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The Life Cycle and Social Organization of Bees of the Genus *Exoneura* and their Parasite, *Inquilina* (Hymenoptera: Xylocopinae)[1]

By

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This paper consists of an account of biological observations on several species of bees of the genus *Exoneura* and on their social parasite and close relative, *Inquilina.* These bees belong to the same section of the xylocopine tribe Ceratinini as the genera *Allodape, Allodapula, Exoneuridia,* etc. This group of genera is virtually restricted to Africa and the Indo-Australian region and is well known as the only group of bees other than *Apis* and *Bombus* which practices progressive feeding of the larvae.

GENERAL ACCOUNT OF THE LIFE HISTORY OF *EXONEURA*

Sakagami (1960) has given a review of the biology of this group of genera, most of which make their nests in hollow or pithy dry stems. The nests of most *Exoneura* are burrows through pith or rotting stems that are as soft as pith. Sometimes they clean the pithlike frass out of beetle burrows in wood (Rayment, 1935) or nest in cavities in galls (Rayment, 1951) but probably most species do not habitually occupy beetle burrows as does *Allodapula* in Australia (Michener, 1962). However, nests of three species have been recorded from beetle burrows in solid fence posts and spars (Rayment, 1954).

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Beetle burrows in branches and twigs are also used (e.g., Rayment, 1956) by some species. Data on the related genus or subgenus *Exoneurella* are presented elsewhere (Michener, 1964).

Exoneura makes no separate cells, all young being reared together in the burrow. Rayment's early (1935) references to cell partitions are in error. I never saw the threads on the walls of the nest tubes reported by Rayment (e.g., 1951).

Nest entrances are regularly constricted, either being excavated in that way or narrowed by a constructed collar made of bits of the material removed from the burrow. The narrow entrance is important in defense of the nest. At a small disturbance, a female in the nest may bite at an intruder or a fine fiber held at the nest entrance, but usually she quickly turns and blocks the hole firmly with the flattened dorso-apical part of the abdomen. The females also secrete from the mouth region, seemingly from the mandibular glands, a brown liquid having the odor of tenebrionid or carabid beetles. They emit this material either at the nest or, if captured or greatly disturbed, away from the nest. On one occasion I found females of *E. bicolor* so common (11 miles south of Uralla, New South Wales, on November 5, 1958) visiting the flowers of *Daviesia latifolia* that when the bushes bearing the flowers were beaten with a net, the odor could be perceived several feet away.

The effectiveness of adult females in defending their nests is shown by a series of nests of *E. variabilis* set up for observation in Brisbane. Within a day those containing no adults were robbed of all immature stages by ants. Those containing adults mostly survived for many days.

Eggs of most species are laid in a mass (usually criss-crossed) at the bottom of the burrow, not attached to the burrow walls. However, in some species the eggs are attached by their posterior ends to the wall of the burrow and project into the lumen of the nest (Rayment, 1948, 1951; Erickson and Rayment, 1951; and *E. aterrima* discussed below). In some cases such attached eggs are placed in a row; in other cases they are scattered about on the inner nest wall. The duration of the egg stage was not determined by me but is obviously long enough that numerous eggs (10 or more) may accumuyate in a single nest, probably laid by a single female, before the first ones hatch. The ovaries mature only one egg at a time, as in most bees, although three or four may be nearly mature (Figs. 77, 78). Rayment (1948) showed that at the temperatures of late winter in Sydney the egg stage lasted between two and three weeks.

Larvae hatching from loose eggs remain in a cluster at the bottom of the nest until they grow large enough to maintain a position above the bottom. Larvae hatching from attached eggs may retain their positions on the nest walls for a time and may be fed pollen in this position.

The larvae are fed progressively with pollen mixed with a liquid (nectar?)

to form a rather sticky but firm mass. Sometimes more than one larva feeds from a single mass and this may be the usual way of feeding small larvae lying in groups. Larger and sometimes even the smallest larvae (e.g., in *E. aterrima,* see below) are fed by individual pollen masses placed on their venters. Even within a species the manner of feeding varies, as was noted for *E. variabilis* (see below) and for *E. roddiana* by Rayment (1948), who observed both communal and individual pollen stores, depending on the arrangement of the larvae in the nest.

At any one time the number of larvae having pollen supplies on which to feed is small. For example, in one group of nests of *E. variabilis* (see below) only eight larvae out of 74 had food available when the nests were opened. Rayment (1951) showed that in 17 nests of *E. richardsoni* containing 209 larvae, only six nests contained food and these had a total of only 23 pollen masses.

Rayment has repeatedly (1946c, 1951; Erickson and Rayment, 1951) described the feeding of larvae, especially young ones, by a liquid from the mouthparts of females which he stated was "pap" from the pharyngeal glands. The scarcity of larvae feeding on pollen supports this idea. However, the long larval life suggests sporadic feeding. Moreover, the finding of very young larvae feeding on pollen indicates the inaccuracy of the idea that young larvae must be fed only liquid. (For *E. aterrima,* see below; for *E. angophorae, asimillima, richardsoni,* etc., see Rayment, 1951, in which publication pollen is reported among the eggs and very small larvae lying in a cluster at the bottom of the nest.) Disturbed adults often move the larvae about in the nest with their jaws and mouth the larvae; such movements might simulate feeding and cause erroneous accounts of feeding. Feeding of larvae by glandular secretion (or by other liquid from the mouth of the adult) requires verification, although it seems probable in view of the detailed accounts of Rayment.

The young larvae lack ventrolateral lobes but have strong subspiracular ridges (Figs. 4, 53, and 57). Ventrolateral lobes appear on the mesothorax in the penultimate larval stage and exist on most segments in the ultimate larval stage. The mesothoracic arms are much the largest of such lobes (Syed, 1963). As described below for *E. variabilis,* these lobes (arms, or pseudopodia) are partially retractile in the last larval stage but shrivel in the prepupal part of the last stadium. Rayment (1948) appears to have been correct in regarding these lobes as non-secretory protuberances. His subsequent certainty (e.g., 1951) that they have secretory importance is not supported by my observations of their external and internal structure. As Rayment said, the mesothoracic arms are often mouthed and chewed by larvae but so are any other small soft objects which the larvae can reach. This activity therefore does not indicate any exudation. In contrast to *Allodapula* (Michener, 1962), larvae of *Exoneura* are constantly active, bending about as though reaching for something. Immature stages generally lie roughly in order of youngest at the bottom to oldest near the entrance of a nest. Food, therefore, has to be carried past a series of pupae and prepupae to the larvae which are being fed. Feces are produced while larvae are still feeding (Rayment, 1951) and must be carried out of the nest by adult bees.

The duration of the immature stages is not well known but is long, as Rayment clearly showed. Rayment (1951) thought that development from egg to adult of *E. rufitarsis* and *richardsoni* required from early July (midwinter) to early December (early summer). He also showed (1948) that both larvae and adults could survive up to 90 days closed in a container without food, and Erickson and Rayment (1951) showed survival of adults for over 100 days at 10°C. Thus survival of both larvae and adults during periods of drought when flowers are scarce and during the winter is not surprising. Overwintering of larvae certainly occurs (Rayment, 1946b, 1951). It is probable in some of the species discussed in detail below. However, the principal way of overwintering is by means of fertilized adult females. Often several females overwinter together. In the spring new colonies are commonly established by single females (*E. variabilis,* see below; *E. concinnula,* see Rayment, 1951). Sometimes, however, two or more adult females are present in nests in spring (*E. illustris,* see Erickson and Rayment, 1951; *E. richardsoni,* see Rayment, 1951). Whether or not supernumerary females later disperse from such nests, leaving monogynous colonies, is not known, but in *E. variabilis* such dispersal is suggested by the polygynous October (early spring) nests and the largely monogynous November nests. Some species maintain more nearly continuous reproductive activity than does *E. variabilis,* as is quite clearly the case for *E. roddiana, concinnula,* and *rufitarsis* which had many eggs in their nests in July (midwinter) (Rayment, 1951).

At least in summer many nests contain two ore more adult females. Large groups usually consist in part of young individuals which have not yet dispersed, but as many as three or four females may be long term inhabitants of a nest. Such groups, as will be shown in detail later, commonly consist of one or sometimes two egg layers[3] and one or more workers. The important role of workers in pollen collecting has been shown by Michener (1963). Further information on the division of labor and social organization is presented in the body of this paper and in brief form, in the summary.

Rayment (1951) described males as guarding nests, leaving and returning to them, and in short constituting a significant part of the society. His observations were probably made in winter and early spring when low temperatures presumably prolong all activities. Data obtained by me show that males

[3] I have not used the word queens, because so many of the nests at least in the species I studied contained only one female, which was like the egg layer in nests containing more than one female.

are produced in rather large numbers but after reaching maturity stay in nests for much shorter periods of time than females, so that adult nest populations are predominantly female. Presumably under warm conditions males leave the nests and soon mate and die.

A swarm of males of *E. hamulata* was found about noon of April 5, 1959, on Noosa Hill in Noosa National Park, Queensland. A few hundred males were flying about in the sun between large bushes, sometimes only two or three in a place, sometimes 25 forming a loose flying swarm. The bees never seemed to alight but remained in flight continually. No females were seen, but I have little doubt about this being a mating swarm. Probably only those species with large eyed, hairy males indulge in such swarming.

METHODS

The principal method used was to collect nests, plug the entrances in the field, bring them to the laboratory, and preserve for study the entire contents of each nest. Nests were mostly taken in early morning, late afternoon, or on cool or rainy days when all the bees would presumably have been in their nests.

Each female bee was examined using the methods described by Michener, Cross, Daly, Rettenmeyer and Wille (1955). The wings of *E. variabilis* do not often become much worn. The number of nicks on the forewing margins was recorded in the belief that it provides some rough index of previous flight activity. For purposes of the present paper, these data are given as unworn (no nicks), slightly worn (1 to 5 nicks in total on both wing margins), well worn (6 to 10 nicks in total on both wing margins), and much worn (11 or more nicks in total). The last category was very rare. Mandibular wear was rather slight and recording of it was abandoned.

Spermathecae were never found partially empty and it seems probable that once mated, a female retains a supply of sperm for life.

For the ovaries, the maximum width of each was measured as well as the length of the longest developing egg. The average width of the two ovaries is correlated with the length of the longest developing egg (see figure 1), and the latter has been used in the following sections of this paper on the theory that it better represents the reproductive activity of the female concerned (see also figures 65 to 82).

For convenience in expression, ovaries with the longest oocyte 0.50 mm. long or longer are considered to be enlarged in the discussions which follow. As can be seen from figure 1, this means enlargement beyond the initial stages common among slender ovaries.

The whitish areas noted in the section on ovaries of *E. variabilis* were used as an aid in judging age and egg laying by bees in the latter part of the study, after their meaning was realized.

In the following discussions the words "adult" or "female" always mean adult female except when otherwise specified. Callow adults are those showing paler coloration than mature adults. The youngest callows have milky wings but the wings harden and become transparent long before full colora-

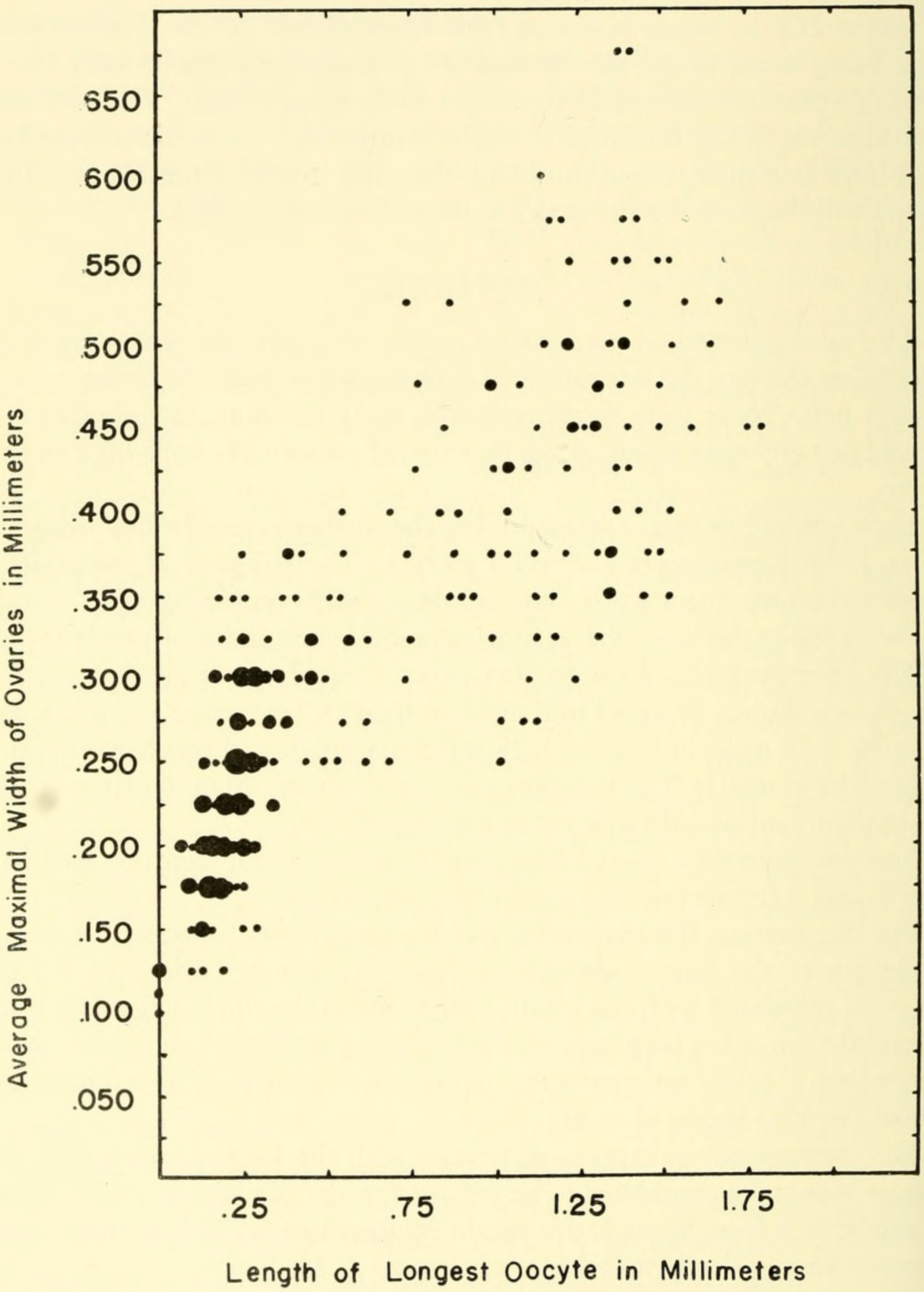

Fig. 1. Scatter diagram showing relations between ovarian width (maximum width of each ovary measured and averaged for each individual) and length of the longest oocyte in *Exoneura variabilis*. Small dots represent one individual; numbers of individuals represented by larger dots may be estimated by their diameters.

tion of the body is attained. Callows are unfertilized, with unworn wings, and with regularly formed, slender ovaries (longest oocyte less than 0.22 mm.) having no whitish areas in the bases or stalks. Fully colored but otherwise similar females are also considered as young but are not recorded as callows, being listed as mature adults.

EXONEURA VARIABILIS RAYMENT

Habitat: Observations were all made in southeastern Queensland. Nests were found in large numbers at the margins of the rain forest areas which occur on the higher mountains of this region. None was found in *Eucalyptus* savanna or in the depths of the rain forest, but breaks in the forest caused by roads as well as natural forest margins provided suitable habitats.

The localities where series of nests were taken for study are as follows: (1) roadside at summit of Cunningham's Gap, near Mount Edwards (October 3, November 9, December 27, February 25); (2) forest margins in Lamington Naional Park, near Binna Burra, in the McPherson Range (December 8, January 11-13); and (3) roadside and forest margins on Tamborine Mountain, on the side nearest to the town of Tamborine (December 18, February 15, March 22).

Nests: From the localities and dates listed above, 233 nests or at least burrows occupied by one or more *Exoneura variabilis* were opened for study. A few of these were merely burrows in which bees were resting, or were probably nests in the process of excavation, but 221 were nests in later stages of development.

The nests are simple burrows in broken or cut, standing, dry, pithy stems of bushes, brambles, or vines. Rarely, they are in stems that are soft because of rotting rather than because of pithyness. The holes are obviously made by the bees themselves, as in most other *Exoneura* and in contrast to species of *Allodapula* (see Michener, 1962). They enter the stems at the broken or cut ends. In slender stems the burrows are nearly straight while in thick stems with much pith the burrows are often sinuous. The stems are typically erect and the nests more or less vertical, but they often also occur in slanting, horizontal, or even hanging stems. In the last case, the entrance is the lowest part of the nest. Such orientation is especially common in roadside bushes of *Lantana* whose dead stems have been cut or broken.

Plants utilized for nesting sites were the following: *Rubus rosaefolius* (most nests at Cunningham's Gap, many at Binna Burra, few at Tamborine Mountain), *Lantana camara* (most nests at Tamborine Mountain, few at Binna Burra), *Eupatorium adenophorum* and *Plectranthus graveolens* (many from each at Binna Burra), *Homalanthus populifolius* (some from Tamborine Mountain), *Erigeron* (few from Cunningham's Gap), *Deeringia baccata* (few from Binna Burra), cultivated *Hydrangia* (one from Binna Burra), dead stems of rain forest vines (few from Binna Burra), and rotten stems of various plants (few from Binna Burra). Rayment (1949b) recorded a nest from a dead stem of a "reedy grass or sedge."

A few nests in *Lantana* and *Deeringia* were excavated through the dry portions of the stems and terminated at the beginning of moist living material. The same phenomenon was common in nests of *Exoneurella lawsoni* (Rayment) (see Michener, 1964) and was shown to influence the length of the burrows. These few nests of *Exoneura variabilis* in such stems were excluded from consideration in the following paragraphs on nest size and growth although all of them are within the extremes noted for nests in dry stems. No significant correlation was noted between nest measurements and the kind of stem in which the nest was located.

The nests are burrows 2.0 to 3.0 mm. in diameter. The mean of 140 measurements of burrow diameters is 2.5 mm. At the entrances the burrows are narrowed to 1.5 to 1.6 mm. in diameter. The burrows are excavated with narrow entrances. However, if an entrance is artificially enlarged or if the apex of a stem, including the constricted part of a burrow, is broken off, the *Exoneura* narrows the entrance by means of small pieces of pith stuck to each other and to the wall of the burrow near the entrance. Often such pieces of pith can be noted at nest entrances not altered in any way by an experimenter.

Nests in dead, dry twigs or stems and containing immature stages were 24-295 mm. in depth. The nests are seemingly deepened during the time that the young are being reared and the nest reused, as shown by the following data: Nests containing a single adult female and eggs or small larvae but no older immature stages ranged from 24-190 mm. in depth, mean 70.6 ± 8.65 mm. ($n=32$). Older nests, containing a single adult female and immature stages up to pupae, but no young adults, were 25-260 mm. in depth, mean 83.2 ± 5.95 mm. ($n=71$). Still older nests containing more than one adult or containing a young egg layer and also older immatures apparently her sisters (i.e., nests whose use is continuing beyond the brood of the founding female) ranged from 38-290 mm. in depth, mean 118.4 ± 11.41 mm. ($n=33$). Differences in depth between the latter group of nests and each of the others are significant ($p < .01$) but the differences between the first two is not ($.50 < p > .10$).

A few nests were found which contained larvae or pupae and at the same time had loose bits of pith outside the entrances; this observation corroborates the statistical evidence that pith is sometimes and perhaps regularly removed from the bottom of a nest and pushed past the brood and out the nest entrance by adult bees with resulting lengthening of the burrow.

Seasonal variation in nest depth was suggested, but the differences between seasons were not significant. Nests in October and November were

24-143 mm. in depth, mean 79.5 ± 9.84 mm. ($n = 13$). In February and March depths were about the same, 25-295 mm., mean 78.0 ± 9.58 mm. ($n = 28$). In summer, however, nests seemed deeper, 25-260 mm. in December and January, mean 95.3 ± 6.12 mm. ($n = 95$).

Life History Data: Group 1. This species was first encountered by me at Cunningham's Gap in the spring, on October 3, 1958. Nine nests were found; in them were 17 adult females and no adult males. Three of the nests contained only one adult; all of these lacked immature stages and were presumably excavated for establishment of new nests. The remaining six nests contained two or three adults each and five of them contained larvae, four to six each, mostly small; middle sized and large larvae were present in only one nest. Since there were no eggs nor pupae, I thought at first that these larvae had passed the winter in the nests and did not hatch from eggs early in the spring.

At least 65 percent of the females taken from the nests in October, including all that were alone in their nests, contained no sperm cells in the spermathecae. In all but two the largest developing egg was less than 0.45 mm. long; one was 1.00 and another 1.38 mm. in length. Most of the females, therefore, were unfertilized with scarcely enlarged ovaries, and most did not show any wing or mandibular wear. These data are in various ways confusing. If they represent an overwintered population, there should be adult males to fertilize at least the isolated unfertilized females; also they do not correspond with data from the overwintering fall populations (groups 8 and 9) which were studied in much larger numbers and which included no young larvae, very few mature ones, and few unfertilized females. It is my tentative supposition that the high percentage of unfertilized females and the lack of eggs represent sampling errors (the sample size was small) and that the young larvae found in five of the nests hatched from eggs laid in September.

Group 2 consists of 11 nests from the same locality taken on November 9. Each contained only a single adult female, except for one with two. Immature stages were absent in three of the nests. In one nest, the only immature individual present was a single prepupa. In one nest there were seven small larvae and five eggs. In the remaining six nests there were two to 11 (average 5.5) eggs and no other young. The nest with two adult females was the one with 11 eggs.

All of the adults that were successfully dissected (9) were fertilized. Those with eggs in the nest had enlarged ovaries with the longest oocyte 1.00 mm. or longer. Those without eggs had more slender ovaries with the longest oocyte .035-0.50 mm. in length. Of the 12 females, eight had one or more nicks in the wings and two were much worn.

Clearly conditions had changed since the preceding month, most of the females being alone, fertilized, and in egg laying condition.

TABLE 1. *Exoneura variabilis.* Numbers of Young and Adults in Nests of Group 3, taken on December 8. (Each horizontal row represents a nest. Nests without immature stages or with only eggs were omitted. Under adults C=callows. "I" indicates the parasitic bee, *Inquilina.*)

Nest No.	Eggs	Small Larvae	Medium Larvae	Large Larvae	Prepupae	Pupae	Total Young	Adult ♀♀	Adult ♂♂
274	3	1	..	..	..	..	4	1	..
300B	2	2	..	..	..	..	4	1	..
287	2	1	1	2	..	..	6	1	..
276	..	..	..	..	..	7	7	1+1I	..
269	..	..	..	..	2	..	2	1	..
278	..	..	..	2	4	..	6	1	..
280	..	..	..	1I	2I?	2	5	1	..
285	..	..	..	2	..	..	2	1	..
294B	..	..	2	..	..	..	2	1	..
297B	..	..	..	1	..	..	1	1	..
303B	..	..	..	..	1I	11I	12	2	..
304B	..	..	2	..	..	..	2	1	..
310B	..	..	..	3	3	1	7	1	..
311B	..	..	..	2	..	1	3	1	..
312B	..	..	..	2	..	1	3	1	..
317B	..	..	2	2	..	..	4	2	..
321B	..	..	..	..	..	1	1	2+1C	1C
322B	..	..	2	..	..	..	2	2	..
318B	..	2	..	..	..	..	2	1	..
273	4	..	..	..	..	..	4	2	..
272	7	3	..	..	..	..	10	2	..
270	13	..	..	..	..	7	20	1	..
275	11	3	3	..	..	..	17	2	..
281	..	1	2	..	..	..	3	1	..
286	5	..	..	..	..	3	8	1	..
288	10	..	..	2	1	3	16	3	..
289	..	1	..	1	..	..	2	1	..
296B	3	..	..	..	..	1	4	1+2C	..
298B	6	4	..	2	..	..	12	3	..
301B	2	4	..	4	2	..	12	2+2C	..
302B	2	..	..	..	4I	16I	22	3+1I	..
306B	11	8	..	1	..	4	24	2C	4C
308B	1	1	..	7	1	14	24	5+1C	5C
314B	20	..	..	..	..	10	30	2+4C	3C
315B	11	6	6	8	3	6	40	3+10C	10C
316B	6	..	..	..	1	5	12	2	..
319B	1	2	2	..	..	..	5	1	..

Group 3 consists of 44 nests taken at Binna Burra on December 8. Of these, four were only burrows without immature stages, three of them only 10 to 18 mm. deep, apparently being excavated. Each contained a single fertilized adult female, two with slender and two with enlarged ovaries.

Three of these four bees showed some wear of the wing margins. Apparently new nests were being established at this season.

Three other nests had progressed somewhat farther and contained one to four eggs each but no other young. A single adult female was in each of these nests; all three were fertilized, one had enlarged ovaries while two had slender ovaries, one showed some wing wear.

The contents of the remaining 38 nests in Group 3 are indicated in Table 1. Nests 274, 300B, and 287 were like those discussed in the preceding paragraph except that some of the eggs had hatched. The majority of the nests were older and their interpretations more complex, as indicated below.

Several nests (269-322B) contained only older larvae or pupae. Except for 303B, 317B, 321B, and 322B, these contained only one adult, which had been fertilized. About half of these females were unworn; the remainder showed wing wear. The ovaries were slender (longest oocyte 0.18-0.28 mm.) except for 276 and 310B which had swollen ovaries (longest oocyte 1.23 and 1.00 mm.). Presumably at least some of these adult females were of the same generation as the immature stages; others may have been mothers of the immatures in their nests. Those with enlarged ovaries would presumably soon have laid eggs, so that their nests would have been similar to those discussed below with young as well as old immature stages. Nest 322B contained two adults, both fertilized and with worn wings, one with slender ovaries, one with rather enlarged ovaries (longest oocyte 0.78 mm). Nest 303B contained two adults, both unfertilized, with very slender ovaries, and worn wings. Nest 317B also contained two adults, one fertilized and unworn, one unfertilized with worn wing margins (worker). Both had slender ovaries. Nest 275 contained two adults; their spermathecae were lost in dissection; both had worn wings; one had slender, the other enlarged ovaries.

The remaining nests contained immatures of various ages, often young ones (eggs or small larvae) and older ones (prepupae, pupae, or callow or young adults) with few intermediates. For example, nests 272 and 273 contained eggs and young larvae as well as unworn adults with very slender ovaries without whitish areas; in addition 273 contained a fertilized, well worn adult with more robust ovaries (longest oocyte 0.55 mm.) with whitish areas in the stalks. The latter individual must have laid the eggs and could have been also the mother of the young adult. As shown in Table 1, most of the nests (numbers 272-319B) had a larger number of immature stages than did 273. One of these nests (306B) contained only callow adults and another (272) only young adults with slender ovaries. In spite of the eggs, no old adults were in these nests. Presumably they had died by the time I opened the nests. Nests 273, 281, 286, 288, 289, 296B, 315B, and 319B contained only one mature adult each. (In nests 288 and 315B, two of the three adults shown in Table 1 were probably young, perhaps only slightly older than those recognized as callows. Perhaps they were workers.) These mature adults were fertilized; those in nests 273, 286, 288, and 315B had worn wing margins and swollen ovaries (longest oocyte 0.55-1.42 mm.) while those in nests 281, 289, 296B, and 319B had unworn wings and slender or slightly enlarged ovaries (longest oocyte 0.17-0.87 mm.). Those having the longest oocytes, 0.87 mm. or longer, had eggs in the nests; the others (except for 273 in which the longest oocyte was 0.55 mm.) did not. Probably only the worn individuals, and perhaps not all of them, were mothers of the older immatures in the nests. The other nests (298B, 301B, 302B, 308B, 314B, and 316B) contained two or three seemingly mature adults each. In 298B and 301B, the mature females were all fertilized; one in each nest had somewhat enlarged ovaries (longest oocyte 0.55 and 1.08 mm.) and worn wing margins, the others had slender ovaries and unworn wings. Nests 302B, 314B and 316B had ovaries of all mature females enlarged (longest oocytes 1.03 to 1.70 mm.). All were fertilized except one in 302B. Most showed wing wear but one each in 314B and 316B did not. The five mature females in 308B included two with swollen ovaries (longest oocytes 0.70 and 1.35 mm.) and worn wing margins which were probably fertilized. The other three had slender ovaries. One was unfertilized with worn wings, one fertilized with worn wings, and one fertilized with unworn wings.

Group 4 consists of 35 nests taken at Tamborine Mountain on December 18. Of these, one was only 11 mm. deep and contained only an unfertilized, unworn adult with slender ovaries. One lacked immature stages but contained an unworn adult with large ovaries, probably ready to start laying. Another contained a similar but somewhat worn adult. Three nests contained two, four, and five eggs respectively but no other young, and a single fertilized adult with large ovaries (longest oocytes 1.13 and 1.3 mm.) was in each; one had unworn wings, another slightly worn wings, and the third had much worn wings as though she had had some other activity before laying the few eggs observed. Such a bee might come from a nest that had been destroyed, or might be a worker that later became a reproductive.

Two nests lacked immature stages entirely but contained two and four adults respectively. Each contained one fertilized adult with somewhat enlarged ovaries (longest oocyte 0.75-1.20 mm.); the others were unfertilized with slender or slightly enlarged ovaries (longest oocytes 0.23-0.63 mm.). The wings were unworn or nearly so. Presumably these were adults of the same brood, reared in these nests. In each nest the fertilized bee would presumably soon have started laying; the others might have dispersed or remained as workers.

The contents of the remaining nests in Group 4 are indicated in Table 2. Nest 311T seems to have passed just beyond the stage of those discussed in the preceding paragraph in that eggs had been laid. One adult, the egg layer, was fertilized with enlarged ovaries (longest oocyte 1.23 mm.) while the other was unfertilized with slender ovaries and must have been a worker. Both had worn wings.

The nests listed as 297T to 326 in Table 2 contained only older larvae and pupae. In those containing only one female (297T, 308T, 324, 326), she was fertilized, and except for 324, had much enlarged ovaries (longest oocyte 1.13-1.50 mm.), suggesting that egg laying was about to begin. Nests with two adult females (302T, 318T) contained one adult each that was fertilized with enlarged ovaries (longest oocyte 0.63 mm.) and one each that was unfertilized with slender ovaries. The first would presumably have soon started egg laying while the second, probably a sister in each case, would have remained as a worker or perhaps left to start a new nest.

Table 2. *Exoneura variabilis.* Numbers of Young and Adults in Nests of Group 3, taken on December 18. (Each horizontal row represents a nest. Nests without immature stages or with only eggs were omitted. Under adult females, C=callows. "I" indicates the parasitic bee *Inquilina.*)

Nest No.	Eggs	Small Larvae	Medium Larvae	Large Larvae	Prepupae	Pupae	Total Young	Adult ♀♀	Adult ♂♂
311T	6	..	..	..	..	..	6	2	..
297T	..	..	..	..	..	3	3	1	..
302T	..	..	..	4	..	..	4	2	..
308T	..	..	..	1	..	6	7	1	..
318T	.	..	..	..	..	3	3	2	1
324	..	..	..	1	1	..	2	1	..
326	..	..	..	..	..	3	3	1	..
305T	..	..	1	2	..	..	3	1	..
313T	5	2	..	..	..	4	11	1	..
321T	5	..	..	..	..	2	7	1	..
322T	4	..	..	..	..	1	5	1	..
323	3	..	..	..	..	2	5	1	..
293T	2	7	1	..	..	..	10	6	..
294T	1	..	3	3	..	..	7	3	..
298T	8	3	..	..	3	7	21	4	..
301T	2	1	..	6	..	..	9	4	..
303T	8	..	..	2	..	3	13	2+1I	..
307T	3	1	..	..	..	4	8	2	..
310T	6	2	1	6	..	..	15	5+1C	1
314T	8	..	1	1	..	1	11	2	..
317T	2	..	..	1	..	1	4	2	..
319T	3	2	3	..	..	..	8	2	..
320T	6	3	2	..	..	..	11	5	..
325	8	4	2	..	1	..	15	3	..
316T	10	2	..	2	2	5	21	2	..
304T	1	..	..	8I	..	..	1+8I	3+1I	..
328	9	2	..	2	1	5	19	2	..

Nests 305T, 313T, 321T, 322T, and 323 contained only one adult each. All were fertilized except the one in 313T which was unfertilized, unworn, with slender ovaries, and could not have laid the eggs in the nest. The adult in 305T had slender ovaries and worn wings; the adults in 321T, 322T, and 323 had enlarged ovaries and those in the first two had unworn wings. It is very likely that such unworn individuals and perhaps the others as well are not mothers of the older immature stages in their nests; probably they are their sisters. They are, however, mothers of the eggs, and presumably care for and protect the older larvae and pupae present as well as their own offspring.

Nests 293T to 325 on Table 2 all contained more than one adult. In each case one was fertilized, with large ovaries, and in a few cases with worn wings, while the other individuals were unfertilized, with slender ovaries and usually unworn wings. The unfertilized individuals may function as workers; presumably they are sisters of the egg layer in each nest and also of the pupae and prepupae when present. Nest 316T was similar except that the individual with slender ovaries was fertilized. Nests 304T and 328 contained only unfertilized individuals with slender ovaries which could not have produced the eggs found in those nests.

Group 5 consists of 23 nests. Some were taken from Tamborine Mountain on December 18, established in Brisbane for observation, and opened on December 26; the others were taken at Cunningham's Gap on December 27. Two lacked immature stages and contained one adult each. One of these adults was fertilized, unworn, with enlarged ovaries (longest oocyte 1.18 mm.). The other had slender ovaries but its other characteristics were not ascertained.

Three nests contained one, two, and seven eggs each and no other immature stages. The first two contained one adult each, fertilized, one with worn wing margins, the other unworn, both with enlarged ovaries (longest oocyte 0.90 and 1.35 mm.). The third nest contained two females, both fertilized with well worn wing margins, one with enlarged ovaries (longest oocyte 1.48 mm.), the other with long slender ovaries except for one large oocyte 1.45 mm. in length. The latter, although fertilized, may have been more or less workerlike in function.

The contents of the remaining 18 nests of Group 5 are indicated in Table 3. Nests 331 to 379 in Table 3 contained only older larvae and pupae. Of the two adults in 331, one was fertilized with enlarged ovaries (longest oocyte 1.18 mm.) and the other was unfertilized, unworn, with slender ovaries (longest oocyte 0.15 mm.), probably a worker. Nests 376, 377, and 379 each contained a fertilized, unworn adult with somewhat enlarged ovaries. Probably eggs would soon have been laid; also it seems very probable that these adults were sisters rather than mothers of the pupae and prepupae in their nests.

Table 3. *Exoneura variabilis.* Numbers of Young and Adults in Nests of Group 3, taken on December 26. (Each horizontal row represents a nest. Nests without immature stages or with only eggs were omitted. Under adults, C=callows. "I" indicates the parasitic bee *Inquilina.*)

Nest No.	Eggs	Small Larvae	Medium Larvae	Large Larvae	Prepupae	Pupae	Total Young	Adult ♀♀	Adult ♂♂
331	..	..	..	61	..	..	61	2	..
376	..	..	..	..	3	..	3	1	..
377	..	..	..	..	2	..	2	1	..
379	..	..	..	..	..	2	2	1	..
374	1	..	..	..	..	2	3	1	..
382	9	1	2	10	..	2	24	1+4C	4C
386	10	5	..	..	1	5	21	1	..
388	2	..	..	..	2	2	6	1	..
329	2	..	1	4	3	..	10	2+2C	..
330	4	3	2	5	1	4	19	2+1I	..
332	5	1	4	2	..	1	13	4	1
373	..	2	2	2	..	..	6	3	..
375	8	5	1	5	..	..	19	6+2C	..
381	7	1	..	..	..	4	12	3+1I	..
385	11	5	..	..	..	4	20	2+1C	..
389	8	..	..	..	..	4	12	2	..
390	8	..	..	..	..	2	10	2	..
391	6	..	..	..	3	1	10	2	..

The remaining nests contained a variety of immature stages. Nests 374, 382, 386, and 388 contained only one adult each (if callows are ignored); in every case this adult was fertilized, with worn wings, and with much enlarged ovaries (longest oocyte 1.50 to 1.68 mm.). Nests 329, 331, 332, 373, 375, and 381 had one fertilized individual with swollen ovaries (longest oocyte 1.18-1.58 mm.) in each. Two had worn wing margins, three did not. The other adults in each of these nests were unfertilized, unworn, with slender ovaries, and in some cases were known to function as workers. Nest 390 was similar except that the probable worker was fertilized, although with slender ovaries. Nests 385, 389, and 391 had two mature adults each, both fertilized; most were worn and all had enlarged ovaries (longest oocyte 0.85-1.52 mm.). Nest 330 contained two unfertilized adults with slender ovaries, one with worn wing margins. Probably both functioned as workers.

Group 6 consists of seven nests taken at Binna Burra, January 11-13. They show no differences from those of Group 5 except that the small number of eggs may be significant. Five of the nests contained eggs, but three contained only one each, the others two each. Only two of the nests contained small larvae, one five, the other one. Correlated with the small number of eggs was the few adults with enlarged ovaries; there were only two. One was in a nest without other adults and with one pupa; presumably the adult would soon have laid eggs. The other was in a nest containing young from the egg to pupal stages and two other adults, unfertilized, with slender ovaries, probably functioning as workers.

Group 7 consists of 31 nests taken at Tamborine Mountain on February 15. The approach of autumn was already obvious. Fourteen of the nests contained no immature stages. Of the 17 remaining nests, only three contained eggs. Two others contained small larvae, so that five or about one sixth of the nests contained eggs or small larvae. Ten contained prepupae or pupae. The number of immature stages, even in nests containing some, was small (1-4) with the exception of three nests. These three contained eggs, small larvae, medium sized larvae, large larvae, prepupae, and pupae respectively, in the following numbers: (nest 421) 0, 0, 0, 3, 4, 15; (nest 443) 5, 5, 3, 3, 1, 0; and (nest 445) 7, 4, 4, 4, 0, 1.

The 31 nests of group 7 contained a total of 50 adults, one to seven per nest. Twenty-two, or nearly half, were unfertilized, the rest fertilized; 14 showed some damage to the wing margins, the others showed no wear. Only five had enlarged ovaries; all five were fertilized but their distribution among the nests was not intelligible. Of the three nests containing eggs only one also contained a bee with enlarged ovaries. Probably the egg layers in the other two had died. The other four adults with enlarged ovaries were in nests with no young or only older larvae or pupae. Two were the only adults in their nests and two were in nests with another adult each.

Apparently fertilized and unfertilized adults with slender ovaries were functioning as workers to feed larvae in most of the nests containing larvae.

Group 8 consists of 13 nests taken at Cunningham's Gap on February 25. One large larva, two dead prepupae, and one pupa were the only immature stages; these were distributed among three nests. Callow adults were present in another nest. Of the 17 adults, about 50 percent were fertilized, six showed worn wings, and none had enlarged ovaries (longest oocyte .25 mm.).

Group 9 consists of 48 nests from Tamborine Mountain taken on March 22. Immature stages were present in only five of these and callow adults in a sixth. Dead parasitized[4] prepupae were present in three others. The youngest immatures were large larvae, of which there was one each in three different nests. The total number of living immatures per nest was one in each of three nests and seven in each of two other nests.

The 70 adults in the 48 nests were from one to six per nest. Twenty two were unfertilized; the rest fertilized; 28 showed worn wing margins, eight of them well worn or much worn; all had slender ovaries (longest oocyte 0.13-.35 mm.).

Summary of Discussion of Life History: The data for groups 8 and 9

[4] Parasitization was by chalcidoid wasps similar to those recorded by Rayment (1949b).

above show that this species goes into winter primarily as fertilized adult females with slender ovaries. Young immature stages had disappeared by February 25 (late summer) and only a few older larvae and pupae remained. As shown in Table 4, about half of the adult females were worn, showing that many females that had been active earlier were now preparing for overwintering. Most of the nests contained one or two adult females. Those with more than two often contained callows, showing that the larger number was usually due to a recently matured brood; probably such individuals would not remain together throughout the winter.

In the spring, ovarian enlargement of some individuals occurs and eggs are laid in some nests in September and October. The presence of a few large immature stages suggests that a small number pass the winter in such stages rather than as adults. Reproduction goes on in September and October while several individuals are still in some nests, but group 2 (early November) indicates that by that time nearly all females have dispersed from overwintered groups and each has her own nest. Presumably each overwintered female ultimately develops enlarged ovaries and rears her offspring.

Production of eggs and of young adults goes on throughout the summer as shown in the preceding section and in Table 4. New nests seem to be established throughout the summer by single females. Old nests often contain several females but the large groups are usually mostly young individuals, often partly callows.

As shown in Table 4, production of immature stages is reduced by February 15 and many nests already lack immatures completely (see paragraphs above on group 7). Only 16 percent of the nests contained a female with enlarged ovaries (nearly all fertilized). However, the two nests containing several eggs and young larvae (443, 445) lacked egg layers; care of the young was by bees with slender ovaries, mostly unfertilized. Thus well before the end of summer the bees are progressing toward the overwintering condition.

The Reproductive Cycle Within Nests: In order to better understand the summer part of the life cycle, the social interactions and reproductive cycle must be examined. Many nests, especially as summer advances, are difficult to interpret, but others, with greater or lesser certainty, can be placed in one or another of the groups discussed in the following paragraphs. Those that cannot be so placed are often difficult to interpret because of lack of knowledge of the age of the egg-laying female; one may not be able to decide whether she is a sister or the mother of her associates. Examples of nests of various types are given below; further details on the same nests can be obtained from Tables 1-3 or the commentary in preceding sections.

Nest establishment and the egg layer with her first brood are exemplified as follows: Burrows without immature stages, usually containing only one adult and presumed to be young nests, were found throughout the summer.

TABLE 4. *Exoneura variabilis.* Average Number of Individuals per Nest in Various Developmental Stages on Different Dates. (In parentheses are percentages of nests taken on each date that contained each stage.)

Group No. Date No. of Nests	1 X-3 9	2 XI-9 11	3 XII-8 44	4 XII-18 35	5 XII-27 23	6 I-11 7	7 II-15 31	8 II-25 13	9 III-22 48
Eggs	....	3.5(64)	2.9(50)	3.2(66)	4.0(70)	1.0(71)	.5(10)	....	....
Small larvae	1.2(56)	.6 (9)	.9(32)	.8(31)	1.0(35)	.9(29)	.4(13)	....	....
Medium larvae	.2(11)	....	.5(20)	.3(23)	.5(30)	.1(14)	.4(20)	....	....
Large larvae	.1(11)	....	1.0(41)	1.1(37)	1.5(30)	2.1(43)	.7(32)	.1 (8)	.1 (6)
Prepupae	....	.1 (9)	.5(23)	.2(14)	.7(30)	.1(14)	.6(23)	....	.1 (4)
Pupae	....	....	2.0(32)	1.4(43)	1.4(52)	1.7(43)	.7(20)	.1 (8)	.2 (6)
Total immatures	1.5(56)	4.2(73)	7.8(93)	7.1(86)	9.0(78)	6.0(100)	3.2(55)	.2(15)	.4(10)
Adult ♀♀ (total)	1.9(100)	1.1(100)	2.0(100)	2.1(100)	2.3(100)	1.9(100)	1.6(100)	1.3(100)	1.5(100)
Callows	....	....	.5(16)	.0 (3)	.4(17)	.4(29)	.1 (3)	.2 (8)	.1 (4)
Fertilized	.4(33)	1.0(100)	1.2(84)	.9(86)	1.2(91)	.6(57)	.9(81)	.6(62)	1.0(83)
Worn	1.0(67)	.7(73)	.8(57)	.7(50)	1.0(61)	.3(29)	.5(35)	.5(46)	.6(54)
With enlarged ovaries	.2(22)	.7(64)	.7(52)	.9(83)	1.1(91)	.3(29)	.2(16)	....	....
Workerlike	.8(67)	....	.3(20)	1.1(51)	.6(30)	.7(43)	.7(35)	.5(46)	.4(31)
Adult ♂♂	....	....	.5(11)	.1 (6)	.2 (9)	.1(14)	.2 (7)	.1 (8)	.2 (8)

Similar beginning nests, but with eggs already laid, were also found in each sample of nests studied. Other nests contained only eggs and young larvae; examples are nests 274 and 319B. Such nests usually contain a single fertilized adult female each; if she is continuing to lay eggs, her ovaries are enlarged. Usually several eggs are laid over a relatively short period, after which egg-laying by the mother ceases at least for a time, as shown by nests such as 276, 278, 310B, and 297T in which the several young are large larvae or pupae but younger immatures are lacking. The mothers in such nests are fertilized, often with some wing wear as one would expect, and the ovaries usually somewhat enlarged. In other cases, however, the egg production seems to have been more protracted. Nest 287, for example, had young throughout the range from eggs to large larvae. The mother, as would be expected, was fertilized, with some wing wear, and with enlarged ovaries. The number of young in nests such as those described in this paragraph does not usually exceed seven or eight.

Most egg layers probable survive to lay a second batch of eggs. Nests are rather common in which a group of older, immature individuals is present, and in which, in addition, there is a group of eggs or small larvae, young of intermediate ages being absent. When the egg-laying adult in such a nest shows considerable wing wear, I have interpreted the evidence as indicating resumption of egg laying by the same mother that produced the older offspring. An example is nest 270, in which the adult bee was much worn, fertilized, with much enlarged ovaries. The fact that, in addition to the seven pupae in the nest, there were 13 eggs may suggest that in addition to the old mother, another individual, possibly a sister of the pupal individuals, had contributed to the egg cluster. This seems unlikely because of the lack of callows or other young adults; this nest was taken at 5:00 a.m. when almost certainly all individuals living in it would have been present. Nests 286 and 323 are other examples showing probable resumption of egg laying by a worn, fertilized female with large ovaries.

Such nests can sometimes also be recognized at a later stage when some or all of the individuals of the first brood have reached adulthood. For example, in nest 273, in addition to eggs, there was an old, fertilized adult with well worn wings and enlarged ovaries and an unfertilized, unworn female with slender ovaries. The latter presumably represented the first brood of young; males and any other females of that brood must already have dispersed. The eggs represented the second brood of young. The unworn female would probably have remained and functioned as a worker or might have mated and become reproductive. Nest 311T was the same except that the unmated individual with slender ovaries already had three nicks in one wing margin. Nest 288 presents a similar picture, six large immatures and two presumably young adults[5] (unworn, unfertilized, with slender ovaries)

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[5] One of the young adults was teritological, lacking one front leg and one side of the prothorax. The mesonotum was so shaped that the bee probably could not fly.

apparently representing the first brood and ten eggs representing the second brood of a worn, fertilized female with enlarged ovaries.

Nests 314B and 316B are similar to those described above in having only young and old immature stages, without intermediate ages. Each also had a worn, fertilized female with enlarged ovaries. In addition, each contained an unworn, fertilized female with enlarged ovaries. No doubt both individuals contributed to the clusters of eggs, as indicated by the large number of eggs (20) in nest 314B. The 17 pupae and callow adults in the same nest suggest a double source for the earlier brood also. The sources of the unworn egg layers cannot be established but probably they are older sisters of the pupae and callow adults in these nests.

Nest 315B also may contain one of its founders; at least there was a well-worn, fertilized female with large ovaries in the nest. The other adults in the nest were unworn, unfertilized, with slender ovaries, and no doubt were sisters of the callow adults and pupae. The large number of immature stages suggests that more than one egg layer was involved in their production.

Nests such as 270 and 288 suggest that the second brood of a female may be larger than the first. This may be reasonable since there is often more than one female to care for young of the second brood, while the first brood ordinarily must be cared for by the mother alone.

There is evidence that the founder of a nest does not generally survive long after laying the eggs for her second bood. Only 24 well and much worn females were found in the course of the study; they become no more common as the season advances and are no more common in large colonies than in small ones. These facts argue against long survival of a colony-founding mother such as occurs in *Lasioglossum malachurum* (Noll, 1931) or *L. inconspicuum* (Michener and Wille, 1961). Further support of this interpretation is provided by Skaife's (1953) observations on *Allodape* and by the many nests containing immature stages, obviously being fed, yet lacking any individual that could have been their mother. Obviously care of young is taken over by other individuals, probably usually older sisters of the young concerned. The nests discussed below illustrate such phenomena.

Nest 272, containing eggs and young larvae, was inhabited by two adult females, both unworn, one fertilized, one unknown because the spermatheca was lost in dissection, both with slender ovaries lacking white areas. Such ovaries could not have produced the eggs found in the nest. Presumably these adults were from the first brood of a female; her second brood consisted of the eggs and young larvae being cared for by the individuals of the first brood. This nest was taken at about 5:00 a.m., long before the bees become active. Hence it is unlikely that any surviving inhabitants were away from the nest. Nest 313T was similar in that it contained young immatures. It also contained pupae and one unworn, unfertilized adult with slender ovaries; these must represent the first brood of a female no longer present, whose second brood was the eggs and young larvae. The young adult was obviously caring for the eggs and young in the nest.

Nest 421 contained large larvae as well as prepupae and pupae. Of the seven adult females in the nest, only one was fertilized, three showed slight wing wear, and all had slender ovaries with no white areas. Obviously these adults were caring for the larvae although no one of them could have been their mother.

Nests 443 and 445 both contained numerous immature individuals and several adults. One adult in each nest was fertilized, that in 443 slightly worn, but none of the adults had enlarged ovaries. Obviously one or more older bees, presumably dead by the date when the nest was taken, must have been the mothers of the immatures in each nest. Young bees were clearly caring for the eggs and larvae.

Not only are young commonly cared for by their older, workerlike sisters, but some of the sisters also replace their mothers as egg layers, as indicated in the following paragraphs. Nest 295T is interesting in that it contained no immatures. The original egg layer must have failed to produce a second brood. The four bees in the nest were all unworn, only one was fertilized and she had enlarged ovaries. Presumably she would soon have laid a group of eggs. One of the unfertilized females had slightly enlarged ovaries (longest oocyte 0.55 mm.).

It is my unverified suspicion that nests such as 275 (both adults with slightly worn wings, only one fertilized with enlarged ovaries) and 301B (one of the noncallow adults unworn, unfertilized, with slender ovaries; the other only slightly worn, fertilized, with enlarged ovaries) had lost their original founders and that each contained another egg layer which was presumably one of the offspring of the founder. The principal reason for this surmise is the slight amount of wear of the wings of the individuals with enlarged ovaries.

In other cases it seems clearer that the founder of a nest has died and been replaced by another egg layer. Nest 296B contained eggs, a pupa, callow adults, and one mature, unworn, fertilized adult with enlarged ovaries. It seems most likely that this individual is a sister of the pupa and callows but the mother of the eggs. Nest 293T was similar in that it contained young immature stages and young adults. Five of the adults were unworn, unfertilized, with slender ovaries. The remaining adult differed in being fertilized, with enlarged ovaries. Presumably she was a sister of the other five adults and mother of the eggs and young larvae. Nest 463 can be interpreted along similar lines; the three adults were unworn, only one was fertilized with enlarged ovaries.

Division of labor: From the above paragraphs it is evident that the typical nest population contains only one fertilized adult female with enlarged ovaries. During the main reproductive period in summer (December), over half of the nests contain only one mature (i.e., not callow) female and at other seasons the percentage of monogynous nests is even higher. However, in some nests, additional mature females are present. Thus of 102 nests taken during December (groups 3-5), 48 contained more than one mature female. As shown in Table 5, 30 of these 48 nests contained two mature females and

Table 5. *Exoneura variabilis.* Frequencies of December Nests with Two or More Mature Females (out of total of 102 nests) and, among these, Frequencies of Nests with Varying Numbers of Reproductive Females.

No. of mature ♀♀	0	1	2	3	4	5	6
Frequencies of nests with 2 or more mature ♀♀.	--	--	30	8	5	3	2
Frequencies of such nests having varying nos. of ♀♀ with enlarged ovaries.	4	29	12	3	--	--	--
Frequencies of such nests having varying nos. of fertilized ♀♀.	2	28	15	3	--	--	--

only small numbers had three or more. Table 5 also shows, as was suggested from less specific data at the beginning of this paragraph, that in most nests (28 or 29 out of 48) containing two or more mature females, only one is fertilized and only one has enlarged ovaries. In the great majority of cases the same individual shows both of these features and is obviously the only reproductive individual in the nest. However, among the 131 mature females in the 48 nests, 13 were fertilized but had slender ovaries. The 54 monogynous December nests contained 16 fertilized females with slender ovaries. This 27 to 30 percent fertilized individuals with slender ovaries consists of (1) individuals, probably relatively young, in their parental nests, sometimes associated with fully reproductive individuals, (2) individuals starting new nests (among the monogynous nests only), and (3) individuals that have laid their first brood of eggs and whose ovaries have regressed. There may be other conditions under which such individuals appear; from available data it is often difficult to place specific individuals in one or another of these classes. My impression is that classes (1) and (3) are about equally numerous and (2) less so.

In addition to fertilized individuals with slender ovaries, there were among the 48 nests containing more than one female, three females with enlarged ovaries but no sperm cells in the spermathecae. One of these actually had only one oocyte enlarged (0.55 mm. long), so that its ovaries barely qualified as "enlarged"; it was in a nest (295T) containing two other young mature adults (unfertilized with slender ovaries) in addition to a fully reproductive female, and was undoubtedly only a young female which for some reason had an unusually enlarged oocyte. The other two unfertilized females with enlarged ovaries both had worn wings and the longest oocytes of each were 1.03 and 1.10 mm. long. Both had ovaries smaller than average for such large oocytes (0.25-0.30 mm. wide), as shown in Fig. 1, a fact which suggests that the ovarian enlargement may have been incomplete. One was in a nest (385) with a fully reproductive female, a callow female, and brood; the other was in a nest (302B) with two fully reproductive females and a female of the parasite *Inquilina*. Apparently such individuals are more or less in the nature of abnormalities.

Among the December nests there were eight in which two of the females were fully reproductive. In several nests these were the only adults present while in other cases other mature adults were also present.

Among the 131 mature females in the 48 December nests containing more than one mature female, 53 had enlarged ovaries and were fertilized. Such individuals are the principal reproductives and, as shown above, are usually distributed one per nest. At least many of the remaining individuals function as workers. This was established by capturing pollen collectors returning to their nests and dissecting them along with the other females in the nests. The pollen collectors were, in all cases studied, unfertilized bees with slender ovaries, and can be called workers. As examples, nest 332 contained a well worn reproductive, a worker, and two other individuals which seemed workerlike and probably also served as workers. Probably the reproductive was the mother of the workers which were therefore functioning in the presence of a queen mother just as in many halictids and other social bees. Nest 329 contained a reproductive, a worker, and two callows. Since all were unworn, they were probably all sisters. Nest 331 contained a reproductive and a worker. Because the reproductive's wings were damaged in capture, it is not known whether she was an old bee or not. All the larvae in the nest were *Inquilina;* the reproductive evidently had not yet started to lay and was most likely a sister of the worker. Finally, in nest 330 there was no reproductive, the two females being unfertilized, with slender ovaries. At least one of them, however, was bringing pollen into the nest, presumably to feed larvae which probably were her sisters. Nests such as 330 substantiate the view already presented that young adults take over the work of caring for any young in the nest when the old adults die.

The importance of workers in foraging in this and other species of *Exoneura* has been shown elsewhere (Michener, 1963) by dissections of pollen collecting individuals taken on flowers. At least at some seasons more than 80 percent of the pollen collectors were shown to be unfertilized and an even higher percentage have slender ovaries. The high percentage of workers collecting pollen indicates the inactivity of egg layers in such work, for less than 50 percent of the mature females from nearby nests were workers.

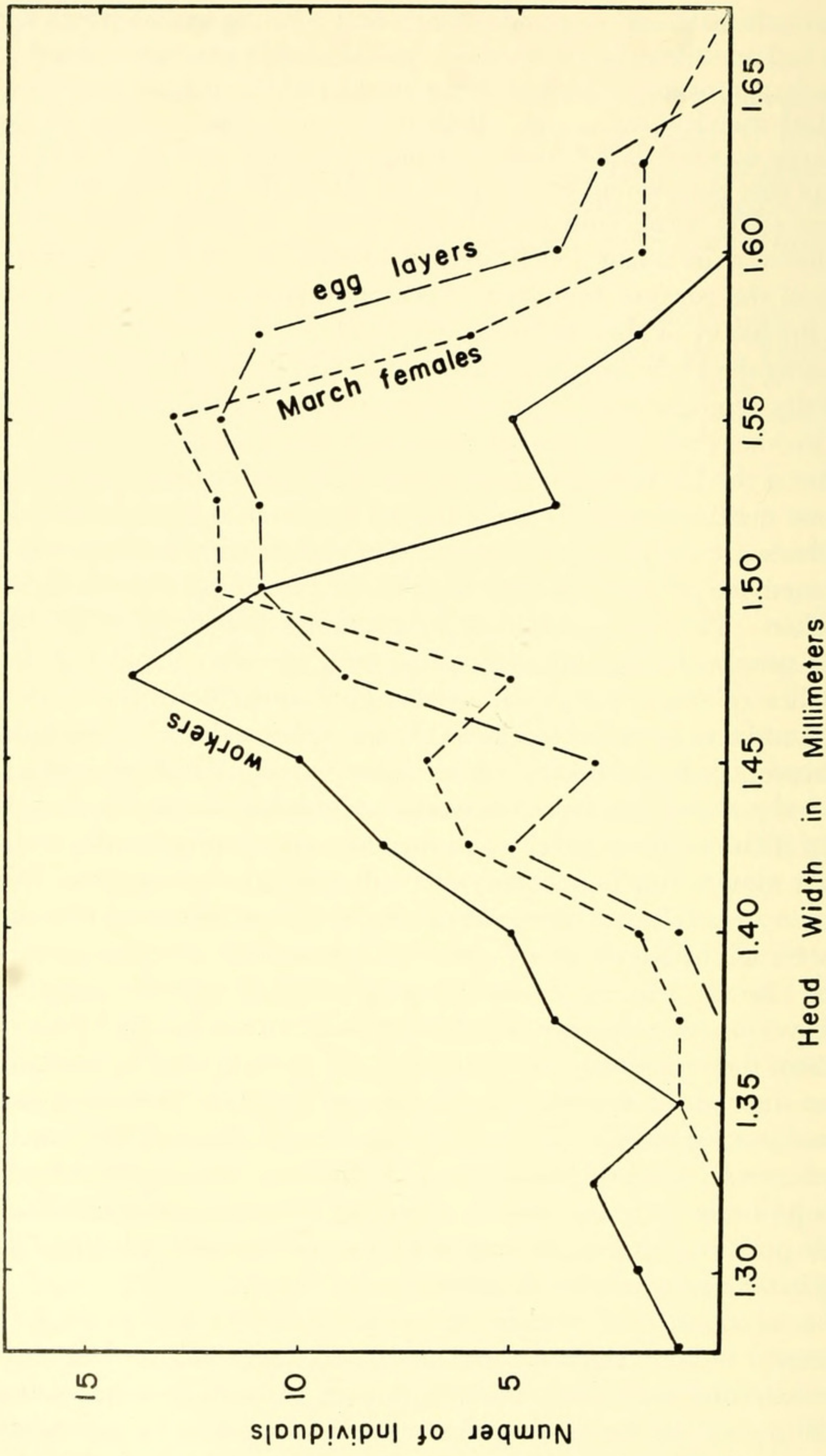


Fig. 2. Frequency distribution of head widths of females of *Exoneura variabilis*, based on 70 egg layers taken in December, 70 workers and presumed workers taken in December, and 70 females taken in March.

Since most workers are unworn, the problem arises as to whether workers die off as such or ultimately mate and disperse to establish new nests. The abundance of immature stages compared to the small number of adults (Table 1 to 3) suggests that the workers are short lived in this capacity—they either die after a short adult life or they disperse and cease to be workers. The number of new nests found in each group during the summer was small, as indicated in the discussion of nest groups 3 to 5. It is therefore my belief that most workers are relatively short lived, as in other social bees, and that they die before their wings become very worn. On the other hand the seemingly new nests sometimes found being established by worn bees may suggest that some workers do become reproductives later (see first paragraph in discussion of Group 4 above). The idea that the workers, or at least many of them, represent a caste rather than a stage in the adult life of females is further supported by the average size difference between workers and egg layers. Seventy fertilized individuals with large ovaries taken in December were compared with 70 unfertilized mature adults with slender ovaries taken in the same month and presumed to be workers (including 19 known to be workers from behavioral observations). Head width was used as a measure of size. The mean head width of the 70 egg layers was $60.9 \pm .257$ micrometer divisions, that of the 70 presumed workers was $58.1 \pm .101$. These means are significantly different as shown by a t-test ($p < .01$). These data are shown in millimeters in Fig. 2. There was no significant or even suggestive size difference between lone egg layers and those in company with workers or other females. In the same figure is presented comparable data for 70 females taken on March 22. There was no significant difference between these females, prepared to overwinter, and the summer egg laying females.

The difference in size between egg layers and workers is more clearly shown by comparing sizes in various nests separately. Among 33 nests taken in December and January in which egg layers and workers could be distinguished with some degree of assurance, 24 had the egg layer larger than any worker in the same nest (Table 6). Moreover, 61 of the 71 workerlike individuals from these nests were smaller than the accompanying egg layers.

Adults produced in December, as judged by callows, included a few individuals of maximum size but most were the size of workers; 21 of the 24 callows taken in December with accompanying egg layers were smaller than those egg layers. In February, however, of six callows in three nests that contained egg layers, two were larger, two smaller, and two equal in size to those egg layers. These data, although few, suggest that at that time callows become overwintering egg layers rather than workers.

Sex Ratio: The sex ratio may support the idea of a worker caste somewhat similar to that of social halictines for there is an excess of females produced. December and January pupae, callow adults, plus a few prepupae

TABLE 6. Relation of Size of Workers (W) to Egg Layers in Various Nests of *Exoneura variabilis* taken in December and January.

Relation	No. of nests	No. of workers
W $<$ egg layer	24	54
W $=$ egg layer	4	4
W $>$ egg layer	2	2
W $<>$* egg layer	1	2
W $<=$* egg layer	1	6†
W $>=<$*egg layer	1	3
Totals	33	71

* Multiple symbols indicate that some workers are smaller than, others larger than or equal to the egg layer.
† These six consisted of 5 smaller than and one equal to the egg layer.

reared to the pupal stage for determination of sex, numbered 207. Of these only 40.1 percent were males.

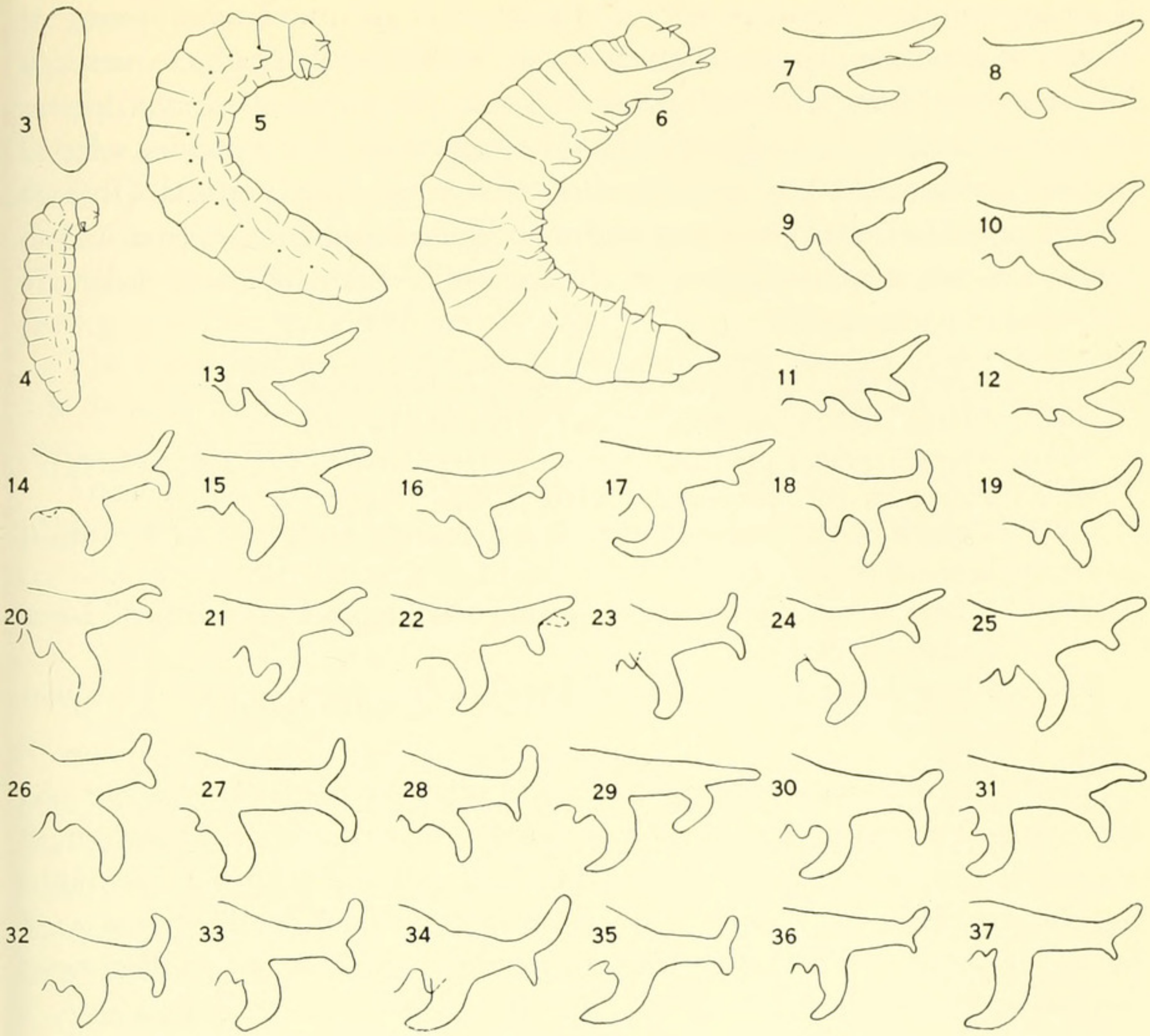
Males are generally short lived or leave the nests when young, for the number of noncallow males found in the nests is small (see Tables 1 to 3).

Ovarian Development: The various stages of ovarian development among adults, from young callows to mature egg layers and workers and overwintering individuals, are shown in Figures 65 to 82. The explanations of the illustrations are given in some detail and make an extended account here unnecessary. Drawings are based on specimens fixed in Kahle's (Dietrich's) solution. There are four ovarioles per ovary, and in each several oocytes enlarge simultaneously, thus permitting the laying of several eggs at about the same time. This is in sharp contrast to *Allodapula* and *Exoneurella* (see Michener, 1962 and 1965).

The white areas found in the posterior parts of some ovaries presumably result from resorption of eggs or from the laying of eggs or both and are therefore of value in giving some idea of previous ovarian activity.

Immature Stages: The occurrence of immature stages in nests is given in detail in the section on Life History Data, including Tables 1 to 3. The details of larval form and structure are given by Syed (1963), who showed that there are probably four larval stages. His drawings were from fixed specimens; Figures 3-13 were made from living material.

The mesothoracic arms of the last stage larvae vary more than Syed indicated, as shown by Figures 7-37. These arms are sticky and soft in life. Branches may stick together or even to the body wall and then practically disappear. There is thus a good probability of observational errors in studies based on living material. Moreover, the arms are partially retractile; in inactive individuals they are not fully exerted. Tactile stimulation, for example with a needle, especially in the head region, results in full extension of the arms, as though by blood pressure; after a short time they retract.



FIGS. 3-37. *Exoneura variabilis.* 3, egg (length 1.75 mm.); 4, small, probably second stage, larva (maximum diam. 0.58 mm.); 5, half grown (third stage) larva (maximum diam. 0.75 mm.); 6, mature larva. Figures 7-37 represent maximally exerted mesothoracic arms of mature larvae before the prepupal stage. Figures 7-13 were drawn from live or freshly dead specimens. Figures 14-37, which tend to have the branches recurved, were drawn from specimens that had been fixed for weeks in Kahle's (Dietrich's) solution. Broken lines in some locations represent projections present on one side of the body, absent on other side of the same larva. Figures based on larvae from the same nests are 7 and 8, 9 and 10, 11 and 12, 17 to 19, 20 to 22, 23 and 24, 25 and 26, 27 to 31, and 32 to 37.

Adult bees passing through the nest must cause this reaction which must be related to providing the pollen mass by the adults and its handling by the larger larvae.

In the prepupal stage the larval appendages shrivel.

The small projections on the mesothorax of third (?) stage larvae are not retractile.

Specimens dropped alive into Kahle's (Dietrich's) solution have fully extended appendages which after a time tend to have recurved branches as shown in Figures 14-37.

In the nests the immature stages are usually arranged from oldest above to youngest below. Perhaps because there are larger numbers of young of about the same age than in *Allodapula* (see Michener, 1962), the sequence is not so precisely kept as in that genus. For example, pupae of various degrees of pigmentation are usually mixed. The following lists illustrate selected cases in which marked irregularities in the usual sequence occurred. (In each list the nest number is given first and then the immature stages from top to bottom. Groups of immatures in clumps rather than in linear order are indicated in parentheses.)

288: 2 large larvae, 1 prepupa, 1 white pupa, 2 black pupae (10 eggs).
306B: 1 large larva, 4 pupae (11 eggs, 8 very small larvae).
308B: 6 large larvae, 1 prepupa, 14 pupae, 1 large larva (1 egg, 1 small larva).
310B: 3 large larvae, 3 prepupae, 1 white pupa.
289T: 2 black pupae, 5 white pupae, 3 prepupae (1 small larva, 2 very small larvae, 8 eggs).
316T: 2 large larvae, 2 prepupae, 3 pupae, 1 small larva, 1 pupa, 1 small larva, 1 pupa (10 eggs).
382: 10 large larvae (8 eggs, 1 small larva), 1 dead pupa, 1 pupa; 2 medium sized larvae, 1 egg.

Feeding of the larvae is progressive, as in other members of the genus. At any one time relatively few larvae have food. For example, on December 18 a series of nests was collected during the cloudy afternoon after a fine morning during which the *Exoneura* were common on flowers. The nests were opened in the evening. At that time only eight of the 74 larvae in these nests had pollen masses on them. These eight included larvae of all sizes.

I have two records of two small larvae curled around a single pollen mass but in general there is one mass per larva. The mass is on the ventral surface of the larva; the larva lies on its dorsal side and curls around the pollen as in the sketches reproduced in Figures 38-41.

FIGS. 38-41. *Exoneura variabilis* larvae feeding on pollen masses. 38, very small larvae feeding on pollen mass which has been largely consumed (maximum dimension of pollen mass 1 mm.); 39, third stage (?) larva; 40 and 41, last stage larvae.

Eggs and small larvae are somewhat sticky and cling together in irregular clumps. The eggs are not attached in any way to the walls of the nest burrows.

Larvae removed from nests produce feces from middle size onward. Feces are never found in the nests, however; they must be removed by the adults.

Variation among adults: Rayment's name for this species is appropriate for there is more variability in coloration in this species than in any other *Exoneura* known to me. The face of the female is rarely wholly black. Commonly there is a small cream colored mark on the lower part of each paraocular area and sometimes these marks are rather large, nearly attaining the level of the summit of the clypeus. Commonly there is a longitudinal median clypeal mark, sometimes broadened at the summit to the full upper width of the clypeus. The clypeal mark may be present without the paraocular marks, or vice versa, or both may be present.

The females in any one nest *tend* to resemble one another in the markings but there is enough variation within nests to show that all the variation described is intraspecific.

There is also geographical variation. The abdomen, in specimens from Cunningham's Gap, is orange. In specimens from the other localities it is considerably darker because of broad basal blackish bands on the segments, and sometimes it is almost wholly black.

INQUILINA EXCAVATA (COCKERELL)

This bee is similar in size and appearance to *Exoneura variabilis* and inhabits the nests of that *Exoneura.* As was pointed out by Michener (1961), the females of *Inquilina* do not possess a fully formed scopa. They have not been seen to collect pollen and appear to be social parasites in the nests of *E. variabilis.* This habit explains some of the "heterospecific companionship" discussed by Sakagami (1960). The details of the larval structure of *I. excavata* have been described and figured by Syed (1963). Variation in the mesothoracic arms of mature larvae is illustrated in Figures 42-49.

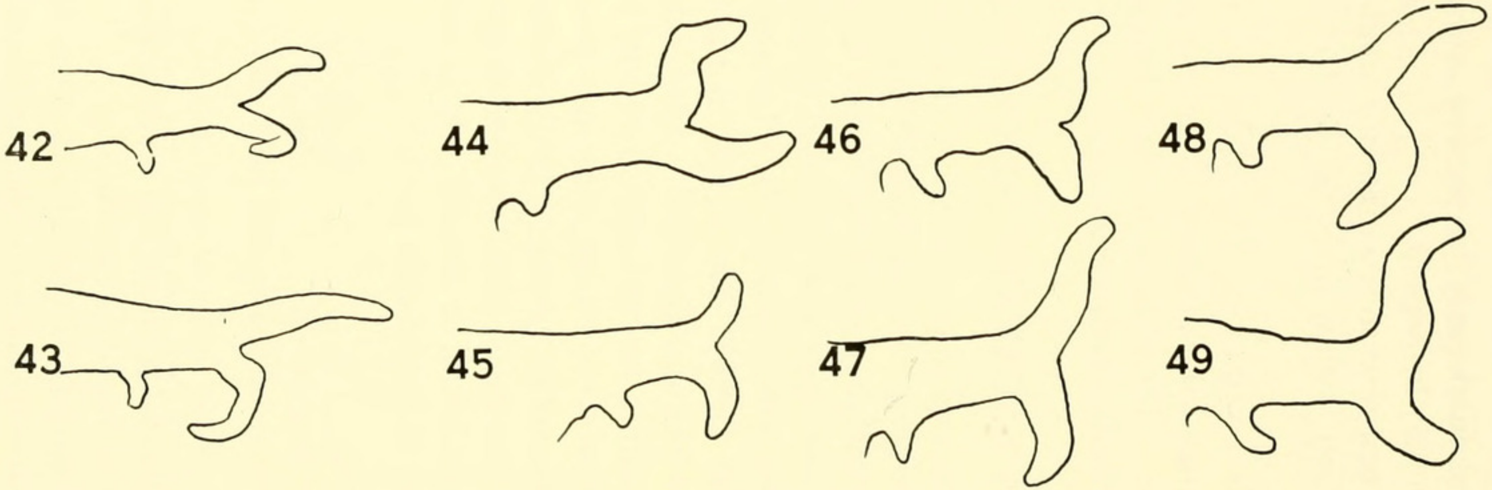
No specimens of *Inquilina* were found with nest groups 1 and 2 of *E. variabilis.* Occurrence in December (groups 3 to 5) is shown in Tables 1 to 3. In January (group 6) three nests (not included in previously presented statistics on *E. variabilis*) were found to contain only *Inquilina.* The contents were as follows (nest number at first of each line):

460: seven adult females.
461: two adult females, six large larvae.
464: five adult females, two adult males, one black pupa, one prepupa, seven large larvae.

In another nest one female of *Inquilina* was associated with a female, two small larvae, and seven large larvae of *E. variabilis.*

In February and March (groups 7 and 8) a total of eight *Inquilina,* all adult females, was taken, one in each of eight nests, and in every case in the company of one or more adult *E. variabilis* and sometimes with *variabilis* larvae.

The relation of *Inquilina* to the *Exoneura* cannot be learned in detail from



FIGS. 42-49. Sketches of mesothoracic arms of mature larvae of *Inquilina excavata*, based on fixed specimens. Figures 42 and 43 are based on larvae from one nest, the others, on larvae from another nest.

FIGS. 50-51. *Exoneura aterrima*. 50, lower end of nest, showing positions of eggs; 51, newly hatched larva, with posterior part of body still in chorion attached to wall of burrow, and with pollen mass already on venter of larva.

available data. It is obvious that the parasite must invade nests of *Exoneura* and lay eggs there. From the fact that whole groups of larvae and pupae in certain nests (302B, 303B, 304T, 331) were *Inquilina,* and from the frequency of adults in the nests, it seems clear that the *Inquilina* take up residence in association with *Exoneura,* rather than merely entering to lay an egg and then leaving.

The larvae of *Inquilina* must obviously be fed by the *Exoneura,* since the parasite cannot collect pollen. The *Inquilina* probably prevents the production of brood of the host in some way or destroys *Exoneura* eggs, in view of the seven nests (302B, 303B, 304T, 331, 460, 461, and 464) in which the whole broods seem to have been *Inquilina.* In some cases, e.g., 460, 461, and 464, the *Exoneura* appear to have reared their parasites and died, leaving the nest entirely to the parasite. In other cases, it seems that the *Exoneura* survive. For example, nest 331 was inhabited by two adult *Exoneura,* one of which was apparently about to start laying eggs. Perhaps such *Exoneura* resulted from larvae somewhat older than those of the parasites reared in the same nest; perhaps in the absence of *Exoneura* larvae of that age, the destruction of the *Exoneura* colony by the parasite is complete.

The individual females of *Inquilina* isolated in nests of *Exoneura* were nearly all fertilized, not or slightly worn, with slender ovaries. Only two with enlarged ovaries were found; these were the adult females in nests 302B and 381. Both were in nests with females of *Exoneura* which were also fertilized and with enlarged ovaries. From this it seems likely that egg-laying *Inquilina* live in nests where female *Exoneura* are actively laying eggs. The species of the eggs and young larvae in nests 302B and 381 is unknown, but it is reasonable to suppose that they were those of the *Inquilina* which probably destroyed host eggs.

EXONEURA HAMULATA COCKERELL

Habitat: This species was studied at the nearby localities of Beerwah and Tibrogargen, in southeastern Queensland. The area is *Eucalyptus* savanna.

Nests: Nests of this species have been recorded previously by Rayment (1946c, 1948). Twenty five nests of *E. hamulata* were found by me. All were burrows in standing dead, dry, flowering stems of *Xanthorrhoea.* Usually there was only one burrow in such a stem, but in one case two and in another case four burrows were parallel to one another in the pith, so close together as to be separated by only one half to one fourth of a millimeter of pith for considerable distances, yet never connecting. *E. hamulata,* like *E. variabilis,* makes its own burrows; it enters stems cut off by an insect which leaves a smoothly cut end. Stems broken or cut by man have rough ends and were not utilized.

Nest burrows sufficiently advanced to contain young are 30-310 mm. deep (mean of 21 measurements, 164 mm.). The entrances of the burrows are narrowed to 2.0-2.5 mm. (mean of six measurements, 2.4 mm.).

The entrance may be narrowed by means of bits of pith forming a neat collar or the burrow may be excavated with a narrow entrance; perhaps all are first constructed in the latter way and a collar built only if the original entrance is damaged. The diameter of the burrow below the entrance is 2.5-4 mm., usually being 3 mm. or more (mean of 39 measurements, 3.4 mm.).

Life History and Reproductive Data: Information on the nest contents of the 21 nests that contained young is given in Table 7. These data suggest

TABLE 7. Numbers of Young and Adults in Nests of *Exoneura hamulata*. (Each horizontal row represents a nest. Nests without immature stages or callows and containing only a single adult were omitted from this table. Under adults, C=callows.)

Nest No.	Date	Eggs	Small Larvae	Medium Larvae	Large Larvae	Prepupae	Pupae	Total Young	Adult ♀♀	Adult ♂♂
88	X-17	..	..	2	2	..	..	4	2	..
89	X-17	..	..	..	..	3	12	15	2	..
90	X-17	7	..	7	..	..	10	24	4	..
92	X-17	..	..	4	4	..	..	8	3	..
245	XI-24	4	..	..	..	..	1	5	2+5C	..
253	XI-24	6	..	..	..	..	1	7	3+17C	6C
400	I-6	3	2	..	..	..	..	5	1+1C	..
401	I-6	1	..	..	..	..	1	2	2C	..
402	I-6	9	4	..	3	..	..	16	3	..
403	I-6	10	2	..	..	..	..	12	1+3C	..
404	I-6	9	..	..	..	..	10	19	1+8C	2C
405	I-6	4	1	2	6	..	2	15	5	..
406	I-6	1	..	..	4	..	..	5	2	..
407	I-6	4	..	..	..	..	..	4	2	..
408	I-6	..	..	..	4	1	..	5	3	..
409	I-6	15	..	..	..	..	4	19	3+6C	1C
410	I-6	..	..	..	..	..	..	0	2+1C	..
416	I-6	..	..	..	4	..	..	4	2	..
419	I-6	..	..	..	..	..	1	1	1	..
420	I-6	1	..	..	..	..	..	1	1+1C	..
465	II-19	4	..	..	2	1	..	7	2	..

that nests are active more nearly continuously than in *E. variabilis* for nests full of immature stages were found both in October and February. October and February nests of *variabilis* do not contain such a variety of immature stages. A longer season for *hamulata* is not surprising in view of its warmer habitat, not far above sea level. Perhaps immature stages are numerous throughout the winter in these nests but adults were not taken on flowers in spring until mid-September nor in fall after April. Two lone females were found making new nest burrows on November 24, two others on January 6. It is likely that new nests may be established at various seasons, as in *E. variabilis*. None of the nests containing immature stages was recently established by a lone female, however; all contained older young and most contained more than one mature female.

Obviously, as in *E. variabilis,* females lay considerable numbers of eggs over a short period and then rest, probably laying a second group of eggs later. The result is the normal occurrence of young of two very different ages (e.g., eggs and pupae, as in nest 404) in the nests. Occasionally (nest 405) a more or less continuous sequence of young exists in a nest, perhaps because of the presence of more than one egg laying female.

The rather numerous callow adults in the nests (see Table 7) no doubt originated from the same groups of eggs as the pupae usually found in the same nests.

Division of Labor: Consideration of mature adults in the nests suggests the existence of the same sort of colony organization at least from October through January or February as exists during December for *E. variabilis*. Nests with a single mature female exist (e.g., 400, 403, 404). All show a major gap between young and older immature stages. The adult females in nests 400, 403, and 404 were well worn, fertilized, with enlarged ovaries, as might be expected of females laying their second groups of eggs.

Nests with several mature females are more common than in *E. variabilis,* as shown in Table 7; 15 of the nests contained two to five mature females each. The features of the mature females in these 15 nests are shown in Table 8. One or more fertilized bees were present in each nest. One fully reproductive individual (fertilized and with large ovaries) was found in each of six polygynous nests (90, 406, 408, 409, 416, and 465) and two in five nests (245, 253, 402, 407, and 410). Most of the remaining bees were (1) unworn, fertilized individuals, not yet laying eggs (no white areas in ovaries), but caring for larvae which could not have been their progeny (e.g., all females in nests 88 and 92); or (2) unfertilized individuals, either worn or not, almost all of which had slender ovaries. These are presumably workers, except perhaps for a few which would later mate and become egg layers. The presence of worn workers (e.g., the last bee listed in nest 90, Table 8) supports the view of workers as a distinct caste rather than as a phase in the life cycle, as elaborated in the discussion of *E. variabilis*. Wing wear is much more evident in larger bees than in smaller; it is therefore not surprising to find it more useful in studies of the large species, *hamulata,* than in *variabilis*. Workers are relatively abundant in *E. hamulata*.

The size of workers in *E. hamulata* probably averages smaller than that of egg layers. Workers in four nests were smaller than the associated egg layers, in a fifth, the reverse was true. Most of the callows were also smaller than associated egg layers.

TABLE 8. Data on Mature Females in Nests of *Exoneura hamulata* Containing Two or More Such Females. (Degrees of wing wear are from unworn, —, to very much worn, ++++.)

Nest No.	Fertilized	Worn Wings	Enlarged Ovaries	Nest No.	Fertilized	Worn Wings	Enlarged Ovaries
88	+	—	—	405	—	—	—
	+	—	—		+	++++	+
89	—	—	—		—	—	—
	+	—	—		?	—	—
90	—	—	—		—	—	—
	+	++++	+	406	+	—	—
	—	—	—		+	—	+
	—	++	—	407	+	+	+
92	+	—	—		+	++	+
	+	—	—	408	—	—	—
	+	—	—		+	++++	+
245	+	—	+		—	—	—
	+	+++	+	409	—	+	—
253	+	—	+		—	+	+
	+	++++	+		+	+	+
	+	+	—	410	+	++	+
402	+	—	—		+	—	+
	+	—	+	416	—	—	—
	+	—	+		+	—	+
				465	?	--	—
					+	—	+

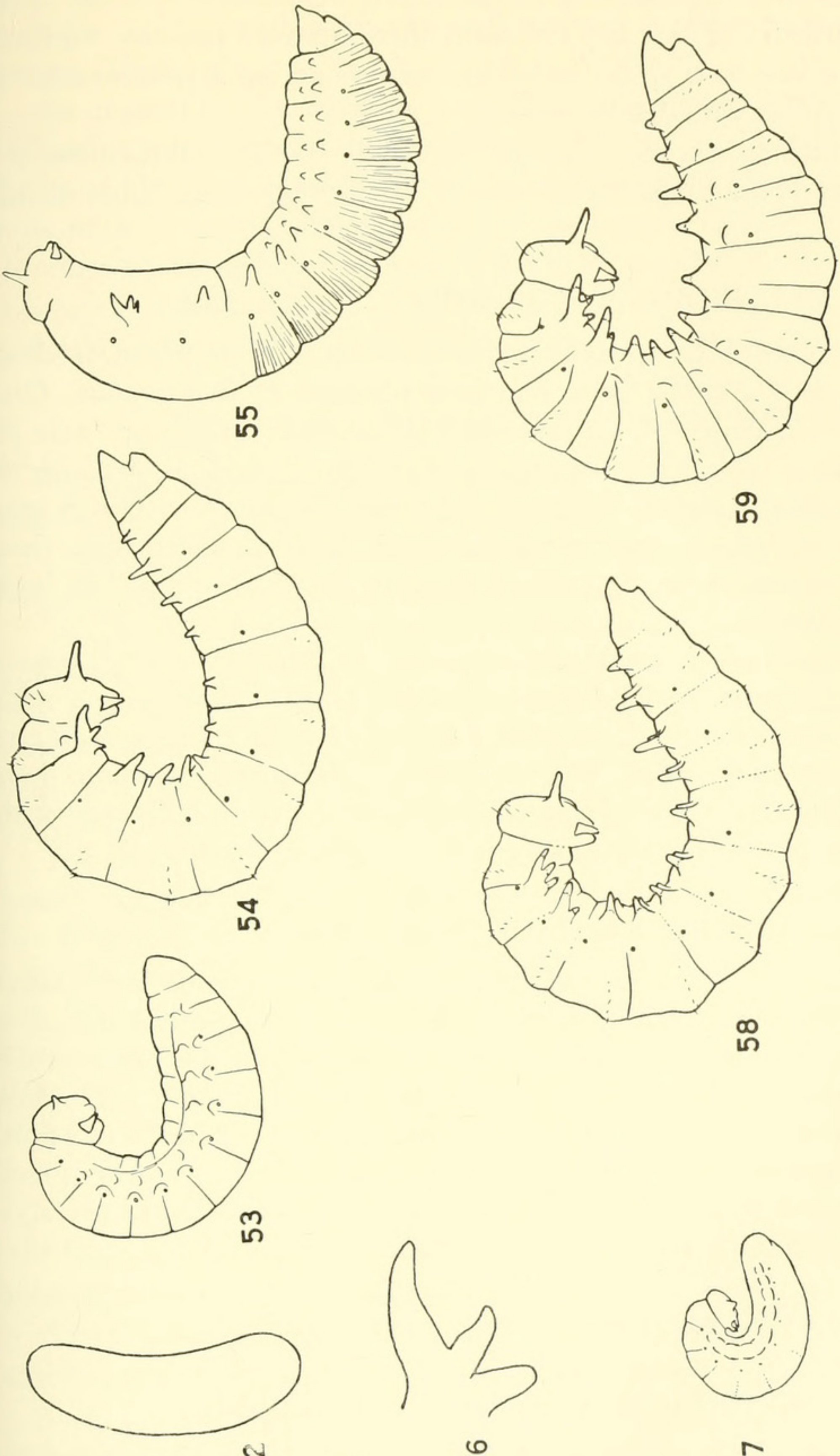
Sex Ratio: Of 93 pupae and callow adults, only 42 percent were males. This is in almost exact agreement with *variabilis.*

Ovarian Development: No differences in ovarian development were noted between *E. hamulata* and *E. variabilis.*

Immature Stages: The details of larval structure were given by Syed (1963). The figures presented in the present paper (Figures 52-56) were based on living specimens. The arrangement of the stages in the nests is similar to that of *E. variabilis,* perhaps less regular.

EXONEURA OBSCURIPES MICHENER

Six nests of this species were found, all in Lamington National Park near Binna Burra in the McPherson Range, Southeastern Queensland. They were in rotting, broken stems of vines in the rainforest, three of the six in a single broken stem. Nests containing immature stages ranged from 55 to 125 mm. in depth; diameters were 3 to 3.5 mm., with entrances narrowed to 2 mm. Eggs, small larvae, and large larvae were found both on December 8 and January 11. A new nest was being excavated by a lone, fertilized, unworn female on December 8.



Figs. 52-56. *Exoneura hamulata.* 52, egg (length 2.15 mm.); 53, small larva (rear part of body was still in egg shell before it was pulled out for sketching); 54, mature larva; 55, prepupa, hairs omitted; 56, mesothoracic arm of mature larva.

Figs. 57-59. *Exoneura obscuripes.* 57, small larva (rear portion of body was still in egg shell before it was pulled out for sketching); 58 and 59, larvae in last stadium, 59 older. In these drawings dotted lines show lengths of appendages when not exserted.

In Figures 54 and 59 the inner small row of abdominal tubercles does not show.

Nests with one, two, and three mature adults were found. The one with three contained an egg layer and two unfertilized, unworn probable workers. In each of the two nests with two adults, one was an egg layer, the other a fertilized, worn bee with slender ovaries.

Larval structure was described by Syed (1963). The illustrations included herein (Figures 57-59) are based on sketches made from living specimens.

EXONEURA ANGOPHORAE COCKERELL

Only two nests of this species were found, both at Tibrogargen, in dead flowering stems of *Xanthorrhoea,* like those occupied by *E. hamulata.* One was taken on November 24, the other on February 19. These nests were 62 and 94 mm. deep with diameters varying from 3.5 to 5 mm., the entrance of one (for other not recorded) narrowed to 1.5 mm. Each nest contained eggs and small larvae but no other immature stages. Each contained more than one adult, however, suggesting that a previous brood of young had been reared in the nest.

The nest taken on November 24 contained (1) a fertilized, worn female with enlarged ovaries, obviously the egg layer; (2) two unworn bees with slender ovaries, one fertilized, the other not, probably both acting as workers; and (3) three mature males. The nest taken on February 19 contained an unworn egg layer (fertilized, enlarged ovaries) and a worn individual with slender ovaries probably acting as a worker although fertilized.

EXONEURA HACKERI COCKERELL

Two nests of this species (which is apparently the same as *insularis* Cockerell) were found, both in stems in the rainforest margin in Lamington National Park near Binna Burra, southeastern Queensland. One entered the stem through a beetle hole in the side of the stem instead of through a broken end. Lengths of the nests were 63 and 210 mm., diameters were 2.5 to 3 mm.

One of the nests contained 12 eggs, one pupa, and two worn, fertilized females, neither with greatly enlarged ovaries. The other contained ten large larvae and six mature females, four fertilized, one unfertilized, and one doubtful. Two of the fertilized individuals were worn, the other adults were unworn. One worn and one unworn fertilized female had enlarged ovaries.

EXONEURA ATERRIMA COCKERELL

A single nest of this species was found at Tibrogargen on November 24, 1958 in a dead flowering stem of *Xanthorrhoea.* The entrance was through a hole (made by a beetle?) in the side of the stem rather than through a broken end. The burrow was only 19 mm. long, 3 mm. in diameter, narrowed to 1.5 mm. at the entrance. It contained four eggs and one very young larva with the rear half still in the egg shell but with a pollen mass on its under surface (Figure 51).

An unusual feature, differing from all other *Exoneura* studied by me but resembling certain species studied by Rayment (1948, 1951) and Erickson and Rayment (1951), was the attachment of the eggs, usually by their posterior ends, to the burrow wall near the end of the burrow (Figure 50). The eggs therefore do not lie loose and form a clump as in other species dealt with in this paper. The chorion of the one egg that had hatched kept this position and held the young larva in the position shown in Figure 51.

EXONEURA SUBBACULIFERA RAYMENT

Five nests were found in dead, cut stubs of *Rubus* stems at Cunningham's Gap on November 9. The nests ranged from 60-148 mm. in depth and from 2.5-3 mm. in diameter. Some of them were being deepened (as shown by pith fragments thrown out of the entrances) in spite of the presence of brood.

Like nests of *E. variabilis* found on the same date, those of *subbaculifera* contained eggs, one of them also with small and medium sized larvae. The nests contained two to four females each, all but one fertilized, mostly worn, and one or two in each nest with enlarged oocytes. The one unfertilized individual is of interest because it was well worn with slender ovaries; it was probably a worker or workerlike individual that had survived the winter.

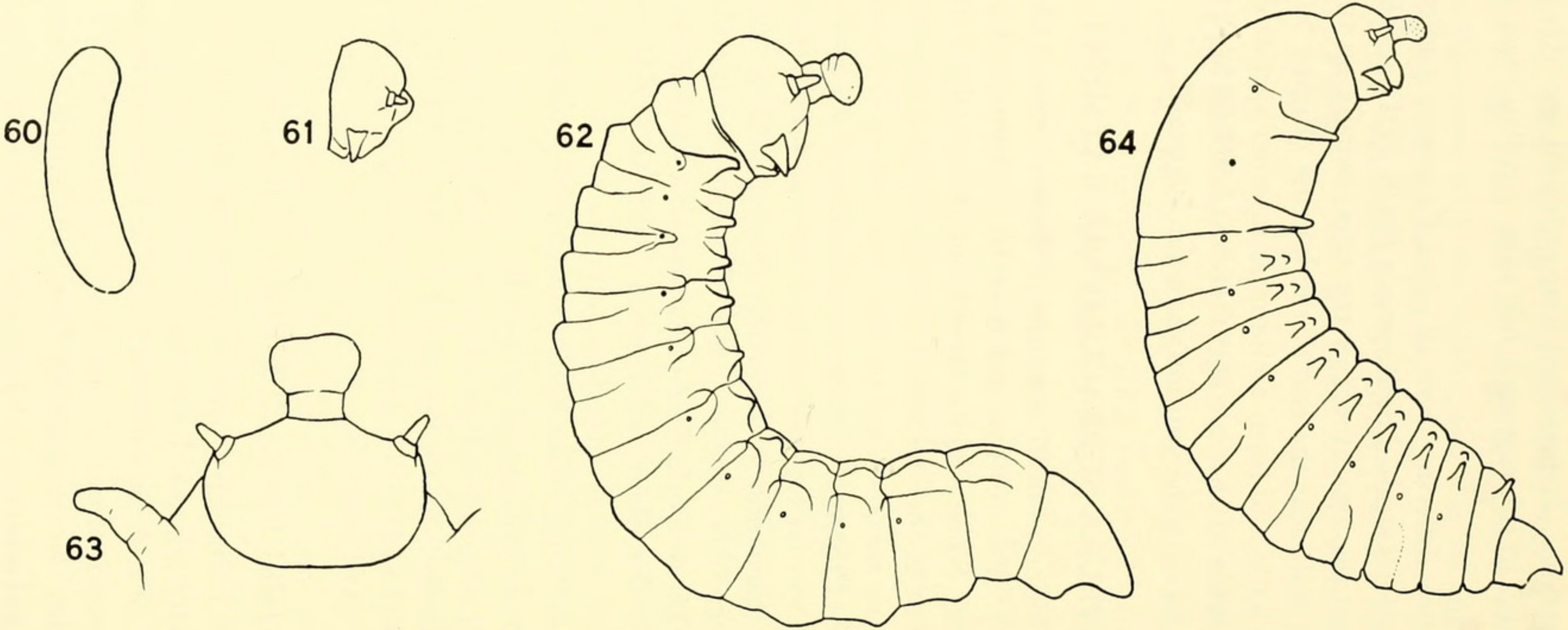
The larvae were described and figured by Syed (1963) and are noteworthy for the large frontal projection, also shown in Figures 62 and 63 based upon fresh material. Like the ventrolateral projections of this and other *Exoneura,* the frontal projection can be exserted; all are shown in the exserted position in the figures but when withdrawn the apical part of the frontal projection is reduced in size and less turgid and the abdominal appendages are all mere convexities, like those shown on the eighth and ninth abdominal segments in Figure 62.

EXONEURA BACULIFERA COCKERELL

Two nests were found in broken stems at the edge of the rainforest in Lamington National Park near Binna Burra.

The nests were 30 and 260 mm. deep, 2.75 to 4 mm. in diameter, the constriction at the entrance of one of them had a diameter of 1.75 mm.

The shallow nest was apparently new, containing a single fertilized female with enlarged ovaries and four eggs. The deep nest contained six mature females, five callow females, 13 males, six pupae, and three eggs. Two of the mature females were fertilized, worn, with enlarged ovaries. The other four were unfertilized, unworn (except for one nick in one wing), three



FIGS. 60-63. *Exoneura subbaculifera.* 60, egg (length 1.78 mm.); 61, head of third stage (?) larva (head width 0.60 mm.); 62, mature larva (head width 0.80 mm.); 63, dorsal view of head and front of thorax of same.

FIG. 64. Prepupa of *Exoneura baculifera* (maximum diameter 1.70 mm.).

with slender ovaries, the fourth, surprisingly, with enlarged ovaries.

The prepupa of this species is shown in Figure 64. The frontal projection is similar to that of *E. subbaculifera.*

SUMMARY

This paper consists mainly of an account of the life cycle and social organization of *Exoneura variabilis,* with less complete data on several other species of *Exoneura* and on the socially parasitic bee, *Inquilina excavata.* The bulk of the information was derived from statistical examinations of nest populations, spermathecal content, wing wear, number and stages of the immature forms, and the like, rather than from direct observation of behavior in the nests.

E. variabilis nests in simple burrows, not divided into cells, in dry pithy stems in rainforest boarder regions. It overwinters in such burrows, primarily as fertilized adult females of varying ages (or amounts of wing wear). One to three females inhabit a single nest. A few larvae apparently also overwinter.

In spring the bees disperse so that most nests contain one female. Egg laying occurs throughout spring and summer and adults of both sexes are produced. New nests are established throughout the active season by lone females. However, apparently the majority of the young adult females do not leave the parental nest but remain there. Some replace the original egg laying female who dies soon after laying two, sometimes incompletely separated, batches of eggs. Since the larvae are fed progressively, those hatching from the second batch are usually reared by one or more of their adult sisters from the first batch of eggs. Such an individual may coexist for a time with the worn mother, but in many nests larvae are cared for in the absence of any individual that could be their mother. Commonly such sisters are workerlike, having slender ovaries and being unmated, but others mate and replace their mothers as egg layers.

At all seasons over half the nests opened contained only one mature female (recently emerged adult females are not counted). However, especially in summer, some nests (e.g., 48 out of 102 in December, the first summer month) contained more than one mature female, usually two but rarely as many as five or six. Usually only one but sometimes more are egg layers; the rest have slender ovaries and are often unfertilized workers; they were seen to be active in collecting pollen for nests containing egg layers which did not leave during the period of observation. (Rarely unfertilized individuals have enlarged ovaries.) Workers average smaller in size than egg layers and are probably short lived compared to egg layers.

A worker can be either daughter or (usually) sister of an egg layer in her nest. Female bees care for their younger sisters, their own progeny, and

progeny of their sisters. Both workers and egg layers care for whatever young are in the nest, although egg layers in nests that also contain workers do little or no foraging.

About 40 percent of the young produced are males. Adult males do not remain long in the nests, and are probably short lived.

Ovarian development was studied and illustrated. In contrast to halictids, conspicuous white masses are formed, presumably indicating both resorption of eggs and prior laying.

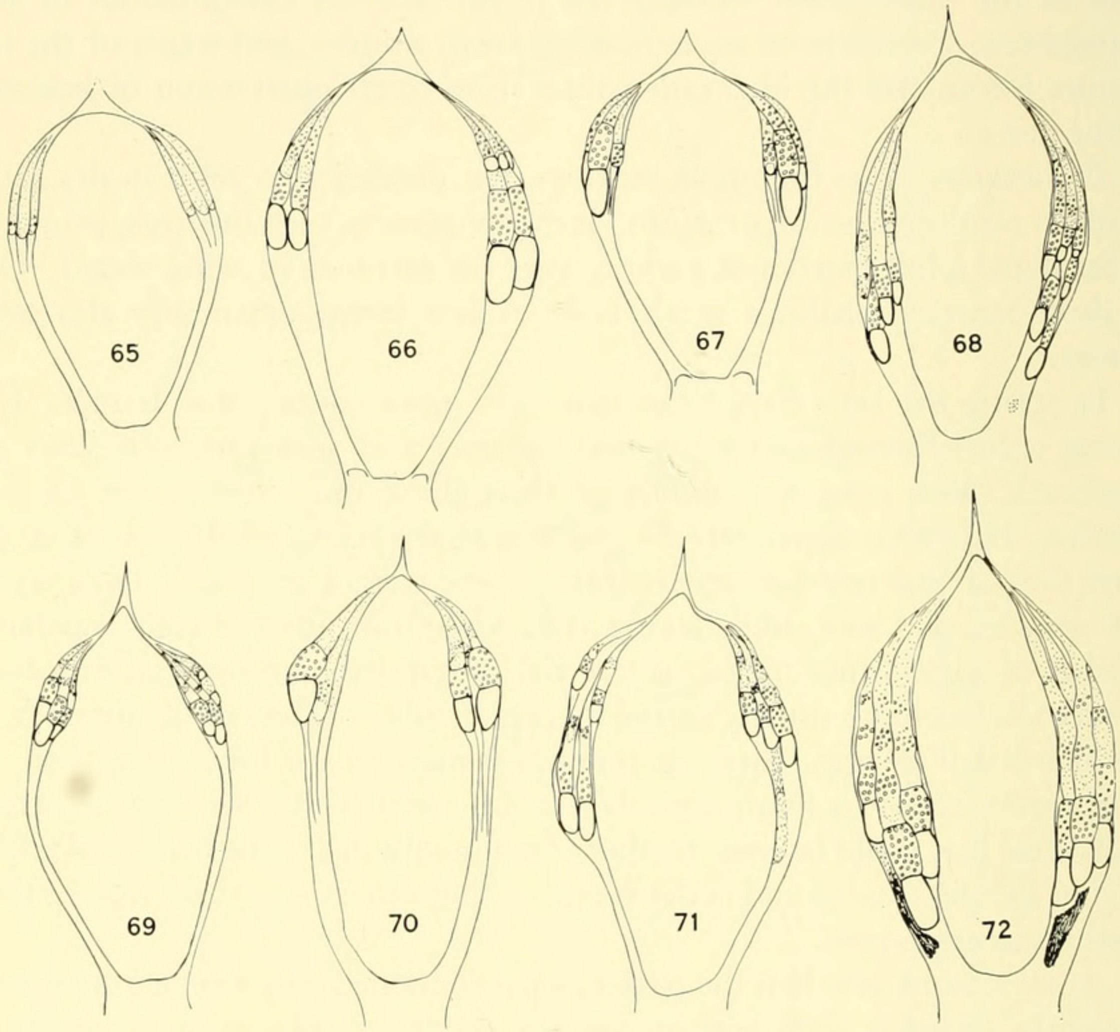
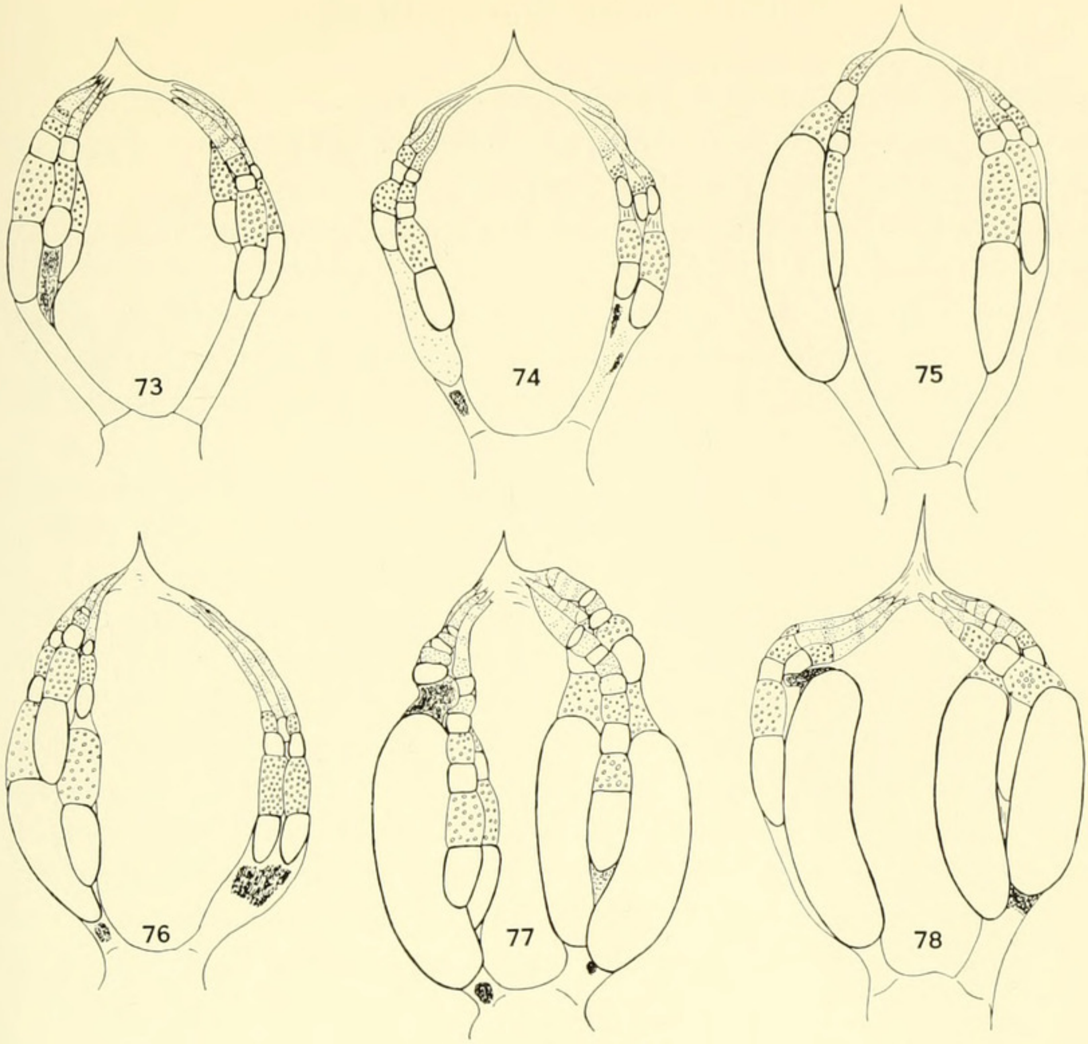
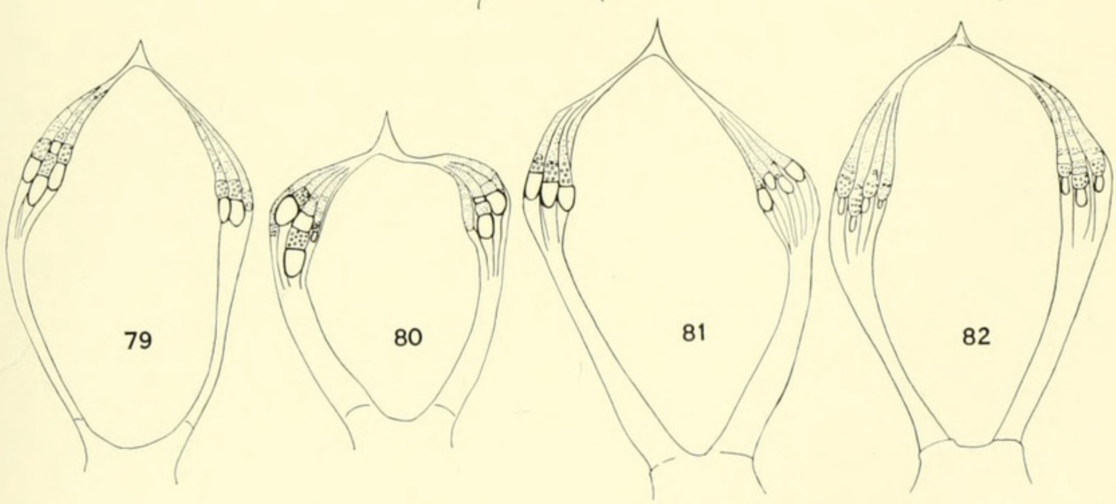


FIG. 65. Ovaries of soft, pale, young callow. Note that oocytes at the lower ends of the ovarioles are scarcely enlarged.

FIGS. 66 AND 67. Ovaries of callows. Note enlarged oocytes and well formed groups of nurse cells; in the right ovary of figure 66 each of the ovarioles has a second enlarging oocyte. There are no white bodies indicating oosorption or remains of nurse cells.

FIGS. 68-72. Ovaries of overwintering bees taken from nests and fixed on March 22, 1959. Figures 68 and 69 were from unfertilized bees with unworn wings, 70 and 71 from fertilized bees with unworn wings, and 72 from a fertilized bee with worn wing margins. Figures 68, 71, and 72 show white areas (dark in figures) in one or both of the lateral oviducts indicating oosorption. Figures 69 and 70 seem to show an anterior retreat of the ovarioles as compared to the callows. This is common in overwintering bees. There is commonly only one distinct enlarged oocyte per ovariole but there may be none (some ovarioles, figs. 67 and 68) or as many as three (right side, fig. 68). The bee that had worn wings and was therefore presumably older than the others had larger ovaries, but none of the oocytes was very large (Fig. 72). Apparently at this season oocytes of only moderate size are resorbed.





Figs. 73-78. Ovaries of some adults taken on December 26, 1959. Figures 73 (fertilized) and 74 (unfertilized) are based on bees with worn wings. They might have been either workers, or egg layers for some reason not at the moment laying eggs, and therefore with rather slender ovaries. The left hand ovary in figure 74 evidently produced a large oocyte, now being resorbed (lightly stippled). White areas (dark in figures) below the ovarioles indicate oosorption or remains of nurse cells. Figures 75 to 78 represent bees apparently in or approaching egg laying condition. Figure 75 shows no white areas below the ovarioles; this bee probably never laid an egg. Figures 77 and 78 (left side of each) show the break down of groups of nurse cells above fully formed eggs. Similar white masses (dark in figures) below the eggs probably are of this origin and indicate prior egg laying.

Figs. 79-82. Ovaries of unfertilized workers taken on December 26, 1959. Often such ovaries are flattened against the wall of the crop so that all four ovarioles are in a single plane and visible from one view, as shown on one or both sides of figures 80 to 82. The lack of white areas suggests that these bees never laid eggs. Narrow apical oocytes such as are shown in figure 82 are very rare.

Immature stages are kept more or less in age groups in the nest. Food masses are placed on the ventral surfaces of the larvae. Occasionally two small larvae may curl around a single food mass.

Life cycles and social organization of other *Exoneura* species seem similar to those of *E. variabilis.* In *E. hamulata* the colonies average larger and the active season longer. In *E. aterrima* the eggs, instead of being placed together in a batch at the bottom of the nest, are stuck by their posterior ends to the walls of the nest and the young larvae retain this position and are fed there.

Inquilina excavata is a social parasite in the nests of *Exoneura variabilis* and is closely related to *Exoneura. Inquilina* cannot collect pollen. Its females invade nests of *E. variabilis* and take up residence there in association with the *Exoneura.* Apparently the *Inquilina* prevent the laying or survival of *Exoneura* eggs in some way, for production seems to go wholly to *Inquilina,* but adult *Exoneura* (workers) must be present to bring food for the parasite. The only two *Inquilina* found with enlarged ovaries, ready to lay eggs, were in *Exoneura* nests containing a female *Exoneura* having similar ovaries. Perhaps the *Inquilina* synchronize their laying with that of the *Exoneura* in order to fit into the social system of the latter. Ultimately the *Exoneura* die off, leaving the nest to the by now maturing *Inquilina,* or some *Exoneura* survive and probably may reestablish the *Exoneura* colony.

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