Biological Notes on *Dioxys pomonae pomonae* and on its Host, *Osmia nigrobarbata* (Hymenoptera: Megachilidae)

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Abstract: Biological observations on the parasitic bee *Dioxys pomonae pomonae* Cockerell are presented covering the following points: searching habits of female, oviposition, elimination of immatures of the host, feeding habits, and cocoon. Additional observations, including nest structure, are given for the host bee *Osmia nigrobarbata* Cockerell.

With the exception of a paper by Micheli (1936), apparently nothing was known heretofore concerning the biology of the cleptoparasitic bee genus *Dioxys* beyond the host associations of some of the species (Hurd, 1958; Jaycox, 1966). For this reason, we present the following observations concerning *Dioxys pomonae pomonae* Cockerell, a North American representative of this distinctive Holarctic genus. Brief notes are also given on the biology of the host bee, *Osmia* (*Acanthosmioides*) *nigrobarbata* Cockerell. An accompanying paper (Rozen, 1967) describes the immature stages of *D. pomonae pomonae*.

We would like to thank the following people for identifications of adults associated with this study: Dr. Paul D. Hurd, Jr., University of California, Berkeley; Dr. Elbert R. Jaycox, University of Illinois, Urbana; and Dr. Charles D. Michener, the University of Kansas, Lawrence. The literature search was aided by the Bibliography of Apoid Biology under Dr. Michener's supervision. This study was carried out at the Southwestern Research Station of The American Museum of Natural History, Portal, Arizona.

DESCRIPTION OF NESTING AREA: All observations were made at 3 miles north of Apache, Cochise County, Arizona, between April 28 and May 5, 1966. The *Osmia* burrows were widely scattered over nearly horizontal ground sparsely covered by low vegetation consisting of *Malacothrix*, *Gaillardia*, *Phacelia*, a number of grasses, and other low-growing plants (Fig. 1). Several possible hosts of *Dioxys* were active including *Osmia* (*Acanthosmioides*) *nigrobarbata* Cockerell (determined C. D. Michener) and *Anthidium emarginatum* (Say) (determined E. R. Jaycox). Both the *Osmia* and *Anthidium* collected pollen from *Astragalus*. Three species of *Dioxys* flew in the area: *D. productus subruber* (Cockerell), *D. pomonae pomonae* Cockerell, and *D. pacificus pacificus* Cockerell (all identified by P. D. Hurd). Females of *D. pomonae pomonae* were seen both entering and waiting by the burrows of *Osmia nigrobarbata*, and a female was reared from an *Osmia* cell. The hosts of the other species are not known.

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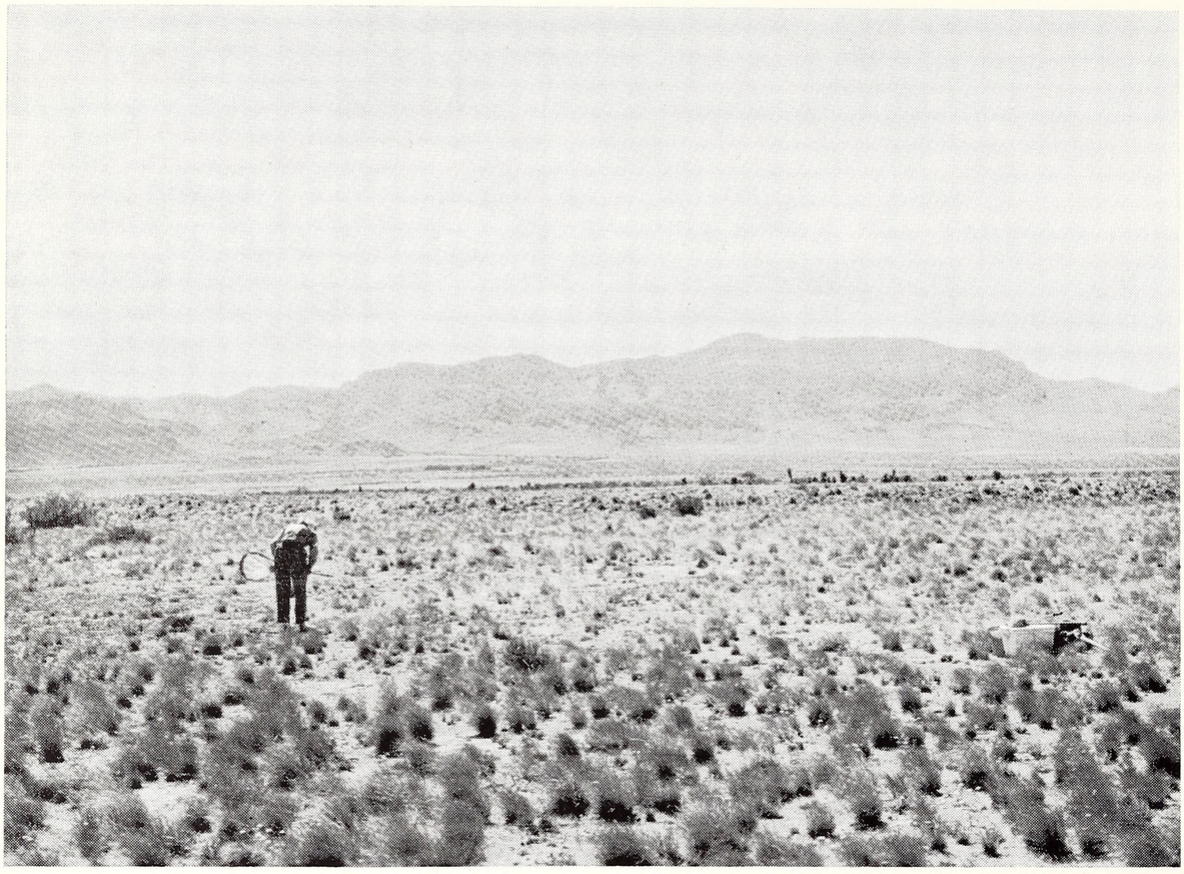


FIG. 1. Nesting area of *Osmia nigrobarbata* Cockerell.

OBSERVATIONS ON THE BIOLOGY OF *Osmia nigrobarbata*: Nests of this species were widely scattered and entrances were usually found at the bases of low plants or at the edge of shallow depressions. The burrows entered the ground at a slight angle from the horizontal and each tumulus was piled on one side of the entrance. Burrows were open and their direction was unpredictable, for some turned sharply to the side or downward. They were short, measuring only a few inches long, and the cells were situated within two or three inches of the surface. Some cells were encountered barely below the loose, dry surface layer of soil.

The nearly horizontal cells are constructed from a mastic of plant tissue. The source of this material is unknown, but because it was uniform for all cells encountered, it must be gathered from a particular plant. At first bright green, its color fades, so that cells several months old are nearly brown. The cell wall, approximately 0.5–1.0 mm thick, is quite hard; the inside cell dimensions are approximately 8.0 mm long and 5.0 mm in maximum diameter. The cell closure consists of the same plant material as that of the wall and is nearly flat on the inside and concave on the outside.

The arrangement of the cells is extremely variable. Some single cells were found which were probably the beginning of a nest series; the other cells were

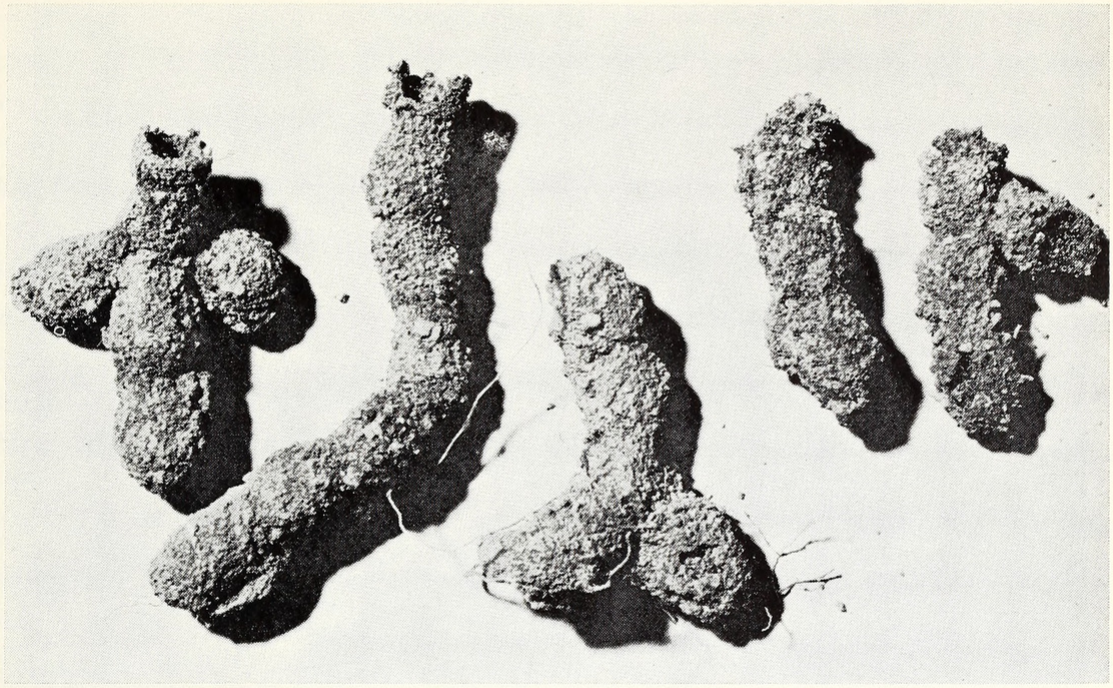
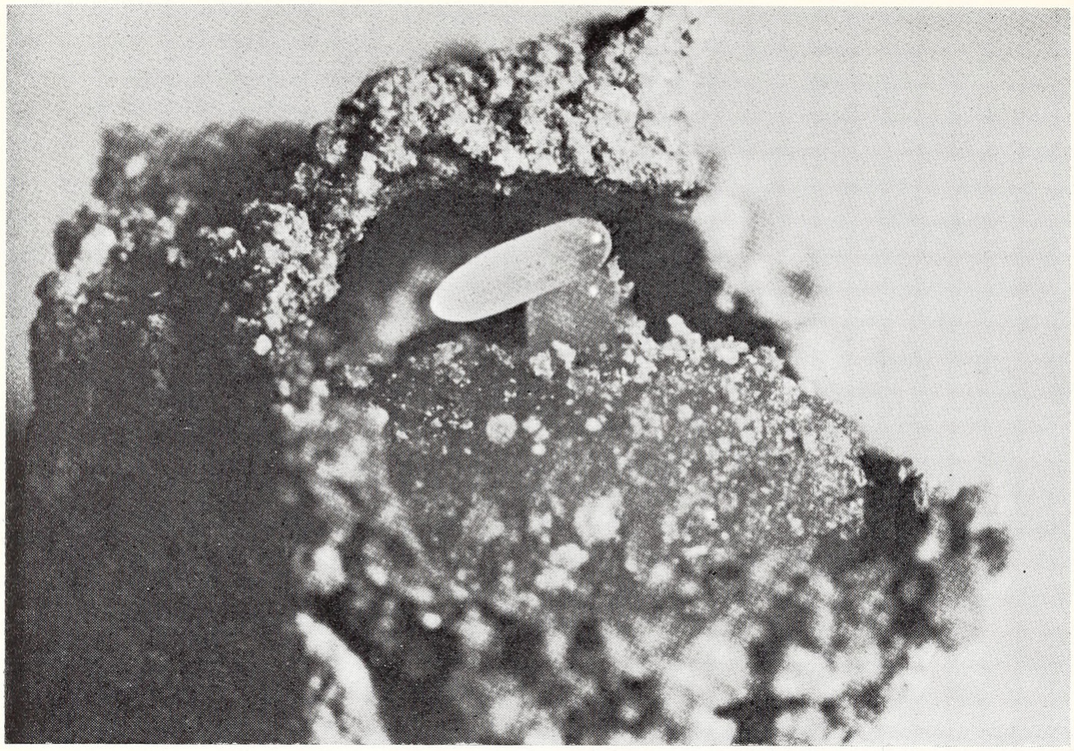
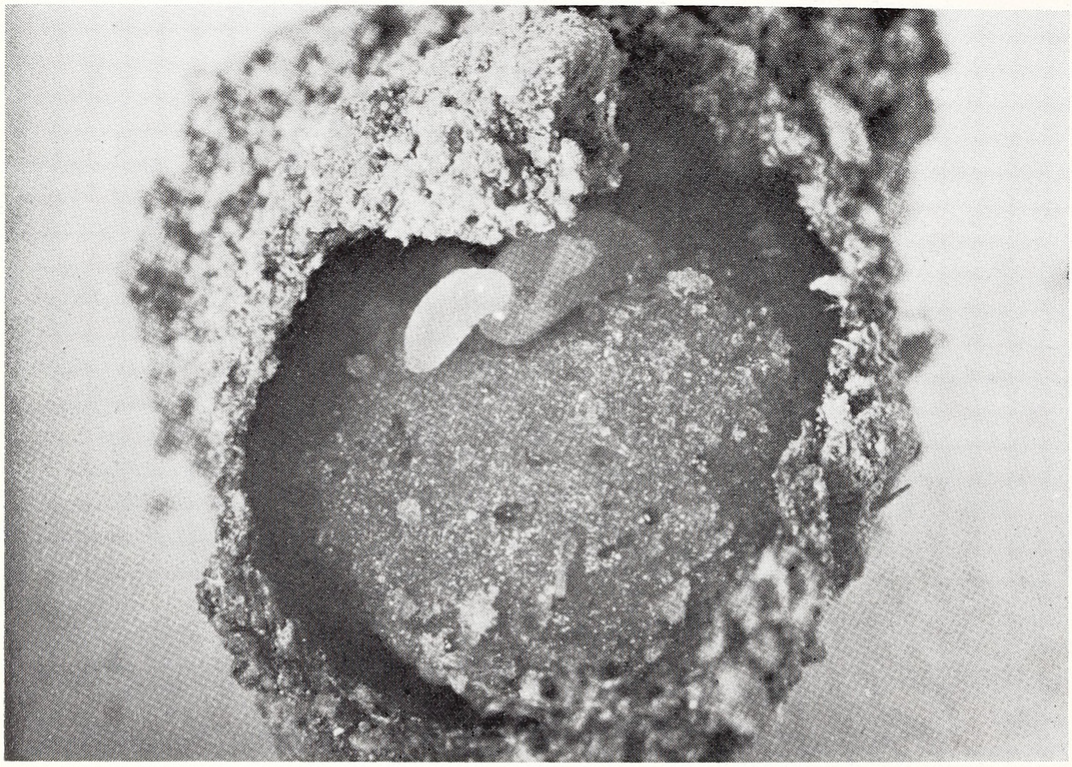


FIG. 2. Nests of *Osmia nigrobarbata* Cockerell. Swellings represent individual cells.
FIG. 3. Opened cell of *Osmia nigrobarbata* Cockerell showing food loaf and egg, from side.

arranged in a basically linear series that branched in an infinite number of ways (Fig. 2). Cells in the series were all interconnected so that four or five cells could often be removed from the ground without their separating. Each cell was a complete unit in that the rear end (or side) of one cell was not the





FIGS. 4, 5. Cell of *Osmia nigrobarbata* Cockerell, with front end removed. 4. Freshly deposited egg of *Dioxys pomonae pomonae* Cockerell adhering to anterior end of the *Osmia* egg. 5. Same cell, viewed from above, just before *Dioxys* egg hatched. Notice chorion adhering closely to the *Dioxys* embryo.

cap of the previous cell. Hence in a series, individual cells could be broken off without any of the cells being damaged. The strings of cells lay approximately horizontally in the ground.

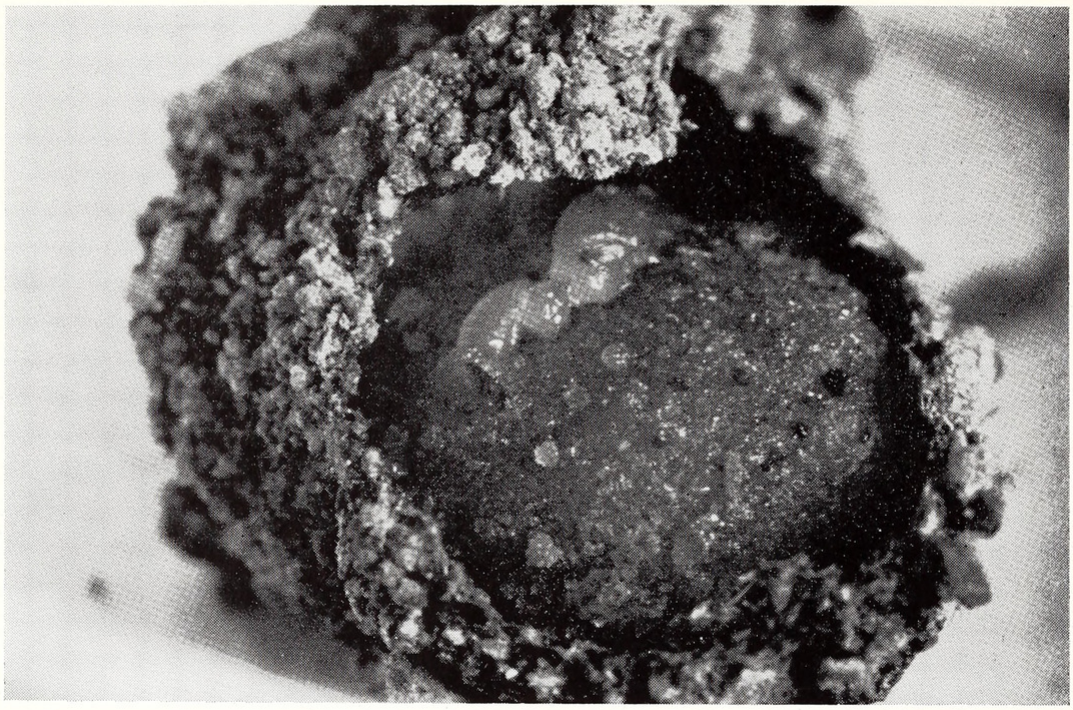
Only one female was responsible for a cell series, and each cell was constructed, provisioned, and closed before the next one was started.

Provisions of nectar and pollen were formed into a large, elongate, moist loaf (Fig. 3) occupying most of the cell. All eggs were uniformly placed on top of the provisions, forward of the center, in the sagittal plane of the cell. The eggs were laid either on the surface of provisions or with the rear of the egg slightly embedded. The anterior end rested on or, perhaps more frequently, projected into the lumen of the cell and pointed toward the cell closure.

The mature larva of *Osmia* spins a well-developed cocoon which consists of a loosely woven, tan outer layer and a tough (leathery), polished (on the inner surface) inner layer that is almost black. The cocoon lacks a nipple at the anterior end.

BIOLOGICAL NOTES ON *Dioxys*: The females of *D. pomonae pomonae* and *pacificus pacificus* fly slowly close to the surface of the ground and stop briefly at spots that presumably have certain characteristics of the nest entrances of the hosts. The flight appears "deliberate" and unhurried. Occasionally a female suddenly flies swiftly a short distance and then again starts her slow searching. Although the path meanders, it tends to lead in one direction, so that the female travels a considerable distance. As the *Osmia* nests were widely scattered over a number of acres, this behavior pattern of *D. pomonae pomonae* appears to be functional. In contrast, the meanderings of such parasitic bees as *Oreopasites*, *Holcopasites*, and *Neopasites* carry the bee back and forth over a limited area; this restricted search pattern appears to be an adaptation to the gregarious nesting habits of host species. Now and then, the *Dioxys* females land on the ground and clean their wings and antennae as do females of the nomadine genera. Once, after finding a burrow of *Osmia*, a female of *D. pomonae pomonae* examined the entrance, then retreated a few inches, and sat on a twig where it waited, as if for the departure of the host female. Several other times a female was noticed entering an *Osmia* burrow but came out within a half a minute.

Over 470 cells of *Osmia* were opened during our search for the immatures of *Dioxys*, with the result that we found seven larvae and two eggs of the parasite. One egg (Fig. 4) adhered loosely to the anterior end of the host egg. A small slit in the cell wall above the posterior end of the *Dioxys* egg apparently marked the spot through which the egg was inserted into the sealed cell. The other egg was partly embedded lengthwise in the under surface of the pollen-nectar mass so that somewhat more than half of it was visible. The chorion is shiny and translucent white. Resembling the host egg in almost all respects, the egg of *Dioxys* is somewhat smaller: length, 1.5–1.8 mm, width, 0.6 mm.



FIGS. 6, 7. Cells of *Osmia nigrobarbata* Cockerell. 6. Same cell as in Figs. 4 and 5. First instar *Dioxys* with its large head next to *Osmia* egg, which has been recently killed. 7. Intermediate stage larva of *Dioxys pomonae pomonae* Cockerell.

Each of the *Dioxys* larvae was found in a cell with a dead egg, first instar, or second instar of *Osmia*. The host is killed with the sharp mandibles which are present during the first three larval stages (Rozen, 1967). One first instar larva was discovered on the underside of the pollen-nectar loaf, whereas the other larvae, presumably second instars, rested on the side or top part of the food. The egg found adhering to the *Osmia* egg hatched in the laboratory, and the first instar immediately killed the host egg (Figs. 4–6). However, at least the first and second instars were active and, if touched with forceps, opened their jaws widely and actively moved the anterior part of their bodies from side to side. These actions, plus the large, sharp-pointed mandibles of the first three instars, suggest that the host may be eliminated by the second or third instar as well as the first. Never more than one *Dioxys* was found in a cell; the female *Dioxys* probably deposits only a single egg in a nest. In contrast, females of many of the Nomadinae lay more than one egg per cell.

As with most other bee larvae, the duration of the feeding period is short, lasting for two to three weeks. The larva, while feeding, moves about on the provisions (Fig. 7). Four larval instars were observed (but see Rozen, 1967). The fourth instar begins to defecate before it finishes feeding; the feces are extruded as elongate semisolid pellets.

The thin outer layer of the cocoon is composed of very loose strands of silk to which some of the fecal pellets adhere. Defecation is completed before the next layer is deposited. The second layer, black in color, is comparable to the inner, leathery layer of the *Osmia* cocoon but is thicker and imparts a greater rigidity to the finished case. The innermost face of the one *Dioxys* cocoon examined consisted of yet another layer, at least toward the anterior end of the cocoon. Loose and light brown, it formed a cellophane-like coating even though some individual silk strands were detected. Except toward the rear where the inner layer adhered more or less closely to the rigid layer, the inner face did not possess the polished, nearly black surface of the *Osmia* cocoon. The cocoon of *D. pomonae pomonae* possessed a distinct nipple at the anterior end, so that the shape of the cocoon was identical to that of *Dioxys cincta* (Jurine) (Micheli, 1936, Fig. 6).

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Received for Publication June 13, 1967