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Bees: Their Nests and Nesting Sites

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as reported by GEORGE E. BOHART and WILLIAM P. NYE, U.S.D.A., Agr. Res. Serv., Entomology Research Branch, in cooperation with Utah Agricultural Experiment Station.

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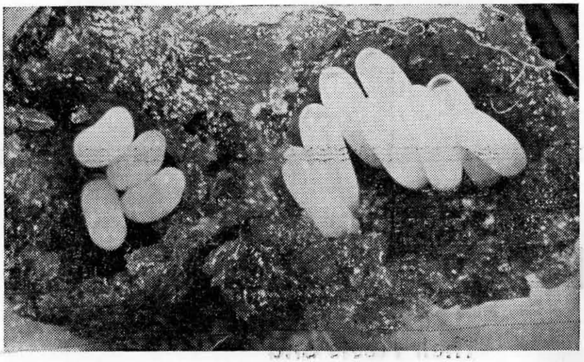


Fig. 1. Egg chamber from a bumblebees nest (opened for photograph).

Artisans of Many Kinds

NOWHERE is there greater diversity among bees than in their nesting habits. This applies both to their choice of home sites and to their architecture. Most bees construct their nests as burrows in soil or wood. They may place their brood cells singly at the end of branch tunnels or in linear series. Other kinds of bees merely partition ready-made burrows or other tubular cavities into a linear series of cells. There are also bees that occupy large cavities of various shapes. They usually arrange their cells in clusters or in flat combs. Finally, there are a number of bees that construct one or more cells in the open as independent structures. Thus, there are burrowers, borrowers, cave dwellers, carpenters, and open-air builders. Then, there are the many species of cuckoo bees that make no nests at all.

Brood Cells

The number of cells per nest ranges from one to many thousands. For solitary bees the maximum number is probably about 25. Some of the social sweat bees make only a few more than this. On the other end of the scale, the record holders are probably certain stingless bees that are supposed to construct several hundred thousand cells under ideal conditions.

Private nursery cells are the rule among bees. However, one genus of African carpenter bees raises its young in wardrooms formed by hollow stems or by the hollow interiors of giant thorns. Most species of bumblebees start their brood in wax chambers holding from 4 to 15 or 20 eggs, but they partition the quarters as the young develop (Fig. 1).

Nest Entrances

Ground-nesting bees sometimes conceal their nest entrances in loose sand under clods or in dense vegetation. However, most of them leave some kind of mound or other tell-tale mark at the entrance. **Nomadopsis** (Andrenidae) makes a mound with a shallow crater at the summit and a closed entrance. The alkali bee (**Nomia melanderi**) makes a conical nest mound with an open entrance at the summit (Fig. 2). A near relative, **Nomia triangulifera,** constructs a horizontal vestibule inside the mound leading to a closed entrance at the side. **Halictus farinosus** also makes a side entrance, but she leaves it open and sweeps away a trail in front. **Anthophora pacifica** makes no mound but wears a deep trail in front of her concealed entrance. Bees of the genus **Emphor** (Anthophoridae) make a short, flared turret over the nest entrance and kick pellets of earth in all directions (Fig. 3). When the nest is complete, they break down the turret and use its fragments to plug the entrance. Related bees in the gensus **Diadasia** build a cylindrical turret and leave it in place.

The nesting habits of bees often seem to fit in with their position on the family tree, but in some cases there is no apparent agreement. Some of the most striking nesting habits are more characteristic of individual genera, and even species, than of larger groupings. In general, we have tried to choose for the following discussion habits that are fairly consistent for large groups.

Colletids Make Their Own "Cellophane"

The primitive family Colletidae is divided taxonomically and biologically into two main groups. One group, represented principally by **Hylaeus,** is a borrower. It chooses hollow stems and old bee burrows or other tubular cavities. If you collect a few hollow stems containing **Hylaeus** nests and place them in a sheltered place with a large bundle of empty stems, the emerging bees will probably use the new stems

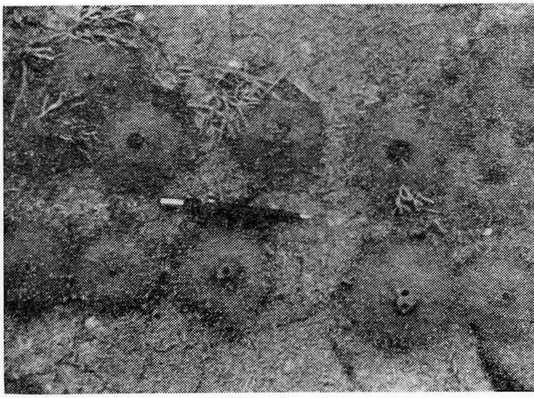


Fig. 2. Entrance mounds of the alkali bee (Nomia melanderi Ckll.).

Fig. 3. Emphor sumichrasti (Cresson) entering turret surrounded by dirt pellets (photo by G. D. Butler).

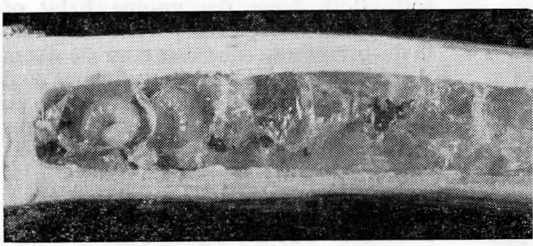


Fig. 4. Nest of Hylaeus cressoni (Ckll.) in hemlock stalk. Note transparent, irregular cells.

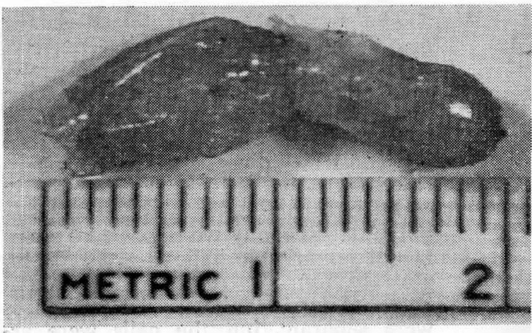


Fig. 5. Cells of Colletes phaceliae (Ckll.) showing transparent, jugshaped walls.

and build up a thriving population, The other group of colletids, represented by **Colletes,** digs its own burrows in the soil. Both have the unique habit of making delicate, transparent cells for their offspring. These are made from secretions of the maxillary gland and are probably fashioned with the broad, bilobed glossa. The cells of **Hylaeus** are irregular or conform to the nest cavity chosen (Fig. 4), whereas those of **Colletes** are shaped like vases (Fig. 5).

Halictids "Put the Squeeze on" at the Nest Entrance

The sweat bees (Halictidae) usually nest in the soil and dig vertical burrows with short, horizontal branch burrows that end in horizontal cells. Often the main burrow extends deeper than the cells. A few halictids, like the alkali bee and its relatives (**Nomia**), have burrows with the cells hanging down in series from one or two horizontal side burrows. Recently we observed a number of remarkable halictid nests (**Lasioglossum** sp.) constructed in the rotted cores of large timbers. The entrances were separate, but the cells were arranged in a labyrinth of interconnecting branch burrows that made no distinction between nests.

In spite of a few such divergent plans, it is easy to tell halictid nests by the burrow diameters. The entrances and the branch burrows are just wide enough to admit the bee, but the main burrow is considerably wider. Halictids apply a delicate varnish to the walls but not to the ceiling of their cells. As in the colletids, this lining is secreted by glands in the head and is applied with the mouthparts.

Fig. 6. Unvarnished cell of Nomadopsis scutellaris (Fowler) with pollen ball apparently coated by a waxy substance.

Fig. 7. Nest tube composed of three cells of Dianthidum curvatum sayi (Ckll.) taken from burrow of Anthophora occidentalis (Cresson). Cell walls composed of gravel and other debris cemented with sunflower resin.

Andrenids Are Secret Miners

The andrenids are all burrowers. Most of them make long, twisting tunnels with long branch burrows ending in single vertical cells. Some species have conspicuous nest mounds in the open (especially **Nomadopsis**), but most of them practice the art of concealment. Species of **Andrena** often crawl under several inches of loose sand or ground litter before starting their vertical burrows.

Andrena lines her cells with a fine varnish, but **Nomadopsis** paints the varnish on the pollen ball instead (Fig. 6). The andrenids usually close the burrow entrance when they leave for the field, and soue species close it while they are in the nest. In this they differ from many of the halictids, which leave the nest entrance wide open.

Melittids — Their Labors Go Unheralded

The Melittidae is too small a family on this continent to merit much discussion in a brief survey like this one. For the most part its nesting habits resemble those of the Andrenidae, which family it rather closely resembles. Some members of this family have larvae that spin cocoons. Otherwise this habit is reserved for the four higher families. Strangely enough, cocoon spinning is

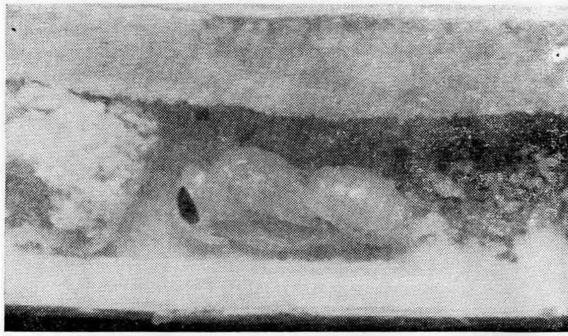


Fig. 8. Brood cell of Ceratina sp. in hemlock stalk. Note pith plug, pupal bee, and fecal pellets.

common among the sphecid wasps, which are supposed to be the ancestors of bees. Was the cocoon-spinning habit retained among ancient members of short-tongued families until it could be passed on to the forerunners of the higher families? Or did it disappear altogether, only to reappear independently among the higher bees? Could it also be argued that the peculiar distri-

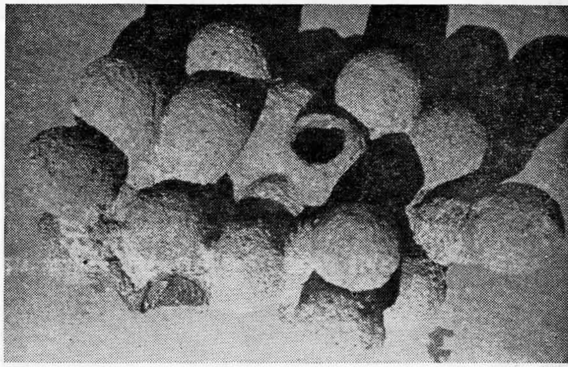


Fig. 9. Cell cluster of Diadasia enavata (Cresson) (worm's-eye view).

bution of cocoon spinning on the family tree shows that we will have to build another tree? You can see that many questions remain unanswered.

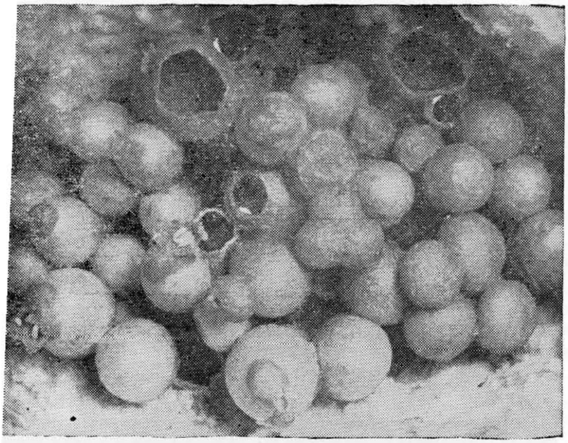
Megachilids — Master Craftsmen

The family Megachilidae, which includes the well-known leaf-cutting bees, has the fascinating habit of lining its brood cells with specific materials. According to the genus (and in many cases the species) of bee, some of the materials used are: leaf or flower pieces; leaf pulp, resin, resin and leaf pulp, resin and gravel (Fig. 7); mud; mud and leaf pulp; and stem hairs. The artistry, industry, and individuality which megachilids show in the construction of their brood cells contrast sharply with the simplicity of their nest pattern. Most of the species merely borrow ready-made burrows in soil, wood, or stems and place in them a linear series of cells. Sometimes the cells are fitted into spaces between clods of earth or in shallow rock depressions. Some of the resin bees use limb crotches. In general, the more simple the megachilids make their nests, the more care they lavish on their brood cells. After the larvae have finished feeding, they further protect themselves for the coming periods of hibernation and transformation by spinning tough cocoons composed of fibers embedded in a stout varnish.

Like the honeybees, many megachilids place their provisions and eggs in the empty cocoons of preceding generations. Once we found eight cocoons neatly nested into a single cell. The bee that emerged from the final cell was perforce less than half the size of many of its fellows.

Xylocopids Earn Their Name

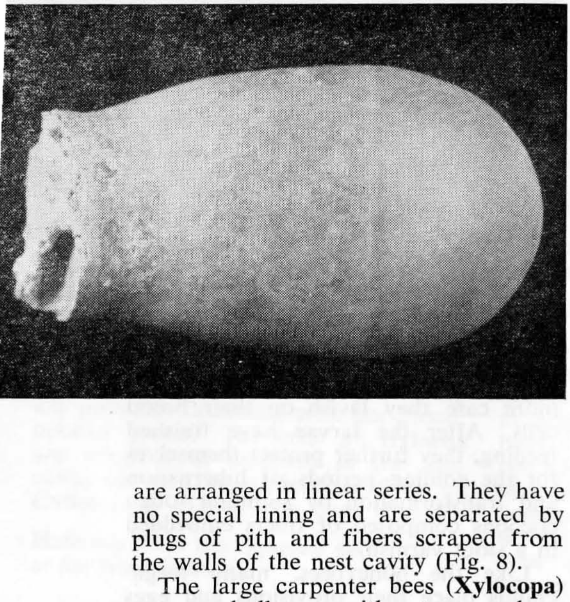
The carpenter bees (family Xylocopidae), as the name implies, construct their nests in wood. The small carpenter bees (**Ceratina**) usually choose hollow stems, but they also tunnel through pithy stems when necessary. The cells



body shape. Early on the stem of anthophorid evolution there appeared the ancestors of a large stock of parasitic bees. These cuckoo bees build no nests, but if you ever follow a female searching for the nest of her host you will come to respect her diligence. We can guarantee that your patience will never match hers.

Nearly all of the nonparasitic anthophorids nest in the soil. However, a few species of **Anthophora** nest in decaying wood, and at least one gnaws its burrows into sandstone. In general,

Fig. 10. Inner lining of Emphoropsis cell composed of a plaster-like anal secretion.



the more primitive anthophorids, such as **Melissodes** and **Tetralonia**, place single cells at the ends of branch burrows. The more advanced forms have linear series of three or four cells placed in short branch burrows. Sometimes the arrangement resembles a cluster of grapes except for the attachment of one

Fig. 11. A bumblebee nest (Bombus morrisoni Cresson) showing (a) pollen pot, (b) original honey pot, (c) honey stored in old cocoon, (d) egg baskets, (e) cluster of three wax brood cells, (f) cocoons, (g) mattress lined with wax.

are arranged in linear series. They have no special lining and are separated by plugs of pith and fibers scraped from the walls of the nest cavity (Fig. 8).

The large carpenter bees (**Xylocopa**) may use hollow or pithy stems such as bamboo or century plant, but they also drill through solid timber when easier methods are not available. These nests have short horizontal branches across grain and long parallel burrows with linear series of cells running with the grain. Sometimes their extensive galleries seriously damage building supports and other structures.

Anthophorids are Diversified

The family Anthophoridae is a large one, diverse in nesting habits as well as

cell to the next (Fig. 9). **Anthophora** and its closest relatives line their mud cells with a white shell-like substance that appears to be secreted from rectal glands. The impervious shell holds the watery syrup that covers the pollen in the cell (Fig. 10).

Conspicuous features of many **Anthopora** nests and those of **Diadasia** and its relatives are the clay turrets guarding the entrances. Some students of bees believe they are for protection against those egg bombardiers, the bombyliid flies, but the protection seems to be inadequate at best.

The Apidae — Workers in Wax

The family Apidae is the most highly advanced of the bee families in structure, nesting habits, and social development. Strangely enough, the tropical **Euglossa** and **Eulaema,** which are among the most highly developed apids structurally, have no true social development and make their cells in clusters much like those of certain anthophorids.

The nests of other aphids are characterized by two main features—wax cells and the aggregation of many cells into flat combs. The bumblebees (**Bombus**) and the tropical stingless bees (**Melipona** and **Trigona**) place their cells vertically on the upper sides of horizontal combs. The honeybees (**Apis**) orient their cells nearly horizontally on both sides of vertical combs, thus conserving space and eliminating the weight problem encountered when many combs are piled on top of each other. There may be only one comb, as in the case of the giant honeybee of India (**Apis dorsata**), or many, as in the common honeybee.

The bumblebees generally have one active brood comb composed of several brood clusters. The cocoons of older combs beneath are stripped of their wax and used for honey storage. Interspersed among the combs may be a few large pollen cells (Fig. 11).

The stingless bees generally make separate cells for pollen, honey storage, and brood. Some of them make honey pots as large as Japanese saki cups. The nests of stingless bees are rerarkable for the free use of a material called cerumen, composed of mud, pitch, wax, and other materials in various proportions. This material is used for struts between the combs and for a cavitatious insulating envelope around the nest.

We could expound at great length on the fascinating details of apid nests. None of the other families have nests that approach them in size, complexity, or specialization. Unfortunately these are the very features that make it impossible to describe them adequately in this brief article.

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