zu unterscheiden. – Die Gattung *Hebridochernes* zeigt einige Parallelen zum Cheliferiden-Genus *Ellingsenius*, wie den Besitz von 3 Galealborsten und die mit Seitenrandleisten versehenen Abdominaltergite des Männchens; sie gehört jedoch eindeutig zu den Chernetiden, da die Palpenfinger mit Nebenzähnen versehen sind und nur der bewegliche Finger einen Giftapparat besitzt.

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THE BIONOMICS OF EXONEURELLA, A SOLITARY RELATIVE OF EXONEURA

(Hymenoptera: Apoidea: Ceratinini)[1]

By Charles D. Michener[2]

Abstract: Numerous nests of *Exoneurella lawsoni* of eastern Australia were studied throughout the active season. Larvae are fed progressively and have curious morphological modifications presumably associated with this method of feeding and with the absence of separate cells. Winter is passed by adults of both sexes in nests in pithy weed stems. Mating occurs in the spring and each ♀ starts her own nest. Females maturing during the summer may start their own nests or, when the overwintered mother dies, one of the daughters may remain in the nest, care for her immature siblings, as well as lay her own eggs. This species is much more nearly solitary than are the species of the related genus *Exoneura*.

It is well known (see recent review by Sakagami 1960) that numerous bees of the genera *Allodape*, *Exoneura*, and their relatives live in small colonies in hollow stems and rear their larvae by progressive feeding. The present paper concerns an Australian species, *Exoneurella lawsoni* (Rayment), which is noteworthy because it is essentially solitary, each female usually rearing her own young. Like the other species of the group, and unlike all other bees, the larvae are not reared in cells but live together in a hollow stem. The

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basically solitary habit of *E. lawsoni* may be primitive, as is perhaps suggested by some of the unique features of the species which have caused it to be placed in a monotypic genus (Michener 1963a). The combination of solitary nesting and progressive feeding of larvae is not known elsewhere among bees and if progressive feeding arises only among social groups, then the solitary habit must be a reversion rather than a primitive feature. The seasonal fluctuation in sex ratio, described below, is also a feature to be expected in social forms and suggests that the lack of a worker caste in *E. lawsoni* may be a derived feature.

Habitat

Observations were made in southern Queensland and in the New England area of New South Wales. All localities were in areas of rather dry *Eucalyptus* savanna, not near the coast nor in or near rain forest areas. Collecting localities may be divided into two groups, as follows:

Lowland Localities: 6, 8, and 19 km S of Warwick, Queensland; Moore, Queensland; and Heifer Creek Road, 22 km SW of Gatton, Queensland.

Upland Localities: 8 km N of Deepwater, New South Wales; 13 km W of Armidale, New South Wales; 18 km S of Uralla, New South Wales; 24 km S of Tenterfield, New South Wales; and Stanthorpe, Queensland.

The lowland localities are at altitudes of 450 m or less and hence activity begins earlier than in upland localities on the Great Dividing Range and the New England plateau at altitudes of 840–1050 m.

Most of the specimens were found in nests. A very few were taken on flowers of *Wahlenbergia* and pollen of that plant was commonly found in guts of the bees or in the nests, but pollen of other plants was also found in the bees of their nests.

Nests

A total of 225 nests of *Exoneurella lawsoni* was examined and the contents studied during 1958–59 and 1964. Three of these nests were in unidentified dead pithy weed stems but 222 were in cut or broken, standing dead stems of *Verbena bonarensis*. This is a common introduced weed and roadside stands of it were the source of nearly all nests of *Exoneurella* found. The bee is absent in similar stands of *V. bonarensis* near the coast (e. g., Brisbane). It seems likely that the bee is far more common than before the establishment of this pithy stemmed weed in Australia. *Exoneurella* enters stems only where they are cut or broken and makes its own burrow into the pith. When living stems have been cut the upper portions of the stubs often die while the bases of the plants remain green. Burrows made into the dead stubs of such plants may extend a few millimeters into slightly greenish tissue but moist or living material limits the depth of the burrows.

The nests are simple burrows in dry pith, 1.1 to 1.6 (usually about 1.5) mm in diameter at the entrances. Many are of about the same diameter below the entrances, but others are slightly larger. Forty four measurements of burrow diameters below the entrances averaged 1.7 mm (extremes of 1.5 and 2.0).

The mean depth of 109 nests containing eggs or young was 80.4 cm (extremes 230 and 20). Nests made in dry stalks of plants green at the bases extended down only to green tissue, as indicated above. The mean depth of 24 such nests containing eggs or young was

only 33.6 cm (extremes 51 and 20). There is no evidence that production of young was less successful in such nests than in deeper nests. The mean depth of 85 nests made in wholly dead stalks was 93.6 cm (extremes 230 and 27).

Some deepening of the burrows may occur after the first eggs are laid. This is suggested by the following observation: 35 nests from dry stems taken near Warwick, in November and December, and containing large larvae or pupae, had a mean depth of 88.1 ± 7.05 cm; 11 nests, also in dry stems, from the same locality and dates and containing eggs or very small larvae but no older larvae or pupae had a mean depth of 69.0 ± 3.43 cm. This difference in means is highly significant ($P < .001$).

A seasonal change in burrow depth was also noted. The data are based on nests from dry stems taken near Warwick, as follows: 19 nests taken 8. XI had a mean depth of 92.4 ± 11.84 cm; 26 nests taken 27. XII had a mean depth of 77.8 ± 6.32 cm; 15 nests taken 25. II had a mean depth 62.5 ± 7.41 cm. The differences in means are highly significant ($P < .01$). The decreasing average depth as summer advances may result from the starting of numerous new nests as a result of summer reproductivity.

Seasonal cycle

Group 1. Exoneurella lawsoni was first found by me in spring, on 1. X. 1958, near Warwick, a lowland locality. Only four nests were discovered; in them were 12 adult males and 23 adult females. There were also two half grown larvae (alive but with no evidence of recent feeding, no pollen in gut) in one of the nests. The cool weather, lack of eggs in the nests, and lack of flowers in the area suggested that the bees were in hibernating condition and that the two larvae had survived the winter with the adults.

Examination of the females showed slender ovaries, .13 to .25 mm in width, either with no large oocytes or with the largest not over .48 mm long. The spermathecae were empty in the six females in which these organs were examined. All the females had unworn wings. From these data (corroborated by autumn data, see Group 9), it seems that winter is passed as young adult males and females in groups, probably family groups (with a few larvae), in the nests made during the preceding season, the females being mostly unfertilized until spring.

Group 2. From the standpoint of seasonal progress, the next material consisted of 85 nests from all of the upland localities, taken 1–8. XI. 1958. Eight of these nests were occupied by one to four males each. The remaining 77 all contained a single live female each. One also contained two dead females and ten (13%) contained one or two males in addition to the female. A total of 77 females and 21 males were found in the material.

Obviously the females in overwintering nests such as those described under Group 1 had dispersed. Some of them remained in the overwintering nests, as suggested by the presence of large larvae and dead adults in some nests, while others started new nests. However, in no case was more than one live female in a single nest. Some of the females were still excavating their nests, as shown by the pith being pushed from the entrances. Others had nests in which they were laying eggs, or beginning to rear larvae.

Of the 85 nests, 39 already contained one or more eggs or larvae, as shown in Table 1. Six contained more or less large larvae, showing again the survival through the winter (which is quite cold, regularly dropping below freezing, at these upland localities) of larvae

Table 1. Numbers of nests of group 2 containing various numbers of young; Upland localities 1-8.XI.1958. (Totals are shown in the bottom row, all nests contained a single adult ♀.)

Eggs	Small larvae	Medium larvae	Large larvae	Prepupae	Number of nests
1					6
1	1				1
2					8
3					5
3	1				1
44					3
5					1
6					1
5	2				1
2	5				1
6	1				1
7					1
6	2				2
9					1
			1		2
	1		1		1
		1	2		1
3		3			1
3	2		3	2	1
111	17	4	8	2	39

of various sizes in a small percentage of nests. The table shows that eggs were being laid in some of the nests with overwintered larvae; from the nature of the Group 9 population it seems probable that the egg layers were not the mothers of the older larvae.

Examinations of the spermathecae of 16 females showed all to have been fertilized. Comparison with Group 1 indicates that overwintering females (or at least many of them) mate in early spring. As would be expected, ovarian development was much greater than in the Group 1 females. Ovarian widths ranged from .20 to .45 mm and the longest oocyte in each female ranged from .63 to .98 mm, the larger ones being eggs apparently ready to lay. Such measurements are equivalent to those of egg laying individuals at any season; the maximum ovarian width measured at any time was .55 mm and the maximum length of any egg ready to be laid was 1.0 mm. One fourth of the females of Group 2 had one or two nicks in their wing margins.

Group 3. This group consisted of only four nests found at Moore on 25. X. 1958. Although the date was earlier than for Group 2, the seasonal cycle was farther advanced because of the warm conditions at low altitudes. Each nest contained a single adult female. In two of the nests there were only eggs and small larvae; in the third there were five eggs, one small larva, one half grown larva; in the fourth were six eggs, three larvae, two prepupae, one brown eyed pupa, and one black eyed pupa. Dissections of the females showed them to be similar to those of Group 2.

Group 4. This group consisted of 25 nests taken on 8. XI near Warwick. Each nest

Table 2. Numbers of young in nests of group 4 from near Warwick (lowland), 8. XI. 1958. (Each horizontal row represents a nest; totals are shown in bottom row. Each nest contained one adult ♀.)

Eggs	Small larvae	Medium larvae	Large larvae	Prepupae	Total young
2					2
1	1				2
			4		4
4					4
4					4
4					4
4	1				5
5					5
3	1	2			6
	2	2	2		6
6					6
3	1	2			6
1	1		5		7
1	2	2	3		8
7	1	1	1		10
5	2	3			10
10					10
4	3	2	2		11
4	1	1	3	2	11
3	3		5	1	12
3	2	3	3	1	12
6	1	2	4		13
5	2		4	2	13
6	3	2	3	1	15
8	2	2	4	1	17
99	28	25	43	8	203

contained a single adult female. Four contained adult males (one contained two of them), so that there were five living males to the 25 females. Two dead males suggested that the overwintered males were dying off. Immature stages seemed similar to those of Group 3 although there were no pupae. Table 2 shows the distribution of immature stages. A few nests seemed to have been started quite recently and contained only eggs but most contained large larvae as well as younger stages. Obviously eggs were still being laid in virtually all nests, however.

Dissections of females gave results similar to those for Group 2 except that two females did not have any eggs nearly ready to lay, their longest oocytes being .35 and .45 mm. One half of the females had one to three nicks in their forewing margins, indicating continuing wear as compared to Group 2.

One female was a striking exception to the above statements. Although she had well developed ovaries and occupied a nest with young, she had no sperm cells in her spermatheca. Presumably she had never mated. No evidence was obtained that the sperm is ever depleated; I believe that once mated, a female carries sperm cells for life. This

individual also had well worn mandibles (not seen in any others) and four and five nicks in the margins of her forewings. Evidently she had worked more than the mated individuals. This is interesting in relation to comparable observations made for a halictid bee, *Augochloropsis sparsilis* (Vachal) (Michener & Lange 1959) but is not easily understood for a solitary bee like *Exoneurella lawsoni*.

Group 5. At Stanthorpe (highlands) three nests were taken on 29. XII. 1958. The nests were similar to those described as Group 4 but two of the nests contained a total of nine pupae. Eggs were still being laid and young of all stages were present. The three nests contained 12, 20, and 22 eggs and young. The single female in each nest was fertilized, with well developed ovaries, like those of Group 2. All three had nicks in the wing margins. Clearly they were still the overwintered females.

Group 6. As shown by Group 5, the nest founders were soon to be joined by their first adult offspring by late December in highland localities. In lowland localities young adults were already being produced as shown by the 35 nests of Group 6 taken near Warwick on 27. XII. 1958. Seven of these nests were inhabited by single females, with 0 to 11 eggs and no other young; obviously these females were establishing new nests just like the bees described in Group 2. Four burrows contained only males, as did some Group 2 nests. Either these males made their own burrows or crawled into holes made and abandoned by females. Males were found in some of the new nests as well as in old nests, indicating that they may enter any nest hole and do not necessarily remain in the burrows where they were born.

The total number of adults taken in all the nests was 49 females and 18 males. Of the 49 females, only seven had nicks in the wings and might well have been surviving overwintered females. Three of these seven were in new nests and probably, therefore were not overwintered bees; the four asterisks in Table 3 represent one female each that might be a survivor of the preceding, overwintered generation although the existence of equally worn individuals believed to be of the summer generation suggests that there may be no survivors at this season in the lowlands. All the other 42 females were unworn. Of these, 26 were obviously young, being more or less callow (brown rather than black in color), unworn, and unfertilized, with slender ovaries while 16 were fully black, mostly fertilized, and often with well developed ovaries. All intergradations between these two classes existed in the material of Group 6. However, examination of these features shows clearly that for most nests there was one female with well developed ovaries and sperm cells in the spermatheca. These mature females, in at least most nests, seemed to be replacements for the overwintered females.

There is no evidence that any of the females were acting as workers, as they do in the related genera *Exoneura* and *Allodapula* (Michener 1963b, 1964). This matter will be discussed further under Group 7. The only possible exception appears in the nest shown in Table 3 with two asterisks in the right hand column. Each asterisk represents a female with well developed ovaries and nicks in the wing margin. That there should be two such females in one nest is unusual; they are equivalent to the females in the nests marked "b" and "c" in Table 4. One of them was unfertilized which suggests that she may have been more or less like a worker. The data for the next groups of nests show that the nests continue to be cared for, at least primarily, by a single female each and that associations of adults jointly caring for the young probably do not regularly arise, as they do

Table 3. Numbers of young and of adult ♀♀ in nests of group 6 from near Warwick (lowland), 27. XII. 1958. (Each horizontal row represents a nest; totals are shown in the bottom row. Nests without immature stages or with only eggs were omitted. Asterisks are explained in the text.)

Eggs	Small larvae	Medium larvae	Large larvae	Prepupae	Pupae	Total young	Adults
2					1	3	3**
			1	1	1	3	2
1		1	1			3	1
1	1	1				3	1
		1	2		1	4	1
1		1	1		2	5	1
3				2	1	6	3
4		1	2	1		8	1
7			1		1	9	1
4	4	1	1	1	1	12	2
5	2	1	2		2	12	1
6	2	2	2		1	13	1
4	3	3	1	1	1	13	1
5	3	2	3	1		14	2
8		1	3	1	1	14	2?
6	3	1	3	1		14	3
8	2	1	2	1	1	15	1
7	1	3	3		1	15	2
8	1		6	1		16	2
9		1	5	1	1	17	4*
11	1	2	3			17	3*
9			9	1	3	22	2
11	7	6	2	1	1	28	2
120	30	29	53	14	20	266	42

in *Exoneura* (see Michener 1964).

Table 3 lists the immature stages in each nest (except those containing only eggs). It is obvious that, as in the next group, a wide variety of stages was present in each nest. The older stages such as prepupae and pupae must have been progeny of the overwintered females while most or all of the eggs and some of the smaller larvae must have been progeny of the replacement owner of each nest. Presumably when an overwintered owner dies, her place is taken by one of her progeny and the progressive feeding of the young is continued. The several nests shown in Table 3 with eggs, large larvae, prepupae, and pupae, but without small larvae, support the idea of a change in egg layers resulting in a break in continuity of laying. Similar gaps in productivity can be seen in some nests in Table 4. In the genus *Exoneura* such gaps often result from cessation of egg-laying by the mother, followed by its resumption so that a second batch of eggs is produced (Michener 1964). Egg layers in nests with such gaps in *Exoneurella* usually are unworn, indicating that they are relatively young and not old mothers laying a second batch of eggs.

Group 7 consists of 35 nests from 19 km S of Warwick, 23–25. I. 1964, taken by Mr. G. Monteith who kindly fixed the contents of each nest separately and sent them to me.

Eleven nests contained lone females, mostly not at all worn and with the ovaries enlarged, but with no immature stages. Three nests each contained a similar female and from three to six eggs. One nest contained only a single male. Data for the remaining 20 nests are given in Table 4. Obviously many bees were establishing nests, as shown by the eleven females alone in burrows but with large ovaries, and by those with only eggs, as well as by those with only eggs and young larvae (see the upper part of Table 4).

The total number of adults taken in all the nests was 64 females and seven males. There is no reason to believe that any of the adults had overwintered. Eleven of the females had nicks in their wings. Of these, five were in nests containing only a single adult. One of these had no immature stages, one only eggs and young larvae, the other three had older immature stages. The other six females with worn wings were in nests with other females in them.

Among the nine nests containing more than one female, the female populations of four consisted of one individual obviously the oldest, with enlarged ovaries, little fat in the body cavity, with sperm cells in the spermathecae, and often with nicks in the wings; and varying numbers of younger females, often partially callow, but even if fully pigmented, recognized by abundant fat in the abdominal cavity, slender to enlarged ovaries, spermatheca without or sometimes with sperm cells, and no wing nicks. These obviously younger adults presumably would soon leave to establish new nests, as suggested by the numerous new nests

Table 4. Number of young and of adult ♀♀ in nests of group 7 from near Warwick (lowland), 23-25. I. 1964. (Each horizontal row represents a nest; totals are shown in the bottom row. Nests without immature stages or with only eggs were omitted. Letters are explained in the text.)

Eggs	Small larvae	Medium larvae	Large larvae	Prepupae	Pupae	Total young	Adults
5	1					6	1
6	1					7	1
6	2					8	1
3	3					6	1
1	1	4				6	1
2			2			4	1
	1	1	1			3	1
			1		2	3	1
			1		2	3	2b
3		2	3	2	3	13	1
6	3	3	2			14	1
6	2	2	4	1	3	18	1
2	5	2	7		7	23	5a
2	3	2	4		5	16	5
1		8	13		4	26	3d
1			5	4	4	14	7
4	4	4	3	2		17	5
7	4				3	14	3a
			7	3	11	21	6
					6	6	3c
55	30	28	53	12	50	228	50

being established. Nearly all of the young adult females, however, not only in these nests but also in those containing two older females (discussed below), as well as those mentioned in the discussion of Group 6, had pollen in the gut, suggesting trips to flowers. The fact that some were fertilized also suggests trips away from the nest. The question therefore arises as to the extent of workerlike activity in such nests. Do such females help to feed the larvae and are any of them inhibited reproductively?

The remaining nests in Group 7 might be expected to shed some light on these questions. Nests marked "a" (right hand column, Table 4) contained three and five adults, all young with rather slender ovaries, the best developed having the largest oocyte .70 mm long. None of them could be mothers of the eggs and small larvae; the mothers must have died or escaped capture. Nest "b" contained two old fertilized adults, both with nicks in the wings and somewhat to fully enlarged ovaries. In the absence of most immature stages, there is no evidence that either one was workerlike. Nest "c" is similar except that one teneral adult female was also present and neither of the older adults had worn wings. Probably in "b" and "c", one of the older adults would soon have started laying and perhaps the other would have left to establish a new nest. Only in nest "d" were there two old females and young of various ages. (There was also one young female with slender ovaries and much fat in the abdomen.) The old females both were fertilized, with wing nicks and with enlarged ovaries; both may well have been laying eggs. There is no evidence for a worker caste in these data.

However, workers of *Exoneura* are commonly unworn and relatively young bees (Michener 1964). Could some of the young bees, some of them callows, in the nests in Groups 6 and 7 be functioning as workers? The fact that a young adult female appears able to take over care of immature stages (brothers and sisters of the young adult, no doubt) when the mother dies, as is indicated by the presence of eggs together with old larvae (still being fed) and pupae in nests whose only adult is a young female (see discussion of Group 6) suggests that young adults might well also take on feeding of their younger brothers and sisters while the mother is still present. This would be workerlike activity. The large numbers of new nests of *Exoneurella* during the summer, the obvious immaturity of most of the young adult females in nests with other adults, and the lack of significant size differences between older and younger (possibly workerlike) females (such size differences exist in *Exoneura*) argue against regular workerlike activity in *Exoneurella* and suggest that young females merely remain in the parental nest for a time before dispersing.

Group 8 consists of 15 nests from near Warwick and from Heifer Creek Road (lowland localities), 25 and 26. II. 1959. One nest contained only a single male. Data for the remaining 14 are given in Table 5. The total number of adults taken in all the nests was 19 females and 16 males. Of the females, four marked by asterisks in Table 5, were fertilized, had large ovaries, and nicks in the wing margins. Eggs were present in the nests of these four. Only one other nest contained eggs; one of the females in it had large ovaries and nicked wing margins, but was unfertilized. All the other females had slender ovaries, unworn wings, and those whose spermathecae were examined had not mated; most of them were obviously still callows. The older individuals were presumably members of the summer population, already being largely replaced by the overwintering generation. Reproduction was diminishing, as shown by the small number of eggs compared to other stages (compare with Tables 3 & 4.)

Table 5. Number of young and of adult ♀♀ in nests of group 8 from lowland localities, 25 and 26. II. 1959. (Each horizontal row represents a nest; totals are shown in the bottom row. Asterisks are explained in the text.)

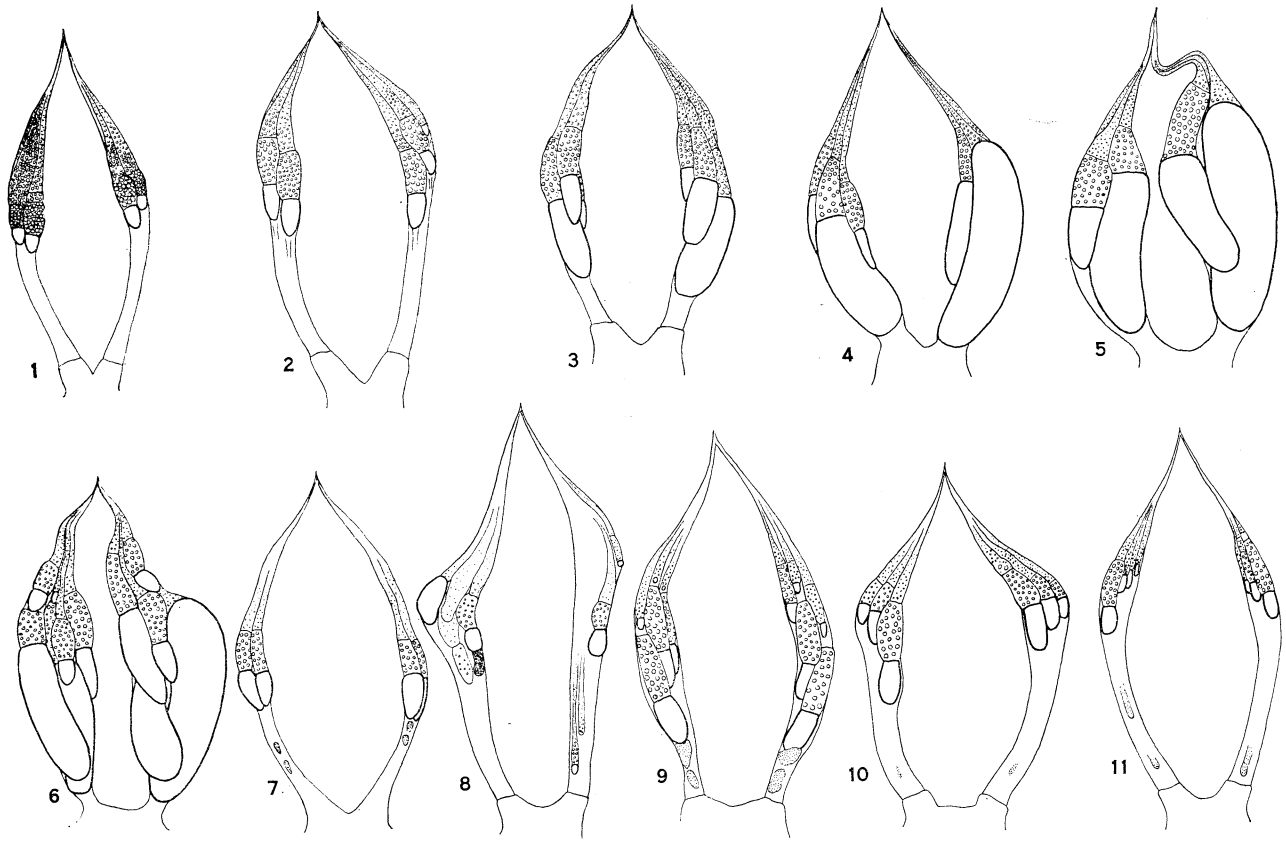
Eggs	Small larvae	Medium larvae	Large larvae	Prepupae	Pupae	Total young	Adults ♀♂
			2			2	
			2			2	
	1	1	1			3	4
1			2			3	
				1	3	4	1
			3		2	5	1*
	2	1	3			6	
			3		5	8	1
6	2	1				9	1*
				1	9	10	1
	1		4	1	4	10	1
			1		10	11	5
3	2	2	3	1	3	14	1*
3	4	2	2		4	15	1*
2	3	1	3	1	5	15	2
15	15	8	29	5	45	117	19

Group 9. This group, taken in the fall (16. III. 1959) to get information on conditions at the approach of winter, consisted of 19 nests from near Warwick. The adults in these nests were almost all without nicks in the wings and unfertilized with slender ovaries (widths .10 to .25 mm; longest oocyte .13 to .33 mm.) comparable to those of early spring bees (see Group 1). One female was fertilized with two and five nicks in the margins of the forewings. She was in a nest with one pupa and one callow adult. Although slender (widths .13 and .15 mm, longest oocyte .15 mm), the ovaries showed white areas posteriorly indicating resorbtion or possibly laying of eggs (fig. 9). Presumably she was an old female that had laid eggs, but unlike most, now seemed prepared for overwintering. The only other fertilized female was just like most in her ovarian condition and had unnicked wings. Two unfertilized females had one or two nicks in the forewing margins. This is not surprising since all of them had pollen in the gut, showing that they had been flying about. Except as indicated above, no adults showed any evidence of work, of egg laying, or of mating. There were 34 females, 36 males.

In eight of the 19 nests there still remained immature stages, totals of seven large larvae, four prepupae, and 30 pupae. One nest contained 12 pupae; otherwise no nest contained more than six preimaginal individuals.

REPRODUCTION AND IMMATURE STAGES

Ovaries and eggs: Examination of the ovaries (figs. 4–6) shows that only one egg is ready to be laid at a time. There is only one large oocyte or developing egg in each ovariole at any one time or, in the midst of active egg laying, two growing eggs may be seen in certain ovarioles (fig. 6). This is intermediate between *Allodapula* in which only one growing egg is seen per ovariole (Michener 1962) and *Exoneura* in which many may



Figs. 1–11. 1–6. Ovaries of individuals of *Exoneurella lawsoni* (Rayment) taken from nests 8 km S of Warwick, Queensland, 27. XII. 1958 and fixed in Kahle's (Dietrich's) solution before dissection. 1, callow (unfertilized) with no pollen in gut (Some young adults, otherwise similar, were black and hence not recognizable as callows); 2 & 3, callow (unfertilized) with crop and hind gut full of pollen; 4 & 5, unfertilized ♀♀, not callows (Some young fertilized ♀♀ have ovaries that look like fig. 5); 6, fertilized ♀. 7–8. Same locality, 25.II.1959. 7, old fertilized ♀; 8, old unfertilized ♀. That these individuals were old was judged by worn wings. 9–11. Same locality, 16 III.1959. Presumably all these individuals were going into hibernation. 9, the only fertilized ♀ with worn wings found on this date; 10, unusually robust ovaries for unworn, unfertilized, overwintering ♀; 11, Ordinary type of ovaries of unworn, unfertilized, overwintering ♀ (Ovaries of unworn fertilized individuals were similar).

be seen in each ovariole (Michener 1964). The frequent existence of a cluster of sometimes up to 11 eggs in the bottom of a nest shows that the female of *Exoneurella* can produce eggs in fairly rapid succession and that they do not hatch promptly.

Captions for figs. 1–11 give my interpretation, based on examinations of many individuals, of the various degrees of ovarian development shown. Each ovary has four ovarioles. Young individuals from emergence to and including active egg layers (figs. 1–6) show a relatively easily understood progression in ovarian development. Overwintering individuals (figs. 9–11, 9 being a rare worn individual that would perhaps have overwintered) have ovaries similar to those of young adults but with whitish areas (in fixed material) suggesting resorbtion of some oocytes. Old and no longer egg-laying summer females (fig. 7) have similar ovaries, while an old unfertilized summer female (fig. 8) had very peculiar ovaries, the ovarioles widely separated, not all of them ending in large oocytes.

Eggs (fig. 12) are about .95 mm long, .38 mm in maximum diameter, white, slightly curved, with a coarse reticulate pattern, faint at the small end. They are laid loose in the bottom of the nest. Being slightly sticky, they often adhere to one another in a clump, or even stick to larvae.

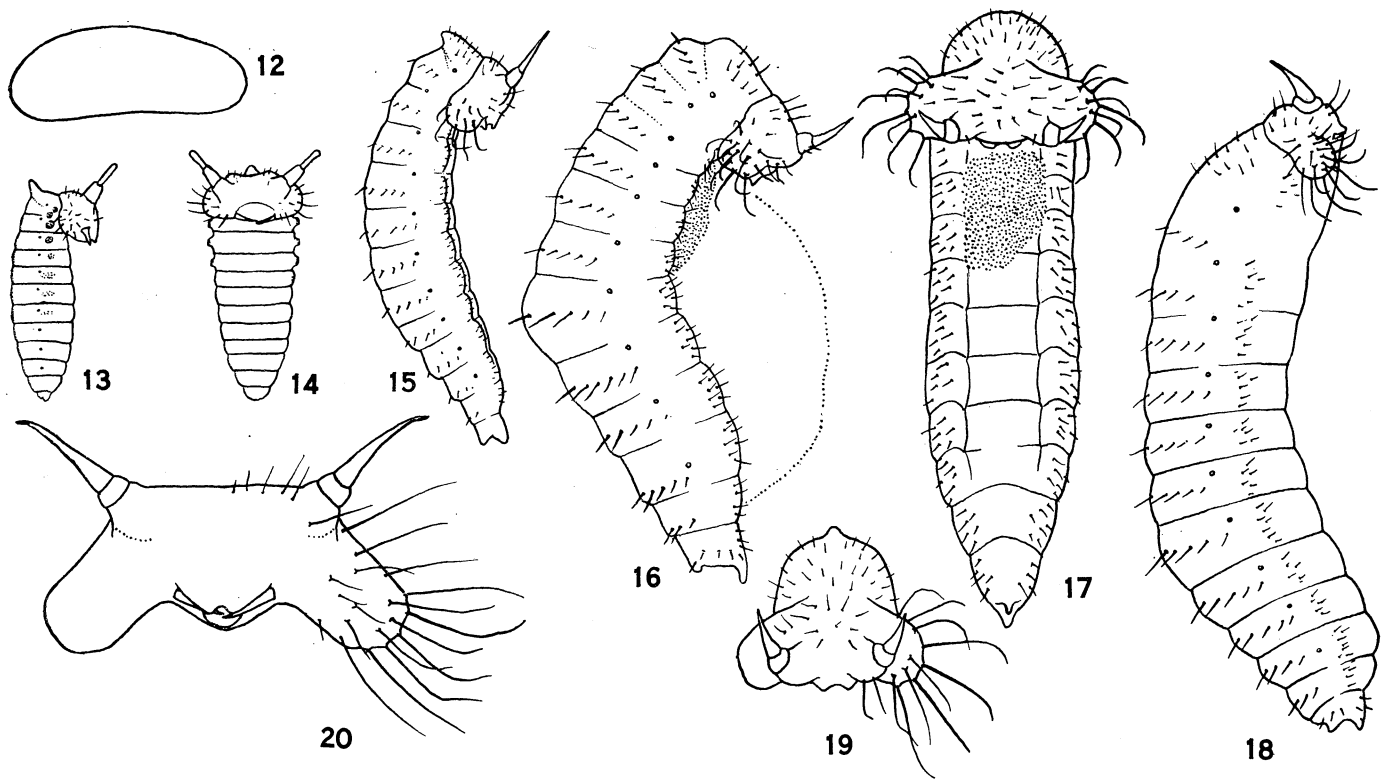
Larvae: As in *Allodapula* (Michener 1962), the immature stages are kept in order in each nest from youngest at the bottom to oldest above. Even pupae with different degrees of darkening are consistently in this sequence, the darkest being uppermost. The female bee therefore has to crowd past pupae, prepupae, and the larger larvae to feed the smaller larvae near the bottom of the nest. Details of larval structures have been given by Syed (1963), and the number of larval stadia determined as probably four. His account is based entirely on preserved material. The comments and drawings herein were based on living specimens.

The small larvae (I believe first and second stadia) are too small to support themselves in the nest and often lie near or among the eggs so that there is a lack of regular arrangement among the smallest young. They have long, blunt antennae (figs. 13 & 14), a middorsal prothoracic tubercle, and small, roughened lateral tubercles on the thoracic segments and small roughened, not projecting areas on the sides of some of the abdominal segments. The sides of the head are not much expanded.

When small larvae are disturbed, they swallow a great deal of air and distend themselves. My illustrations (figs. 13 & 14) show somewhat distended individuals; Syed's (1963) illustrations of preserved specimens are perhaps based on much distended individuals which may explain his failure to see certain tubercles.

Middle sized larvae (third stadium ?) have pointed antennae (fig. 15), a middorsal prothoracic tubercle, somewhat swollen ventrolateral or subspiracular ridges along the body forming a rather broad and only gently convex venter, and broad, hairy, jowllike, posterolateral lobes on the head. These lobes are sufficiently laterad in position that they do not interfere with the bending of head to feed from the venter of the larva. Such larvae lack the lateral thoracic tubercles of smaller larvae and the hinge in the middle of the body of larger ones.

Middle sized larvae probably support themselves in the nest not only by their slight stickiness but by stretching across the burrow, supported by the prothoracic tubercle pressed against one wall and the apex of the abdomen against the opposite wall.



Figs. 12–20. Sketches made from living individuals of *Exoneurella lawsoni* (Rayment). 12, egg (length .95 mm); 13 & 14, young larva, lateral and ventral views; 15, 3rd (?) stage larva, lateral view (length 2.50 mm); 16 & 17, 4th (?) stage larva, lateral and ventral views (length 3.25 mm), dotted areas represent an ordinary sized pollen mass; the dotted line represents the largest pollen mass seen on a larva; 18, prepupa (length 3.75 mm); 19, head and prothorax of young 4th stage, showing small dorsal prothoracic tubercle (view the same as for fig. 6); 20, facial view of head of 4th stage larva.

Large larvae (fourth stadium ?) are similar to the middle sized ones except for the lack of the prothoracic tubercle (smaller larvae of the stadium show it weakly, fig. 19), the flatter venter between the strong ventrolateral ridges, and the dorsal swelling of the fifth abdominal segment (fig. 16). This swelling forms a noticeable hinge for the movements of the body; flexion can push the larva up or down the burrow. Commonly the posterior part of the body extends across the diameter of the burrow and the anterior part is directed upward in the burrow. The rather coarse dorsal hairs of the posterior part of the body probably help in movements in the nest.

It is interesting to note how the comparable problem of maintaining larvae of *Allodapula* in their positions in nests has been solved by a parallel structural development, namely a large dorsal tubercle on the first abdominal segment (Michener 1962).

Prepupae and pupae: These stages are found heads uppermost, above the level of the larvae in the nest. Their size, hairs, and roughness of the burrow walls must hold them in position since they are not sticky.

The pupa is similar to that of *Allodapula* (Michener 1962). The face and vertex have long, erect hairs; there are groups of particularly long hairs about the summit of each eye and on the frons above the antennal bases, and there are hairs nearly as long on the clypeus. The thorax is hairless. The metasomal terga two to five have long subapical lateral hairs, three to five also have shorter subapical dorsal hairs. Special pupal structures (such as coxal spines, etc.) are absent.

The pupae of *Exoneurella* differ from those of *Allodapula* by the absence of coxal and trochanteral spines and by the details of the arrangement of the hair on the head and metasoma.

Sex Ratio: The relative numbers of the adults of the two sexes seem to vary through the year, from approximately equal in winter to many more females than males in summer (Table 6). It seemed probable that adult males have shorter lives than females, as in most bees and as was indicated by the reduction in relative numbers of males during the spring when little or no production of adults was occurring. The sex ratio of pupae was therefore examined. It was found that in summer many more females than males emerge but that in autumn the numbers are more nearly equal or males are in excess (Table 6).

Table 6. Numbers of adults and pupae of each sex at different seasons of the year.

	Adults			Pupae		
Nest groups	♂	♀	♂/♀	♂	♀	♂/♀
1 (Oct.)	12	23	.52	0	0	
2 (Nov.)	21	77	.27	0	0	
3 (Oct.)	0	4		0	0	
4 (Nov.)	5	25	.20	0	0	
5 (Dec.)	0	3		0	8	
6 (Dec.)	18	49	.37	5	15	.33
7 (Jan.)	7	64	.11	18	32	.56
8 (Feb.)	16	19	.84	18	26	.69
9 (Mar.)	36	34	1.06	19	10	1.90

Such results would not be surprising for a social species which would produce an excess of female workers during the spring and early summer. They may indicate that *Exoneurella lawsoni* is derived from social ancestors with a worker caste (or something like a worker caste) such as *Exoneura* and *Allodapula* have.

Feeding of larvae: In every nest, most of the larvae had no pollen supplies from which they were feeding. Most of them had pollen in the gut, showing, as would be expected, regular feeding. However, only one out of ten or more larvae, and often much less, were feeding or had available food when the nests were opened. These larvae, like those of *Allodapula* (Michener 1962), had masses of moistened, sticky pollen on their under surfaces, and fed by curling the head region until the mouthparts contacted the food mass. Once two small larvae seemed to be feeding from a single pollen mass but this situation may have resulted from snapping of the stem in which the nest was located. Figs. 16 & 17 show maximal and ordinary sized pollen masses.

The flat venter and large ventrolateral ridges of large larvae seem to be adapted for supporting pollen masses. The large lobes on the sides of the head and their hairs may, even more, serve to locate the pollen mass or to guide the female bee in placing it on the venter of the larva.

Feces of larvae are never found in the nests and must be removed by the adults.

Duration of Immature Stages: Comparison of Groups 2 & 5 suggests that about two months are required for development from egg laying to pupa under highland conditions in spring and early summer. At lower, warmer, altitudes, progress may be more rapid. The pupal stage alone, at room temperature in Brisbane in March, required 15 days.

SUMMARY

Exoneurella lawsoni (Rayment), a bee that nests in burrows in pithy stems in eastern Australia, was studied by examining 225 nests taken at different seasons. Larvae live together (not in separate cells) and are fed progressively by the mother or by her successor (daughter ?). In each nest they are arranged from the oldest near the nest entrance to the youngest at the bottom, except that small larvae and eggs may be mixed in a cluster. Moderate sized and large larvae have curious structural modifications for maintaining their positions in the vertical burrow. Food is placed by the mother on the venter of the larva and eaten by curling the head region. The period from egg to adult is two months or more.

Winter is passed by young adult males and unfertilized females in about equal numbers in (family ?) groups in the nests, along with a very small number of larvae of various ages. Mating occurs in spring (October or in the highlands, early November) and the females disperse, only one remaining in each original nest, the others making new nests. The females start laying eggs, some of them in nests containing overwintered larvae which are progeny of females of the preceding generation. The females keep laying eggs more or less continuously so that by early summer the number of young of all ages per nest averages as high as 8 (8. XI) or 11.5 (27. XII) and reaches a maximum of 28. Meanwhile, however, some families are small, perhaps being started late by overwintered females or by adults emerging in spring from overwintered larvae.

By late December numerous adults are maturing from the eggs laid in spring. By this

time most of the overwintered females seem to have died and in most nests a female, presumably a daughter of the overwintered spring mother, seems to care for the larvae and to continue the egg laying in the nest. The other young females remain in the nest while they are still callows but soon after they become fully black, they leave and establish new nests. Since young of all ages are present in the nests, the maturation of adults continues through the summer and establishment of new nests does also. By late February, however, egg laying has ceased in most of the nests. By mid March nearly all old adults are dead. Numerous adults of both sexes (the females almost all unfertilized) are in the nests, together with a few larvae which probably pass the winter in that stage and prepupae and pupae which will produce additional young adults before winter.

Relatively few of the young emerging in early summer are males; by fall many are males. Such an arrangement would be expected only with social forms having a worker caste produced in summer. This fact, together with the progressive feeding, may indicate that *Exoneurella* had a social ancestor such as *Exoneura* or *Allodapula* with a worker caste or workerlike individuals.

LITERATURE CITED

Michener, Charles D. 1962. Biological observations on the primitively social bees of the genus "*Allodapula*" in the Australian region (Hymenoptera, Xylocopinae). Insectes Sociaux **9**: 355–73.

1963a. New Ceratinini from Australia (Hymenoptera, Apoidea). Univ. Kansas Sci. Bull. **44**: 257–61.

1963b. Division of labor among primitively social bees. Science **141**: 434–35.

1964. The life cycle and social organization of bees of the genus *Exoneura* and its parasite, *Inquilina* (Hymenoptera: Xylocopidae). Univ. Kansas Sci. Bull., in press.

Michener, Charles D. & Rudolf B. Lange. 1959. Observations on the behavior of Brazilian halictid bees (Hymenoptera, Apoidea), IV *Augochloropsis*. Amer. Mus. Novit. **1924**: 1–41.

Sakagami, Shoichi F. 1960. Ethological peculiarities of the primitive social bees, *Allodape* Lepeltier (*sic*) and allied genera. Insectes Sociaux **7**: 231–49.

Syed, I. H. 1963. Comparative studies of larvae of Australian ceratinine bees (Hymenoptera, Apoidea). Univ. Kansas Sci. Bull. **44**: 263–80.