50-90s investigators of halictines, in spite of certain defects of the methods applied, obtained superb results and made a number of discoveries concerning different aspects of within-nest behaviour of the bees. Particular interest held in halictines is due not only to the fact of their eusociality itself, but even more to the existence in halictines of several sociality levels, from that of solitary species up to primitively-eusocial colonies; moreover, even closely related species happen to be far distant on this scale. This has made halictines a promising object for searching for intermediate phases leading to eusocial organisation. Halictine colonies have provided a sort of field data for verification of various consequences and predictions following from different hypotheses on the origins of eusociality in Hymenoptera. Some of the discoveries directly confirm predictions of the HAMILTON's (1964) haplodiploidy hypothesis of the origin of eusociality: 'insubordination' of the workers to the egg-laying female unrelated to them (SMITH, 1987); workers' ability in primitively-eusocial species of controlling the sex ratio in the brood (PLATEAUX-QUÉNU, 1983); prevention of multiple mating of females due to chemical marker left by males on the body of females after copulation (KUKUK, 1985). In addition, being established the fact of obligatory control over the brood's development in eusocial halictine species (BATRA, 1968; KNERER, 1969a), it is clear that subsocial organisation constitutes the only way of the rise of eusociality. Nevertheless, the data concerning eusocial halictine species remain to be rather scarce. Apart from the general reasons (presently we know something about the nesting of only 3 % of the species of the world Apoidea fauna), this is also caused by the relative lateness of the discovery of eusociality in halictines, which makes it imperative to carry out profound and specific investigations in order to establish the fact of solitary/eusocial mode of their life.

Distribution of eusocial species among halictine taxa. In the present time, solitary mode of life is unequivocally established for only 25 halictine species. In this connection the list of halictine taxa in which eusocial species fail to appear, as well as the ratio of social and solitary species in other taxa, is a matter of debate. With sufficient confidence one may presently state that there is no eusocial life in the tribe Nomioidini, as well as in such a great and relatively well studied genera of the tribe Halictini as *Caenohalictus*, *Habralictus*, *Homalictus*, and *Lasioglossum*[1], in *Agapostemon* group of genera, and in some others. By contrast to the Halictini, in the tribe Augochlorini, the genera, which include only solitary species, seem to be very few. In total, eusocial life is discovered in 74 species of 100 halictine species whose biology is sufficiently studied (these species are listed by RADCHENKO, 1993; RADCHENKO & PESENKO, 1994; EICKWORT et al., 1996).

In the tribe Halictini, which includes 44 genera of non-parasitic bees, eusocial species are found in three genera: *Evylaeus (+Dialictus)*, *Halictus*, and *Seladonia*. In the genus *Seladonia* all of the well-studied species lead eusocial life. Only for *S. virgatellus* the possibility of solitary life is admitted (PACKER et al., 1989). Eusocial life appears to be characteristic of the most species of the genus *Halictus*. Thus in this genus out of 17 well-studied species eusocial life is established in 14 ones, while only three species, namely *Halictus quadricinctus* (GROZDANIĆ, 1969), *H. sexcinctus* (KNERER, 1980b), and *H. tsingtouensis* (SAKAGAMI, 1980), definitely lead solitary life. Judging by such indirect indications as the males' flight at the end of the season only, and overwhelming female predominance in collections, it is likely that many other species of the genus *Halictus* also lead eusocial life. In the most numerous and well-studied halictine genus *Evylaeus* eusociality is already attested for 35 species. Solitary mode of life is uncontroversially established in 17 species only: *Evylaeus opacus* (MICHENER & LANGE, 1958b), *E. oenotherae* (KNERER & MACKAY, 1969), *E. villosulus* (PLATEAUX-QUÉNU et al., 1989), *E. allodalus*,

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[1] PACKER (1997, 1998), basing on indirect data, believes that *Lasiglossum aegyptiellum*, inhabiting the Mediterranean basin and Central Asia, is possibly eusocial.

E. nitidiusculus, *E. parvulus* (SAKAGAMI et al., 1985), *E. quadrinotatulus* (SITDIKOV, 1987), *E. nupricola* (SAKAGAMI, 1988), and several others.

Of 30 non-parasitic genera of the tribe Augochlorini, eusocial species are detected in seven. The overall picture of distribution of eusociality in the Augochlorini is far from being clear. For instance, from 131 species of the genus *Augochlora* and 138 species of *Augochloropsis*, eusociality is established in two species of each, while the data concerning the rest of the species of these genera remains to be extremely poor. However, in some great genera eusociality is established in considerable number of species.

Foundation of nest. In temperate regions eusocial colonies are usually founded by overwintered single foundresses. As well as those of other primitively eusocial species, halictine foundresses, having been fertilised in autumn, early in the spring leave their hibernating quarters. In this period their ovaries are underdeveloped. Two to four weeks later the ovaries develop due to nectar and pollen nutrition, and young foundresses start the foundation of nests. In some species new nests are normally founded at the place of, or close to the matrifilial nest, which results in rise of nest aggregations, while in other ones young foundresses dissipate over considerable territory building isolated nests. Sometimes several individuals take part in the nest foundation, with the outcome of a polygynous colony coming into existence (see below).

In tropics young foundresses also happen to fall into diapause similar to the winter diapause in temperate areas, which falls on the dry, or inversely, the rainy season, depending on the concrete species and the region (MICHENER, 1974), but typically no diapause occurs, being the nests founded all over the year. After the death of the foundress its place is often taken by a working female which morphologically and physiologically can be not different from the foundress. The duration of nest foundation may vary territorially within one and the same species.

Polygynous colony foundation. Among many halictine species several young females co-operate in the nest foundation; also cases are noted where a bee, which has solitarily founded a nest, is joined by one or two other females. The view of polygynous colony foundation as a necessary phase of development of the majority of halictine eusocial colonies, held by some authors (Michener, 1958, 1969a, 1974; KNERER & PLATEAUX-QUÉNU, 1966a), was not supported by the later comparative studies (PACKER & KNERER, 1985). Characteristically polygynous foundation is realised by sisters overwintered together in their mother's nest. In construction of the new nest, the main burrow of the maternal one is made use of. However, the connection between joint wintering and foundation of polygynous nest is not obligatory. First, only two or three individuals usually co-operate for nest foundation, whereas much more spend the winter in the same nest; consequently, remaining females found their new nests in different places and by themselves. Second, in a few instances the nest is founded by females, which did not hibernate together. Third, in some species, e.g. in *Evylaeus marginatus*, future foundresses always winter jointly in the maternal nest, but afterwards every of them independently founds a new nest (PLATEAUX-QUÉNU, 1962).

In a short time the members of jointly founded colony divide into castes according to their ovarian development. In polygynous nests typically there is only one female with normally developed ovaries which lays eggs; other females serve the function of working individuals, although they are fertilised and potentially reproductive. In polygynous nests normally the largest individual becomes the egg-laying female. However the body size not always predetermines the position of a female in the caste hierarchy. Thus, if into a colony of *Evylaeus zephyrus* founded by a solitary female one or two days later young females are introduced, then it is the older female which becomes the egg-layer, regardless of its size (BROTHERS & MICHENER, 1974). This is evidently due to more advanced ovarian development in the bees that emerge earlier and feed for a longer time. In our opinion, among overwintered females having founded nests the caste determination may depend on when a specific individual leaves its wintering place: the earlier it happens, the more advanced is ovarial development, which increases the female's chances of becoming an egg-layer. Only in case the jointly hibernating females emerge almost simultaneously, the body size acquires the decisive importance.

Only at the initial stages the egg-laying female of polygynously founded colony takes part in all nest building, cell construction and cell provisioning works. Later it spends most of time within the nest, being only busy forming the pollen ball, laying eggs and sealing the cells with caps, if they are available. All the rest of the work about construction, protection and foraging of the cells are carried out by female co-foundresses, which serve the function of working individuals. Among the advantages of polygynous nest foundation as compared to the monogynous one, we should name, first, the opportunity of organising almost constant protection of the nest against various enemies; second, higher productivity of the polygynously founded colony as calculated per one female foundress (for the relevant data on *Evylaeus zephyrus* see KUKUK, 1983); third, less wearing of the egg-laying individual; fourth, earlier establishment of cells for the first brood of workers.

In polygynously founded nests females serving the worker function usually either die even before the first brood of workers emerges, or get banished from the nest by the egg-laying female. Anyway, by the emergence of the first brood only one female is typically left in the nest. The banished females either die, or possibly excavate new burrows for their nests, or – as noted with respect to *Halictus scabiosae* (KNERER & PLATEAUX-QUÉNU, 1967a) – occupy the nests formerly built by females of other bee species.

Structure of the foundress nest. The foundress nests of eusocial halictine species in their location and structure are similar to the nests of related species leading solitary or subsocial mode of life. The main restrictions on the nest architecture of eusocial (as well as subsocial) halictines, obligatory both for the foundress nests and family nests, consist in non-linear arrangement of cells, and in absence of long laterals leading to the cells. After the cells are sealed, the laterals that lead to them must be filled with soil. Linear cell arrangement and long lateral burrows exclude the mother's contacts with its offspring, therefore they are met in the nests of only a few solitary halictine species. Having chosen the place for the nest, the foundress excavates all the initial depth of the main burrow, including the lower blind burrow. As far as the spring nest is normally built by one foundress, its depth is moderate as against that of the summer eusocial nest, which is excavated by several (or many) working individuals of the already existent eusocial colony. The soil brought out during burrow excavation gets piled at the nest entrance. The soil tumulus appearing in result of this usually encircles the nest entrance like a ring.

The foundress does not construct a nest tube or a turret, and does not make the entrance opening and the adjacent part of the main burrow narrowed in comparison with the diameter of its rest. Here is the difference between the foundress nest and the one into which it will be re-constructed by workers. By contrast to the family nest, among the majority of species in the foundress nest the walls of the upper part of the burrow do not get cemented. On having excavated the main burrow, the foundress starts constructing the cells. In their architecture the foundress nests of halictines may be of two main types. In the first, simpler one, the cells are located at the sides of the main burrow, extending up or down by groups, or being scattered along it (Figs. 50-52, 54). The cells either adjoin the burrow or communicate with it through very short laterals, whose length characteristically does not exceed that of the cell. The second, more complex, type of halictine nest is presented by chambered nests where the cells group into honeycomb clusters surrounded by a full or partial chamber (Figs. 55-58). The ways of construction of chambered nests vary considerably.

In the majority of eusocial halictine species the cells are oriented more or less horizontally, which, in our view, makes unsealing the cells easier for females and less dangerous for feeding larvae; this procedure is occasionally carried out by females in order to monitor the development of the brood. Only in *Evylaeus laticeps* cells sometimes happen to be deflected from the horizontal by 45° (PACKER, 1983). The structure and form of cells are similar enough among all of the halictines.

Acting alone, the foundress usually constructs only four to six cells, e.g. in *Evylaeus marginatus* two to six cells (PLATEAUX-QUÉNU, 1962), in *E. duplex* three to nine cells (SAKAGAMI & HAYASHIDA, 1961) are constructed. For separate halictine species larger number of cells established by the foundress for the first brood is indicated in the literature. In our view, such an information most certainly concerns the former polygynous nests in which by the moment of their inspection the egg-laying female has already lost its assistants. On having completed the works about establishing the cells for the first brood, the foundress immures itself within the nest.

The functioning of its ovaries stops or sharply slows down, being resumed not before the offspring emerges (GOUKON et al., 1987). Evidently the foundress spends this time immobilised, although it is not excluded that sometimes it activates in order to inspect the development of the offspring. Direct observations of the foundress' behaviour in the preimaginal period of the first brood are virtually absent.

Occasionally the question of incubation of offspring by halictines is raised in the literature. The hypothesis of incubation of cells located within chambers was spelled by VERHOEFF (1897), and later supported by MICHENER (1974: 198). In our belief, it is unconvincing assumption, since incubation of brood implies great energy loss, which is possible only on the condition of active feeding of the foundress. Therefore during the development of the first brood it should either periodically leave the nest, or accumulate forage therein. But neither actually happen.

Composition of the first and the following broods. The development of the first brood at the majority of eusocial halictines is relatively fast, taking only 1-1.5 month, and soon there appear young bees in the nest. At once after leaving the cells, they meet with their mother, which from this moment on becomes a queen. The vacated cells and chambers are filled with soil by young bees, to the exception of rare instances where they are used again.

The composition of the first brood differs seriously among different species of eusocial halictines; it may include either working individuals only, or a compound of workers and males, sometimes with an admixture of future foundresses. Great proportion of males in the first brood is typically linked to low development of social life among a given species. Thus, in species with lower level of eusociality males form a considerable part (in some cases even a half) of the first brood. For example, in *Evylaeus laticeps* this parameter averages 23.8% (PACKER, 1983), in *Halictus rubicundus* 25% (fluctuating in different years from 17.7 to 32.4%; YANEGA, 1988), in *Evylaeus rhytidophorus* 41% (MICHENER & LANGE, 1958c), and in *E. albipes* more than 50% (PLATEAUX- QUÉNU, 1988).

In halictines with higher eusociality level, males are either absolutely absent in the first brood, e.g. in *Evylaeus marginatus* (PLATEAUX-QUÉNU, 1962; POURSIN & PLATEAUX-QUÉNU, 1982), *E. imitatus* (MICHENER & WILLE, 1961), and *E. rohweri* (BREED, 1975a), or their proportion in the total number of the bees emerged in the first brood does not exceed 5-10%, e.g. in *Evylaeus duplex* (GOUKON et al., 1986), *E. malachurus* (NOLL, 1931), *E. nigripes* (KNERER & PLATEAUX-QUÉNU, 1970), and *E.umbripennis*; WILLE & OROZCO, 1970).

PLATEAUX-QUÉNU's (1983) experiments carried out on artificial nests of *Evylaeus calceatus* have shown that the sex of eggs which a female lays to produce the first brood depends on the weight of pollen balls. As their weight gets experimentally increased, the proportion of fertilised eggs yielding workers considerably rises. The results of this experiment demonstrate that the foundress can always control the sex of its offspring. It is not excluded that production of males in the

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first brood of eusocial halictines has to do with an early start of rearing a part of future foundresses, which have a long diapause. This can be concluded judging by the information on Halictus rubicundus (Yanega, 1988). In the nests of this species about a half of the first brood females copulate at once after their emergence, and shortly leave the maternal nest hiding till the next spring. In result, a part of the females of the species population permanently lead quasi-solitary mode of life.

At the vast majority of well-studied eusocial halictines only one brood of workers is reared before the production of future foundresses. To be sure, working individuals occasionally happen to appear in the second brood too. However, the formation of the second brood is usually vastly extended in time, so that the workers which mostly emerge first manage to participate in rearing of the reproductive offspring. Only in *Evylaeus malachurus* (LEGEWIE, 1925a; BONELLI, 1948; POURSIN & PLATEAUX-QUÉNU, 1982) and in *E. pauxillus* (SMITH & WELLER, 1989; PACKER, 1991) during a season two consecutive broods, and in southern regions in the former species sometimes even three consecutive broods of workers are produced, after whose rearing the production of future reproductive offspring begins.

A specific perennial life cycle is proper to *Evylaeus marginatus* (see description of its bionomics in Chapter IV).

Caste differentiation. Sufficiently distinct dimorphism in females (reflected even on the taxonomic level), being queens always by 15-20% larger than workers, is established for only the following eight species, which have probably reached the highest social organisation among halictines: *Evylaeus malachurus* (KNERER & PLATEAUX-QUÉNU, 1967b), *E. linearis* (KNERER, 1983), *E. pauxillus* (PACKER & KNERER, 1985), *E. cinctipes* (KNERER & ATWOOD, 1966; see another opinion in PACKER et al., 1989), *E.exiguus* (PACKER, 1986b), some populations of *E. umbripennis* (WILLE & OROZCO, 1970; for different data see EICKWORT & EICKWORT, 1971), *Halictus latisignatus* (SAKAGAMI & WAIN, 1966), and *Seladonia hespera* (BROOKS & ROUBIK, 1983; PACKER, 1985). It is *S. hespera* that exhibits the most pronounced morphologic caste differentiation – apart from greater body size, its queens have disproportionately huge hypostomal tooth. In addition, in the above species only insignificant part of working individuals have relatively developed ovaries, and as a rule all of the workers are unfertilised. Thus, in *E. linearis* only 3.2 to 13.6% of workers have more or less developed ovaries, while the fertilised ones number 0.5% only (KNERER, 1983). It should be also noted that among the species with non-overlapping caste polymorphism the average body size of workers usually increases during the season.

In the most eusocial halictines the castes are under-differentiated due to a large size overlap between queens and workers. Usually caste affiliation of a female can be established not before its functions in the family are revealed, although for certain species it is possible to uncontroversially identify the queen by the presence of sperm in its spermatheca and by the degree of its ovarian development.

In many halictines working individuals not only fail to exhibit morphologic distinction from queens, but often also have developed ovaries and are typically fertilised. Such are the species *Augochlorella striata, A. persimilis* (MICHENER & LANGE, 1958c; ORDWAY, 1965), *Seladonia confusa* (DOLPHIN, 1966; cited after MICHENER, 1990), *Halictus rubicundus* (YANEGA, 1988), *Evylaeus breedi* (MICHENER et al., 1979), and other halictines with low level of sociality. Among these species castes can be distinguished not so much by differences in the ovarian size as by the number of developed ovarioles and by the presence therein of mature oocytes. Nevertheless, the mere fact of fertilisation in a series of instances also fails to play the decisive role in the caste determination. It is possible that in halictines, similarly to other eusocial bees, the caste differentiation is determined, apart from the body size and fertility, by the titre of the juvenile hormone, on which the ovarian development is dependent.

Mechanisms for supporting of caste structure. Such mechanisms remain extremely under-studied: the pheromone control over the workers on the part of the queen is established for neither of halictine species; unclear is also the question as to its behavioural dominance. One variety of the latter is impeding the copulation of workers by the queen. The simplest way of doing it is decreasing, down to full cessation, the production of males in the first brood, which however rather reflects only the general rise of the level of eusocial life among halictines (see above). As well, several other modes of workers copulation prevention are revealed.

The queen's aggressive behaviour directed at suppressing the ovarian development in workers (Figs. 94-97), which is proper to other primitively eusocial bees (e.g., bumble bees), as the main mechanism of the queen's behavioural dominance in its overt form was attested in true eusocial colonies of neither of the studied halictines: *Evylaeus zephyrus* (BATRA, 1966b; MICHENER et al., 1971a; BREED et al., 1978), *E. calceatus* (PLATEAUX-QUÉNU, 1974), *E. duplex* (SAKAGAMI & HAYASHIDA, 1968), *E. versatus*, and *E.imitatus* (BATRA, 1968). All the data on the aggressive behaviour whereby the dominant halictine female preserves the caste structure of the family (see MICHENER et al., 1971b; BROTHERS & MICHENER, 1974; MICHENER & BROTHERS, 1974; BREED & GAMBOA, 1977; GREENBERG & BUCKLE, 1981, BUCKLE, 1982a, 1982b, 1984; SMITH, 1987) concern the artificially composed 'semisocial' groups comprised of only young females of one generation of the first (summer) brood. The role of the queen in such groups is usually served by the most robust and active female with the most fully developed ovaries which in the experiments was provided the opportunity of copulation.

Clearly, the behaviour of the female dominating over its sisters or contemporaries must widely differ from that of an authentic queen having experienced diapause and being the mother of all the rest of the colony members. In artificial colonies one observes high aggressiveness of the egg-laying female that seeks to inhibit the ovarian development among its sisters or contemporaries. In the capacity of

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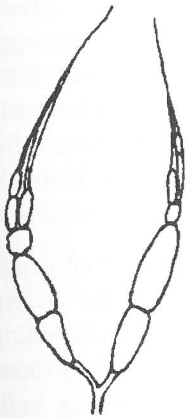

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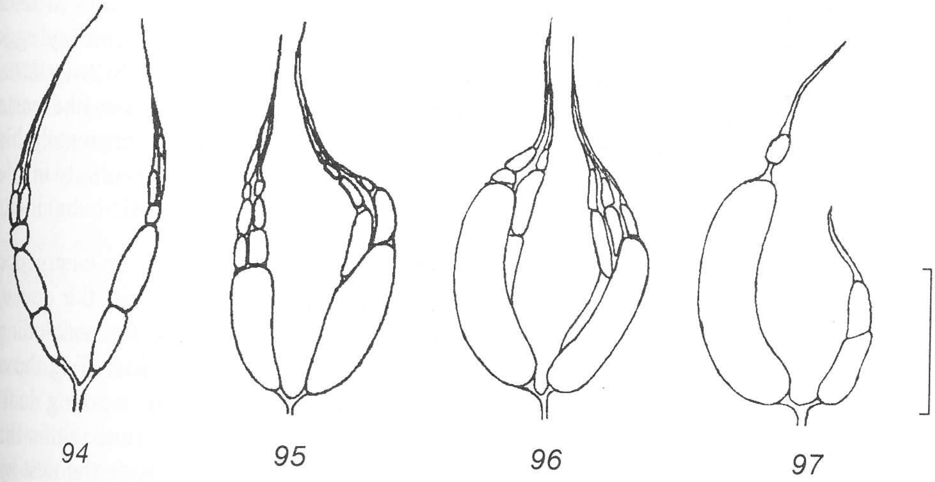
behavioural patterns leading to such an inhibition, the following types of interaction between the female and the working individual are distinguished (Michener & Brothers, 1974; Brothers & Michener, 1974; Michener, 1977; Smith, 1987):

nudging – the face-to-face contact with the worker; realised by a short fast movement and possibly accompanied by inflicting slight trauma on the worker;

backing – leading the worker after itself, backing the female deep into the nest; realised with slightly raised head and antennae stretched forward; after each short 'backing' the dominant female waits for the worker, and in case of its stopping 'pushes' it;

lunge – a sharp forward movement without contacting the worker.



Figs. 94-97. Dissected ovaries of workers of *Evylaeus nigripes* in a matrifilial (*94*, *95*), queenless (*96*), and own nest (*97*) (from Knerer & Plateaux- Quénu, 1970: Figs. 22-25). Scale lines represent 1 mm.

Replacement of queens by workers and usurpation of nests by other females. In the most studied halictines the queens that in the spring successfully established the nest and reared the first brood, live at least till the autumn. Only for a few species, e.g. for *Evylaeus zephyrus* (Batra, 1965), it is noted that queens often die shortly after the emergence of the first brood, being the place of the dead queen occupied by one of its daughters.

Halictine workers, in spite of their relatively high reproductive status, do not reveal aggression against the true queen and evidently never banish it from the nest (with the exception of cases where it totally switches to production of non-fertilised eggs). In case the queen dies, it is normally replaced by the oldest working bee, regardless of its body size. The older bees' higher chances to replace the queen are probably due to their more advanced ovarian development. Throughout several days after the replacement occurs, the ovaries of the new queen rapidly develop and on the average reach the size of the ovaries of the true queen. However, if the first female replacing the queen gets removed, in the next dominant individual the ovarial development proves to be slower. Unlike authentic queens living for a year or more, the queen-replacing females are shortly worn. For example, those of *Halictus rubicundus* live no more than three weeks (YANEGA, 1989).

Apart from the above described intra-familiar queen replacement, sometimes one observes in halictines the usurpation of alien nests by females from the same, and occasionally another species. Thus, described is facultative cleptoparasitism exhibited by females of *Halictus scabiosae*, which occupy both the nests of their own species and those of *Evylaeus nigripes*. They kill the host bee and lay eggs into the cells already provided with the pollen ball (KNERER & PLATEAUX-QUÉNU, 1967a). PACKER (1986a) noted the existence of intra-specific cuckoo-like caste among the females of subtropic populations of *Halictus ligatus*. Unfortunately his work fails to present unequivocal data on the behaviour of such individuals inside of alien nests, so that one can make only a guess of their cleptoparasitic behaviour.

Within-nest behaviour and general division of labour. After the emergence of the first brood the foundress, which from this moment on becomes the queen, enters into active state, but occupies itself only with inspecting the cells, concluding the formation of the pollen ball, and laying eggs. All other works, including those about constructing and foraging the cells, are carried out now by working individuals. After their emergence the queen spends all, or almost all the time within the nest, leaving it not even for its own feeding. The latter is realised inside the nest by consummation of a part of forage from the cells while they are being filled with provision. Inside the nest the bees are normally arranged in chain along the main burrow, occupying the queen the lowest position.

Among non-reproductive members of colonies, in many halictines one finds a division of functions: some workers are responsible for the protection of the nest, while others for foraging. Occasionally even morphological differentiation of subcastes is exhibited. At the same time, typical of such species as *Evylaeus politus* and *E. glabriusculus* is constant division of workers according to the kind of work fulfilled, although these subcastes have no external differences (KNERER, 1981). A part of workers are not functionally specialised, and at different times realise either nest protection, or foraging the cells. Such individuals usually have more developed ovaries than other workers, but they are scarcely active, or even not inclined to do any work whatever (KUKUK, 1980). These bees are likely to be the first candidates for replacement of the dead queen.

Division of labour in halictines – to which it is proper – can be observed even in colonies comprising no more than three individuals, being the first of them the queen, the second a guard, and the third a forager (BROTHERS & MICHENER, 1974).

Still, in a number of species the division of functions between workers is not established. For instance, in colonies of *Evylaeus nigripes* (KNERER & PLATEAUX-QUÉNU, 1970) and *E. linearis* (KNERER, 1983) working individuals occupied with nest protection are lacking. Functional specialisation among workers arises several days after their emergence. The concrete specialisation, as well as the general behaviour of an individual, is tightly linked to its reproductive status.

Apart from protecting the nest, constructing and foraging the cells, separate workers assist the queen with inspecting the cells with the developing offspring. The queens of certain eusocial halictines keep the cells almost constantly open for supervision over the developing offspring, as well as for removal of excrement and larval sloughs. The cells with dead or anomalous individuals being at preimaginal stages of development get immured by workers (KNERER, 1969a). In *Evylaeus malachurus* the cells remain unclosed only in the period of larval feeding; they are opened shortly after the emergence of the larva from the egg and get closed again when the feeding is concluded. At other species, e.g. in *Evylaeus imitatus, E. versatus*, and *E. zephyrus*, whose cells are sealed with caps, monitoring is realised by periodical opening of the caps. In the course of inspection the cells with normally developing larvae get immediately re-closed, while those with dead offspring get tightly filled with soil (BATRA, 1968).

Construction works. After the emergence of workers new cells are typically established at a greater depth as compared to those set up by the female foundress. Such a deepening of nests can last for all the season long. Unlike the nests established in the spring by a solitary female, at the period of workers' activity the family nests have narrower entrance (as against the rest of the main burrow), which plays an important role in the nest protection (see below). Workers narrow down the entrance by means of creating built-in walls of the soil excavated from the inside of the nest. As well, some species line the upper narrowed part of the burrow with secreted materials. Often the narrowed part of the burrow protrudes above the ground in a form of a turret (Fig. 65), which was not yet present in the nest when built by the foundress.

Normally several bees take part in the construction of the burrow, yet each one works independently of others. Only during removal of soil from the excavation place co-operation is possible: loose soil is transported to a short distance, then another bee picks it up. Different halictines use different ways of soil transportation inside the nests. As the family grows, so does the number of the cells constructed. Typically, in its architecture the family nest does not differ radically from the one built by the female foundress, with the natural reservation as to a greater depth, ramifiedness, and a larger number of cells. It is worth noting that, unlike, e.g. *Evylaeus duplex* (SAKAGAMI & HAYASHIDA, 1960), *E. laticeps* (PACKER, 1983), and E. calceatus (Bonelli, 1965a), which for all the season long construct chambered nests. The workers of *E. malachurus* fail to make chambers in their summer nests, although during solitary nest establishment their queens often excavate chambers around the cell clusters (Bott, 1937; Knerer & Plateaux-Quénu, 1967b; GROZDANIĆ & VASIĆ, 1970).

In eusocial colonies the cells are usually constructed co-operatively by several workers shifting one another in execution of separate procedures. Halictines do their construction works mainly at the night-time. Besides intranidal workers, some part in cell construction is taken also by forager workers that at different times can be occupied both with supplying the nest with provisions for pollen ball formation, and with constructive work. According to BATRA's (1964) observations, the cells of *Evylaeus zephyrus* which fail to get filled with larval forage on the very day they are constructed, on the next day get re-lined with secretory material. Older cells, unused for several days after their construction, get not only re-lined with secretory film but preliminarily covered with a new thin layer of soil. Therefore, the bees storage pollen only in newly lined cells.

Foraging. The food collection is realised by halictine workers without co-operation with each other (MICHENER, 1974). Moreover, they seem not only to forage independently but also to have no adequate notion of the family's forage necessities. Not infrequently a foraging bee returned with its load of pollen fails to find any cell open for putting the food into it. In result the forager rambles for a long time within the nest in search for a vacant cell, and having not found it leaves the pollen at the end of the blind burrow, as far as halictines do not accumulate whatever other food reserves. Adult individuals which do not fly out from the nest for feeding eat pollen from partly provisioned cells (BATRA, 1968).

Provisioning of every cell is realised co-operatively by several working individuals. Normally for the formation of one pollen ball, the amount of food brought in 6-8 trips is enough, and in *Evylaeus umbripennis* creation of the pollen ball often takes just 5 pollen loads. In provisioning one cell of *Evylaeus zephyrus* sometimes up to 6 females take part (Batra, 1964), but still every forager usually prefers to fill one and the same cell. If at the moment of the forager's return the cell is occupied by another bee, the former one passes on to the next cell, and later brings new portions of pollen directly to it. Foraging workers, e.g. those of *Evylaeus imitatus*, make daily up to 7 trips (MICHENER & WILLE, 1961).

Nectar usually gets added to pollen not before its supply is already sufficient for formation of a pollen ball. On its return to the nest, the forager can leave pollen in one cell while regurgitating nectar into another. Pollen and nectar mixture is formed into a pollen ball consecutively by several bees. Aside from foragers, a part in this process is taken also by intranidal workers and the queen, which realises the final treatment of the pollen ball immediately before laying an egg. After doing so, the queen at once seals the cell with a soil cap (being exception those species failing to make caps). If no egg is laid on the pollen ball in two days, workers fill such a cell with soil.

BATRA (1964) and KNERER (1969a) made suggestion that in halictines 'progressive' larva feeding is possible, being pollen and nectar periodically added to the cells with feeding larvae. This view finds its support in the facts that, first, workers now and again unseal the cells with the brood, and second, the weight of grown larvae palpably exceeds that of the initially formed pollen ball together with the egg itself. However, as has been shown later, the cell unsealing is realised in order to only control the larval development, and the increase of the weight of larvae is due to absorption of moisture by pollen balls (MAY, 1970; BATRA & BOHART, 1970). To be sure, it is not excluded that provision in the cells gets wet with nectar in the species which do not produce cell caps (in particular, *Evylaeus malachurus* should be mentioned here) and therefore cannot keep up high humidity inside of cells. Still, in certain more recent works (BUTLER, 1975; DIETZ, 1982; POPOVA & BLAGOVESCHENSKAYA, 1989) erroneous indications of 'progressive' larvae's feeding in halictines continue to appear.

Nest protection and identification of colony members. Guards spend all the day at the entrance part of the nest in a head-up position, being their heads approximately level with the ground surface. In the narrowed entrance part of the nest there is enough room for one individual only, so that in order to let a forager pass the guard moves down to the wider part of the burrow. Only the colony members are let into the nest. The guard bee both blocks the way for all other insects and turns them back threatening them with its mandibles. The guard never abandons the entrance opening. If the undesirable object fails to move away or, on the contrary, demonstrates aggression at its attempt at penetrating into the nest, then the guard bee rapidly moves down to the wide part of the burrow, turns around and goes up blocking the entrance with its metasoma. In such a position it holds so strongly that it can be barely moved even with considerable effort. If such a bee nevertheless gets extracted from the burrow, another worker instantly takes its place. In case of consecutive removal of all guards, their role is played by foragers.

The guard bee easily enough turns out various smaller enemies and parasites, but its resistance does not present a serious obstacle to a cleptoparasitic bee of the genus Sphecodes that, being in its size comparable with halictines, easily does away both with guards and the rest of the family members, which fact is reported for many halictine species (MARÈCHAL, 1890, 1894; FERTON, 1898; NIELSEN, 1903; BLÜTHGEN, 1923; LEGEWIE, 1925c; ORDWAY, 1964, RADCHENKO & PESENKO, 1994).

At most halictines the nest protection is realised only during the daylight hours. For the night, as well as at the days of unfavourable weather conditions the nest entrance gets stopped up with a plug, for whose construction loose soil and small stones are used (KNERER, 1969b). Only separate species, belonging all of them to those constructing turrets, in particular *Evylaeus linearis* and *E. marginatus*, leave the nest entrance open and unprotected for the night (KNERER &

PLATEAUX-QUÉNU, 1970). However these species' nests, as well as nests of some other halictines, e.g. *E. nigripes*, have no constant protection even in the day.

Guard bees identify the members of their own nest by their smell (BARROWS et al., 1975; MICHENER, 1982). The sources of odours used for identification are most probably macrocyclic lactones secreted by Dufour's gland (SMITH & WENZEL, 1988). These smells are genetically determined; they seem to be very unstable and, evaporating, do not communicate from one individual to another during joint keeping of bees from unrelated colonies (GREENBERG, 1979). At the same time, in artificially mixed groups bees remember and freely admit to the nest not only those group members unrelated to them yet also alien individuals related to the latter ones (BUCKLE & GREENBERG, 1981). Still, in isolation bees soon forget the smells of the colony members. Thus, after 12 days isolation guard bees of *Evylaeus zephyrus* let pass only about 10% of the members of their group (KUKUK et al., 1977).

GREENBERG (1979) establishes distinct positive correlation between the quotient of the relatedness of the guard bee to a bee artificially introduced into the nest, and the frequency with which the guard lets this bee enter the nest. However special experiments of BUCKLE & GREENBERG (1981) have demonstrated that actually the guard bee admits all the bees which are genetically related to the members of its nest, not to this bee itself.

Rearing of sexual forms. The start of rearing reproductive females in eusocial halictines with annual families depends both on external factors (air temperature and day duration), and on the size of colony and the average size of bees (KAMM, 1974; KUMAR, 1975; see also: KNERER & PLATEAUX-QUÉNU, 1967d; PLATEAUX-QUÉNU & PLATEAUX, 1979, 1980a). The concrete mechanisms of a halictine family's switching to production of reproductive individuals remain to be unclear. It is known only that in the species whose castes differ in size, appearance of future queens is determined by increase of size of pollen balls stocked.

In what concerns the majority of those halictine species having no considerable difference between the size of workers and queens, it is more accurate to speak not of appearance of reproductive females but of disappearance of workers in broods, due to the fact that as time goes more and more emerged females have the opportunity of copulation. The males' percent goes up especially sharply in the last brood where their number no less than 50%. The males emerge first, and copulate with practically all emerging females, which evidently plays the key role in becoming the latter reproductive.

Among some species, e.g. in *Evylaeus zephyrus*, the early, i.e. occurring already in the first brood, rearing of males is explained by frequent perishing of female foundresses, which makes it imperative that workers replacing them have the opportunity of copulation and laying eggs producing females (BREED, 1975a). The emergence of future female foundresses from eggs laid by fertilised workers was observed also in *E. calceatus* (PLATEAUX-QUÉNU, 1985). Besides that, early rearing of males leads to appearance of such future female foundresses that fall into diapause long before the autumnal break-up of the colony. This phenomenon is recorded, in particular, for *Halictus rubicundus*. The most of unfertilised eggs bearing males are laid in halictine colonies by working individuals (Noll, 1931; Plateaux-Quénu, 1960a, 1962; Batra, 1964, 1968; Michener, 1974; Sakagami, 1974). Such an egg laying is often accompanied by cannibalism. Great workers of *Evylaeus* marginatus and E. zephyrus unseal the cells, eat the eggs, lay eggs of their own, and re-seal the cells (Plateaux-Quénu, 1960a; Batra, 1964). Interestingly, some workers of E. zephyrus and E. versatus, having laid eggs, on the same day fulfil their routine functions of providing forage (Batra, 1968). These data are also curious in the respect that usually foraging workers have the lowest reproductive status in the colony.

Copulation. Males of eusocial halictine species can copulate with females at different places both inside and outside of nests: on flowers, on the ground surface etc. (see reviews in Barrows, 1975, 1976a, 1976b; Alcock et al., 1978). Only in *Evylaeus marginatus*, males copulate solely inside of nests, since young foundresses do not leave their maternal nests till the next spring. In the flight period of males, the nests of *E. marginatus* where there are young reproductive females remain constantly open, so that males easily penetrate into them, visiting different nests with unrelated individuals.

Males of some species, in particular *Evylaeus rohweri* possess patrolled areas where they wait for females (Barrows, 1976b). Besides that, in the first 2-8 days of their life females of many species excrete pheromones attracting males. The role of the sexual pheromone is at least partly served by one of the substances that Dufour's gland produces (Smith et al., 1985). Thus, in Kukuk's (1985) experiments males of *Evylaeus zephyrus* were effectively attracted by imitations of females presenting a stick wrapped around with nylon covered with an extract from female Dufour's gland. Males reacted energetically to such models, and made attempts at copulation. It is interesting that after the male's contact with a female dummy on its surface there probably remained a chemical marker, which made the imitation unattractive to other males. Regardless of whether or not chemical markers are left, the male is capable of remembering the smell of the individual it copulated with, since it avoids further contacts both with this female and with its virgin sisters having the same smell (Smith & Ayasse, 1987). According to some data males in general prefer copulation with females from alien nests (Greenberg, 1982b; Wcislo, 1987). Females are as well able to recognise the smell of their brothers, escaping copulation with them (Michener & Smith, 1987).

Packer (1986a) has made observations showing that males of *Halictus ligatus* in tropics, where they fly jointly with females virtually for all the season long, prefer copulation with young and robust females. The reason for such a selectivity, as Michener & Smith (1987) suppose, lies in males' natural drive to avoidance of senseless loss of time and sperm on the females that most probably will become non-reproductive workers. In temperate regions the above problem gets solved by means of phenological segregation in the course of the emergence of workers and males, and/or by means of various behavioural adaptations that exclude or reduce the possibility of copulation between males and working individuals. Among the most graphic examples one may point out the behavioural peculiarities of Evylaeus marginatus, whose males emerge simultaneously with workers but copulation between them is prevented by that in the period of males' flight queens keep the nests with emerged workers constantly closed (PLATEAUX-QUÉNU, 1962).

The size of the family and duration of its existence. The size of families varies widely in eusocial halictine species, on the account of both different number of individuals in different broods, and different number of broods themselves, which to a large extent depends on for how long the family exists. It should be born in mind as well that under natural conditions extremely high mortality of female foundresses is observed. Many of them fail to establish colony, or to leave offspring. Thus, in a series of areas investigated the total number of individuals reared among halictines in the first brood often fails to exceed that of females which established nests in spring (MICHENER, 1974). Later many newly arisen families perish from various enemies and diseases. For this reason one can estimate the size of families only by those having successfully developed and reared reproductive brood.

In tropics, due to that the period when active family life is possible is longer than that in other zones, colonies of some halictines number several hundred individuals. Thus, one of the nests of *Seladonia lutescens* found in Costa Rica contained several males and 342 females, the most of which were probably workers (WILLE & Michener, 1970); this provides grounds for expectation of further increase of bees reared in the colony. Indeed, in Guatemala in a nest of the same species 589 females were detected (Sakagami & Okazawa, 1985). To be sure, the queens of other tropical halictines, in particular *Evylaeus breedi* and *E. seabrae*, produce only 1-3 working individuals, switching at once after that to rearing of reproductive forms (MICHENER et al., 1979).

In temperate zones among the most of halictines families exist for one season only, during which 2-3 broods, totalling on the average 50, or occasionally 100 individuals are reared. Only at *Evylaeus marginatus* the colony lives for 5-6 years, annually growing in size. Thus, according to PLATEAUX-QUÉNU's (1962) information, the brood reared the last before the break-up of the colony numbers up to 590 individuals, and in total the individuals reared throughout the colony existence period number up to 1458. Moreover, in the nests of this species GROZDANIĆ (1956, 1966) has found 676 to 897 individuals in the last brood alone. BONELLI (1965a) admits that among *Evylaeus calceatus* perennial colonies also exist, living their queens at least for two seasons. It has been demonstrated that in laboratory conditions, under constant relatively high temperature and with a long day, colonies of *Evylaeus* *zephyrus* can be kept in active state, but as the queens grew old they were consecutively replaced by new females selected from those not falling into diapause (Greenberg, 1982a).

Evolutionary stages of eusociality. The main initial conditions of the rise of eusociality appear to be similar in all the Aculeata, to the exclusion of specific requirements connected with differences in the biology of species and their groups, in particular with peculiarities of nesting. The number of levels of eusociality development (evolutionary stages of eusociality) in the halictines is higher than in any other group of bees. Those stages are as follows:

I. *Transitional* (to eusociality) stage – the rise of facultative and very primitive eusociality: (1) only a part of females in population lives eusocially; (2) the help afforded by daughters to their mother is very limited; (3) the proportion of males in the worker brood is large; (4) polygynous foundation of colonies often occurs. The species being at this stage are *Evylaeus albipes* (Plateaux-Quénu, 1988), *Seladonia confusa* (Knerer & Plateaux-Quénu, 1967b), *Augochlorella striata* (Packer et al., 1989), *Augochloropsis sparsilis* (Michener & Lange, 1959), *Pseudaugochloropsis nigerrima* (Michener & Kerfoot, 1967) (as well as some non-halictine species from genera *Ceratina*, *Xylocopa*, *Euglossa*).

II. *Lower primitive-eusocial stage* – stabilisation of eusocial life and its expansion to the whole population or species: (1) all wintered females seek to found a reproductive brood using help of worker daughters; (2) the number of individuals in the first ‘worker’ brood is reduced; (3) the proportion of males in the worker brood decreases; (4) facultative division of labour and initial morphological differentiation of castes appear. The species being at this stage are *Evylaeus laticeps* (Packer 1983), *E. versatus* (Michener, 1966), and *E. zephyrus* (Batra, 1966) (as well as many of Allodapini).

III. *Middle primitive-eusocial stage* – colony integration: (1) males in the worker brood disappear; (2) the queen exhibits distinct behavioural or/and pheromone control over its daughters (parental manipulation); (3) non-overlapping morphological differentiation of castes appears. The species being at this stage belong only to the halictines; they are: *Evylaeus cinctipes* (Knerer & Plateaux-Quénu 1967a), *E. linearis* (Knerer, 1983), *E. umbripennis* (Wille & Orozco, 1970), and *Seladonia hespera* (Brooks & Roubik, 1983; Packer, 1985).

IV. *Mature primitive-eusocial stage* – increase in the life efficiency of the colony: (1) the number of worker broods grows; (2) all colonies are founded monogynously. This stage is presented only by the halictines: *Evylaeus malachurus* (Noll et al., 1931) and *E. pauxillus* (Knerer & Plateaux-Quénu 1967b).

Stage IV is the highest in the halictines. The superior stages of the evolution of eusociality in bees are presented by *Bombus* (V. Higher primitive-eusocial stage), Meliponini and *Apis* (VI. Advanced eusocial stage).

Along with progressive development of eusociality, as well reversions occurred. In particular, it is supposed that return to solitary life has occurred in *Halictus quadricinctus*, *H. sexcinctus* and *H. tsingtouensis.* Under severe conditions, where successful rearing of two broods within one season is improbable, even some bee species, whose colonies are close to the middle stage of social life, switch to solitary existence; for example, this is the case with *Evylaeus calceatus* and *Halictus rubicundus*. Sometimes such a reversion has a partial character; for instance, in *E. imitatus* in the Canadian province of Ontario (KNERER & PLATEAUX-QUÉNU, 1967b) the 'working' brood includes many (up to 45%) males, whereas males are absolutely absent in it in the southern parts of the geographical range of this species (MICHENER & WILLE, 1961; MICHENER, 1969).

Even in the species that achieved the highest (among the halictines) stages of sociality (for example, in *Evylaeus malachurus* and *E. marginatus*) the colony nests almost fail to be different from those of solitary halictine species, except for a larger number of cells (the colonies of *E. marginatus* often comprise hundreds of individuals), and frequent complication of the structure of the nest entrance, making it better protected by guard bees. The conservative stability of halictine nest architecture is due both to retention of the former nesting substrate (i.e., soil), and to morphobiologic peculiarities of these bees, unable to construct cells in any manner other than excavating them in soil, with later building in and lining their inner walls.

Existing two main ways of arranging cells in the nests of eusocial halictines (implying the first that cells are placed at the extremities of very short laterals or close to the main burrow, and the second that they are arranged in groups inside of chambers), the second looks more progressive, since it promotes more frequent contacts between individuals, which is important for development of communication among colony members, and in principle provides opportunity for the rise of nest thermoregulation. Nevertheless, the prospective of that even colonies of the halictines, which construct chambered nests, would evolve to the social organisation level achieved by bumble bee families (stage V) may be estimated as nil.

One of fundamental factors limiting the evolution of sociality in the halictines is non-plasticity of the building material used. Non-plasticity of soil impedes creation of sufficiently large nest chambers, and most importantly, considering the way of cell construction adopted by the halictines (i.e., excavation, rather than modelling), excludes the simultaneous work of several working individuals in building one cell, which is necessary for development of communicational links and complication of social behaviour, including the functional specialisation of workers observed in the colonies of advanced eusocial bees. As well, non-plasticity of building material prevents re-use of cells. In addition, hygroscopicity of soil, along with typically horizontal orientation of cells, deprives bees of the possibility of accumulating a stock of nectar (or honey) in the nest for feeding imagoes, which renders unrealisable thermoregulation and incubation of the brood.

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However, the variety of halictine colonies in the level of social life and wide distribution of eusociality in many genera, subgenera, and even groups of species of this subfamily show that biologic features of the halictines offer fairly good possibilities of independent and repeated rise of eusociality, which is observed in some species even at present.

Cleptoparasites. Obligatory cleptoparasites of eusocial halictines are presented by related to them parasitic bees of the genera Austrosphecodes, Echthralictus, Eupetersia, Microsphecodes, Paradialictus, Paralictus, Parathrincostoma, Ptilocleptis, and Sphecodes, belonging to the tribe Halictini, Temnosoma to the tribe Augochlorini, as well as Nomada belonging to the family Anthophoridae. To be sure, the Nomada, which do not kill the host bee, seemingly can lay eggs only into the nests of halictine foundresses. There exist data to the effect that the species Microsphecodes (Eickwort & Eickwort, 1976), some species of Sphecodes (Knerer, 1980), and Paralictus asteris (Wcislo, 1997b) behave as social cleptoparasites. The main cleptoparasites of nest-building halictines in the Palaearctic region are representatives of the genus Sphecodes.

Main reference: FABRE, 1902: 1-27; MALYSHEV, 1936: 201-309; SAKAGAMI & MICHENER, 1962: 1-135; KNERER & ATWOOD, 1966: 1337-1339; EICKWORT, 1969: 652-660; PLATEAUX-QUÉNU, 1972: 1-200; MICHENER, 1974: 261-313, 1990: 77-121; SAKAGAMI, 1974: 257-293; EICKWORT & SAKAGAMI, 1979: 28-87; PACKER, 1991: 153-160; 1993: 215-233; RADCHENKO, 1993: 1-60; RADCHENKO & PESENKO, 1994: 171-195; KNERER & WCISLO; 1997: 316-332; DANFORTH & EICKWORT, 1997: 270-292; WCISLO; 1997a: 316-332; YANEGA, 1997: 293-315.