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Biology of the Bee Genus *Conanthalictus* (Halictidae, Dufoureinae)

JEROME G. ROZEN, JR.[1] AND RONALD J. MCGINLEY[2]

ABSTRACT

The following details of the nesting biology of *Conanthalictus* (*Sphecodosoma*) *dicksoni* Timberlake and *C.* (*C.*) *conanthi* (Cockerell) are given and where possible are compared and contrasted with the biologies of *Dufourea* and the other dufoureines: choice of nesting site, number of females to a nest, nest description, pollen plant preference, provisioning habits, appearance of eggs and larvae, feeding activities of larvae, cocoon construction and appearance, number of generations per year, adult activities, and nest associates. The Dufoureinae appears to be a homogeneous and distinctive taxon in terms of its nesting habits.

INTRODUCTION

The present paper provides the first published information on the nesting biology of the dufoureine genus *Conanthalictus*. These are small to minute, slender bees distinguished from other North American dufoureines, except *Protodufourea*, in that adults possess three submarginal cells, a character shared with the Old World *Systropha* and the Chilean *Penapis*. *Protodufourea* and *Conanthalictus* can be separated by characteristics presented in Timberlake (1955). The genus has been divided into three subgenera. *Conanthalictus conanthi* (Cockerell) and *dicksoni* Timberlake, whose biologies are described here and compared with those of other dufoureines, represent the subgenera *Conanthalictus*, *sensu stricto*, and *Sphecodosoma* respectively.

Adults associated with nests were kindly identified by Prof. P. H. Timberlake, University of California, Riverside, who (1961) revised the genus. Mr. Larry Pardue of the New York Botanical Garden identified the pollen plant. Support for the study came from National Science Foundation grant GB32193. Adults, larvae, a single pupa, and cells and burrows are deposited in the collections of the American Museum of Natural History.

CHARACTERISTICS OF NESTING AREA

We studied both species at 21 miles south of Animas, Hidalgo County, New Mexico (fig. 1) in a predominantly arid grassland region having also scattered mesquite bushes. *Conanthalictus dicksoni* was first found flying on August 10, 1975, and a nesting site was discovered seven days later on a surface sloping 20 to 30 degrees to a drainage ditch along a dirt roadway running along the

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broad bottom of the Animas Valley. The pollen plant, *Nama hispidum* Gray var. *mentzelii* Brand (Hydrophyllaceae), grew sparsely in the vicinity of the nest area; the closest flowering clump occurred approximately 25 feet from the site of this species, although other clumps apparently dead or at least no longer blooming were somewhat closer. We discovered adults of *C. conanthi* on August 24, 1975, not only on the same species of *Nama* but also on the clump closest to the nest site of *C. dicksoni*. A nest of *C. conanthi* was found and excavated on August 25, 1975, near a clump of *Nama* on the same sloping surface as, and about 25 feet from, the nests of *C. dicksoni*. Although both bee species visited the same plants and therefore possibly competed for food, population levels were so low that evidence of temporal niche partitioning could not be ascertained in the time we had available.

The sloping nest surface of these bees was sparsely vegetated with widely scattered, low-growing plants (including the pollen plant) so that the nest entrances were not shaded. The soil was fine, almost without stones or pebbles at the site of *C. dicksoni*, but had some small stones and gravel where *C. conanthi* nested. Dry on the surface, the ground was moist below because of recent thunderstorms. Although the drainage ditch received considerable water during these storms, nest entrances were sufficiently high so that they were not flooded.

Conanthalictus (*Specodosoma*) *dicksoni* Timberlake

Description of Nests. Eleven nests, actively being provisioned by females, were all within a 1-square meter area. The entrances 4 to 70 cm. apart were randomly arranged. While excavating the active ones, we encountered several other nests apparently no longer being provisioned. More than one female entered a number of burrows, an action indicating that some nests were composites. However, nests are probably

FIG. 1. Nesting area of *Conanthalictus dicksoni* and *conanthi*, 21 miles south of Animas, Hidalgo County, New Mexico. Figure in background excavating nests of *C. dicksoni*; figure in foreground pointing to nest of *C. conanthi*.

never inhabited by more than two or three females. No nest contained mature adult males.

Nests (fig. 3) are rather uniform. Entrances were open, unconstricted, without turrets and, although occurring on a surface that sloped 20 to 30 degrees from horizontal, were usually at the base of small irregularities where the immediate surface was 45 to 90 degrees from the horizontal. The tumulus was dry, loose, moderately coarse, and on the downhill side of the entrance. Main tunnels, open, unlined, and circular in cross section, penetrated into the sloping surface at about 30 degrees from horizontal, extended in an irregular fashion 3 to 5 cm., and then curved downward being thereafter essentially vertical but still meandering. Because of the fine-grained, uniform nature of the soil, the meandering did not seem to be caused by hard inclusions in the substrate.

At cell depth, laterals 7.0 to 13.5 mm. long (six measurements) curved from the main tunnels. Still-open laterals led slightly downward to open or partly provisioned cells. Circular in cross section, they appeared to be the same diameter as the main tunnel but narrowed to 1.75 mm. in diameter (one measurement) at the cell mouth. Laterals are filled with soil after provisioning and egg laying.

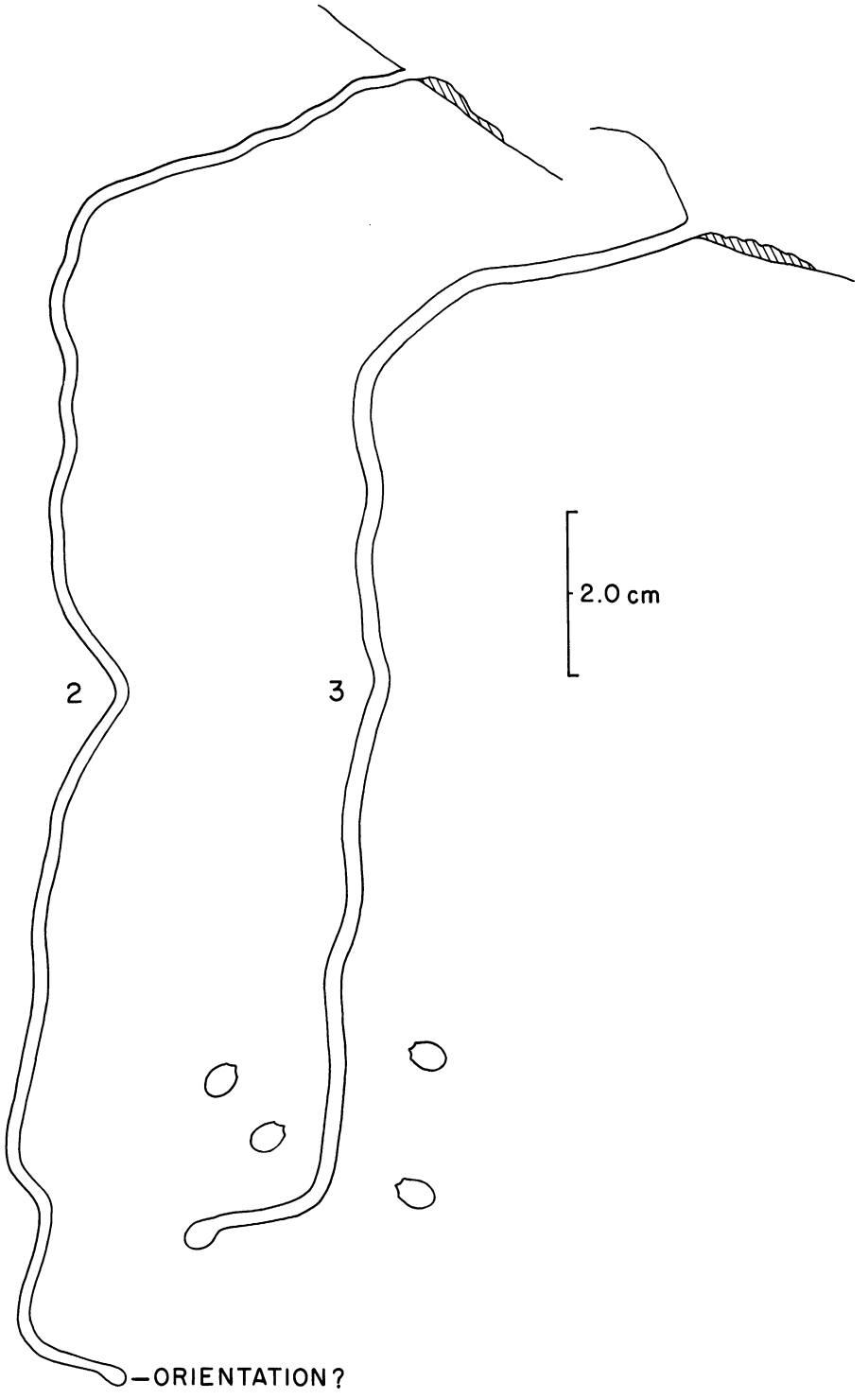
Cells, always arranged singly, occurred at depths from 10 to 14 cm. (12 measurements) and were 4.0 to 5.0 mm. long (three measurements) and 3.0 mm. in maximum diameter (four measurements). Newly constructed cells were found at the lowest level in nests; cells containing the oldest larvae were closest to the surface. All cells were tipped to the rear at 30 to 45 degrees from the horizontal, and seemed unusually globular compared with those of most bees. Although they were small and therefore difficult to observe, the roof may have been somewhat longer than the floor; if so, they were not symmetrical around their long axis. Their inner surface was dull and nonwaterproof above but apparently somewhat waterproof on the floor, for a droplet of water placed there was absorbed slowly. Only on the floor was there a trace of a darkened lining. The cell wall, although lacking signs of a special lining, apparently had been impregnated as it was slightly harder than the surrounding soil in some cases. The cell closure was strongly concave on the inside and exhibited a distinct spiral with approximately three rows to the radius.

Provisioning. Pollen was transported by the female as a rather loose, irregular, perhaps slightly moistened mass primarily on the anterior surfaces of the hind tibiae and femora. By excavating and examining numerous cells, we concluded that in the cell, she shapes the first load of provisions into a complete sphere that is enlarged with one or more subsequent loads. One sphere representing incomplete provisions measured 1.0 mm. in diameter and two completed spheres carrying eggs measured 2.0 and 2.5 mm. The pollen in all balls was firmly packed, mealy-moist, homogeneous, possessed no waterproof covering, and rested in the middle of the floor of the cell.

Development. Deposited on completed provisions, eggs were strongly curved with one end (presumably the anterior) distinctly more blunt than the other. The chorion was smooth and shiny and the egg translucent white. One egg *in situ* rested on top of the pollen mass, with both ends touching the mass, in the sagittal plane of the cell and had the blunt end closest to the cell closure.

Although few feeding larvae were encountered, young larvae apparently crawl around the pollen mass while they feed, for partly consumed provisions maintained a roughly spherical shape. Larvae nearly through feeding held the remains of the provisions cradled on their venter.

Only three cocoons were found and, although all corresponding to the shape of the cell, the variability in their appearance and structure remains somewhat of an enigma. One cocoon (apparently remaining from the previous year) contained a quiescent postdefecating larva that was slightly moldy but apparently alive. It consisted of three thin layers of material. The tan, dull, parchment-like outer layer was composed of fine, matted fibers. The inner layer was slightly paler, more yellowish, and had a glistening sheen; its surface was bumpy and exhibited indistinct silk fibers that were less conspicuous than those of the outer layer. Sandwiched between these two layers was a thin filling of yellow feces distributed evenly over almost the entire surface (in contrast to the posterior placement of feces in the cocoon of *Dufourea mulleri*, Torchio et al., 1967); only at the cell closure was the cocoon



FIGS. 2, 3. *Conanthalictus*, side view of nests. 2. *Conanthalictus conanthi.* 3. *Conanthalictus dicksoni.*

without feces. No fecal material adhered to the cell wall, indicating that defecation did not commence until after the outer layer was spun. A mass of dull, white amorphous material was smeared on the inside of one part of the cocoon and probably represented the final meconioid discharge although it did not exhibit pollen grains. Although the cocoon possessed no raised nipple, the closure end was apparently slightly flatter. Because of this and because it lacked feces, it appeared slightly different from the rest of the cocoon. The postdefecating larva was folded on itself so that its anal area was appressed to the venter just behind the head; the head was next to the cell closure.

The two other cocoons encountered each consisted of only a single layer of silk, less rigid, and thinner (less than 0.05 mm. thick) than the cocoon described above. Both were a pale tan, lighter than the cocoon containing the postdefecating larva, but otherwise of the same general exterior appearance. One contained no feces whatsoever but enclosed a bombyliid larva and the remains of a *Conanthalictus* larva that had obviously succumbed to the bombyliid after cocoon spinning. The other, partly opened while being excavated, contained a defecating larva, which then pupated within seven days of being found. The feces were in the form of long, yellow pellets some of which were loose, others more or less appressed and fused into a mass at the posterior end of the cocoon. Neither of these cocoons contained an inner layer of silk.

We hypothesize that this bee, which is apparently bivoltine (or multivoltine), may spin a single layer cocoon when the larva pupates immediately after defecating but that it constructs a more substantial and rigid three-layer cocoon when the postdefecating larva overwinters.

Mature larvae like those of other dufoureines known to us (*Systropha*, *Rophites*, and *Dufourea*) possess paired conical dorsal tubercles on most body segments and have the first pair markedly smaller than the following. All of these larvae also possess protuberant labiomaxillary regions as is characteristic of most cocoon spinning bees. Because of the reduction of the first pair of dorsal tubercles and the pronounced labiomaxillary region, dufoureine larvae can be immediately distinguished from panurgine larvae, in which the first pair of dorsal tubercles is not reduced and the labiomaxillary region is recessed. The larvae of the dufoureine genera as well as of other halictids will be described comparatively subsequently.

Adult Activity. Males and females were active during the heat of the day although we made no observations early in the morning nor late in the afternoon. We saw females both collecting pollen from the flowers and also returning to and egressing from nests. Males were never seen at the nest sites but were seen flying in rapid zigzag fashion around pollen plants and resting on flowers. We concluded that mating takes place in the vicinity of the pollen plant, not at the nesting site.

Females, upon emerging from nests, meander back-and-forth in an orientation flight over the entrances before departing.

Parasitism. Although several species of *Sphecodes* and at least one of *Neolarra* occasionally flew over the nesting site of *Conanthalictus dicksoni*, no other cuckoo bee was seen investigating entrances of any *Conanthalictus* nest and no cuckoo bee larvae were found in the cells. Bombyliid adults were extremely common in the area and the larvae were abundant in the nests of *Conanthalictus*, with perhaps more than half of the older bee larvae parasitized by them.

Conanthalictus (*Conanthalictus*) *conanthi* (Cockerell)

Description of Nest and Provisioning. In most respects the single nest (fig. 2) of this species was similar to the nests of *Conanthalictus dicksoni.* The entrance was open and exhibited a loose, dry tumulus on the downhill side. The main tunnel, 1.5 mm. in diameter, meandered at a 30 degree angle from horizontal into the slope. Becoming vertical after the first 4.5 cm. of length, it dropped in a meandering fashion to the depth of 16 cm., curved, and opened into a single cell containing an incomplete, spherical pollen mass, 1.25 mm. in diameter, of mealy-moist, yellow pollen. The orientation of this cell was uncertain but was probably similar to that of *C. dicksoni.* The lateral was 0.7 cm. long, and the diameter at the cell opening 1.2 mm. The cell was 3.75 mm.

long and 2.25 mm. in maximum diameter and possessed a dull, somewhat rough wall with no visible lining. The cell wall appeared somewhat firmer than the surrounding soil and may have been impregnated by some secretion.

Adult Activity. Males and females, less common than those of *Conanthalictus dicksoni*, were encountered on and near *Nama hispidum* var. *mentzelii* during the heat of the day.

Parasitism. There was no indication of parasitism either by bee or bombyliid in this nest.

DISCUSSION AND CONCLUSIONS

The biologies of *Conanthalictus dicksoni* and *conanthi* discussed here closely parallel those of *Dufourea* as presented in Torchio et al., 1967. Significant points of similarity between the two genera are: *Nesting*: nest entrance usually open and with asymmetrical or eccentric tumulus; main burrow open, descending in somewhat meandering fashion, not branching except in *Dufourea pulchricornis* (Cockerell); laterals present (i.e., cells not sessile), filled after closure; cells arranged singly (but also in short series in some species of *Dufourea*), globular (i.e., with relatively short long axis); lining dull, retardant to water at least on floor. *Provisioning*: provisions shaped after each load is deposited in cell into spherical form, mealy-moist and without waterproof coating. *Development*: eggs strongly arched, placed on top of provisions in sagittal plane of cell; larvae mobile while feeding, at least during early instars; defecation commencing after start of cocoon construction; cocoon, at least of over-wintering larva, consisting of two layers of silk with feces sandwiched in between. *Adult Activity*: adults active during heat of day.

Although very few species of dufoureines have been studied, the biology of *Conanthalictus* seems to differ to some extent from that of *Dufourea*, as follows: with more than one female to a burrow, at least in some nests of *C. dicksoni*; burrows without vestibule near entrance (some species of *Dufourea* with such vestibule); laterals tending to be rather uniform in length (laterals of some species of *Dufourea* varying greatly in length); feces applied over entire inner surface of the outer layer of the over-wintering cocoon (in *Dufourea*, feces at rear end of cocoon); two kinds of cocoons apparently present, one associated with over-wintering larva, the other with larva that pupates immediately after defecation (in *Dufourea*, only one kind of cocoon known); at least some species bivoltine or multivoltine; *Conanthalictus* without known cuckoo bee parasites (some species of *Dufourea* parasitized by *Neopasites*).

Probably many of the above differences between the two genera will be found untrue after other species are studied, judging by the variation we have found studying other genera of bees. The uniformity between *Dufourea* and *Conanthalictus* as presented confirms the conclusions made by Torchio et al. (1967) that the subfamily is "a homogeneous and distinctive taxon."

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