

BIOLOGIES OF AFRICAN
ALLODAPINE BEES
(HYMENOPTERA, XYLOCOPINAE)

CHARLES D. MICHENER

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INTRODUCTION

THE PRESENT PAPER reports on a study of allodapine bees made during most of a year in southern and eastern Africa. It concerns nests and behavior, including evidence of social organization when present. Some comparative West African data are included although my study of two species in Cameroon has been published elsewhere (Michener, 1968). In the introductory section, before the accounts of the species, a general statement on allodapine nesting biology is provided including comparative data from Australian and other species. These same sections, in reviewing various aspects of allodapine biology, provide a synthesis of certain of the findings presented in Species Accounts.

The allodapines are a group of genera of the tribe Ceratinini (family Anthophoridae, subfamily Xylocopinae) limited to Old World tropical and austral regions (Africa, Asia Minor, southern Asia eastward to Formosa and the Solomon Islands, and south through Australia to Tasmania). African genera of nonparasitic allodapine bees are *Allodape*, *Allodapula* (with a subgenus *Allodapulodes*), *Braunsapis*, *Exoneurula*, *Halterapis*, and *Macrogalea*. For a taxonomic summary, see Michener, 1969a. A fuller taxonomic treatment of the African forms are given by Michener (MS) and the distinctive and often behavior-related larval structures are described in a subsequent paper. The parasitic forms in Africa, some included in *Allodape*, *Allodapula*, *Braunsapis*, and *Macrogalea*, others in the exclusively parasitic genera *Eucondylops* and *Nasutapis*, have been treated taxonomically by Michener (1970b).

Outside of Africa, the allodapine fauna is far less diversified. *Exoneurula* reaches across the Red Sea to Asia Minor. *Braunsapis*, the largest and most widespread genus, occurs not only in Africa but in Madagascar, India, and eastward to Formosa, the Solomon Islands, and the northern half of Australia. *Allodape* reaches Madagascar. Genera not found in Africa are *Exoneuridia* from Asia Minor and *Exoneurella*, *Exoneura*, and its parasite *Inquilina*, all from Australia.

Nests and larvae are known for all allodapine genera except *Exoneuridia*.

To relate the names here used and put forward

by Michener (1969a, 1970b) to previous biological work, it is necessary to indicate the currently accepted names and generic assignments for species whose biologies have been studied in the past. This is done in table 1, not only for African forms but for others on which there is biological information in the literature. When there is no difference between a prior and current name, the reference is included in the table only if it is of special biological significance.

ACKNOWLEDGMENTS

My work in Africa was made possible by a John Simon Guggenheim Memorial Fellowship supplemented by National Science Foundation Grant No. G 11967 (providing limited travel funds for behavioral work).

The success of my studies was the result of help from many sources. Lack of space prevents the listing of many names that I would like to acknowledge, but persons listed below gave some of the more meaningful aid: The use of interesting areas for field study was permitted thanks to the courtesy of Dr. S. H. Skaife, Hout Bay, Cape Province (who not only permitted use of his property, Tierbos, where he had studied allodapine bees, but gave freely of his knowledge of South African bees and other insects); Miss C. E. Godman of Horsham, Sussex, England (who permitted use of her Noordhoek Estate on the Cape Peninsula as well as the help of Mr. D. R. Meredith); Prof. H. B. Rycroft (who arranged for my studies at the Kirstenbosch Botanical Gardens, Cape Town, and the Karoo Gardens, Worcester, Cape Province); Dr. and Mrs. Kurt Strauss of Pietermaritzburg who permitted studies on their property at Salt Rock, Natal, as well as use of their house there; Brother Austin Dolan, O.S.F. of St. Peter's Teacher Training College, Bambui, Bamenda, West Cameroon (who also arranged for living accommodations in an area that would otherwise have been difficult to work in); and the Natal Parks Board which permitted my field work in Hluhluwe and Ndumu Game Reserves.

For very much help in indicating the best collecting areas and sometimes providing transportation to interesting places, I wish to thank Dr. A. J. Hesse and Mr. F. W. Gess of the South

TABLE 1
CURRENT NAMES AND GENERIC ASSIGNMENTS OF SPECIES STUDIED PREVIOUSLY

Previous Study	Current Name
<i>Allodape abdominalis</i> (Skaife, 1953)	<i>Allodape rufogastra</i> Lepeletier
<i>Allodape angulata</i> (Skaife, 1950, 1953)	<i>Allodape mucronata</i> Smith
<i>Allodape ceratinoides</i> (Brauns, 1926)	<i>Allodape ceratinoides</i> Gribodo and <i>A. panurgoides</i> Smith
<i>Allodape elizabethana</i> (Brauns, 1926)	<i>Braunsapis elizabethana</i> (Strand)
<i>Allodape halictoides</i> (Skaife, 1953)	<i>Allodapula acutigera</i> Cockerell
<i>Allodape marginata</i> (Iwata, 1938; Yasumatsu, 1938)	<i>Braunsapis sauteriella</i> (Cockerell)
<i>Allodape paradoxa</i> (Brauns, 1926)	<i>Braunsapis paradoxa</i> (Strand)
<i>Allodape pringlei</i> (Brauns, 1926)	<i>Allodapula variegata</i> (Smith)
<i>Allodape strandi</i> (Masi, 1930; Paoli, 1930)	<i>Braunsapis strandi</i> (Masi)
<i>Allodapula foveata</i> (Michener, 1968)	<i>Braunsapis foveata</i> (Smith)
<i>Allodapula grandiceps</i> (Michener, 1968)	<i>Braunsapis leptozonia</i> (Vachal)
<i>Braunsapis convexa</i> (Michener, 1970a)	<i>Braunsapis luapulana</i> (Cockerell)
<i>Braunsapis grandiceps</i> (Michener, 1970a)	<i>Braunsapis leptozonia</i> (Vachal)
<i>Braunsapis kenyae</i> (Michener, 1970a)	<i>Braunsapis gorillarum</i> (Cockerell)
<i>Braunsapis rufipes</i> (Michener, 1970a)	<i>Braunsapis bouyssoui</i> (Vachal)
<i>Eucondylops konowi</i> (Brauns, 1902, 1926)	<i>Eucondylops konowi</i> (Brauns)
<i>Exoneura</i> spp. (references in Michener, 1965)	<i>Exoneura</i> spp.
<i>Exoneurella lawsoni</i> (Michener, 1964)	<i>Exoneurella lawsoni</i> (Rayment)
<i>Inquilina excavata</i> (Michener, 1965)	<i>Inquilina excavata</i> (Cockerell)
Asiatic (including Formosan) to Australian species placed in <i>Allodape</i> or <i>Allodapula</i> (references in Sakagami, 1960; Sakagami and Yoshikawa, 1961; Michener, 1962)	<i>Braunsapis</i> spp.
Sakagami's (1960) Ethogroup I	<i>Halterapis nigrinervis</i> (Cameron) group

African Museum, Cape Town; Messrs. R. C. Littlewood and F. J. Stayner of the Karoo Gardens, Worcester; Mr. C. Jacot-Guillarmod, Director of the Albany Museum, Grahamstown; Mr. B. R. Stuckenberg of the Natal Museum, Pietermaritzburg, who more than anyone else helped to organize my entire trip; Dr. M. Soulé of the University of California, San Diego, then of the University of Malawi, Limbe, who also provided accommodation when it was needed in Malawi; Mr. D. H. Eccles of the Fisheries Research Unit, Monkey Bay, Malawi; Dr. E. C. G. Pinhey, National Museum, Bulawayo, Rhodesia; Mr. G. R. Cunningham-van Someren of Karen, Nairobi; Mr. L. D. Vesey-FitzGerald of Ngurdoto National Park, Arusha, Tanzania; and Dr. D. G. Greathead of the Commonwealth Institute of Biological Control, Kawanda Re-

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It is a pleasure also to acknowledge the field and laboratory help, for certain periods during my study in Africa, of my wife, Mary H. Michener; my daughter Mrs. Barbara M. Turner; and Mr. Denis J. Brothers then of Rhodes University, Grahamstown, now at the University of Kansas. Mr. Brothers and Mrs. Gisela K. Fashing also did the necessary statistical work and he and Mr. Edward M. Barrows made the thousands of dissections of female bees connected with studies of social levels. The secretarial and editorial help of Mrs. Joetta Weaver is gratefully acknowledged.

ALLODAPINE BIOLOGY

NESTS

ALLODAPINE BEES nest in small, simple burrows in dead, dry, hollow or pithy stems, less commonly in pithy thorns, galls, rotting stems, or holes in dead branches or twigs. Brauns (1926) said that these bees may nest in earthen banks where suitable stems are scarce; I have not seen such behavior but Brauns was a good observer. Ecological details on African nesting sites, including their relations to human and animal activity, fire, stem taxonomy, stem diameter, shade, etc., have been presented by Michener (1970a).

The nests of the forms treated in Species Accounts below were nearly all in dead twigs or stems. The bees mostly enter where breaks occur exposing natural hollows, hollows made by borers, or pithy centers which the bees can excavate. Less commonly the bees enter unbroken stems through openings made by borers. In many cases it was difficult to determine, for a given nest, whether the bees used a burrow made by other insects or excavated their own.

All nests are simple burrows, rather uniform in diameter (except for some species of *Allo-dapula*). The dimensions for all species treated are indicated in table 3.

The entrance is constricted. In some nests the entrance seems clearly to have been excavated into pith and left smaller in diameter than the rest of the burrow. Such entrances were noted specifically for some nests of *Allodape mucronata* and *panurgoides*, *Braunsapis trochanterata*, *foveata*, and in Australia, *Exoneura variabilis* and *hamulata*. Entrances constructed in this way show that the bee excavated the burrow rather than using a pre-existing one. Except in the Australian *Exoneurella lawsoni* the nest entrance is further constricted, or the constriction made or maintained by building a collar. If it is destroyed, the bees can rebuild it. The collar is constructed of bits of pith or fibers from inside the burrow stuck together with an invisible material making a neat, round entrance hole, which the female bees can defend either with the head and jaws, or by reversing and closing the entrance with the flattened dorsum of the apical terga. At the opposite end the nest burrow is neatly rounded. If excavated in pith, the burrow simply ends in this

form, but if the nest is in a naturally hollow stem or one bored by another insect, the bottom may be wholly or partly made of bits of pith or fibers, stuck together as in the case of the entrance collar. Thus in location and structure the nests are as described earlier for species studied in Africa, Asia, and Australia (for earlier references see Sakagami, 1960; Sakagami and Yoshikawa, 1961; Michener, 1962, 1964, 1965, 1968).

There is variation among the genera in the size and perfection of the entrance collar. It is well developed in most genera but in the *Allo-dape* of South Africa it is poorly elaborated and, as indicated above, it is absent in *Exoneurella*.

Nests may be deepened during occupancy, as first noted by Iwata (1938). Michener (1965) showed seasonal deepening of nests in *Exoneura variabilis* and *subbaculifera* and noted that nests inhabited by several bees averaged deeper than those occupied by only one. Moreover, freshly excavated pith was sometimes found pushed out of nest entrances containing immature stages, showing that pith was carried past the eggs and young from the bottom of the burrow to the entrance. Similar observations were made for *Braunsapis* in Cameroon (Michener, 1968). Seasonally progressive nest deepening was also noted for *Exoneurella* (Michener, 1964), and Iwata's (1938) data showed the larger (older) colonies of *Braunsapis sauteriella* to have deeper nests than those occupied by lone adult females and their young.

TABLE 2
MEAN NEST DEPTHS^a
(Measurements are in Centimeters)

	Depth (N) of Young Nests	Depth (N) of Mature Nests	Signifi- cance of Difference (Kruskal- Wallis tests)
<i>Allodape mucronata</i>	14.3 (27)	18.8 (29)	0.001
<i>Allodapula acutigera</i>	9.0 (28)	10.7 (62)	0.02
<i>Allodapula dichroa</i>	6.0 (28)	8.1 (21)	0.05

^aYoung nests contained lone females and eggs or small larvae; mature nests contained medium-sized larvae or older young.

TABLE 3

NEST DIMENSIONS OF AFRICAN ALLODAPINE BEES

	Entrance Diam- eter (mm.)	Nest Diam- eter (mm.)	Nest Depth (cm.) ^a	
			Young Nests	Mature Nests
<i>Allodape mucronata</i>	4-4.5	4.5-6	7-28	6-42
<i>A. panurgoides</i>	2.5-3	3.5-5	2.5-16	4.5-15
<i>A. ceratinoides</i>	—	4-5.5	8	4-20
<i>A. friesei</i>	3.8-4	3.5-5.5	4.5-8.5	4-30
<i>A. rufogastra</i>	2.5-3.5	4-5.5	5.5-24	5-29
<i>A. exoloma</i>	1.9-2.8	2.5-4	4-12	4-12
<i>A. pictifrons</i>	3	3.3-4.5	4.5	—
<i>A. quadrilineata</i>	—	3.5-4	6.5	7.5-18
<i>A. stellarum</i>	2.5-3	2.6-3.5	—	3-9.5
<i>A. pernix</i>	—	3.5-5	—	6-9.5
<i>A. interrupta</i>	2.5-3	3.4-4.5	—	4.5-11
<i>A. brachycephala</i>	2.4	3	8.5	—
<i>A. derufata</i>	—	3.5	5-27	—
<i>A. dapa</i>	3-3.5	4-4.5	4-4.5	—
<i>Braunsapis</i> <i>trochanterata</i>	2.5-3.2	2.7-5	—	4.5-21
<i>B. facialis</i> (Natal)	1.5-2	2-3	3-15	1.5-15
<i>B. bouyssoui</i>	1.5-1.7	1.5-2.5	—	2-14
<i>B. leptozonia</i>	1.4-1.9	1.6-3	3.5-9	2-21.5
<i>B. foveata</i>	2.2-2.6	2.5-4	4-10	3.3-22
<i>B. luapulana</i>	—	1.8-2.6	2-7	2.5-14.5
<i>B. draconis</i>	1.5-2.0	2.0-2.5	—	4-26
<i>B. rhodesi</i>	—	2-3	—	2.3-16
<i>B. stuckenbergerorum</i>	1.0-1.5	1.5-2.5	—	2.5-16
<i>B. rolini</i>	1.5-2.5	—	—	2-7
<i>B. gorillarum</i>	—	1.9-3.2	—	3-18.5

^aYoung and mature nests are distinguished as indicated in table 2.

The species treated below sometimes show evidence of similar nest deepening, as indicated in table 2. For most of the species listed in table 3, however, evidence for such deepening is lacking, although for some (e.g., *Allodapula variegata*) young nests average deeper (not significantly) than old nests. I made no special effort to gather data pertinent to this subject, and depths of many nests went unrecorded because of the need to gather other sorts of data; I take it as established that many allopapines that make their own burrows in soft materials do extend them during the period of use.

CARE OF THE YOUNG

Allodapine bees are unique in that, except for

TABLE 3-(Continued)

NEST DIMENSIONS OF AFRICAN ALLODAPINE BEES

	Entrance Diam- eter (mm.)	Nest Diam- eter (mm.)	Nest Depth (cm.) ^a	
			Young Nests	Mature Nests
<i>B. simplicipes</i>	—	1.8-2.5	—	2-15.5
<i>B. elizabethana</i>	—	2-2.5	—	3.5-22
group				
<i>B. paradoxa</i>	—	1.5-2.5	—	6-9.5
<i>B. vitrea</i>	—	3	—	9
<i>B. albitarsis</i>	—	2.4-2.6	—	10
<i>Allodapula</i> <i>acutigera</i>	2-2.5	3-5.5	3-25	3-33
<i>A. dichroa</i> west	2-2.5	2.5-4.5	—	9-25
east	1.5-2	2.5-5.5	2.5-11	4-18
<i>A. variegata</i>	1.5-2	2.3-6.0	4.5-22	2.5-23
<i>A. rozeni</i>	—	4	—	9
<i>A. melanopus</i> and <i>turneri</i>	1.5-2	3-4.5	7-12	6.5-26
<i>A. vitatticeps</i>	—	3.5-4.5	—	17-21
<i>A. xerica</i>	2	3.5	—	10-12
<i>A. hessei</i>	—	3.5-4.0	—	4-11
<i>A. maculithorax</i>	—	3-3.8	3-4.5	—
<i>Exoneurula</i> <i>stigmoides</i>	—	2-2.5	—	6-24.5
<i>Macrogalea</i> <i>candida</i>	3-4	3.5-5.5	—	2.5-40
<i>Halterapis</i> <i>nigrinervis</i> group	1.3-1.75	2-3	2-4.5	1.5-16

the genus *Halterapis* and presumably during part of larval growth, the genus *Exoneurula*, young are reared together and progressively fed, often in contact with one another and often being moved about by the adult or adults in the nest. They are thus subsocial (except for *Halterapis*) in the sense of Wheeler (1923) and subsequent authors (Michener, 1969b). *Halterapis* mass provisions its larvae but the other genera feed progressively. In most cases each larva receives periodically a mixture of pollen and a liquid, presumably nectar, or sometimes nectar alone, on its venter, and the larva eats from this until the supply is exhausted. In *Allodapula* regularly and in *Exoneurula* at least sometimes for the youngest larvae, feeding is from a common food mass. As an occasional event in some other genera two larvae

may be seen feeding from a single food mass. Earlier reports of direct feeding of larvae with glandular secretions or crop contents of adults should be discounted unless verified.

At any one time, except for *Allodapula*, *Halterapis*, and probably *Exoneurula*, most larvae do not have a food supply. This must be related to their slow rate of growth. Attainment of full size takes weeks or, through winter or perhaps dry season periods, months, compared with days for most bee larvae.

Removal of larval feces is a behavior pattern that has arisen independently whenever practical in bees. In most bees in which each larva is in a sealed cell, such behavior is impractical, and in the Apini it occurs only after emergence of adult bees. But in the few halictines that leave the cells open, feces are removed before pupation. In allodapines, feces start to be voided well before larvae reach full size, as detailed with references by Sakagami (1960). They are dry pellets and are removed more or less as they are produced, so that they cannot ordinarily be found in the nest in any genera except *Halterapis* and *Allodapula*. In these genera, either because of mass provisioning or because of a clump of larvae around a food mass, adults in the nest do not have access to lower parts of the nest where feces accumulate. Ultimately, however, when maturation of the brood permits such access, larval feces are removed even in these genera, although sometimes slowly and incompletely, as for example in *Allodapula melanopus*.

Some species of *Braunsapis*, *Exoneurula*, and *Halterapis* on occasion utilize nesting stems that slope downward to the opening instead of standing more or less erect. Reeds in thatch, with nest entrances at the edge of the roof, are the most easily found and studied. Such stems are probably useless for species whose eggs are loose, since the eggs would roll out. In such nests eggs and feeding and growing larvae have their normal positions with relation to the nest entrances. On entering the prepupal stage, however, orientation must be in relation to gravity rather than to the nest entrance, for prepupae and pupae in such nests have their heads directed away from the entrances. Emergence and subsequent behavior of adults is entirely normal. In various other genera (*Allodapula*, *Macrogalea*) an occasional pupa is seen reversed in position, as shown in figure 91. Such inversion may occur in nearly horizontal stems; since I broke

off most stems and examined them later indoors, I lack adequate data on their slopes in relation to pupal inversions.

OCCURRENCE OF COLONIES CONTAINING TWO OR MORE FEMALES¹

Nests of all species are started by lone females, and in progressively feeding species each is soon inhabited by the mother and a group of eggs, larvae, or pupae, i.e., a subsocial group. With maturation of the young, some species regularly or facultatively have nests inhabited by two or more mature females. Among such females there is often division of labor, with an unfertilized female caste, although external caste differences are limited to mean size. This is the only group of the Anthophoridae exhibiting such social behavior and polymorphism.

Elucidation of the group behavior of allodapines depends in part on the view that these bees do not readily or often enter and live in nests other than their own. If they regularly invaded other conspecific nests, explanations of the bees in a nest would be quite different from those here offered, for I have considered the inhabitants of a nest as familial relatives. Evidence favoring this interpretation comes from sources including the following: (1) Using 50 nests in Cameroon and 150 in South Africa, I put pressure on the bees to enter nearby nests, but they did not do so (see Michener, 1970a, for the method). (2) The bees in a given nest often show family resemblances in color pattern, etc. Unrelated invaders would often be quite different even though conspecific.

As pointed out by Michener (1969b), social organization when found in allodapine bees involves cooperative activity among whatever adult females are in the nest, whether mother and daughters or a group of daughters. The young cared for by such adults may be either their own offspring, their younger brothers and sisters, or presumably sometimes their nieces and nephews. Terms like semisocial and eusocial (Michener, 1969b) therefore do not apply usefully to species of this group although they can be applied to individual nests.

In related bees such as *Xylocopa* and *Ceratina*, nest burrows often contain several adults during

¹This and the next section, somewhat modified, appear in German as a chapter in Schmidt (In press).

TABLE 4

PERCENTAGES OF NESTS BELIEVED TO HAVE BEEN INHABITED FOR SOME TIME IN THE ACTIVE SEASON BY TWO OR MORE MATURE ADULT FEMALE ALLODAPINE BEES. *Exoneura*, *Exoneurella*, AND *Braunsapis simillima* AND *unicolor* ARE AUSTRALIAN FORMS; ALL OTHERS ARE AFRICAN

	Percentage of all Nests	Percentage of Nests with Eggs or Young	No. of Nests	No. of Nests with Eggs or Young	Season	Account of Life Cycle
<i>Exoneurella lawsoni</i>	6	8	64	51	Dec.-Jan.	Michener, 1964
<i>Allodape mucronata</i>	6	7	106	86	Sept.-Nov.	See below
<i>A. panurgoides</i> and <i>ceratinoides</i>	4	6	105	70	Oct.-Dec.	See below
<i>A. panurgoides</i> and <i>ceratinoides</i>	9	15	34	20	Feb.	See below
<i>Allodapula dichroa</i>	3	4	150	123	Sept.-Feb.	See below
<i>A. variegata</i>	7	10	55	40	Dec.-Feb.	See below
<i>A. acutigera</i>	10	13	187	141	Sept.-Nov.	See below
<i>A. melanopus</i> and <i>turneri</i>	20	23	103	91	Oct.-Feb.	See below
<i>Braunsapis facialis</i>	34	43	166	131	Dec.-March	See below
<i>B. leptozonia</i> (Natal)	38	44	73	63	Dec.-Feb.	See below
<i>B. foveata</i> and <i>leptozonia</i> (Cameroon)	28	40	90	63	July-Aug.	Michener, 1968
<i>B. simillima</i> and <i>unicolor</i>	29	36	17	14	July-Nov.	Michener, 1962
<i>Exoneura variabilis</i>	27	30	109	100	Dec.-Jan.	Michener, 1965
<i>Exoneura variabilis</i> ^a	32	36	109	100	Dec.-Jan.	Michener, 1965

^aPercentages in this line are based on more liberal judgments as to maturity of the females than for those in the preceding line.

the inactive season, for example, winter. The same is true of some of the allodapine bees. Moreover, young adults frequently stay in their natal nests for a time so that in the active season nests can often be opened containing several adults. Ordinarily, however, only one adult female works in the nest of *Xylocopa* or *Ceratina* at any one time. In some species of allodapines, on the other hand, colonies containing two or more active females arise during the course of the brood-rearing season. More rarely, as an occasional event in certain species, two or more females that presumably overwintered together remain in the same nest, forming a small colony during the active season. The development of small colonies has been known in certain species for many years (see especially Brauns, 1926; Iwata, 1936; Sakagami and Yoshikawa, 1961).

The frequencies of nests containing two or more active females are indicated for several species in table 4. When young are maturing, a more or less continuous process during much of the active season, there are commonly young adult females in the nests. The continuous establishment of new nests in most species indicates that some such young females must leave their parental nests, but some remain to become

working cohabitants in the nest in which they matured. There is therefore every intergradation among the females in nests between young adult females, unworn, unmated, with slender ovaries and soft, pallid integument (teneral or callows) and old adults with worn wings, often mated, often with enlarged ovaries, and with fully darkened integument. The percentages given in table 4, therefore, commonly represent arbitrary decisions as to which females in each nest are young adults that are likely to leave and probably are not yet active in foraging and care of young and which, on the contrary, represent mature adults, working in the nest, and so far as is known likely to stay there. For some species observations of foraging helped in making such decisions. For species that attain mature coloration late so that acquisition of such coloration coincides with the age when most females leave their natal nests, nearly all females with such coloration were considered as probable permanent residents. For other species, which attain mature coloration earlier, judgments had to be based on dissections and examinations of wing margins and even then were quite arbitrary.

As shown in table 4, the percentages of nests containing two or more fully mature females is

low for species in the upper half of the table, considerably higher although under 50 per cent in the lower half. Presumably in the allodapine *Halterapis*, as in most *Ceratina*, essentially no nests contain two or more mature working females. The low figure, even for the most social species, results from two facts: (1) At any season at least in tropical areas some of the nests are newly established and hence contain only the founding female, commonly with her eggs and larvae. (2) Some of the old nests are abandoned by all but one of the mature adult females, sometimes the old founder, sometimes a daughter (probably when the founder has died). The only nests represented in the percentage columns in table 4 are those in which young females mature in a nest and stay, either with or without their mother.

The number of such mature adult females in a nest is in most cases two but sometimes as high as six; it is among them that polymorphism has been investigated. Rarely 20 or more adult females may be found in a nest but most of them are young, often obviously callow.

POLYMORPHISM

Suggestions of division of labor, castes, and polymorphism in allodapines were first described by Michener (1962, 1963). Since that time many pertinent data have been gathered, but the caste system remains difficult to describe because of its flexibility and the feeble differentiation of the castes. Sometimes there are two similar females in the same nest; for example, both may be mated, with enlarged ovaries, and with worn wing margins. No polymorphism is involved in such instances; both bees are apparently working and laying. In most nests inhabited by two or more mature adult females, however, dissection shows that there is one with enlarged ovaries, nearly always mated and usually more worn, whereas others usually have more slender ovaries, are usually not or less worn, and are frequently unmated. The former are the principal egg layers and might be called queens, whereas the latter usually lay fewer eggs, sometimes apparently none, and are often workers. The noncommittal expression, supernumerary females, is used for all such individuals in table 5 because certain of them presumably lay eggs. For example, in the four nests of *Exoneurella lawsoni* containing two mature females each, these females had ovaries of nearly the

TABLE 5
POLYMORPHISM AMONG ALLODAPINE BEES

	1. Percentage of Fertiliza- tion among Super- numerary ♀ ♀ and (N)	2. Mean Size of Super- numerary ♀ ♀ < size of layer	3. More Young in Nests with 2+ ♀ ♀ than in Those with One
<i>Exoneurella lawsoni</i>	75% (4)	?	?
<i>Allodape mucronata</i>	0% (5)	?	yes (NS)
<i>A. panurgoides</i> and <i>ceratinoides</i>	56% (9)	?	? yes
<i>Allodapula dichroa</i>	100% (4)	?	?
<i>A. variegata</i>	40% (5)	?	?
<i>A. acutigera</i>	83% (24)	yes	yes
<i>A. melanopus</i> and <i>turneri</i>	70% (52)	no	yes
<i>Braunsapis facialis</i>	20% (30)	no	yes
<i>B. leptozonia</i> (Natal)	10% (19)	yes	yes
<i>B. foveata</i> and <i>leptozonia</i> (Cameroon)	5% (40)	yes (NS)	yes
<i>Exoneura variabilis</i>	25% (36)	yes	yes

Symbols: NS, not statistically significant by Kruskal-Wallis test. ?, data are too few to form a useful judgment.

same size. The word worker, however, is used below in the more social species (lower part of table 5).

From table 5 it can be seen that in some species (upper part of the table) most supernumerary females are mated (except for the five *A. mucronata* dissected). On the other hand, in *Braunsapis* and *Exoneura* only 5 to 25 per cent of such females are mated.

Data from various species are given in tables accompanying the species accounts to show the variable relations among three attributes of each female in nests containing two or more mature females. These attributes are: ovarian development; prior mating; and prior activity as judged by wing wear (details are explained under Methods). For example, out of 187 nests of *Allodapula acutigera*, only 18 contained supernumerary females. As shown in table 5, more than 80 per cent of these were mated, and as shown in table 26, most had ovaries somewhat slender (classes C to F) and some had slight to

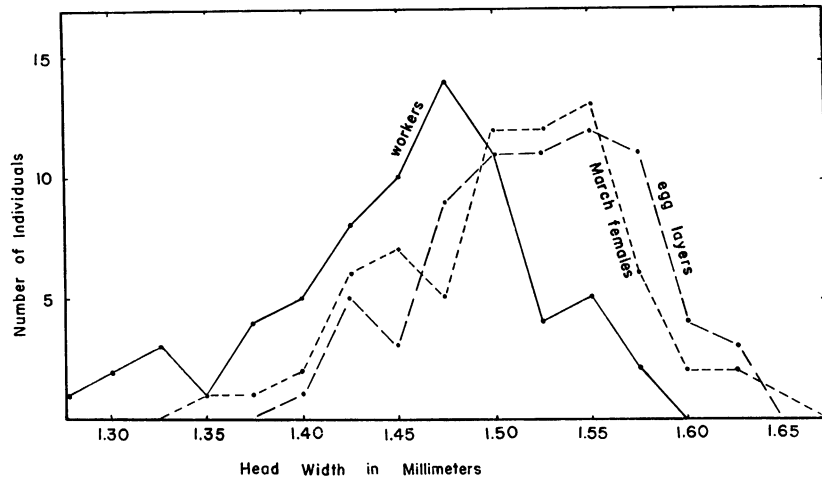


FIG. 1. Frequency distribution of head widths (as a measure of size) of females of *Exoneura variabilis* based on 70 egg layers taken in December (summer), 70 workers and presumed workers taken in December, and 70 females taken in March. The last should be queens that would overwinter to judge by the seasonal cycle of the species. (From Michener, 1965).

considerable wing wear. As another example, out of 109 nests of *Braunsapis facialis* from Natal, 34 per cent contained two or more mature bees (table 5). Bees from 28 such nests were dissected with the results shown in table 19. Most of the supernumerary bees were not mated; most but not all had somewhat slender ovaries, and some showed wing wear.

Column 2 of table 5 shows that at least in species where supernumerary females are relatively common, they have in many cases a smaller mean size than do laying females (queens). This is illustrated for the Australian *Exoneura variabilis* in figure 1 where females that are to overwinter (taken in autumn, the month of March) are seen to have about the same mean size as overwintered egg layers taken in mid-summer (December), whereas workers taken in December averaged smaller. For at least some African *Braunsapis* similar figures could be prepared (see table 5, column 2 and Species Accounts).

The smaller mean size, frequent lack of mating, and usually relatively slender ovaries are all attributes of workers in various primitively social bees and strongly suggest the presence of a worker caste in some nests of at least the species listed in the lower parts of tables 4 and 5. (There are also confusing findings, such as unmated and even unworn bees with enlarged

ovaries, apparently ready to lay eggs. This was especially true of some Australian *Braunsapis* (Michener, 1962). Some anomalous individuals also occur commonly among certain halictids, e.g., *Lasioglossum zephyrum*, see Batra, 1966.)

Observations of foraging behavior justify the conclusion that at least in some species the supernumerary bees function as workers. High percentages of pollen collecting *Exoneura* and *Braunsapis* (called *Allodapula* at that time) were found to be unmated with slender ovaries (Michener, 1962, 1963). For example, in samples totaling 48 pollen collectors of *E. bicolor* and *variabilis*, 83 per cent were unmated and 94 per cent had slender ovaries (classes E and F). Pollen carrying foragers of *Exoneura variabilis* returning to their nests were commonly unmated and with slender ovaries in contrast to other inhabitants of the same nests which were the egg layers (Michener, 1965).

The activity of workers is further shown by a sample of 24 females of *Braunsapis foveata* and *leptozonia* taken collecting pollen (pollen loads on scopas) on flowers (Michener, 1968). Of these only two were fertilized. Most had ovaries of type E although eight had them of type F and one had them of type D. Half had unworn wings but the rest had various numbers of nicks up to 15, and the one with ovaries of type D had 20 nicks.

TABLE 6

MEAN NUMBERS OF EGGS AND YOUNG IN NESTS OF ALLODAPINE BEES CONTAINING ONE MATURE ADULT FEMALE AND TWO OR MORE SUCH FEMALES^a

		1 ♀	2+ ♀♀
<i>Allodape mucronata</i>	(Oct.–Nov.)	6.2	8.3
<i>Allodapula acutigera</i>			
Spring, Sept.–Nov.		2.5	8.0
Summer, Feb.		1.6	4.1
<i>A. melanopus</i> and <i>turneri</i>			
Eggs and small larvae	(Oct.)	2.0	3.2
	(Nov.)	0.5	3.1
Larger young	(Oct.)	6.7	10.2
	(Nov.)	2.3	7.5
<i>Braunsapis facialis</i>			
Eggs and small larvae		0.4	1.9
Total young		1.8	5.9
<i>B. leptozonia</i>			
Eggs and small larvae		1.2	6.4
Total young		2.9	10.8

^aFor further details see Species Accounts.

Of mature (not recognizably young or callow) adult females from nests of the same two species of *Braunsapis*, 52 per cent had been mated and 45 per cent had ovaries enlarged as though active, recently active, or soon to be active egg layers (types A to D). The low frequency of bees with enlarged ovaries or with sperm cells in their spermathecae in the sample of pollen collectors from flowers shows the relative inactivity of fertilized bees and of those with enlarged ovaries, and is surprising in view of the numbers of nests with only one adult female.

It is true that mere carrying of pollen on the scopa does not necessarily indicate worker-like activity because (1) lone bees feed their larvae and (2) allodapine females of all but callow ages often carry pollen into their burrows for later consumption by themselves (Michener, 1968, and present study). The scarcity of fertilized, laying females among the foragers, however, emphasizes the behavioral polymorphism in the allodapine colonies.

The importance of the workers in productivity of allodapines is suggested by the last column of table 5. It is quite possible that in all species or at least those in which supernumerary females are of regular rather than "accidental" occurrence, productivity is increased by the presence of such individuals. The magnitude of the increase is indicated in table 6. In every instance

TABLE 7

NUMBERS OF ADULT FEMALES PER NEST^a

	Mean Total No. of Adult ♀ ♀	Mean No. of Mature Adult ♀ ♀	Maximum No. of Mature Adult ♀ ♀
<i>Exoneurella lawsoni</i>	1.7	1.1	2
<i>Allodape mucronata</i>	1.1	1.1	2
<i>A. panurgoides</i> and <i>ceratinoides</i>	1.1	1.1	3
<i>A. panurgoides</i> and <i>ceratinoides</i> (Feb.)	1.8	1.1	3
<i>Allodapula dichroa</i>	1.2	1.0	2
<i>A. variegata</i>	2.3	1.1	3
<i>A. acutigera</i>	1.2	1.1	3
<i>A. melanopus</i> and <i>turneri</i>	2.6	1.4	6
<i>Braunsapis facialis</i>	1.5	1.4	3
<i>B. leptozonia</i> (Natal)	1.8	1.5	3
<i>B. foveata</i> and <i>leptozonia</i> (Cameroon)	1.4	1.4	4
<i>Exoneura variabilis</i>	2.1	1.9	6

^aSee table 4 for seasons.

except in *Allodape mucronata* the difference in mean numbers of young in nests with one mature adult female from that in nests with two or more is significant at the 0.01 level, in most cases at the 0.001 level, according to Kruskal-Wallis tests. Even a single worker often results in doubling to tripling of productivity, either because of its activity in bringing in food and caring for the young or because of its egg-laying activity (even though normally less than that of the queen) or because of some interaction. It would seem that selection should favor colonial behavior; perhaps the small sizes of the colonies are related to the limited space available in the stems and twigs utilized as nesting sites.

Since so many workers are unworn (e.g., tables 19 and 26), the question arises as to whether they constitute a distinct caste and die as workers or ultimately mate and disperse to establish new nests. The data strongly support the view that they are short-lived compared with queens and that at least most do not disperse and establish their own nests. (No data are available for forms in which supernumerary females are scarce, such as those listed in the upper parts of tables 4 and 5). In favor of this view is the smaller mean size of workers of various species; they

belong to a different statistical population than the queens. Also, some of them do become worn and show moderate ovarian activity, unlike the young, usually mated bees (queens) that establish new nests. The abundance of immature stages (table 6) compared with the small number of adults suggests that the workers are short lived. The scarcity of new nests established during the active season when workers are most common indicates that they do not mostly disperse, develop into queens, and establish their own nests. Of course such dispersal is the rule in forms that do not normally have workers.

Since recognition of a bee as a worker is arbitrary, especially for unworn, unmated individuals, and since the burden of proof has been to establish the existence of polymorphism in these bees, I have probably been too conservative in recognizing workers and have classified many young workers as young adults of unknown caste. Thus the true number of workers per colony is probably higher than indicated by my data on mature adult females, for example in table 7.

In conclusion, allodapines are unique among insects with social polymorphism in the small sizes of the populations of adults in their colonies and in the failure of many nests, even of the more social species, to acquire workers at all. They range from those like *Exoneurella lawsoni* or *Allodape mucronata* in which each nest normally contains only a single bee and additional mature adult females seem almost accidental, to those in which nearly 40 per cent of the nests contain two or more adult females. Mean and maximum numbers of mature adult females per nest are shown in table 7.

Even in the small and facultative groups of adult females, however, weak polymorphism among the females arises. This is shown behaviorally in that certain females (workers) do most of the foraging, others (queens) do little foraging when workers are present. Moreover, workers often do not mate. Polymorphism is shown physiologically in that many workers, unlike queens, do not experience much ovarian development, although others do and probably lay some eggs. Furthermore, there is meager evidence that workers are short-lived compared with queens. The polymorphism is also indicated morphologically in some species in that the mean size of workers is less than that of queens. In all these features (except, of course, mating) inter-

TABLE 8
SEX RATIOS OF ALLODAPINE BEES

	No. of Pupae	% ♂	% ♀
<i>Allodape mucronata</i>	73	54.8	45.2
<i>A. panurgoides</i> and <i>ceratinoides</i>	107	29.0	71.0
<i>A. friesei</i>	29	41.4	58.6
<i>A. rufogastra</i>	79	29.1	70.9
<i>A. exoloma</i>	64	12.5	87.5
<i>Braunsapis facialis</i>	180	30.0	70.0
<i>B. bouyssoui</i> (Natal)	45	24.4	75.6
<i>B. leptozonia</i> (Natal)	71	14.1	85.9
<i>B. foveata</i> (Natal)	47	6.4	93.6
<i>B. foveata</i> and <i>leptozonia</i> (Cameroon) ^a	65	23.1	76.9
<i>B. luapulana</i>	39	41.0	59.0
<i>B. draconis</i>	34	55.9	44.1
<i>B. stuckenbergorum</i>	25	16.0	84.0
<i>B. simplicipes</i>	60	40.0	60.0
<i>Allodapula acutigera</i>	165	37.0	63.0
<i>A. dichroa</i>	137	42.3	57.7
<i>A. variegata</i>	59	30.5	69.5
<i>A. melanopus</i>	172	37.8	62.2
<i>Halterapis nigrinervis</i> group	27	11.1	88.9
<i>Exoneurella lawsoni</i> (summer) ^b	114	36.0	64.0
<i>E. lawsoni</i> (autumn) ^b	29	65.5	34.5
<i>Exoneura variabilis</i> ^c	207	40.1	59.9
<i>E. hamulata</i> ^c	93	42.0	58.0

^aMichener, 1968.

^bMichener, 1964.

^cMichener, 1965.

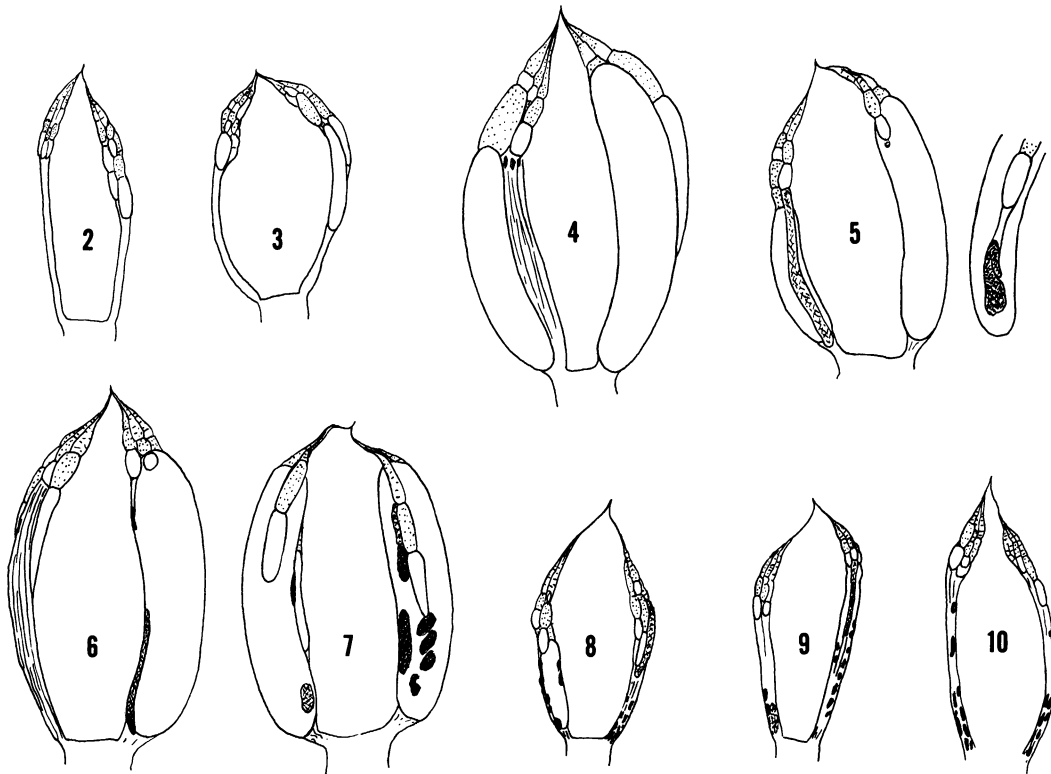
mediacy is common and many bees can be placed as to caste only arbitrarily.

There is no evidence as to the causation of the polymorphism.

FEEDING BEHAVIOR OF ADULTS

So far as known all allodapines are polylectic although preferences for certain flowers may exist. (For further details see Michener, 1970a.)

As shown in greater detail by Michener (1968), allodapine females, at least in the genera *Braunsapis*, *Allodape* (see *mucronata* below), and *Allodapula*, sometimes carry pollen to the nest and place it, loose and dry, on the burrow wall. Such pollen masses may occur even in the absence of brood in *Braunsapis*; if there is brood the pollen is placed above the brood. These food supplies, however, are not commonly seen in nests of most genera and are used up quickly as food by adult bees and as food for larvae. Pollen transport by



FIGS. 2-10. Sketches of ovaries of *Allodape mucronata*. 2, A slightly teneral female classified as F-0, in nest Feb. 5. 3, E+1, Feb. 6, very slightly teneral. 4, A+31, Nov. 26. 5, B-24, Sept. 12; at right, posterior end of right ovary from beneath. 6, D+20, Oct. 26. 7, D+39, Oct. 26. 8, C+41, Nov. 26. 9, E+12, Oct. 26. 10, F+40, Nov. 26. Growing eggs are white. Former locations of recently laid eggs are shown by longitudinal lines, representing wrinkling. Clusters of nurse cells are indicated by stippling. Eggs presumably being resorbed are indicated by crosshatching which becomes darker the denser and whiter the bodies become (see text). For symbols see page 238.

adult females of such forms is not necessarily an indication that they are feeding larvae.

In *Allodapula acutigera*, however, dry pollen masses were found in only one nest lacking immature stages and were never found in nests containing only eggs, prepupae, or pupae. They were found in 50 per cent of the nests containing growing larvae. In this species, therefore, pollen transport by adult females probably is normally an indication that they are feeding larvae.

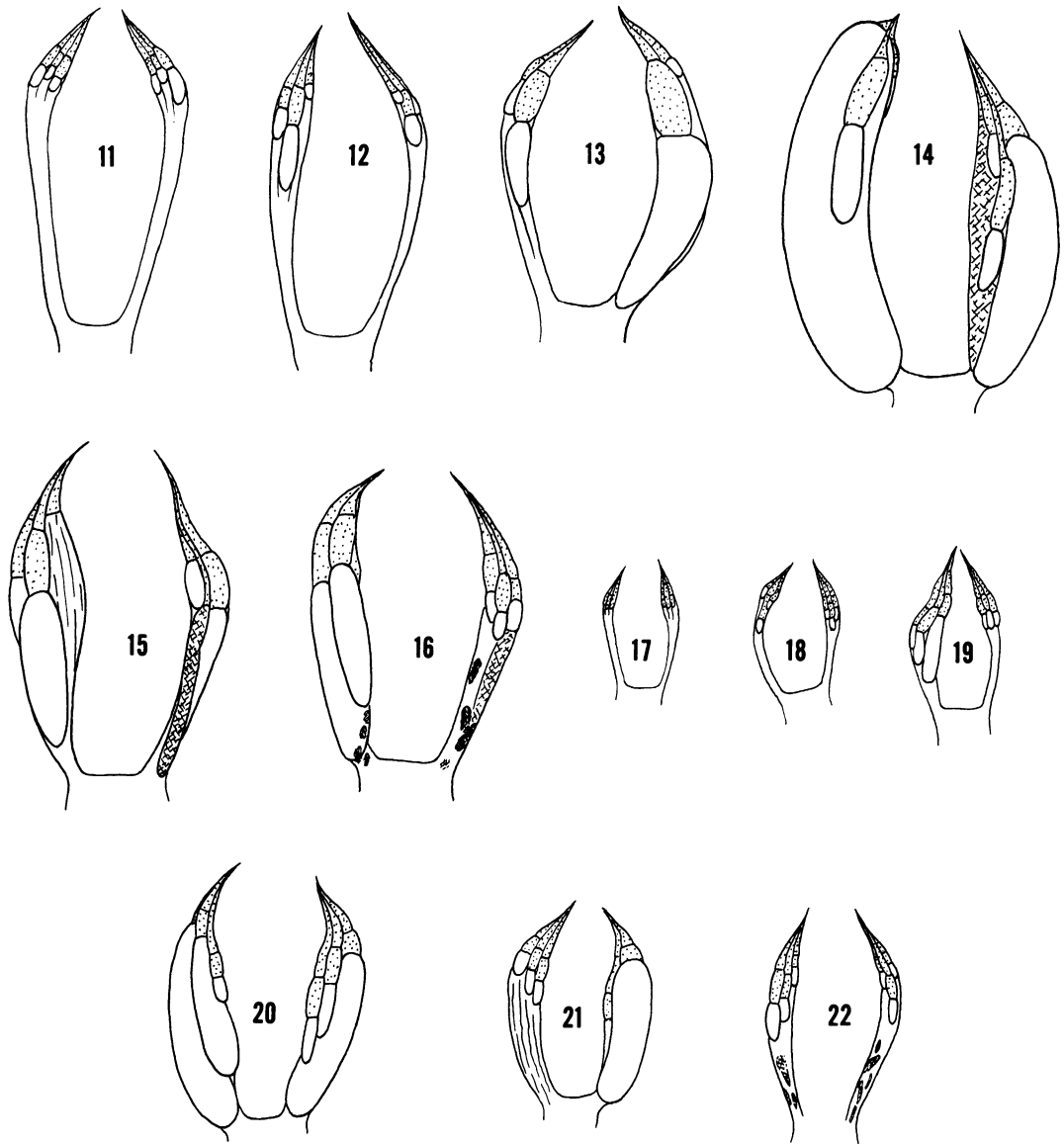
SEX RATIOS

Males are shorter-lived than females and often leave the nests soon after emergence although in *Allodape mucronata* and certain other species they are found in nests for months after emergence. Sex ratios based on adults found in nests are therefore not meaningful with respect to the ratio of production. Table 8 is based on the sex

ratios found among pupae, for species for which adequate samples are available. There is no evidence that these ratios vary with the season, as they do among proterandrous bees and in more highly social bees.

The frequency of low male production is noteworthy, as shown in table 8. Only in *Allodape mucronata* are males produced in numbers equal to, or greater than, females. Even in the solitary forms of *Halterapis* and *Exoneurella*, males are produced in small numbers, a fact which suggests that they arose from social ancestors.

The low male production may support the view expressed earlier that I have been too conservative in recognizing workers and that many of the unmated young females found when colonies are censused remain unmated and are short-lived workers that die before becoming worn or showing other evidence of being workers.



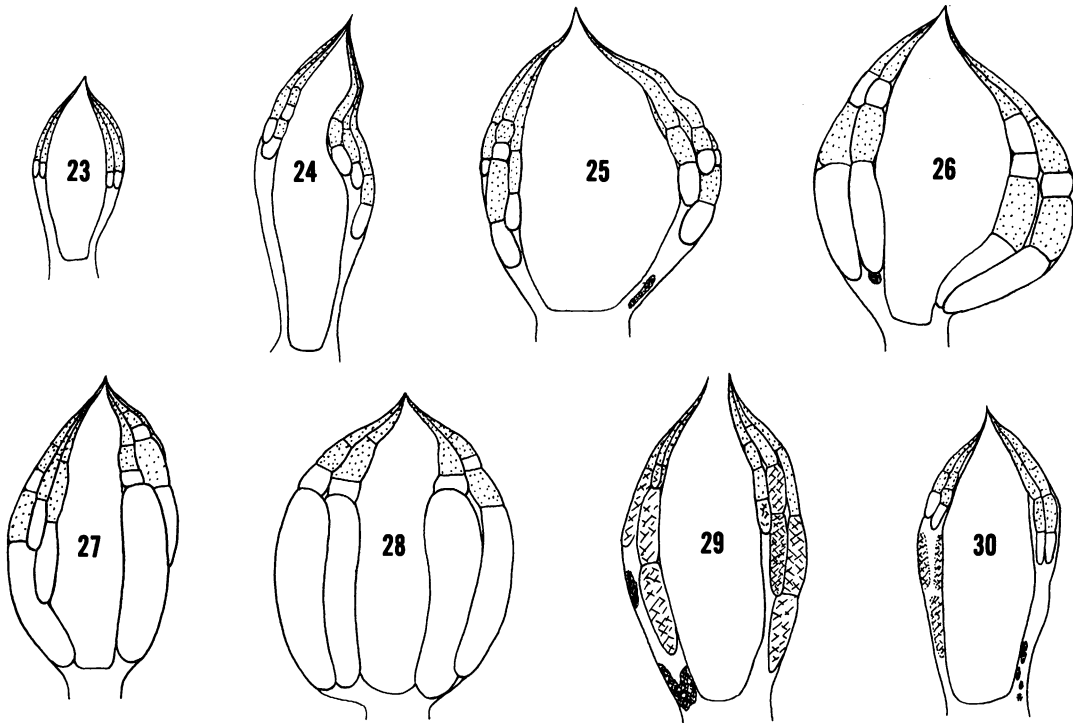
FIGS. 11-16. Sketches of ovaries of *Allodape panurgoides*. 11, A slightly teneral female classified as F-0, in nest Feb. 7. 12, F-2 (approaching E), Feb. 7. 13, C+26, Feb. 5. 14, A+31, Feb. 5. 15, C+0, Feb. 5. 16, C+40, Feb. 5. Explanation as for figs. 2-10.

FIGS. 17-22. Sketches of ovaries of *Braunsapis leptozonia*. 17, A teneral female classified as F-0, taken from a nest on Jan. 6. 18, F-3, from same nest. 19, C+0, from same nest. 20, A+3, from same nest. 21, D+10, Feb. 2. 22, E+21, Feb. 2. Explanation as for figs. 2-10.

THE OVARIAN CYCLE

As a considerable part of the present study depends on examination and interpretation of ovaries, some details concerning them are needed here. Each ovary consists of four ovarioles, which are usually appressed together so

that a maximum of three are fully visible from any one side but occasionally, when small, spread out in a sheet so that all can be seen, as in figure 36. In bees the ovarioles are of the polytrophic type, with oocytes alternating with clumps of nurse cells. In figures 2 to 37 the



FIGS. 23–30. Sketches of ovaries of *Allodapula acutigera*. 23, A teneral female classified as F–0, taken from a nest on Feb. 5. 24, E+0, Feb. 5. 25, E+4, Sept. 12. 26, B+142, Sept. 12. 27, B+3, Sept. 28. 28, A+5, Sept. 12. 29, C+3, Oct. 26. 30, E+33, Feb. 7. Explanation as for figs 2–10.

enlarging oocytes, when large enough to be clearly recognized under the dissecting microscope, are white, whereas the groups of nurse cells anterior to each such oocyte, as well as the more anterior ovariole regions are stippled.

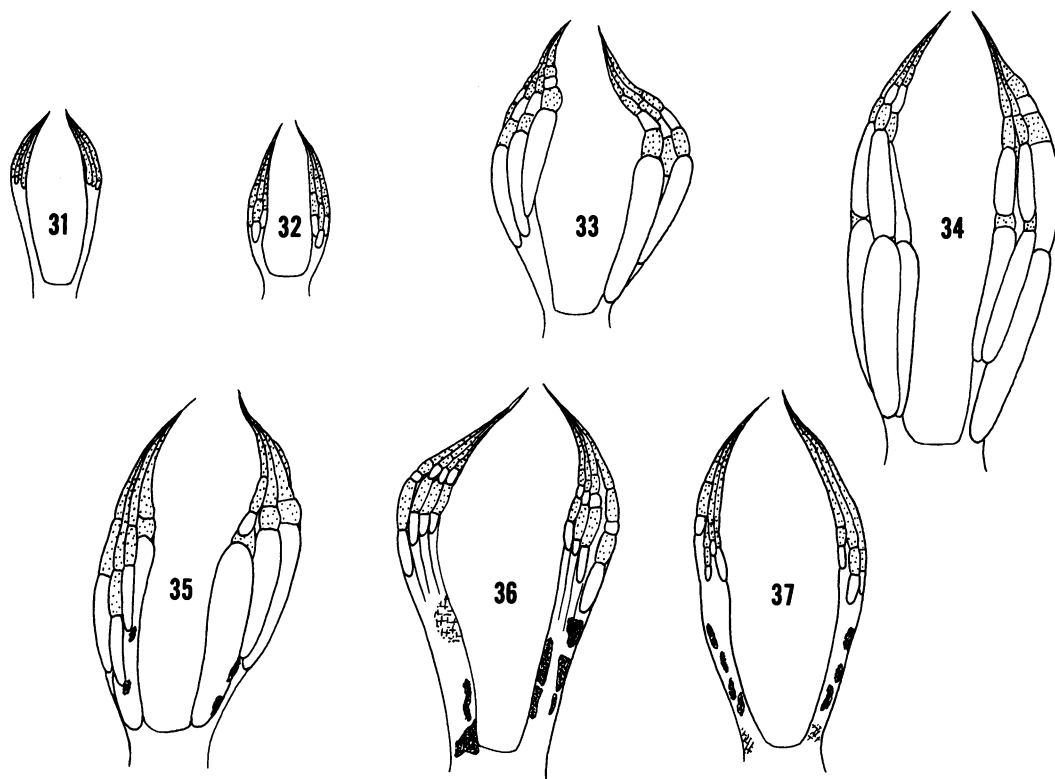
There are some forms (e.g., *Allodape panurgoides*, *Braunsapis facialis*, *leptozonia*, and *simillima*, Michener, 1962) in which eggs are laid at rather long intervals and no ovariole has more than one enlarging oocyte pushing posteriorly toward the oviduct. Moreover, the ovarioles are not at all synchronous, so that only one oocyte attains full egg size at a time. At the other extreme, among forms such as *Allodape melanopus* and *Exoneura* spp. (Michener, 1965) which lay several eggs in a short period and then wait to lay a subsequent group, each ovariole may have two or even three enlarging oocytes. Moreover, the ovarioles are somewhat synchronized so that several eggs may reach maturity at about the same time. Forms like *Allodape mucronata*, *Allodapula acutigera*, and *Exoneurella lawsoni* (Michener, 1964) are intermediate in these respects.

Iwata and Sakagami (1966) have correctly

related the relatively small eggs of *Allodapula* and *Exoneura* to the brood-rearing habit, i.e., to the rearing of batches of young of about the same age. At the other extreme, the larger eggs of some species of *Allodape* and *Braunsapis* reflect longer intervals between laying and broods consisting of young of diversified ages.

Because of the interspecific variation in the ovaries, it is not possible to classify ovarian size on the same scale for each species. Five classes have been recognized, as indicated below under Methods, but have been applied with due regard to the ovarian developmental cycle of each species, as shown by the legends for figures 2 to 37.

Further details of the ovaries have been used in some species to interpret age and other past experience of bees and especially to distinguish ovaries that are slender because they are young from superficially similar ovaries that have regressed in old bees. I am indebted to Denis J. Brothers not only for many dissections but for help in interpreting these matters. The details are explained below for *A. mucronata*, as an example.



FIGS. 31-37. Sketches of ovaries of *Allodapula melanopus*. 31, A teneral female classified as F-0, taken from a nest on Oct. 29. 32, E-0, Oct. 29. 33, B+9, Nov. 24. 34, A+6, Oct. 9. 35, A+2, Oct. 9. 36, E+25, Nov. 11. 37, E+4, Nov. 11. Explanation as for figs 2-10.

Unmated young females, sometimes still callow, have slender, pedunculate ovaries of class F (fig. 2). They grow through the classes E (fig. 3), C, B (and perhaps D), to A (fig. 4). In figure 4 one egg has presumably recently been laid, leaving the wrinkled membrane shown in the left ovary. Eggs are not always laid, however, but are commonly resorbed. Figure 5 at left shows the remains of a long, brownish egg being resorbed; it had probably reached nearly full size and therefore there is nothing left of its nurse cells. Figure 5 (at right) shows an older resorbed egg, the remains now quite dense, white (in Kahle's), and folded over, again without remnants of nurse cells. Often, however, as above the middle of the right ovary of figure 7, resorption destroys a small egg and its group of nurse cells. In this case the egg remnant becomes dense and white and the remnants of the nurse cells are gray and possibly ultimately removed. The number of white bodies is thus presumably a measure of the number of resorbed eggs, al-

though gray and white bodies are not always distinguishable and were lumped in the statistical treatment of the species, below. There is some evidence, still inconclusive, that as eggs are laid white bodies are removed so that they accumulate only in ovaries not releasing eggs for laying. In any case, when bees terminate laying, either temporarily or permanently, the ovaries revert to their original shape (figs. 8-10) but can be recognized as those of old bees by the white and gray bodies.

ASSOCIATES AND PARASITES

No proper study of natural enemies of allopapines has been made. Ants must be among the important enemies (Michener, 1965). Various boring beetles, crickets, and even millipeds and centipedes are sometimes found in hollow stems and may exclude allopapines or even destroy their nests. An interesting insect in this category in South Africa is the peculiarly elongated blaberid roach, *Cyrtotria poduriformis* (Walker)

(det. A. B. Gurney), which is often found in dead hollow stems, small nymphs in small stems such as those used by individuals of *Allodapula* and *Braunsapis*, larger nymphs and adults in large stems such as those used by individuals of *Allodape*.

Parasites of adult allodapines include nematodes sometimes found in the abdominal cavities. Such parasitized allodapines do not have enlarged ovaries and sometimes they are greatly reduced or seemingly absent.

Chalcidoid parasites of immature allodapines found by me in Africa are the following:

1. *Echthrodape africana* Burks, a perilampid whose large larvae are external parasites of pupae of various species of *Braunsapis* in Kenya. Such larvae and the pupae of *Echthrodape* must be moved about in the nest, like bee larvae and pupae, by the adult bees (Michener, 1969c).

2. *Xylencyrtus tridens* Annecke, an encyrtid that is an internal parasite of large larvae or prepupae of various species of *Allodape* and *Braunsapis* from South Africa to Kenya, Uganda, and Cameroon. There is presumably polyembryonic reproduction, for the large larva or prepupa of the host is always completely filled with larval or pupal parasites, leaving only a thin, transparent host cuticle intact. Annecke

(1968), when describing the species, listed all the localities and hosts that I found; this amounted to about 15 nests containing the parasite out of more than 2000 allodapine nests studied. The hosts included four species of *Allodape* and four of *Braunsapis*. The species of the latter were not identified except for *grandiceps* (= *leptozonia*) and were referred to in Annecke's paper by my field species numbers. The names applicable to these numbers are as follows: sp. 1 = *Braunsapis foveata*; sp. 53 = *B. draconis*; sp. 65 = *B. gorillarum*, and sp. 87 = *B. leptozonia*.

3. *Xylencyrtus mumifex* Annecke is another encyrtid internal parasite of large larvae or prepupae, in this case those of *Allodapula melanopus* in Cape Province (Worcester). Larvae of the parasite fill most of the interior of the host. The host then becomes brown, opaque, and sclerotized except for its anterior and posterior extremities which are delicate, dry, and empty. The sclerotized part forms a puparium-like case in which the parasites transform to adults; when I first opened a parasitized *Allodapula* nest I thought I was seeing puparia of a fly associated with the bee. Annecke (1968) has illustrated such a case; another is shown in figure 38. From one to seven *Allodapula* larvae were parasitized in each of several nests from Worcester, Cape Province. The rate of parasitization was much higher than for *X. tridens*, which rarely destroys more than one or two host larvae in a given nest.

METHODS

THE METHODS used are essentially those of Michener (1962, 1965, 1968). They involve fixation of nest populations in Dietrich's (or Kahle's) solution with subsequent measurements of the adult females, examination of wing margins to determine something about the prior activity of the bee, and dissections to determine the amount of ovarian development and the presence or absence of sperm cells in the spermatheca. These data, considered with records of the numbers and stages of the young present, shed considerable light on the activities of the bees. There is no evidence that, once a female has mated, sperm cells ever disappear from her spermatheca.

For convenience in discussing ovarian size, five classes have been recognized as follows:

A. All ovarioles or the maximum for the species enlarged, and one with an egg more or less of a size ready to lay.

B. All ovarioles or the maximum for the species considerably enlarged but no oocyte approaching the size of a mature egg.

C. Ovaries moderately enlarged (about half-way between E and B).

D. Only one or two ovarioles enlarged, sometimes one oocyte greatly enlarged and egg-sized, but the other ovarioles slender.

E. Ovaries slender but not pedunculate.

F. Ovaries slender and pedunculate, i.e., posterior halves or two-thirds mere slender stems containing no oocytes.

The condition of a female can be indicated briefly by three symbols: A letter showing the ovarian development; a symbol indicating the content of the spermatheca, + for sperm-filled, — for empty; a number indicating the total number of nicks in the apical margins of the two forewings. Thus a bee described as A—7 has much enlarged ovaries, is unfertilized, and is

somewhat worn, having seven nicks in the forewing margins. It should be noted that comparisons among species in the number of nicks on the wing margins mean little because as in other bees, large species damage their wings more than small ones, and counts of wing nicks made by different observers at different magnifications differ greatly. Various species were handled by different assistants in the present study.

Except as otherwise noted, the few nests inhabited by females whose abdominal cavities contained nematodes were excluded from nest statistics, and such females were excluded from statistics on ovarian development and the like. The occasional burrows occupied only by male bees were not considered in nest statistics.

A few comments on terminology may be useful, as follows:

The words "teneral" and "callow" are used interchangeably and relate to young adult bees that have not yet developed full mature coloration. Parts of the integument that will ultimately be black are still brownish, and in the youngest callows the wings are milky instead of clear.

The expressions "developmental gap" or "developmental discontinuity" refer to the lack of intermediate immature stages in a nest. In many species females consistently or frequently lay a number of eggs, then cease laying for a time and produce more eggs later. The result for a given nest and time is a group of older immatures such as pupae and another group of younger ones such as eggs and small larvae, without intermediate stages.

In discussing nests the entrance is spoken of as being upward, the other end as the bottom, even though nests may sometimes be horizontal or, at least in species that attach their eggs, may slope downward to the entrance.

SPECIES ACCOUNTS

GENUS *ALLODAPE*

THIS GENUS consists of relatively large bees, including the largest of the allodapines. The species of South Africa are relatively well-known biologically but those of tropical Africa are little known.

Most nests contain only one mature adult female although, as table 5 shows, a few nests in each extensively studied species contained two or more such females, the supernumerary ones being worker-like.

Eggs are loose, one to several in the bottom of the nest. Each larva receives food individually, and the feeding is progressive. The food is placed on the venter of the larva by the adult female. Young larvae lie with the eggs at the bottom of the burrow. As soon as the larvae are old enough, however, they support themselves ventral side up in the burrow by stretching across it, pressing the dorsum of the thorax against one side, the apex of the abdomen against the other. The adult arranges the young from youngest (eggs, small larvae) below to oldest (pupae) above and the arrangement is maintained quite accurately and in detail, dark pupae, for example, being above pale ones.

Allodape mucronata Smith

Figures 2-10, 41-48

This large species was studied at several localities near sea level on the Cape Peninsula (Kirstenbosch Botanical Gardens, Hout Bay, Noordhoek, Cape Nature Reserve), South Africa. One nest was also taken 3 miles south of Avontuur, Cape Province, South Africa, 3500 feet altitude. The nests are in Cape macchia, in stems usually exposed to the sun. Kinds of plants utilized and stem diameters are indicated by Michener (1970a). Nesting area 9 of that paper is typical.

SEASONAL CYCLE: Skaife (1950, 1953) has already dealt with this species and described the life cycle. He noted that the adult bees may be found in their nests at any time of year. There is only one generation per year, the females living for a year, the males for nine or 10 months. Laying begins in winter or early spring (July or early August) in nests typically inhabited by only a single female. An egg is laid every few days,

until a total of up to seven is present in the nest. From time to time, especially during bad weather, the female may eat an egg; the number present therefore need not be the total number laid. Eggs hatch from four to six weeks after laying and larvae are then fed by the mother and reach full size and stop feeding after seven or eight weeks, in November. After about 16 days as prepupae, they pupate. By mid-December all the larvae have pupated. As the pupal stage lasts about five weeks, most adults emerge during January.

Just before or at the time when her young mature, the mother may lay one to four more eggs, but by the end of January the mother is gone, presumably dead. The second brood of young is reared by their own older, mature sisters during the late summer and autumn (February to April). Adults of both sexes (of both broods if there is a second one) remain together through the winter in the nest; Skaife mentioned overwintering groups of a half-dozen. He implied that such groups usually but not always break up in spring so that most nests are occupied by a single female.

My own observations made in the same area, the Cape Peninsula, and in part, thanks to Dr. Skaife's courtesy, on the same property at Hout Bay, to a large extent add data to reinforce the above account drawn from Skaife (1953). Of 109 nests opened in September, October, and November only seven (about 6 per cent) contained more than one adult female, in each case only two. Thus the overwhelmingly usual behavior is for adults to disperse and establish their nests alone. Among these nests only eight males were found, all with worn wings; the last male was found on November 24. It is thus evident that males survive the winter in small numbers. However, of 80 spermathecae from lone females dissected in September, October, and November, only two were empty, showing that most of them mate earlier. Indeed, even in early February, 35 out of 54 females were mated, including some still slightly teneral and not fully colored. Thus mating of a female must usually occur fairly soon after emergence.

Of 22 nests opened on September 12, 1966, 15 had eggs (one to five in number) and only two

TABLE 9
STATISTICS ON EGGS AND YOUNG OF *Allodape mucronata* IN SPRING

	Eggs	Small Larvae	Medium Larvae	Large Larvae	Prepupae	Pupae
September 12 (20 nests; 48 eggs and young)						
1. % of nests containing each stage	73.7	10.5	0	0	0	0
2. % of eggs and young in each stage	93.8	6.2	0	0	0	0
3. Maximum no. of each stage in one nest	5	2	0	0	0	0
4. Mean no. of each stage in nests containing that stage	3.2	1.5	0	0	0	0
5. Mean no. of each stage for all nests	2.4	0.2	0	0	0	0
September 26–October 7 (38 nests; 165 eggs and young)						
1. % of nests containing each stage	70.3	43.3	30.0	24.3	2.7	0
2. % of eggs and young in each stage	52.7	19.8	14.5	12.4	0	0
3. Maximum no. of each stage in one nest	7	2	6	5	2	0
4. Mean no. of each stage in nests containing that stage	3.2	1.8	2.4	2.3	2.0	0
5. Mean no. of each stage for all nests	2.2	0.8	0.7	0.6	0.1	0
October 26–29 (28 nests; 115 eggs and young)						
1. % of nests containing each stage	15.4	34.6	57.7	61.6	27.0	11.5
2. % of eggs and young in each stage	9.6	17.4	27.8	32.1	13.0	0
3. Maximum no. of each stage in one nest	3	3	4	6	4	4
4. Mean no. of each stage in nests containing that stage	2.2	2.2	2.1	2.3	2.8	2.3
5. Mean no. of each stage for all nests	0.4	0.8	1.2	1.4	0.8	0.3
November 24–26 (24 nests; 164 eggs and young)						
1. % of nests containing each stage	20.8	20.8	28.3	54.2	70.8	83.3
2. % of eggs and young in each stage	5.5	4.3	5.5	19.5	26.2	39.0
3. Maximum no. of each stage in one nest	3	3	2	5	4	7
4. Mean no. of each stage in nests containing that stage	1.8	1.4	1.3	2.8	2.5	3.2
5. Mean no. of each stage for all nests	0.4	0.3	0.4	1.4	1.8	2.7

also contained small larvae. The other seven nests contained only a single adult female each, with no eggs or young. By the end of September and early October only three out of 42 nests lacked eggs or young; most had larvae of various sizes. The first prepupa was found on October 19, the first pupa on October 29, earlier than Skaife's account suggested.

In a sample of 24 nests taken November 24 and 26, most of the young were prepupae and pupae (table 9, line 2 for these dates) but in some nests there were eggs or larvae of various sizes. The separation of production into a main brood and a small second brood, noted for this species by Skaife and for various *Braunsapis* and *Exoneura* by Michener (1965, 1968), is not usually apparent in this late November sample; in fact only two nests (e.g., one with one egg, three small larvae, one medium-sized larva, and six pupae) showed the gap in age of young which two separate broods produce. Presumably a sep-

arate second brood may be more evident in December or January, the season when it was noted by Skaife but when I was not in the Cape region. It is clear, however, that, as in the *Braunsapis* and *Exoneura*, some females lay an egg occasionally during the growth of the first group of larvae, so that in their nests there is no discrete second brood but rather a scattering of younger individuals. In late November one-third of the nests contained eggs or small larvae in addition to older young; late laying must be rather common.

Table 9 (e.g., lines numbered 2) shows the progressive development of the main brood of young as well as the continued production of a few eggs. Table 12 shows that the total number of young produced in a nest sometimes exceeds the figures given by Skaife (1953).

By February 5 to 8, when I returned to the Cape Peninsula, the bees had nearly all matured. In 42 nests opened, there were only three pupae.

TABLE 10
PERCENTAGES OF FEMALES OF *Allodape mucronata* SHOWING VARIOUS DEGREES OF WING WEAR

Months	Number of nicks in outer margins of front wings						N
	0	1-2	3-9	10-20	21-47	48-110	
September	10.3	17.2	27.6	20.7	20.7	3.5	29
October	9.1	12.1	21.2	18.1	39.4	—	33
November	4.0	12.0	12.0	36.0	28.0	8.0	25
February	29.1	27.3	20.0	9.1	10.9	3.6	55

One nest, containing two of the three pupae, also contained an egg, a large larva, and a prepupa; another nest contained an egg; and a third a small larva. From this it would appear that only a small percentage (in this sample 7.1 per cent) of the autumn nests contain eggs or larvae and that the partial second brood is, by February, almost insignificant. Skaife placed some emphasis on it but did not indicate its frequency; it may be that it was more frequent in his artificial nests than in the field and it may be more evident in some years than in others.

The 42 nests opened in February contained from one to five adults each, totaling 54 females and 21 males. Two contained only males. None contained more than three females. Of the 40 with females, 30 had only one (sometimes with one or two males). Thus much of the separation of the progenies into individual nests occurs in the summer and fall rather than in the spring, after overwintering.

Except in the late November sample, there was a significant number of nests containing no young, but only an adult female. This is one reason for the low figures in lines 5 of table 9. Females from such nests seemed perfectly normal, being fertilized and with ovaries classified as A or B, with a few to many white bodies, and with wing nicks varying from 15 to 39. The reasons for their lack of offspring are not obvious. If such bees later lay and rear young, this would contribute to the lack of reproductive synchronization in the population.

Examination of the females at any season indicates that there is considerable heterogeneity of the population, perhaps as a result of the production of a partial second brood or perhaps as a result of some females surviving much longer than others. In either case, the result is that at all seasons there are females of very different ages in the population.

Evidence for such age variability is based on data that vary with activity, not age, but the relation to age is rather obvious. Table 10 shows variation in wing wear (see Methods) in females taken from nests in different months. Those obtained in September, October, and November had doubtless overwintered. In early spring (September) most were not or little worn and the mean degree of wear increases during the spring months, as would be expected. However, there were some very worn bees in each month, presumably indicating overwintering of some bees that had worked the previous summer. The summer (February) sample indicates the same thing. Most of the bees were young and unworn, supporting the view that most old females die by about the time of maturation of the first brood of young. However, there were small numbers of much older bees, some of which might die before winter but some of which evidently survive the winter. The few eggs and young larvae found in February were not associated with worn bees.

Another indication of relative age is the number of white or gray bodies in the lateral oviducts and lower parts of the ovaries. These appear to represent resorbed eggs and perhaps remnants of clusters of nurse cells (see The Ovarian Cycle). They may well be lost with egg laying but accumulate so long as no eggs are being laid, for egg production and resorption seem to go on all the time. The relation of these bodies to wing wear is shown in table 11. In February when there is little egg laying and when there are numerous young bees, the positive correlation between the ovarian bodies and wing wear is evident. In spring, when egg laying is going on, one can see that most individuals have some ovarian bodies and a few have many, more or less irrespective of the amount of wing wear.

In early spring (September 12) all females had

TABLE 11

NUMBERS OF WHITE AND GRAY BODIES IN OVIDUCTS AND LOWER PARTS OF OVARIES IN RELATION TO WING WEAR

No. of Wing Nicks	Feb. (N=54)					Sept.-Nov. (N=68)				
	0	1-5	6-10	11-15	16-20	0	1-5	6-10	11-15	16-20
51-55	—	—	—	—	1	—	1	—	—	—
46-50	—	—	1	—	—	—	1	—	—	—
41-45	—	—	—	1	—	—	—	3	—	1
36-40	—	—	1	—	—	—	—	2	—	1
31-35	—	1	—	1	—	—	1	—	—	1
26-30	—	—	1	—	—	—	2	1	—	—
21-25	—	2	—	—	—	—	3	3	—	1
16-20	—	—	2	—	—	—	2	1	—	—
11-15	1	—	2	—	—	—	4	2	1	1
6-10	2	2	—	—	—	2	6	6	—	—
0-5	21	13	1	—	—	3	11	5	2	1

Number of white or gray bodies or resorbing eggs.

ovaries with at least some rather large oocytes except two in ovarian class F. These two were parasitized by nematodes in the abdominal cavity. By late September some individuals had regressed ovaries of class E or F, with gray and white ovarian bodies, and usually with no eggs in their nests, but with older young. In October and November nearly half of the females are like this, i.e., they have produced their first brood and the ovaries have regressed greatly. The other half of the females belong to ovarian classes A to D but A and B are increasingly scarce, especially in November. There seems to be no obvious relation between ovarian development and wing wear at this season. Thus on November 24 among bees taken from nests were individuals classified as follows: A+0, B+26 (large ovaries, unworn and worn wings); F+1, F+41 (much reduced ovaries, almost unworn and much worn).

In February most bees have ovaries in class F, about 9 per cent in E. A similar small percentage have ovaries of class D and such bees must be responsible for the occasional eggs found at this season. Again, there is no relation between wing wear and ovarian class; in a series of nests opened on February 8 were females classified as F+0, F+41 and D+1 and D+54.

Figures 2 to 10 show ovaries of various individuals in a sequence such as they probably pass through in each individual, except that the illustrations do not show that after regression ovaries can enlarge again.

SUMMARY OF SEASONAL CYCLE: Winter is passed in the nests as adults, mainly females but some males. Egg laying (usually less than seven eggs) largely occurs in spring; growth of resulting young is slow, young adults maturing mostly in December and January. Overwintered mothers may lay additional eggs, sometimes one from time to time after the main spring brood and sometimes several about the time of maturation of first brood. In most cases the mothers die at this time and rearing of young from the few late eggs is by older daughters. Most of the females mate when young (November to February), establish themselves one per nest, and although they go out occasionally to feed, lay no eggs until the following spring (August, September, etc.). However, there is enough irregularity in reproduction so that some individuals do not fit this schedule and females of all ages not only survive the winter but may be taken at any season.

It appears that the reproduction largely ceases with the arrival of the arid (and relatively flowerless) summer and autumn of the Cape region, and that in winter the same reproductive inactivity continues, but adults of whatever ages present in autumn can survive the cold.

INTERACTIONS AMONG ADULTS: As indicated above, this is essentially a solitary species, each nest, at least when young are being reared, usually being inhabited by a single adult female. Skaife indicated that some summer and autumn rearing occurs in which one or more young females feed their younger (larval) sisters; I had

no opportunity to study such situations except by dissecting females present in nests taken in early February. In all cases where more than one female was present in a nest, only one was fertilized, or none was fertilized. I therefore suspect that the usual situation is that the bees disperse as soon as fertilized and establish their own nests, except for one daughter that retains the maternal nest. The situation may be comparable with that seen in *Augochlora pura*, a halictid, in which unfertilized females can live together in a single nest but fertilized females become aggressive and all but one is driven from the maternal nest (Stockhammer, 1966).

In the September to November period, however, I encountered seven nests (6 per cent of the total) each containing two mature adult females. Five such pairs of females were successfully dissected. In every such nest one of the females was unfertilized, the other fertilized.

In view of the occurrence of social behavior and castes in some other allodapines, the question arises as to whether the unfertilized individuals in these five nests are sporadically produced workers. In three of the nests the ovaries were quite different in the two females, the unfertilized bees having slender (class F) ovaries, the fertilized bees having ovaries of class A, B, or C. In the other two nests, both the fertilized and unfertilized bees had enlarged ovaries (class A or B) and appeared to be egg layers. The unfertilized individuals did not average smaller than the associated fertilized ones. In four nests the unfertilized bee had unworn wings or nearly so in contrast to worn fertilized associates (19 to 54 nicks); in the fifth nest the two were not greatly different in wear, nine nicks for the fertilized, 13 for the unfertilized bee.

As the workers in social allodapines are often less worn than egg layers, the above particulars do not show whether the occasional unfertilized females could be called workers. Perhaps they are females that matured late in the autumn and failed to find mates; this does not necessarily mean that they are not workers. Observational data on their activities are needed but foraging activity is suggested by the fact that one of the unfertilized females had pollen on her scopae when the nest was opened. The seven nests with two mature adult females contained an average of 7.7 eggs and young, the three taken in November having an average of 8.8. These figures are

TABLE 12
NUMBERS OF EGGS, LARVAE, AND PUPAE OF *Allodape mucronata* PER NEST^a

	Maximum	Mean for Nests Containing Eggs or Young	Mean for all Nests
Sept. 12	5	3.5	2.7
Sept. 26–Oct. 7	9	5.4	4.6
Oct. 16–29	14	5.9	5.0
Nov. 24–26	15	6.9	6.9

^aSee table 9 for N's.

higher than those in the middle column of table 12 and may indicate a greater reproductivity of two bees compared with one but the differences are not statistically significant.

IMMATURE STAGES: The numbers of young of various stages per nest and the relative frequencies of the different stages are shown in table 9 for the spring season when the main brood is being produced. Table 12 shows the sizes of the groups of young bees.

Eggs lie loose in the bottom of the burrow. They are 3.5 to 4 mm. long and curved. The young are arranged from youngest (eggs) at the bottom to oldest (pupae) above, as in other species of *Allodape* and *Braunsapis*. On splitting nests with a knife, occasional irregularities were observed; these could result from the disturbance of the mother when the nests were opened. Skaife (1953) reported that at any disturbance the mother, near the nest entrance, will turn inward and push the young before her with the front of her head until they are all piled near the bottom. Later she respaces the larvae in normal arrangement and with some distance between individual larvae and pupae. She moves the young about as has been described for *Braunsapis* (Michener, 1962, 1968).

As with *Braunsapis* the larvae, in vertical stems, support themselves when large enough by pressing the apex of the abdomen and the dorsum of the thorax against opposite walls of the burrow, the venter facing upward, toward the nest entrance. In horizontal nests they are similarly oriented in relation to the nest entrance but lie on their sides. Pupae are in positions with heads toward the nest entrance and appear to be supported, in vertical nests, by the long pupal hairs.

Larvae are usually fed a pastelike mixture of pollen and a liquid, probably nectar. Pollen is brought in and placed in a dry mass on the wall of the nest above the young, as noted by Skaife (1953) for this species and by me (1968) for *Braunsapis*. I saw such masses rarely when splitting nests of *A. mucronata*. Such pollen is then moistened with a little nectar (?) and the resulting small viscous mass carried to a larva and placed on its venter. Such food may be found on larvae of all ages (except prepupae), even on very small ones only partly out of the egg shell. Skaife's statement that such food is used for older larvae but that clear liquid is the food of the youngest ones is an error. One occasionally sees clear viscous liquid (nectar?) on the ventral surfaces of larvae of any age, as in *Braunsapis* (Michener, 1968), instead of the usual pollen paste.

Feeding of any sort seems infrequent, as was noted also for *Braunsapis* (Michener, 1968). Out of 233 larvae not yet in the prepupal stage, and for which presence or absence of food was recorded, only 50 had any food on them when the nests were opened. Feeding must sometimes occur at inappropriate times for larvae were twice noted with considerable pollen around their posterior extremities, carried there by ecdysis.

Defecation begins when the larvae are about half grown, and the feces as well as shed skins are removed from the nests by the female bees.

Allodape panurgoides Smith AND **A. ceratinoides**
Gribodo

Figures 11–16, 49

These species differ slightly in extremes of coloration but most specimens can be identified only by size. There is nothing in the available biological data to suggest differences in behavior or life history and the two species are therefore treated together. Nests of these species were studied at Cape Nature Reserve, Hout Bay (*panurgoides* only), Kirstenbosch Botanical Gardens, Noordhoek, Mossel Bay, and 40 miles east of Knysna, all in Cape Province. Ten nests (*panurgoides* only) were also taken on top of Table Mountain, Cape Town, at an altitude of 3000 feet; these are not considered in the statistical treatment since, except for one pupa, they contained only eggs and small larvae on December 1 when nests from near sea level contained numerous larger larvae. A series of nests

from 3 miles south of Avontuur, Cape Province, was also not included in the analysis because of the altitude and inland location, although it seemed synchronized with other material.

Like *A. mucronata*, these species nest in Cape macchia, in stems usually exposed to the sun (see Michener, 1970a). Nesting area 9 of that paper is typical for these species.

As in *A. mucronata*, most nests are used by single females. Large larvae were found in five and prepupae in one of the 15 nests opened in September, suggesting that some large larvae and perhaps smaller ones overwinter in the nests. Pupae were first found on October 1 and young adults on October 26. As shown in table 13, young of all ages can be found in the nests, probably throughout the warm season. In February, when almost no young of *A. mucronata* could be found, there were still moderate numbers of young, including eggs, of *A. panurgoides* and *A. ceratinoides*. Moreover, egg laying by the last two species is more uniformly spaced, so that there is no period when the mean number of eggs or size of egg clumps is as large as for September and October in *A. mucronata*. Laying does not cease in spring and begin again in summer, causing a gap in production, as reported by Skaife (1953) and partly verified by me for *mucronata*. As table 13 shows, reproductivity is somewhat diminished in February, when developmental gaps in the series of young (e.g., a nest with three eggs and two large larvae) are more common than from October to December. In September, also, some nests contain large larvae or prepupae and eggs, with no intermediate stages. I take this to be evidence that some females produce some offspring the previous summer, which overwinter as larvae, and that these females resume laying in spring.

Since reproduction appears to be more or less continuous except in winter, it is not surprising that females at all seasons are heterogeneous in wear and doubtless in age. However, since spring is a season of greater reproductivity than summer, more unworn adults are present in February than in the spring months, the percentage with little worn wings (0–3 nicks) being essentially as in *A. mucronata* (table 10). The relative frequency of adult females to males (62:24) in February nests is about as in *mucronata*. Nests containing more than one adult bee were found more commonly than in *mucronata*, especially in February, when out of 34 nests

TABLE 13
STATISTICS ON EGGS AND YOUNG OF *Allodape panurgoides* AND *Allodape ceratinoides*

	Eggs	Small Larvae	Medium Larvae	Large Larvae	Prepupae	Pupae
Sept. 12–Oct. 6 (24 nests; 37 eggs and young)						
1. % of nests containing each stage	22.2	14.8	12.5	28.8	8.4	8.4
2. % of eggs and young in each stage	24.7	10.5	10.5	42.0	4.7	7.7
3. Maximum no. of each stage in one nest	3	1	2	3	1	2
4. Mean no. of each stage in nests containing that stage	1.5	1.0	1.3	2.1	1.0	1.5
5. Mean no. of each stage for all nests	0.4	0.2	0.2	0.6	0.1	0.1
Oct. 15–Nov. 15 (36 nests; 137 eggs and young)						
1. % of nests containing each stage	70.0	22.2	11.1	22.2	25.0	33.3
2. % of eggs and young in each stage	38.0	7.3	2.9	16.8	9.5	25.5
3. Maximum no. of each stage in one nest	6	2	1	10	4	6
4. Mean no. of each stage in nests containing that stage	2.1	1.8	1.0	2.9	1.4	2.9
5. Mean no. of each stage for all nests	1.4	0.3	0.1	0.6	0.3	1.0
Nov. 24–Dec. 4 (45 nests; 216 eggs and young)						
1. % of nests containing each stage	56.0	35.0	40.0	26.7	17.8	40.0
2. % of eggs and young in each stage	26.4	16.7	13.6	7.9	4.2	31.8
3. Maximum no. of each stage in one nest	5	5	4	2	2	14
4. Mean no. of each stage in nests containing that stage	2.4	2.2	1.6	1.3	1.1	3.8
5. Mean no. of each stage for all nests	1.3	0.8	0.6	0.4	0.2	1.5
Feb. 5–7 (34 nests; 91 eggs and young)						
1. % of nests containing each stage	41.2	14.7	14.7	47.1	18.0	26.5
2. % of eggs and young in each stage	25.3	13.2	7.7	22.0	7.7	24.2
3. Maximum no. of each stage in one nest	4	6	3	2	2	4
4. Mean no. of each stage in nests containing that stage	1.7	2.0	1.4	1.3	2.0	2.5
5. Mean no. of each stage for all nests	0.7	0.4	0.2	0.6	0.2	0.6

examined, 15 contained more than one female. Populations attained eight adults, or up to five adult females (see below under Interactions among Adults.)

Throughout the season some nests contained only lone females, without young; observations on such nests parallel those on *A. mucronata*.

The ovaries are less often slender, with long slender posterior parts than in *A. mucronata*. Even in teneral females class E rather than F ovaries are relatively common. Only one large egg is found at a time and it is nearly as long as the ovary (fig. 14). In no case were two enlarging oocytes visible in the same ovariole, as sometimes occurs in *mucronata* (fig. 4). White bodies are much less common, and rarely attain the maximum shown in figure 16. It may be that with a slower rate of egg production and more continuous laying, a higher percentage of the eggs produced is laid than in *mucronata* and there-

fore fewer are resorbed and represented by white bodies.

Figures 11–16 show a sequence of ovarian enlargement and regression as pieced together from dissections of numerous females.

SUMMARY OF SEASONAL CYCLE: Winter is passed in the nests as adults, nearly all females and some large (perhaps some medium-sized) larvae. Egg laying resumes in spring and continues, probably throughout the warm season, but with reduced tempo after the spring months. Females of all ages are present at all seasons, but the maximum number of young females occurs in summer, after the spring period of rearing young. At this season numbers of unmated females are present (see below).

INTERACTIONS AMONG ADULTS: The numbers of nests inhabited by more than one adult female rose as the season advanced: 0 in September (number of nests=16). 2.5 per cent in

TABLE 14

CONDITIONS OF MATURE FEMALES IN COLONIES OF
Allodape panurgoides AND *Allodape ceratinoides*^a

Month	Nest No.
October	433: A+36, A+3
November	502: B+37, C+22, B-0
December	660: B+51, B+0 681: A+26, C+0
February	1256: B+26, C-3 1276: A+15, C-0, F-0, F-0, F-0 1310: D+13, D+0, C-0

^aEach colony contained two or more females, information on which is separated by commas. Letters represent ovarian class (A, largest to F, smallest); the symbols, +, - indicate whether the bee has been fertilized; the number is a total of wing nicks on forewing margins; see Methods. Colonies containing parasitized females are omitted, as are those whose extra females are all recently emerged (callow).

October (N=36), 11.5 per cent in November (N=26), 17.2 per cent in December (N=29), and 44.1 per cent in February (N=35). Doubtless this increase is related to the maturation of young adults as the season advances.

Of the 15 nests taken in February that contained two or more females, four were inhabited only by unfertilized and essentially unworn bees. These were doubtless, in each nest, daughters of an older and presumably dead mother and were caring for their own larval and pupal siblings, as occurs at the same season in *A. mucronata*. In two of these four nests, one containing four bees and one three, one or two females had undergone ovarian enlargement; one was classified as A-0 but there were no eggs, only a small larva. In one other February nest that contained five adult females, all essentially unworn and with slender ovaries (class E or F), one was fertilized (ovaries class D), the others not (ovaries class E and F). Presumably these were also siblings. To what extent, if any, the siblings with enlarged ovaries in such nests function as queens and the others as workers is unknown. Probably dispersal occurs soon after they mate, for nests with two fertilized bees are rare.

Of the remaining nests containing two or more females, about 50 per cent (each month) contained a worn fertilized mother and one (or occasionally more) unworn or scarcely worn, unfertilized daughter with slender ovaries (classes E or F). Some were still teneral. In none of these

TABLE 15

NUMBERS OF EGGS, LARVAE, AND PUPAE OF *Allodape panurgoides* AND *Allodape ceratinoides* PER NEST^a

	Maximum	Mean for Nests Containing Eggs or Young	Mean for all Nests
Sept. 12-Oct. 6	6	2.8	1.4
Oct. 15-Nov. 15	16	4.2	3.8
Nov. 24-Dec. 4	26	7.0	4.7
Feb. 5-7	13	4.0	2.4

^aSee table 13 for N's.

cases can one determine on the basis of available data that such young bees were worker-like; quite likely they would soon mate and leave.

There is a residue of nests, each inhabited by at least two females, in which the females evidently had lived together for some time and were clearly mature adults. The adult inhabitants are classified as shown in table 14.

In nest 502 two worn females, both probably egg layers, were living together, with an unworn but ovarially developed probable daughter. In each of the others there was only one well-worn bee, but in addition there was one (or in 1310, two) not or little worn bees with enlarged ovaries (A to D), sometimes fertilized. It is nearly certain that such bees at least forage and feed the young, as do adult daughters in the absence of mothers. Thus in these few nests there appear to be queens and workers, as in the more common groups of adults found in genera such as *Braunsapis* and *Exoneura*.

Neither unfertilized bees nor other associates of egg layers averaged smaller than a series of egg layers.

IMMATURE STAGES: Table 13 shows the numbers and relative frequencies of the various stages. Table 15 shows the sizes of the groups of young. Compared with *A. mucronata* the groups are smaller in early spring and far larger in February, as indicated before. Several nests contained very large complements of immature stages; the one with 26 (table 15) contained two adult females, one of which was classified as E-0 and was doubtless a recently emerged adult (several of the young were pupae), so that the total number of progeny was at least 27.

The positions of the young and care of them

are as in *A. mucronata*. Larvae with pollen on them were recorded less commonly than for that species. Eggs are more robust than in *A. mucronata*, about 2.5 mm. long in *A. panurgoides*.

***Allodape friesei* Strand**

Figures 50–55

Forty-two nests of this species were studied at localities in Cape Province as follows: Cape Nature Reserve; Hout Bay; Noordhoek; Strandfontein; Kirstenbosch Botanical Gardens; Du Toitskloof; 3 miles south of Avontuur, 3500 feet altitude; Worcester, 1000 feet altitude; 5 miles north of Worcester; and 7 miles west of Robertson. The last three localities are in karroo or marginal karroo vegetation where nests were all in dead flowering stems of *Cotyledon paniculatum*; the others are all in Cape macchia. The species is found in nesting areas 8 and 9 of Michener, 1970a.

There is nothing in the life history data available to suggest differences in life cycle between this species and *A. panurgoides* and *ceratinoides*. Few dissections were made to examine ovaries and spermathecae; evidence from these sources is therefore meager. Only one nest of *A. friesei* was taken in February but it contained eggs, larvae, prepupae, and pupae, not an uncommon finding for *A. panurgoides* and *A. ceratinoides* but unknown for *A. mucronata*. Eggs are similar to those of *A. panurgoides*.

***Allodape rufogastra* Lepeletier**

Figure 56

Skaife (1953) gave a little information about this species under the name *abdominalis*, but provided almost no firm data. The species ranges from the Cape to Natal; Skaife's observations were made at Hout Bay, on the Cape Peninsula. The eastern and western populations differ in appearance and structure and possibly represent different species. Data on the two are segregated below.

CAPE POPULATIONS: Nests were studied at Kirstenbosch Botanical Gardens near Cape Town, and a single one at Noordhoek, Cape Peninsula. The species was not seen by me at Hout Bay although 15 to 20 years earlier Skaife (1953) found it in the exact place where I worked. Only 20 nests in all were found. The habitat is that characterized as nesting area 9 by Michener (1970a).

TABLE 16

NUMBER OF EGGS, LARVAE, AND PUPAE OF *Allodape rufogastra* (CAPE FORM) PER NEST

	Maxi- mum	Mean in Nests Contain- ing Eggs or Young	Mean for all Nests	No. of Nests
Sept. 12–Oct. 6	8	8.0	8.0	2
Oct. 15–Nov. 15	19	10.8	10.8	6
Nov. 24–Dec. 4	16	11.7	11.7	6
Feb. 5–7	11	6.3	4.1	6

The life cycle is clearly similar to that of *A. panurgoides* and *ceratinoides*. A difference is that larger numbers of eggs are laid as shown by the following maxima: a nest contained five eggs on September 29, three October nests, seven eggs each, and two February nests, six. The result is larger nest populations of young as shown in table 16 (compare with table 15). Reproduction may be even more uniformly continuous than in *panurgoides* and *ceratinoides*, although it is less intense in summer, as shown by February nests, than in spring. The identity of columns two and three of table 16 for the spring months shows that all the nests found (14) contained some young, in contrast to the situation in *A. mucronata*, *panurgoides*, and *ceratinoides*, in which nests with no young are common. The large number of eggs and young is not a result of more females per nest than in the other species; the average number is about the same and most nests are inhabited by only one adult female.

In both western and eastern populations most nests inhabited by considerable populations of young fail to have them in the usual order from youngest below to oldest above. Although in general such an arrangement is maintained, there are many irregularities. This is in contrast to *A. mucronata*, *panurgoides*, *ceratinoides*, and *friesei* in which irregularities are exceptional.

EASTERN POPULATIONS: Twenty-six nests were studied in December and January in Grahamstown, Cape Province and the following localities in Natal: Pietermaritzburg and vicinity; Richmond, 2800 feet altitude; Umbumbulu; and 7 miles northeast of Kranskop. The habitats are indicated as nesting areas 5 and 7 by Michener (1970a).

TABLE 17
NUMBERS OF EGGS, LARVAE, AND PUPAE OF *Allodape* IN
SUMMER (DECEMBER–FEBRUARY) NESTS FROM NATAL

Species	Maximum	Means in Nests Contain- ing Eggs or Young	Mean for all Nests	No. of Nests
<i>Allodape exoloma</i>	21	7.3	6.6	35
<i>Allodape stellarum</i>	11	3.3	2.8	21
<i>Allodape pernix</i>	4	2.4	2.1	8

The nests from Grahamstown, December 6, suggest spring nests from western Cape Province in the large numbers of immature stages; one contained 26 eggs and young and two young adult females, a total brood of at least 28. One nest, however, had no eggs or young. Some nests from Natal, December 13 to January 11, were suggestive of the February nests from western Cape Province in the smaller numbers of young but others contained a large brood, in one case 30 young, including nine eggs.

Eggs are rather robust, 2.4 to 2.7 mm. long, 0.94 to 1.15 mm. in diameter. The larger figures relate to western populations.

Allodape exoloma Strand

Thirty-eight nests of this principally eastern species were found, at Grahamstown and 17 miles northeast of Knysna, Cape Province and the following localities in Natal: the vicinity of Pietermaritzburg; Karkloof (40 miles north of Pietermaritzburg); Richmond, 2800 feet altitude; Salt Rock; 14 miles east of Bulwer, 3900 feet altitude; and Cathedral Peak Hotel, 28 miles south of Winterton, 4700 feet altitude. These nests were taken in December and January. Habitats are described as nesting areas 4, 5, and 7 by Michener (1970a).

In the large numbers of eggs and young (table 17) this species resembles *A. rufogastra*, to which it is morphologically similar. No meaningful differences in life history between *A. exoloma* and *A. rufogastra* are indicated by available data. Eggs measured about 2.3 mm. long, 0.8 mm. in diameter.

Allodape pictifrons Smith

Only three nests of this species were found and adults were nowhere found on flowers. From the

abundance of this species in collections it must have been sometimes common in the Cape area.

The nests were all taken in October, one at Noordhoek, the others in the Cape Nature Reserve, both localities in Cape macchia on the Cape Peninsula (nesting area 9 of Michener, 1970a).

There is nothing in the meager data to indicate differences in life history from *A. panurgoides* and *ceratinoides* or for that matter, *A. mucronata*. One egg measured 2.6 mm. long.

Allodape quadrilineata (Cameron)

Six nests of this species were taken in the vicinity of Grahamstown, Cape Province, November 18 to 20 (nesting area 6 of Michener, 1970a).

The last paragraph on *A. pictifrons* applies equally to *quadrilineata*.

Allodape stellarum Cockerell

This species is rather common in eastern South Africa. However, only 21 nests were found, all in Natal, during the summer months (December to February), at the following locations: Pietermaritzburg and vicinity; Salt Rock; 7 miles northeast of Kranskop; Tugela Mouth. Typical habitats are described as nesting areas 4 and 5 by Michener (1970a).

As indicated by table 17, the relatively small numbers of eggs and larvae per nest are suggestive of *A. panurgoides* and *ceratinoides*. The relatively short ovaries, with few white or gray bodies are like those of *panurgoides* and *ceratinoides*, as are the eggs.

In two nests containing two females each, only one per nest was fertilized with enlarged ovaries. The other one in each nest was unfertilized with ovaries of class D. Nothing suggests relations among such individuals different from those found in *A. panurgoides* and *ceratinoides*.

Allodape pernix (Bingham)

Seven nests of this species were found at Salt Rock, 7 miles northeast of Kranskop, and Tugela Mouth, Natal. Because of its scarcity, the species does not appear in the account of nest sites (Michener, 1970a) but habitats were described there as nesting areas 4 and 5. Nests were found in both sun and partial shade. Data on the nests and dissections suggest no differences between the life cycle of this species and that of *A. stellarum*. *Allodape pernix* is larger than *A.*

stellarum and the eggs are also larger, 2.7 to 3.0 mm. long, about 1.0 mm. in diameter.

***Allodape interrupta* Vachal AND
A. collaris Vachal**

Twelve nests of *A. interrupta* were found in Uganda, June 22 to 23, 1967, at the following localities: Kawanda, Kampala; 6 miles north of Entebbe; 22 miles west of Tororo. At the last locality one nest of the extremely similar *A. collaris* was found. The nests were in stems of vines and bushes growing at forest edges or in nearly grassy areas and seemed not restricted to shady sites as *A. dapa* and *derufata* appear to be from meager evidence.

Young of all ages were present. The mean number of eggs and young per nest was 3.6, or for the 12 nests containing eggs and young, 3.9. The maximum number of eggs and young in one nest was 10. The maximum number of eggs in one nest was four; the mean for all nests, 1.9; for nests containing eggs, 2.5.

There was only one adult female per nest except in two cases. In both of these there was one unworn, and in one case teneral, female together with a mature and somewhat worn female. Thus in the few nests found there is no evidence of groups of working females.

The eggs measured 2.4 to 2.7 mm. long, 0.70 to 0.75 mm. in diameter, curved, and loose in the bottom of the nest.

***Allodape brachycephala* Michener**

One nest of this species was taken at Kawanda Kampala, Uganda. Other than the unworn adult female it contained only one egg. The egg was loose at the bottom of the burrow, 2.1 mm. long, 0.75 mm. in diameter and slightly curved.

***Allodape derufata* Strand**

Two nests were found at Kawanda near Kampala, Uganda, on June 22, 1967, in broken stems of dead vines along an open path in a bit of streamside jungle. One of the nests lacked young, the other contained two eggs which were loose in the bottom of the nest but no young. Each contained a single adult female and presumably both were newly established nests.

***Allodape dapa* Strand**

Two nests were found on June 23, 1967, 6 miles north of Entebbe, Uganda, in dead stems

at the edge of a patch of forest. One contained a large larva, a prepupa, and a worn adult female; the other contained two eggs, a prepupa, an unworn adult female, and a worn mature female.

The eggs were 3.4 mm. long, 0.8 mm. in diameter, curved with a slight tendency toward being sigmoid, and loose in the bottom of the burrow.

GENUS BRAUNSAPIIS

This is a large genus mainly of small bees, most common in tropical and subtropical regions although it reaches southernmost Africa as well as northern New South Wales in Australia.

In the active season most and perhaps all species have one or more workers in 30 to 45 per cent of the nests that contain eggs or young. Thus workers are rather common and may constitute more than 50 per cent of the total female population.

The comments on eggs and larvae of *Allodape* are applicable to *Braunsapis* except that in some species the eggs, or some of the eggs, are stuck to the bottom of the nest by the convex surface or to the nest wall near the bottom by the posterior end. The small larva makes no use of this egg attachment, so far as known, and the chorion is delicate and disappears soon after hatching, as in *Allodape*.

***Braunsapis trochanterata* (Gerstaecker)**

Fifteen nests of this distinctive species, which resembles a small *Allodape*, were found in stems of *Lantana camara* in partly shaded locations (nesting area 2 of Michener, 1970a) in Nairobi, Kenya, on May 11, 1967.

Young of all ages were present among the nests and sometimes even in a single nest. There was no evidence of developmental gaps. The mean number of eggs and young per nest was 2.5, or for the 13 nests containing eggs and young, 2.9. The maximum number of eggs and young in one nest was six. Six nests contained an egg each, one contained two eggs, the remainder none. Of the six pupae found (one per nest), only one was a male.

The number of adult females per nest was one or two, four nests containing two. In two of these cases, the two females were both worn, indicating that they were mature adults presumably living together on a long-term basis.

TABLE 18
STATISTICS ON EGGS AND YOUNG OF *Braunsapis facialis* FROM NATAL^a

	Eggs	Small Larvae	Medium Larvae	Large Larvae	Prepupae	Pupae
	Dec. 12–Mar. 9 (166 nests; 463 eggs and young)					
1. % of nests containing each stage	46.4	24.4	29.8	38.7	26.8	36.9
2. % of eggs and young in each stage	21.2	10.2	14.1	17.3	11.5	25.3
3. Maximum no. of each stage in one nest	5	2	3	4	3	8
4. Mean no. of each stage in nests containing that stage	1.3	1.1	1.3	1.2	1.2	1.9
5. Mean no. of each stage for all nests	0.6	0.3	0.4	0.5	0.3	0.7

^aLocalities listed in text.

Eggs were 2.1 mm. long, 0.75 mm. in diameter, curved. In the two nests for which the record was made, the egg was stuck to the bottom of the burrow by its convex surface.

***Braunsapis facialis* (Gerstaecker)**

Figures 40, 57

This species is widespread in Africa, ranging from Senegal to Angola in the west and Kenya to Natal in the east. It is quite variable, as explained by Michener (MS), and in some areas two distinguishable populations (species) may ultimately be recognizable, but no differences in behavior or life history between such forms have been noted.

I collected 253 nests in south and east Africa; 20 additional nests were taken by O. W. Richards and C. R. Carroll in Ghana and Liberia respectively. The localities, with numbers of nests and periods of collecting in parentheses after each province or country, are as follows: *Natal* (166, Dec. 12–Mar. 9): Pietermaritzburg; 11 miles south of Pietermaritzburg; St. Lucia Estuary; Salt Rock near Umhlali; Tugela Mouth; Hluhluwe Game Reserve; Scottburgh. *Transvaal* (one, Sept. 1): 17 miles east of Nelspruit, 3000 feet altitude. *Malawi* (22, April): Blantyre; Limbe; Kasungu; Shire River west of Blantyre. *Kenya* (30, May 10–July 11): Nairobi; Karen near Nairobi; 13 miles south of Malindi; Kikuyu Summit. *Tanzania* (six, June): Ngurdoto Crater, Momela Lakes, and Mt. Meru (6000 feet), all in Ngurdoto National Park near Arusha; Mto Wa Mbu, Lake Manyara. *Uganda* (29, June): Kawanda, Kampala; 22 miles west of Tororo. *Ghana* (10, Mar.–Apr.): Legon, Accra. *Liberia* (10, May–

July): Cuttington College, Bong County. Typical habitats are listed as nesting areas 2, 4, and 5 of Michener (1970a).

Groups of nests from each area and season showed about the same numbers of immature forms of all stages. Table 18 shows the frequencies of the developmental forms in the nests from Natal. A reasonable guess is that egg laying ceases or is slowed during the cool, dry winter months in Natal, but there are no data on the subject. The single nest from near Nelspruit, Transvaal, taken in early spring (Sept. 1) contained two large larvae as well as eggs and small larvae, suggesting that larvae pass the winter in the nests. The fact that similar data on nest contents were obtained from the various areas indicates that in tropical Africa the species is probably active rearing young at all seasons. Young seemed as abundant in nests in the early part of the dry season in Malawi as in the wet season in, for example, Uganda. The inadequate series of nests from the Nairobi region taken during the cool, cloudy months in that area did have somewhat fewer young than series from other areas, but all stages were present and the difference could have been sampling error rather than an indication of genuine reproductive depression, such as occurs there with *B. foveata*.

The maximum number of young (eggs to pupae) in a nest in Natal was 17, found in a December nest from Pietermaritzburg and a February nest from Scottburgh, the latter with an additional callow adult. The next highest number was only nine, found in a January and a February nest. One unusually populous nest was found in June at Kawanda, Kampala, Uganda, with 24 young (+one callow adult), although the maximum otherwise from that area was five.

At Blantyre and Kasungu, Malawi, four nests contained 16, 16, 21, and 23 (+ one callow) young although no other nest from the area was found with more than seven. These extraordinarily large groups of young are likely to be results of laying by more than one female.

The mean number of eggs and young per nest for all nests from Natal was 3.1 and for the nests containing eggs and young the corresponding figure was 3.7; these means are based on a total of 166 unparasitized nests, of which 131 contained eggs, young, or both.

As suggested by the rather small numbers in row 4 of table 18, eggs are usually laid at rather long intervals relative to the developmental rate, so that most nests contain young of scattered ages, one or occasionally two of each age class, the maxima listed in row 3 being rarely attained. These figures are high compared with figures for *Halterapis*, roughly the same as in some species of *Allodape*, lower than for species of *Allodapula* and some other species of *Allodape* and *Braunsapis*. The fact that in each nest there are commonly young of a wide variety of ages makes recognition of any tendency to produce young in separate broods difficult.

Males are not only produced in small numbers, as shown in table 8, but must permanently leave the nests when young. From the nests from Natal, which contained 248 fully colored adult females, only 17 mature males were obtained.

In each area and at all seasons a few nests were found with only an adult female and no eggs or young, or eggs and small larvae but no older young with the female. These appear to be newly established nests. Since young adults are produced over a long season, probably throughout the year in the tropics, it is not surprising that they start new nests through a similarly long period. In Pietermaritzburg all nests that could be found were removed from a section of *Abelia* hedge in mid-December. On February 2 seven new nests, one with an egg, the others with no eggs or immature stages were found in the dead twigs in the same section of hedge. One old nest, obviously missed in December, was also found. These data suggest that in this form, as in most other allodapines, nesting, ovarian and egg maturation, and probably also larval growth are slow processes.

Numerous dissections showed ovaries so similar to those of *Allodape panurgoides* that no series of drawings seems necessary.

INTERACTIONS AMONG ADULTS: The average number of adult females per nest is 1.5 (based on unparasitized nests from Natal), the maximum being four. Sixty-one per cent of the nests contained only one adult female. The females rarely show callow coloration and dissections and examination of wing wear show that usually, when two or more females are associated in a single nest, neither is a fresh, young adult. Only 13 per cent of the nests with two or more females could be considered as inhabited by a single mature female, the extra one being recently emerged and likely to leave in the near future. The remaining 87 per cent of such nests, or 34 per cent of all nests, contained two or rarely three mature adult females probably living together in long-term association.

The females were dissected from 28 nests containing two or more fully mature females. There is much diversity in the conditions of the females. In all nests at least one bee was fertilized as determined from spermathecal dissection. As table 19 shows, other bees are often unfertilized and less worn than the fertilized bee (nests 813–1526) or unfertilized and similarly little worn (nests 1044–1487), but commonly have enlarged ovaries, up to class B although not A, often as large as in the fertilized female. Presumably such unfertilized bees do not lay many eggs, or else they mate before doing so; otherwise male production would be higher than it is. Two colonies (nests 1042 and 1477) were unusual in that an unfertilized bee was markedly more worn than the fertilized one. The remainder (nests 819–1464) contained two fertilized bees, usually similar in ovarian development, and similar to very different in wing wear. Presumably such colonies or ones that may occasionally exist with three fertilized females produce the large numbers of young found in an occasional nest (see above). The available data, however, are inadequate to establish such a relationship.

A rare individual like the E-16 in nest 1042 is a typical worker in the sense of being unfertilized, with slender ovaries, yet worn. Most of the unfertilized individuals, however, have somewhat enlarged ovaries (ovarian classes B and C). If workers are to be recognized in this species, they are mostly such individuals. Some have whitish or grayish material in the lateral oviducts or lower parts of certain ovarioles, showing that the ovaries are not newly enlarged but have been producing and resorbing. If such bees became

TABLE 19
CONDITIONS OF FEMALES IN COLONIES OF *Braunsapis*
FROM NATAL^a

Nest No.	Nest No.
<i>Braunsapis facialis</i>	
813: A+16, C-0	1212: B+2, C-0
1045: B+14, B-1	1235: B+0, B-1
1071: B+19, C-1	1239: A+1, B-2
1104: B+8, C-0	1457: A+2, C-3, F-0
1125: A+9, B-1	1458: B+3, B-0
1231: A+17, E-0	1487: C+5, E-3
1242: A+33, C-0	1042: B+2, B-0, E-16
1248: A+23, C-1, E-0	1477: A+1, C-13, E-0
1511: A+15, C-8	819: A+18, B+25, F-0
1526: B+5, B-0, C-0	1115: A+22, A+1
1044: B+0, C-1	1123: A+7, B+0
1045: B+2, B-0, C-0	1217: A+7, C+0
1105: B+0, E-0	1227: B+23, C+0
1118: A+1, B-3, B-0	1464: A+6, B+24
<i>Braunsapis leptozenia</i>	
859: A+9, C-1	1460: B+15, C-2
854: A+7, B-1	1536: A+5, D-0, E-6,
874: A+3, E-6, E-0,	E-0, E-0, E-0
E-0	(callow)
882: A+5, A-0, B-0	853: B+6, E-0
888: A+10, C-1, F-0	799: A+0, A-5
(callow)	
889: A+18, B-0, C-0,	845: A+3, B-3, E-0
E-2	
1046: A+3, C-1, C-0,	1061: B+0, E-3
F-0 (callow)	1226: B+0, C+21
1228: A+12, C-6	1253: B+0, B-0, D+6

^aEach colony consisted of two to six fully colored females, information on which is separated by commas. Symbols as for table 14; see Methods. Parasitized colonies are omitted.

fertilized, they would not be distinguishable from egg layers that had recently laid an egg. There is no size difference (as indicated by head widths and wing lengths) between fertilized egg layers and the unfertilized bees listed in table 19.

The relative productivity of nests with two or occasionally three females versus lone females was tested by comparing numbers of immature stages (eggs to pupae) in nests from Natal with two mature females and with lone females. The mean number of immatures in nests with two females was 5.9, the range 0-17 (based on 50 nests from Natal), with lone females 1.8, the range 0-7 (based on 80 nests from Natal). When only eggs and small larvae were considered, the corresponding means were 1.9, range 0-5, and

0.4, range 0-2. Differences between the number of young associated with two and with lone females are, for both measures, significant at the 0.001 level. It is evident that in this species the acquisition by a female of an associate, probably a daughter, much more than doubles the productivity.

IMMATURE STAGES: The sizes of nest populations of immature stages have already been indicated. Pollen was found on the nest walls in only two of the 253 nests opened, and only rarely was food found on the under surfaces of larvae; when such food was found it was often a clear viscous liquid (nectar?) rather than pollen.

The eggs measured 1.8 to 2.1 mm. long, about 0.7 mm. in diameter. Although often loose in the bottom of the burrow, the egg may be stuck to the concave bottom by its correspondingly convex surface or attached to the side of the burrow very close to the bottom by its posterior end. Sometimes in a single burrow, one egg is loose, another attached either by its end or the convex side.

The small larvae lie in the bottom of the burrow, larger ones support themselves by stretching across the lumen of the burrow as in *Allodape* and other *Braunsapis*. Immature stages are ordinarily kept quite strictly in order from youngest near the bottom of the burrow to oldest near the entrance. Eggs and small larvae may be mixed, and occasionally there is an irregularity in the arrangement elsewhere, but usually not. Food is provided individually, on the ventral surfaces of the larvae, as in other *Braunsapis* and *Allodape*.

As with *Allodape* and other *Braunsapis*, larval feces are not found in the nests and must be removed by adult bees as they are voided. Young are moved about in the nests, as in other species of *Braunsapis* and *Allodape*.

Of 79 nests taken at Salt Rock, 36 contained the parasitic bee *Nasutapis straussorum* and one contained the presumably parasitic species *Braunsapis natalica*.

***Braunsapis bouyssoui* (Vachal)**

Although small numbers of nests of this widespread species were censused by me in east Africa, a substantial number of nests from which useful information on the life cycle and behavior could be obtained was found only in Natal. I collected 75 nests. The localities, with numbers

TABLE 20
STATISTICS ON EGGS AND YOUNG OF *Braunsapis bouyssoui* FROM NATAL^a

	Eggs	Small Larvae	Medium Larvae	Large Larvae	Prepupae	Pupae
	Dec.-Feb. (46 nests; 215 eggs and young)					
1. % of nests containing each stage	60.9	52.2	43.5	54.3	21.7	56.5
2. % of eggs and young in each stage	20.0	17.7	17.2	17.7	5.1	22.3
3. Maximum no. of each stage in one nest	4	5	4	5	3	7
4. Mean no. of each stage in nests containing that stage	1.5	1.6	1.9	1.5	1.1	1.8
5. Mean no. of each stage for all nests	0.9	0.8	0.8	0.8	0.2	1.0

^aLocalities listed in text.

of nests and periods of collecting in parentheses after each province or country, are as follows: Natal (46, Dec.-Feb.): St. Lucia Estuary; Salt Rock near Umhlali; Pietermaritzburg; 6 miles south of Kwa-Mbonambi; Scottburgh. *Transvaal* (three, Sept.): 17 miles east of Nelspruit, 3000 feet altitude. *Malawi* (11, Apr.): Cape McClear; Blantyre. *Kenya* (12, May): Nairobi; 13 miles south of Malindi. *Uganda* (three, June): Kawanda, Kampala. Habitats are described (using the synonymous name *B. rufipes*) as nesting areas 2 (rare), 4, and 5 (rare) by Michener (1970a).

The nests are suggestive of those of *B. facialis* in contents and the following comments are comparative, indicating those few differences noted between that species and *B. bouyssoui*. Table 20 shows the frequencies of developmental stages in nests from Natal.

The species was taken abundantly only in warm areas—the Natal Coast, the Kenya coast, and Blantyre in Malawi. Only four nests were found in the Kenya highlands (Nairobi); they contained young of all stages suggesting that this species does not have the potentiality shown by *B. foveata* to become inactive and nonreproductive in unfavorable seasons. This suggestion is supported by the numerous young in nests taken in the early dry season (April) at Blantyre and Cape McClear, Malawi.

The maximum number of eggs and young found in a nest in Natal was 12, although one with 13 was taken in Uganda, and nests with 16 and 20 were taken at Nairobi.

The mean number of eggs and young per nest from Natal was a little higher than for *B. facialis*, 4.7 for all nests and 5.5 for the nest containing eggs and young (based on 46 nests, 39 of which

contained eggs or young). These means are smaller than for *B. leptozonia* and *foveata*, largely owing to the relative scarcity of eggs, features showing the similarity to *facialis*. As with the latter species, nests tend to contain young of all ages and recognition of developmental gaps indicating production of young in separate broods is not possible.

The average number of adult females per nest in Natal was 1.6, the maximum being four, approximately as in *B. facialis*. Sixty-three per cent of the nests contained only one adult female. Dissections were not made of many females but there is nothing to suggest differences in the nest populations from those observed for *facialis*.

Eggs were about 1.7 mm. long, 0.6 to 0.7 mm. wide, commonly stuck to the bottom of the burrow by the convex surface or to the side of the burrow at the bottom by the posterior end, just as in *B. facialis*.

***Braunsapis leptozonia* (Vachal)**

Figures 17-22

This small species ranges from eastern Cape Province to Kenya and from Angola to Senegal. It is somewhat variable geographically but there seems little doubt that only one species is involved. Its biology was studied in Cameroon (Michener, 1968) in some detail but only for one month. The data now available cover most of the year and a variety of localities, but the longest series of nests was from Natal where detailed comparison with *B. facialis* is therefore possible, as the two species often occur together.

I collected 197 nests; 12 additional nests were taken by O. W. Richards and C. R. Carroll in

TABLE 21

STATISTICS ON EGGS AND YOUNG OF *Braunsapis leptozonia* FROM NATAL^a

	Eggs	Small Larvae	Medium Larvae	Large Larvae	Prepupae	Pupae
	Dec. 12–Feb. 9 (73 nests; 500 eggs and young)					
1. % of nests containing each stage	61.6	35.6	34.2	56.2	37.0	46.6
2. % of eggs and young in each stage	45.4	8.4	9.8	15.6	6.8	14.0
3. Maximum no. of each stage in one nest	12	6	6	7	3	4
4. Mean no. of each stage in nests containing that stage	5.0	1.6	2.0	1.9	1.3	2.1
5. Mean no. of each stage for all nests	3.1	0.6	0.7	1.1	0.5	1.0

^aLocalities listed in text.

Ghana and Liberia, respectively. The localities, with numbers of nests and periods of collecting in parentheses after each province or country, are as follows: *Cape Province* (three, Dec. 6): Grahamstown. *Natal* (73, Dec. 12–Mar. 9): Pietermaritzburg; 11 miles south of Pietermaritzburg; Nagle Dam, 17 miles east of Pietermaritzburg; Richmond; Salt Rock near Umhlali; Scottburgh; Hellahella, 13 miles southwest of Richmond; Cathedral Peak Hotel, 28 miles south of Winterton, 4700 feet altitude; Hluhluwe Wildlife Reserve. *Transvaal* (50, Sept. 1–2): 17 miles east of Nelspruit, 3000 feet altitude; 29 miles west of Nelspruit, 3250 feet altitude. *Malawi* (17, April): Limbe; Lilongwe; Kasungu. *Kenya* (44, May 3–July 3): Karen, Nairobi, 6000 feet altitude; Kikuyu Summit; 40 miles southeast of Eldoret; 30 miles south of Kitale; Ngong Hills. *Uganda* (10, June): Kawanda, Kampala. *Ghana* (eight, Mar.–Apr.): Legon, Accra. *Liberia* (four, May–July): Cuttington College, Bong County. Some habitats are described, using the name *B. grandiceps*, as nesting areas 1, 2, 3, 4 (rare), 5, and 7 by Michener (1970a).

Groups of nests from most of the areas and seasons show nest conditions similar to those indicated for Natal by Table 21. The similarity of this table to the comparable table given by Michener (1968) for nests from Cameroon documents the widespread uniformity of nest conditions. Even in the cool, cloudy season in the Kenya highlands nests were similar, with large numbers of larvae and especially of eggs.

A possible seasonally mediated difference was noted at Limbe and Lilongwe, Malawi, during early dry season (April), when the nine nests taken contained only three eggs, three large

larvae, one prepupa, and one pupa in all. The implication is that in the dry, flowerless season of this savanna area, reproduction may be greatly diminished.

Reduction of reproductivity also occurs during the cool, dry months of winter in Natal. The series of 50 nests from the Nelspruit area in eastern Transvaal, a region having a climate not greatly different from that of Natal, taken in early spring (Sept. 1 and 2), indicates how overwintering must occur. Forty-four per cent of the nests contained eggs (one to five each), 10 per cent contained small larvae; presumably the eggs and small larvae represent a burst of spring activity. Only 9 per cent of the nests contained any older immature stages; the totals for all nests were three medium-sized and eight large larvae, one prepupa, and two pupae. These data indicate that a few medium-sized or large larvae pass the winter in the nests.

The principal overwintering stage is the adult female, of course. Among the 50 nests from the Transvaal 80 per cent contained only one adult female and the mean number per nest was 1.5, with a maximum of eight. There were also four adult males in the nests. About 80 per cent of the overwintered adults were unworn, a higher percentage than found in summer in Natal, although a few were slightly to much-worn (up to 20 wing nicks in total on the forewings). As in summer most nests contained one fertilized female and the additional females in some of them were often unfertilized. The same combinations of ovarian types and the like, shown for summer colonies in table 19, were found in the spring colonies from the Nelspruit area. The only different feature was the abundance of ovarian class D, with only one or two large eggs;

it seems likely that a goodly number of the eggs in the nests must come from such individuals rather than from ovarian classes A and B which are obviously the main sources in summer.

The maximum number of young (eggs to pupae) taken from a nest in Natal (summer) was 31 found in a December nest in Pietermaritzburg. Other high numbers were 26 found in February, 23 in each of two January nests, and 21 in December. Nests with 24 and 20 eggs and young each were found in Kenya in May and June.

The mean number of eggs and young per nest for all nests from Natal was 6.8 and for nests containing eggs and young the corresponding figure was 7.8. These means are based on all 73 available nests, of which 63 contained eggs, young, or both.

Table 21 and figures in the preceding paragraphs and in Michener (1958) show that, compared with *B. facialis*, nests of *B. leptozonia* in both Cameroon and Natal (and, to judge by more meager data, elsewhere) contain many more immature individuals. The large total number of eggs and young per nest (mean of 6.8 compared with 3.1 in *facialis*) is largely owing to the number of eggs (mean of 3.1, or 2.5 for Cameroon, compared with 0.6 for *facialis*). Larvae are also more numerous in *leptozonia* nests than in those of *facialis*; for pupae the difference is less. The explanation of this could be that *B. leptozonia* lays at a more rapid rate than *facialis* but that either the mortality is higher or the larval and pupal growth rate is more rapid so that the number of pupae per nest turns out to be not much different from that found in nests of *facialis*. Alternatively, the laying rate might be the same as in *facialis* if the developmental rate of larvae and especially of eggs were slower, so that larvae and especially eggs accumulate in the nest.

There are commonly young of a wide variety of ages in a given nest. In 37 of the 73 nests studied in Natal, young ranged if not from egg to pupa, then from egg to large larva, or small larva to pupa. In 18 such nests there was a major gap in ages of the brood, as was noted for a similar percentage (19 out of 36) of nests in Cameroon, mostly nests occupied by single adults. This finding is interpreted as indicating that a bee commonly lays several eggs, stops, then lays a few more eggs when her first progeny are nearing maturity. This is a familiar finding

in allodapines, as is the finding in other nests of young of intermediate ages, showing that the cessation in laying may not be complete.

As the larger number of eggs in nests would suggest, *B. leptozonia* has ovaries in which more large oocytes may be found than in *B. facialis* or *Allodape panurgoides*. An egg ready to be laid does not almost destroy the anterior part of the ovary, as in *facialis* and *panurgoides* (compare figs. 14 and 20). A developmental sequence is suggested by figures 17 to 22.

Males are rarely found in nests. Few are produced (table 8) and they must leave the nests promptly; nests from Natal contained 122 fully colored adult females and only four adult males.

In contrast to the situation in Cameroon, new nests (those without young or with only eggs or small larvae) were scarce in Natal in summer; only about two nests per month in this category were found. In Cameroon one-third of the nests were new. In the seasonal climate of Natal, most of the nests are probably started in spring. In the September (spring) series of nests from the Nelspruit area described above, 91 per cent had no young or only eggs or small larvae.

INTERACTIONS AMONG ADULTS: The average number of adult females per nest in the Natal series was 1.8, the maximum six. Fifty-three per cent contained only one adult female. As with *B. facialis*, callow females are not common and usually when two females are present, neither is a fresh, young adult. In only 20 per cent of the nests with two or more females could all but one be considered as young (mostly callow) individuals. These nests were regarded as inhabited by a single mature female, the extra ones being recently emerged, likely to leave, and certainly not yet much involved in the nest activities. The remaining 80 per cent of such nests, or 38 per cent of all nests, contained two or more mature adult females probably living together in long-term association.

The females were dissected from 16 nests from Natal containing two or more mature females. The findings correspond well to those described for *B. facialis* in the present paper and for *B. leptozonia* and *foveata* by Michener (1968). Differences from *facialis* include consistently less wing wear, as would be expected since *leptozonia* is a smaller bee, and greater frequencies of colonies of three or more mature females and of colonies with two individuals having class A ovaries. Colonies such as are mentioned by

Michener (1968) containing no fertilized bees were not found in Natal. The data are given in greater detail in table 19.

The fertilized egg layers or queens average slightly larger in size than unfertilized, fully mature worker associates having at least some ovarian enlargement or wing wear as evidence of age. Mean head width of the first group was 1.35 (N=14), of the second group 1.31 mm. (N=21). The difference was significant according to the Kruskal-Wallis test at the 0.01 level; moreover similar differences (not significant) have been noted for the same species and for *B. foveata* in Cameroon and for other species of the genus in Australia (Michener, 1963, 1968).

The positive relation between number of young in a nest and number of adults for this species and *B. foveata* was shown in Cameroon by Michener (1968). To put it on terms comparable with those used for *B. facialis*, the following data for Natal *B. leptozonia* are provided: The mean number of immature stages (eggs to pupae) in nests with two or more females was 10.8, range 0-31 (based on 36 nests); with lone females, 2.9, range 0-8 (based on 36 nests). When only eggs and small larvae were considered, corresponding means were 6.4, range 0-16, and 1.2, range 0-5.

IMMATURE STAGES: The large size of egg and larval populations compared with *B. facialis* have already been indicated. Contrary to observations made in Cameroon, pollen was rarely found in the nests in Natal and East Africa; this agrees with the rarity of pollen in nests of *facialis* and other allodapines in the same area.

Eggs were about 1.5 mm. long or slightly less, 0.6 mm. in diameter, rather robust and little curved, and usually loose, often in a clump, at the bottom of the burrow.

Comments on larvae of *B. facialis* apply here also, and are not at variance with material presented by Michener (1968) based in part on *B. leptozonia* in Cameroon.

Braunsapis foveata (Smith)

Figure 58

This species, which ranges from Natal to Ethiopia and Angola to Senegal, was studied with *B. leptozonia* in Cameroon by Michener (1968). The data now available are for various additional localities and months, as listed below: Natal (36, Dec.-Feb.): Nagle Dam, 17 miles east

of Pietermaritzburg; Salt Rock near Umhlali; Richmond, 2800 feet altitude; St. Lucia Estuary; 11 miles south of Pietermaritzburg. Transvaal (five, Sept.): 17 miles east of Nelspruit, 3000 feet altitude. Malawi (nine, Apr.): Blantyre; Kasungu; Lilongwe; Limbe. Tanzania (three, June): Ngurdoto National Park near Arusha. Kenya (65, May, June): Nairobi; Karen, Nairobi; 56 miles west of Eldoret; 30 miles south of Kitale. Uganda (three, June): Kawanda, Kampala; 22 miles west of Tororo. Habitats are described as nesting areas 1, 2 (rare), 3, 4, and 5 (rare) by Michener (1970a).

The life cycle and social organization of *B. foveata* closely resemble those of *B. leptozonia*. Fewer nests were found than for *leptozonia* but the account for *leptozonia* appears to be applicable to *foveata* except as indicated below.

In the cool, moist months in the Kenya highlands, unlike *B. leptozonia*, foraging and rearing of larvae nearly stop. During the period May 3 to June 17 in the vicinity of Nairobi, 63 nests of *B. foveata* were found. Most contained one adult female, unworn or with various degrees of wing wear, no larvae and pupae, but one to eight eggs. Sixteen contained neither eggs nor young. Five contained a small larva in addition to the eggs. Only two contained large larvae, prepupae and pupae. During the month and a half period, no change was observed in the frequencies of eggs and immature stages. Only three nests contained more than one adult female; two were the nests with prepupae and pupae each of which had four adult females, the other contained two females. Before arrival of the cool weather, most young must mature, females mate, colonies break down, and nearly every female must establish a nest for herself.

The few nests taken in the lower, warmer climate of Uganda at the same season and in Malawi in the early dry season (April) showed normal numbers of young of all stages, as were found in Cameroon and Natal in warm wet (i.e., favorable) weather. The only other experience with this bee in an unfavorable season was in spring (Sept. 1-2) in the eastern Transvaal, 17 miles east of Nelspruit, where five nests were taken, four each containing only an adult female, the fifth with a single egg in addition to its female. If this small sample is meaningful, the species passes the winter in this area and in climatically similar Natal as lone females without immature stages.

TABLE 22
STATISTICS ON EGGS AND YOUNG OF *Braunsapis foveata* FROM NATAL^a

	Eggs	Small Larvae	Medium Larvae	Large Larvae	Prepupae	Pupae
	December (36 nests, 249 eggs and young)					
1. % of nests containing each stage	77.8	19.4	30.6	25.0	27.8	69.4
2. % of eggs and young in each stage	57.4	3.6	7.2	7.6	5.2	18.9
3. Maximum no. of each stage in one nest	9	3	4	4	3	4
4. Mean no. of each stage in nests containing that stage	5.1	1.3	1.6	2.1	1.3	1.9
5. Mean no. of each stage for all nests	4.0	0.2	0.5	0.5	0.4	1.3

^aLocalities listed in text.

From its absence at the high altitudes and latitudes attained by *B. leptozonia* and from its seemingly greater response to cool weather both in the Kenya highlands and the Transvaal, *B. foveata* can be assumed to be more sensitive to cold than *leptozonia*. The species is scarce even at the altitude of Pietermaritzburg in Natal, but common at lower altitudes such as at Nagle Dam.

In Natal in summer the frequencies of the eggs and immature stages are very similar to those found in Cameroon (Michener, 1968) for this species and *B. leptozonia*, and in Natal for *B. leptozonia*, as shown in table 22. The preponderance of eggs is obvious. The maximum number of eggs and young found in one nest in Natal was 16, but in Blantyre, Malawi, a nest was found with 39 eggs and young. All but three of the 36 nests censused in Natal contained eggs or young; the mean number per nest was 7.2 for all nests, 7.8 for nests containing eggs or young. The similarity to the comparable figures for *B. leptozonia* is obvious. So also is the presence of a major developmental gap in ages of young in about half the nests containing a broad range of ages, the scarcity of males in the nests, and of newly established nests in contrast to the situation in Cameroon.

The following note was made after opening the long series of nests from Nagle Dam, Natal, December 17, 1966: "Seems unusually well synchronized in that most nests showed a major gap between eggs and older young." These eggs presumably represent the second layings of the females and the synchronization is probably a result of the sensitivity of the species to the cold of winter at this warm temperate latitude.

Comments on interactions among adults and

on immature stages in the treatment of *B. leptozonia* apply also to *B. foveata* except that the maximum number of adult females found in a nest was five instead of six, and 61 per cent (instead of 53 per cent) of the summer nests from Natal contained only one adult female. Dissections were not made as the number of nests was not large enough to be particularly useful, but the frequency of nests with two or more fully mature females living together was somewhat smaller than in *leptozonia*. Such a difference between these species was not found in Cameroon (Michener, 1968) and sampling error may explain the apparent difference in Natal.

Eggs were from 2.1 to 2.4 mm. in length, 0.70 to 0.75 mm. wide, slightly curved, and loose in the bottom of the nest.

In the Nairobi area I noted that although the nest burrows had been excavated with narrowed entrances, most of them had the constructed entrance collars found in most allodapine nests weakly developed or absent, so that the nests from the outside resembled those of *Ceratina*. Such observations were not made elsewhere and are probably a reflection of the seasonal inactivity and large number of new nests in the Nairobi sample.

***Braunsapis luapulana* (Cockerell)**

This small species (related to *B. leptozonia*) is found in equatorial Africa from the west coast to the Kenya highlands. Thirty-four nests were found in May and June at the following localities: *Kenya*: Karen, Nairobi; Kikuyu Summit; 30 miles south of Kitale. *Tanzania*: Ngurdoto Crater, Momela Lakes, and Mt. Meru (6000 feet altitude), all in Ngurdoto National Park, near Arusha. *Uganda*: Kawanda, Kampala;

22 miles west of Tororo. A habitat is described as nesting area 3, using the synonymous name *B. convexa*, by Michener (1970a).

The nests are essentially like those of *B. leptozonia* in content, there being even larger numbers of young and especially eggs. The mean number of eggs and young per nest from all nests was 7.8, and for the 27 nests containing eggs and young the corresponding figure was 9.6. Maximum numbers of eggs and young in the three most populous nests were 30, 34, and 36; one contained 13 eggs. The number of eggs per nest is considerably larger than for *leptozonia*, a mean of 4.0 for all nests, 5.2 for the 25 nests containing eggs.

The numbers of adults in the nests was essentially as described for *B. leptozonia*.

Arrangement of eggs and young was also as described for *B. leptozonia*. Eggs were 1.26–1.45 mm. long, 0.50–0.65 mm. in diameter, slightly curved. They are smaller than those of *leptozonia*.

Braunsapis draconis Michener

This is a small species from Natal, of which 32 nests were found during January and February in the following localities: Cathedral Peak Hotel, 28 miles south of Winterton, 4700 feet altitude; Hellahella, 13 miles southwest of Richmond; 14 miles northeast of Bulwer, 3900 feet altitude. All but four of the nests came from the first locality, in dead stems of *Artemisia*.

The nests are similar to those of *B. leptozonia* but differ in containing more young and more adult bees. The average number of eggs and young per nest was 13.8; no nest was found without at least one egg or young. The maximum number of these stages found in a single nest was 41. The number of eggs per nest was impressive, reaching a maximum of 16. The mean was 4.7, or 5.3 for the 29 nests containing eggs. The figures for eggs are about as for *B. luapulana*.

The number of adult females per nest averaged 3.0 with a maximum of six. Two-thirds of the nests contained more than one adult female. The mean is far higher than for similar species but includes some callows and probably other young adults. As shown in table 8, the sex ratio is about 1:1, unusual for an allodapine, but approached by *B. luapulana*.

Arrangement of eggs and young was as in *B. leptozonia*. Eggs were 1.40–1.55 mm. long, 0.6–0.7 mm. wide, slightly curved.

Braunsapis rhodesi (Cockerell) AND

B. stuckenbergorum Michener

These species belong to the group of *B. luapulana*, *draconis*, and *leptozonia*. Relatively few nests of each have been found, as follows:

(1) *rhodesi*, 10 from Natal (Richmond, 2800 feet altitude; Pietermaritzburg; Umbumbulu—Dec.–Jan.) and 10 from Malawi (Limbe; Blantyre; Kasungu; Lilongwe—Apr.) A habitat has been described as nesting area 5 by Michener (1970a).

(2) *stuckenbergorum*, 26 from Natal (Richmond, 2800 feet altitude; Pietermaritzburg; Nagle Dam, 17 miles east of Pietermaritzburg; 11 miles south and 5 miles northwest of Pietermaritzburg; Hellahella, 13 miles southwest of Richmond; 8 miles south of Richmond; Cathedral Peak Hotel, 28 miles south of Winterton, 4700 feet altitude—Dec.–Feb.). A typical habitat is described by Michener (1970a) as nesting area 5.

There is nothing in the data to suggest biological differences from the well-known *B. leptozonia*. The preponderance of female pupae appears to be as in *leptozonia* (table 8).

Eggs of *B. rhodesi* from Malawi were recorded as 1.65 mm. long, width 0.6 mm. Eggs of *B. stuckenbergorum* are among the smallest known for any *Braunsapis*, 1.2 mm. long, 0.5 mm. in diameter, not curved although straight on one side, convex on the opposite.

Braunsapis rolini (Vachal)

This is a rather distinctive looking small species of equatorial Africa, ranging from the Atlantic Coast to the Kenya highlands and to Mozambique. Only 10 nests were found, all in May, June, and July, at Nairobi, Kenya, and 22 miles west of Tororo, Uganda. The nests from Nairobi were from nesting area 2 of Michener (1970a).

With such meager data, one cannot definitely say whether this species fits into the pattern of those that have few eggs in the nest at any one time, like *B. facialis*, or those that commonly have several, like *B. leptozonia* and its relatives, but an intermediate position seems probable. The maximum number of eggs in any of the 10 nests was three; four nests contained none. The maximum number of eggs and young in one nest was 12 but some nests old enough to contain a pupa had only one or two eggs or young in total.

One nest contained three adult females, three contained two, and the rest one each. In all cases only one bee per nest had nicks in the wing margins.

***Braunsapis gorillarum* (Cockerell)**

This is a species of equatorial Africa, common in the Kenya highlands. Forty-five nests were taken in May, June, and July, in nesting areas number 2 and 3 of Michener (1970a). The species was listed there under the *nomen nudum* *B. kenya*. These months are cool and cloudy in that area and the reproductive activity recorded below may or may not be that characteristic of the species in other seasons of the year. Young of all stages were present, however. Nests were found at the following localities: *Kenya*: Karen, Nairobi; Kikuyu Summit; Nairobi.

The mean number of eggs and young per nest was 3.7 for all nests; for the 33 nests containing eggs or young the mean was 5.1. Although all immature stages are present in the sample of nests, only four of the nests contained a more or less continuous series of stages; others contained only certain age groups or showed gaps in productivity, e.g., eggs and pupae or prepupae without intermediate stages. The maximum number of eggs and young in one nest was 25. The number of eggs per nest averaged 1.8, for nests with eggs, 3.1.

The number of young per nest is markedly lower than in *B. leptozonia* and the mean number of adult females per nest is slightly lower, 1.4. Of these some were young and the social organization is probably about as in *B. leptozonia*.

As in *B. leptozonia*, the eggs are loose, 1.71–1.81 mm. long, 0.60–0.70 mm. wide, and distinctly curved.

***Braunsapis simplicipes* Michener**

This east African species is common in the vicinity of Nairobi (nesting area 2 of Michener, 1970a) but otherwise has not been taken in any numbers. Except for a single nest found 2 miles south of Blantyre, Malawi, in April, all 58 nests of the species were found either in Nairobi or its suburb of Karen, during May to July. As for *B. gorillarum*, the cool weather of these months in Nairobi could reduce brood rearing activity. It undoubtedly does for *B. foveata*. But there is no evidence that this is the case for *gorillarum* and *simplicipes*.

The mean number of eggs and young per nest for all nests was 5.6, for the 48 nests with eggs or young, it was 6.7. The maximum number of eggs and young for a given nest was 22. The largest number of eggs in one nest was seven, the mean was 1.7 per nest or 2.8 for the 36 nests containing eggs. There was no evidence of a change in these figures during the three months of observation in Kenya.

The number of adult females in the nests averaged 1.6 with a maximum of four. A number of them were callow; there is nothing to suggest that the social organization differs from that of *B. leptozonia*. In several nests two females with worn wings were found.

Eggs were loose in the nests, from 1.25–1.74 mm. in length, 0.57–0.65 mm. in width, and gently curved.

***Braunsapis elizabethana* (Strand) AND
B. acuticauda Michener**

This is a pair of species found in the Cape macchia from western Cape Province to Port Elizabeth. I found 28 nests in September to November and February at the following localities in the western Cape Province: Hout Bay; Cape Nature Reserve; west side of Pakhuis Pass near Clanwilliam, 2500 feet altitude. A habitat is described as nesting area number 9 by Michener (1970a).

There is nothing to suggest differences in biology between the two species, and the meager data are treated together here.

The four nests found on September 12 each contained a single adult female and one medium sized or small larva. On October 15 and subsequently young of all ages including pupae were present. Only three nests were found in February, with a total of three eggs, one small larva, and one pupa. This may indicate a mid- and late-summer reduction in reproductive activity as is noted in some other Cape allodapines.

In October and November, which may be the chief season of reproductive activity, 21 nests were found. Young of all ages were often present; reproductive or developmental gaps were not evident. The number of eggs and young per nest averaged 8.8 for all nests, 9.2 for the nests containing eggs and young. The maximum number of these stages in one nest was 35. The maximum number of eggs in a single nest was 11, the mean for all 21 nests was 3.0, for those with eggs 4.1.

These figures are suggestive of *B. leptozonia* or even more, of *B. luapulana*.

Also suggestive of the group of *B. leptozonia* are the free eggs; their small size and lack of curvature suggest those of *B. stuckenbergerorum*.

***Braunsapis paradoxa* (Strand)**

This is a species of the Cape macchia ranging from the western Cape Province to Port Elizabeth. Only five nests were taken in October, November, and February at Cape Nature Reserve and the west side of Pakhuis Pass near Clanwilliam, altitude 2500 feet. A habitat is described as nesting area 9 by Michener (1970a).

The averages from so few nests probably mean little but, remarkably, all contained numerous eggs and young, even the two nests taken in February when most species in the Cape area are rather inactive. Numbers of eggs and young per nest ranged from eight to 12 with a mean of 10; numbers of eggs from two to six with a mean of 3.4. The number of adult females per nest ranged from one to four, with a mean of two.

One nest attributed to this species produced progeny of *B. elizabethana*. An error in recording the data is probable, but further study might show parasitism or some other relationship between the species.

The eggs are loose, short and robust, not curved, 1.40×0.67 mm. for one measured.

***Braunsapis* spp.**

There are, in Africa, various other species of *Braunsapis* for which nests have been found. Very little can be learned about a species from one to three or four nests. The comments below give what little information seems worth recording. None of these species showed any biological features in any way unusual for *Braunsapis*.

Braunsapis vitrea (Vachal). One nest, Nagle Dam, 17 miles east of Pietermaritzburg, Natal. Eggs loose, 1.95 mm. long, 0.7 mm. wide, curved.

Braunsapis minutula (Fries) group (see Michener, 1971). Four nests, Blantyre and Limbe, Malawi. Eggs loose, 1.24–1.50 mm. long, 0.5–0.6 mm. in diameter, curved.

Braunsapis albitarsis (Fries). One nest, Timbora, 40 miles southeast of Eldoret, Kenya, 9200 feet altitude. Eggs loose, 1.4 mm. long, 0.5 mm. in diameter, curved.

GENUS ALLODAPULA

This genus, which is restricted to southern Africa, was first recognized because of its peculiar larvae and larval feeding habits.

As indicated by table 4, worker-like or supernumerary individuals vary from scarce, even scarcer than in *Allodape* in *Allodapula dichroa*, to present in one-fifth of the nests or more in *A. melanopus* and its relatives. They are less abundant than in *Braunsapis*, however.

Eggs are small and, unlike *Allodape* and *Braunsapis*, several are laid during a relatively short period of time. They are firmly attached by their posterior ends to the walls of the nest burrow, in curious and often regular patterns which are characteristic of species or groups.

The young larvae do not at first completely leave the egg chorions; their posterior ends remain in the chorions, and the small larvae therefore project into the lumen of the burrow just as did the eggs previously. Even after it is abandoned by the larva, the shriveled chorion is relatively tough, unlike that of *Allodape* and *Braunsapis*, and often has a support function.

The larvae in a nest are usually more or less of the same age and are fed progressively from a single, common food mass. When larvae are small this food mass is supported by the larvae themselves, anchored to the nest wall by the chorions, or by unhatched eggs or by abandoned chorions. Larger larvae always form a clump around the food mass. In some species they form a ring around the food mass and support themselves and the food by pressing against the nest wall.

When feeding is complete, the clump breaks down, and larvae arrange themselves longitudinally in the nest burrow, but with the age sequence noted for *Allodape* and *Braunsapis* erratic or completely broken down.

***Allodapula acutigera* Cockerell**

Figures 23–30, 59–64, 66–70, 72

This is a somewhat large and robust species for its genus and, having an entirely black body, has the appearance of a large species of *Braunsapis* instead of an *Allodapula*. It was studied at several localities near sea level on the Cape Peninsula (Hout Bay; Kirstenbosch Botanical Gardens; Noordhoek; Cape Nature Reserve), South Africa. A few nests were also found 3 miles south of Avontuur, Cape Province,

3500 feet above sea level, and one was taken in Grahamstown. All the localities except Grahams-town were in Cape macchia, in stems usually exposed to the sun, and include nesting area 9 of Michener (1970a). A single nest was found in area number 7. Kinds of plants utilized and stem diameters are indicated in that paper. The account of the life cycle is based on data from the Cape Peninsula but there is no evidence that it is different at the other localities.

SEASONAL CYCLE: Skaife (1953) has already dealt briefly with this species. He indicated that, as in other allodapines, adult bees may be found in nests at any time of year. Egg laying begins in winter or early spring (July or early August) in nests usually each inhabited by only one female which may lay up to eight or nine eggs. Sometimes two females occupy a single nest in which case 12 or 13 eggs may result. Skaife said that some females start laying much later than others so that eggs can be found in nests until the end of September. Sometimes a female will eat an egg and replace it by another. In spring the eggs require five or six weeks for hatching and larvae are fed, usually, until some time in October. After a two-week prepupal period and a three- to four-week pupal stage, adults of the new generation emerge near the end of November and during December.

As in various other species of allodapines, some of the old females lay a few more eggs just before they die, and the young from this second brood can be found in the nest at the end of December and during January. At this season, in the heat of summer, development is more rapid; the eggs hatch in about two weeks, the larvae are fully grown about 15 days later, and the pupal stage lasts only two or three weeks. Thus these adults emerge during February and March. From then onward until the middle of the following July, only adults are found in nests. At this time considerable groups of young adults occupy the parental burrow, but just before egg laying begins in July most of the females leave and establish new nests.

As for *Allodape mucronata*, my own observations were made in the same area as Skaife's and some of them on the same property, thanks to the courtesy of Dr. Skaife. To a considerable extent my observations support those of Skaife. Of 122 nests opened in September and the first half of October, before young adults appeared, eight contained two adult females, seven contained

three; all others (107) were inhabited by only one. Clearly the normal behavior is for adults to disperse and establish their nests alone. In addition to the 144 adult females in these nests, there was only one male (found September 26); males must only rarely survive the winter. Dissections of spermathecae of all the lone females revealed only two that had not been fertilized; presumably mating normally occurs before winter. In early February, out of 66 females with not or scarcely worn wings and hence doubtless young, all taken from nests, 53 per cent were fertilized. Presumably mating usually occurs rather soon after emergence from the pupa.

The production and growth of young is less regular than indicated by Skaife. As shown in table 23, eggs are produced in each month of the spring and also in summer (early February). Data are lacking for December and January. The number of nests containing only an adult female but no young decreased from 45 per cent of the total nests in September to 24 per cent in October to 5 per cent in November, showing that some bees do not get started laying until even later in the spring than Skaife indicated. The large number of eggs in October (table 23) is a surprise, as Skaife's paper indicated that most of the young should be larvae by that time. The data show, however, that by October large numbers of the young resulting from eggs laid in winter and early spring (July, August, and perhaps even September) are prepupae and new batches of eggs are being laid. Many nests in October contain a group of pupae and prepupae and a group of eggs. Thus a second brood is commonly started in October, as well as a second or third brood in summer as Skaife indicated. In contrast to the situation in genera such as *Allodape* and *Braunsapis*, such broods are of necessity discrete in any one nest, as will be explained below, although for the population there is more or less continuous production through the spring and summer.

The first prepupae were found on October 1 and the first pupa on October 26. These dates support the indication of Skaife that in this species no immature stages survive the winter. By late November, as table 23 shows, there are many pupae and adults in large numbers must emerge at that time and, as Skaife says, in December. Meanwhile, other young are still present in considerable numbers as a result of late laying bees and second broods started in

TABLE 23
STATISTICS ON EGGS AND YOUNG OF *Allodapula acutigera*

	Eggs	Small Larvae	Medium Larvae	Large Larvae	Prepupae	Pupae
Sept. 12-27 (76 nests; 206 eggs and young)						
1. % of nests containing each stage	19.7	25.0	26.3	21.0	0	0
2. % of eggs and young in each stage	17.4	29.0	26.6	26.6	0	0
3. Maximum no. of each stage in one nest	5	8	7	12	0	0
4. Mean no. of each stage in nests containing that stage	2.4	3.2	2.8	3.4	0	0
5. Mean no. of each stage for all nests	0.5	0.8	0.7	0.7	0	0
Oct. 1-26 (74 nests; 203 eggs and young)						
1. % of nests containing each stage	37.8	5.4	6.8	16.2	17.6	5.4
2. % of eggs and young in each stage	41.4	4.4	4.9	15.8	24.1	9.4
3. Maximum no. of each stage in one nest	6	4	4	5	7	11
4. Mean no. of each stage in nests containing that stage	3.0	2.3	2.0	2.7	3.8	4.8
5. Mean no. of each stage for all nests	1.1	0.1	0.1	0.4	0.7	0.3
November 24-26 (37 nests; 188 eggs and young)						
1. % of nests containing each stage	18.9	21.6	27.0	24.3	13.5	51.4
2. % of eggs and young in each stage	11.7	8.5	14.4	13.8	4.3	47.4
3. Maximum no. of each stage in one nest	7	5	6	4	3	9
4. Mean no. of each stage in nests containing that stage	3.1	2.0	2.7	2.9	1.6	4.7
5. Mean no. of each stage for all nests	0.6	0.4	0.7	0.7	0.2	2.4
Feb. 5-7 (48 nests; 136 eggs and young)						
1. % of nests containing each stage	29.2	0	6.3	20.8	18.8	27.1
2. % of eggs and young in each stage	22.8	0	8.1	19.1	16.9	33.1
3. Maximum no. of each stage in one nest	9	0	6	6	7	10
4. Mean no. of each stage in nests containing that stage	2.2	0	3.7	2.6	2.6	3.5
5. Mean no. of each stage for all nests	0.6	0	0.2	0.5	0.5	0.9

October; moreover more eggs continue to be laid. The result is presence of young of all stages, presumably throughout the summer. The absence of small larvae in the early February sample of nests and the scarcity of middle-sized larvae may indicate a break in laying in January, but this is more likely due to hot, dry weather and consequent food shortage than to any innate factor, for adults of all ages from newly emerged to badly tattered are found in the February material as well as in the other months (table 25).

Table 24 shows the total numbers of young produced in a nest. Tables 23, 24, and 25 show conditions in February to be, in many ways, similar to those in spring. The reduced frequency of young larvae has already been discussed. The abundance of unworn young adults is higher, no doubt as a result of emergence earlier in the summer of young reared during the spring.

A much higher percentage (39.6 per cent) of the 48 nests taken in February contained two or more adult females than those taken in spring. One contained six females, and the mean number of females per nest was 1.8. Several nests also contained males.

There is more heterogeneity among females at most seasons than in *Allodape mucronata* (compare tables 10 and 25). Overwintered *acutigera* consist of unworn to much worn individuals, as do females at all other seasons.

Young adults still with pale cuticle often have ovaries of class E, not F, and almost as soon as the cuticle is dark they must enlarge to C. Individuals of class D are rare. Many individuals attain ovarian classes B and A while the wings are still unworn or nearly so. Some attain class B before mating, but most unfertilized young bees (e.g., as found in February) have ovaries of

TABLE 24

NUMBERS OF EGGS, LARVAE, AND PUPAE OF *Allodapula acutigera* PER NEST^a

	Maximum	Mean for Nests Containing Eggs or Young	Mean for all Nests
September	12	4.8	2.7
October	15	4.3	2.7
November	15	5.4	5.1
February	18	4.5	2.8

^aFor N's see table 23.

classes E or C. In all months there are considerable numbers of bees with rather slender ovaries, sometimes pedunculate, but longer, less regularly shaped, and with larger oocytes than those in freshly emerged females. Such ovaries are classified as regressed E and F, and most of them contain a few white or gray masses in the oviducts or lower parts of the ovarioles (fig. 30). Females in nests with no eggs but clumps of growing larvae are among those having such ovaries.

For the ovarian classes A, B, and C, as well as for E and F from which the obviously young females have been excluded (therefore largely regressed), females are found with wing wear ranging from 0 to more than 70 nicks. Thus these ovarian classes can all be attained by unworn bees and retained by much worn bees. However, the average degree of wear is higher for classes A and B, as shown by the following mean numbers of nicks per female based on bees taken during the spring months: class A, 50.3 (N=12); B, 21.7 (N=45); C, 10.0 (N=53); E, 7.4 (N=28); F, 12.4 (N=13). The maximal wear noted (166 nicks) was found in bees of class A,

the next in class B. No bee in classes E or F exceeded 100 nicks. These data suggest that while many class E and F bees are regressed, ovarian regression occurs among moderately worn females; badly worn bees with large ovaries (A or B) rarely regress. It may be that such bees are in their last egg laying episode and will soon die, whereas those with large ovaries but less worn wings may regress to E or F and later lay another batch of eggs.

Figures 23-30 show a sequence of ovarian enlargement and regression pieced together from dissections of numerous females.

Perhaps because several eggs are laid in a period of a few days, followed by a period without oviposition, more ovarioles contain well-developed eggs at the same time (fig. 28) than in forms like *Allodape* and *Braunsapis*. The ovaries rarely contain many of the white or gray bodies discussed for *Allodape mucronata*, but one or two, as well as one or two brownish eggs apparently being resorbed, are common.

During each month of the study (September-November, February), females were found in ovarian classes A, B, C, E, and F. In all three spring months frequencies were about 11 per cent A, 28 per cent B, 31 per cent C, 22 per cent E, and 8 per cent F (N=153). In February, however, the frequency of egg layers had dropped, so that the types appeared as 1 per cent A, 14 per cent B, 38 per cent C, 32 per cent E, and 15 per cent F (N=82). The change is partly attributable to the abundance of young bees in February. However, as shown by the near absence of class A, the sizes of the largest ovaries at this season are noticeably smaller than in spring. This suggests that egg laying would not continue long into autumn.

SUMMARY OF THE LIFE CYCLE: Winter is passed in the nests as adult females, with only a very occasional male surviving. Egg laying

TABLE 25

PERCENTAGES OF FEMALE OF *Allodapula acutigera* SHOWING VARIOUS DEGREES OF WING WEAR

Month	Number of nicks in outer margins of front wings							N
	0	1-2	3-9	10-20	21-47	48-110	111-260	
September	38.2	18.0	18.0	10.2	5.1	9.0	2.6	78
October	35.4	10.4	29.1	10.4	6.3	6.3	2.1	48
November	12.2	26.8	26.8	12.2	7.3	14.6	—	41
February	63.2	14.9	4.6	3.5	3.5	8.0	2.3	87

occurs from July at least to February, with maxima for the population in early spring and in October, and perhaps again in early summer. Each bee lays a group of eggs sometime from July to October, another group when the larvae of the first group reach the prepupal stage, and possibly more such groups. Adult females of all ages can be found at any season, some very worn bees being among those that pass the winter. Mating usually occurs early in the adult life of females and nests are established by individual females although some contain two or three females, even in spring, and up to six in summer when there are numerous young, undispersed, and often unmated adults.

INTERACTIONS AMONG ADULTS: As shown above, this is a largely solitary species. Yet in spring there are some nests (more than 12 per cent) inhabited by two or three adult females and in February the frequency of such colonies is higher, largely because of newly emerged and not yet dispersed females. There are no direct observations on the behavior of the females when jointly occupying a nest. As indicated above, however, Skaife stated that such a group lays more eggs than a lone individual, a conclusion supported by brood counts which show for nests with two or more females an average of 8.0 eggs or young per nest in the spring months, 4.1 in February. Only one such nest contained no offspring. In contrast, for nests containing only one adult female, the number of eggs and young averaged 2.5 in spring, 1.6 in February, with numerous nests containing no offspring. (For comparable figures for all nests, see last column of table 24.) The data show that groups not only lay more eggs but also rear more young to the pupal stage and presumably maturity than do lone individuals.

The membership of the groups of females varies considerably. In February and to a minor extent in November, newly emerged females constitute parts of these groups. In September and October, however, the groups consist of individuals that have presumably lived together for months and there is no reason to believe that they will soon disperse; similar groups can be recognized in November because the young adults are all fresh with slender, undeveloped ovaries (class E).

Eighteen nests were found in the three spring months containing two or three adult females, excluding those in late spring in which the extra

TABLE 26
CONDITIONS OF FEMALES IN SPRING COLONIES OF
Allodapula acutigera^a

Nest No.	Nest No.
160: A+105, C-0	69: A+166, C+0, E+0
550: A+78, F+3	113: A+15, C+1, E-0
317: A+23, F-0	144: B+87, C+0, E+5
17: B+142, E+0	7: F+100, F+0
60: B+97, E+0	18: C+28, D+0, E+92
584: B+96, C+2	13: B+6, E-0, F+0
560: B+85, E+3	73: B+0, F+0, F-0
413: B+54, C+0	182: C+0, C+0, E+3
557: B+52, E+8	100: C+2, E+0

^aFor explanation of symbols see table 14. (Nests 7-144 were opened in September, 160-413 in October, and 550-584 in November.)

adults are believed to have been recently emerged, and also excluding one in which the extra adult was parasitized by large nematodes. Of the 18 nests, 11 contained two adults, seven contained three. In most cases one individual, a queen, was much more worn and presumably older than the others, and was fertilized, and had the largest ovaries (classes A or B), as shown for colonies 160 to 144, table 26. Probably this is the mother, perhaps an older sister, of the others, which are usually fertilized but have ovarian sizes C to F. One colony (nest 7) was probably entirely comparable except that the ovaries of the old female had fully regressed; a brood of small larvae was in the nest. Another (18) contained two old, worn bees and one unworn one. In the remaining four colonies all the bees were relatively young, presumably sisters, one or, in colony 182, two of the individuals having ovaries considerably larger than the other.

A striking difference between this species and species of *Allodape* and *Braunsapis* is that the individuals with little-developed ovaries (auxiliaries) in nests with others are usually fertilized; they are often not fertilized in those other genera.

Omitting colonies 18 and 182, table 26, the bees represented by the first expression for each nest, mostly with ovaries of class A or B, average larger than the others. The mean head widths are 1.87 and 1.80 mm. respectively, the difference in means significant by Kruskal-Wallis test at the 0.001 level. Moreover, in 13 of the 16 individual nests, the largest female is the one

represented by the first expression. Among the lone individuals of all ovarian classes taken at different times from nests during the spring, mean head widths varied from 1.86 to 1.88 mm. (no significant difference between means for the ovarian classes), thus corresponding with bees represented in the first expressions of table 26, but some of the lone individuals were almost as small (1.65 mm.) as the smallest auxiliaries or workers (1.63 mm.).

The auxiliaries found in nests with an active egg layer (1) result in increased productivity of the colony, hence probably lay some eggs or stimulate the individual with larger ovaries to produce more than she otherwise would; (2) do not arrive at their status by chance, as they are ordinarily smaller than the principal egg layer. It seems likely that such individuals lay but few eggs, but also are active in foraging, defense, and the like, and are thus worker-like. One was seen carrying pollen which indicates that they forage. Whether on the death of the usually older egg layer such individuals experience greater ovarian development is unknown, but the existence of some nests with single bees and very low productivity (e.g., only one or two young) suggests that they may not. The possibility that such worker-like individuals disperse and start their own nests as the season advances exists but probably is not a general pattern, for the frequency of nests inhabited by two or three females does not decrease as time passes.

IMMATURE STAGES: The numbers of young of various stages and the relative frequencies of these stages in the population during the period of study are shown in table 23, whereas table 24 shows the sizes of the nest populations of young.

The eggs are small, about 1.3 to 1.5 mm. long, as in other species of *Allodapula*, and attached in a circle by their posterior ends around the wall of the nest burrow. They project into the burrow like the spokes of a wheel, but slope downward at an angle of about 45 degrees. When there are numerous eggs (more than four or six), the circle may become double, some eggs being about half a millimeter above the others (fig. 62). Such eggs, however, are not directly above others but alternate with them so that seen from above the "wheel" seems to have more "spokes." The circle of eggs may be within a millimeter of the bottom of the burrow but is usually several centimeters above the bottom. After one egg is laid the second may be placed opposite it or less

commonly at about 45 or 60 degrees from the position of the first. The circle is completed by filling in spaces.

When an egg hatches, the anterior part of the larval body is exposed ventral side up, but the posterior part remains in the base of the egg chorion and attached thereby to the nest wall. Such a young larva is the size of, and occupies the position of, the egg. When only one egg in a circle has hatched, a small amount of moist pollen paste may be put on its venter by the mother. However, other larvae usually hatch soon, for the eggs of any one batch are not many days different in age. Food is normally provided, at this stage in a single roughly spherical common mass of moist paste about 2 mm. in diameter supported in the middle of the nest burrow by the bodies of the young larvae or unhatched eggs. The food mass rests on the front parts of the bodies of the larvae, which therefore can readily feed. Skaife (1953) reported that the food paste is made by regurgitating nectar onto the mass of dry pollen that often lies on one wall of the burrow above the larvae. Such pollen is far more commonly seen in this than in other species; half the nests with larvae in the feeding stage contain such a mass, sometimes 3 mm. wide and 10 mm. or more in length.

After a larva has grown some, possibly at the time of the first molt, it frees itself from the chorion and moves out onto the underside of the food mass, which is still supported by any remaining eggs, younger larvae, and by the crumpled chorion left by any larva that has crawled out onto the food mass. Sometimes several small larvae crawl onto the underside of the food mass, leaving the latter entirely supported by the egg remnants whose distal (anterior) ends are imbedded in it or in the surface moisture on it. More often there is enough difference in age so that support is not left entirely to the egg remnants.

As larvae grow larger, food is added to the top of the food mass by the adult. The larvae feed upward at the sides of the food mass and begin to fill the space between the food and the walls of the burrow. Their bodies thus become oriented lengthwise to the nest instead of transversely as when they are small and on the bottom of the food mass. As soon as two or three larvae occupy this position, the food mass is no longer supported only by the young larvae and egg remnants attached to the burrow wall but by pressure of

the growing larvae. These larvae form a clump, each larva with its back against the burrow wall and its tuberculate venter against the food mass. The heads of all the larvae are directed toward the nest entrance. The mother, meanwhile, adds more to the top of the common food supply which becomes a columnar mass of paste about 5 mm. high and 2 mm. in diameter, with longitudinal concavities or facets caused by pressure and movements of the larvae against it. Old chorions still connect the bottom of the food mass to the burrow walls. Larvae feed from the upper end of the food mass, simply by bending their heads inward. Clumps of larvae with no food are sometimes found but in most cases food is present.

Before the larvae are fully grown the addition of food must cease, for when they reach full size there is no food left. As the larvae stop feeding they usually drop out of the clump, into the space below it, if the clump is far enough above the bottom of the burrow.

Skaife (1953) said that, unlike most species of allodapines, the larvae of *A. acutigera* do not defecate while growing, and I never found feces under clumps of larvae all of which were still feeding. However, as soon as one larva finishes feeding it starts defecating, so that feces often accumulate in the bottom of the nest beneath the clump.

As more larvae mature, the clump breaks down and prepupae, and later, pupae, are arranged along the burrow much as in other genera, except that the oldest young often are near the bottom of the nest instead of the entrance. The egg remnants show that clumps are stationary and do not ordinarily move up or down the burrow. A single remaining larva, even if large, is too small to support the food mass in the usual way and curves around it, more or less like larvae of *Allodape* or *Braunsapis*, or actually more like those of the Australian *Exoneura*, as the larva does not support itself by stretching across the burrow but merely lies in the burrow.

When the clump of larvae is partly broken down by maturation of larvae, the adult bee can get past it into the lower part of the nest. This part is not accessible to her earlier. Feces are now usually removed, and a new circle of eggs is often laid below the lowermost prepupa or pupa. Only a few (one to four) eggs are present in such a second brood. The discrete broods in

individual nests of this species, in contrast to the irregular laying or incompletely separated broods sometimes found in *Allodape* and *Braunsapis*, are easily understood as a necessity, given the type of larval rearing practiced by *A. acutigera*.

The account presented above is based on immature stages in many nests. Some individual and partially unexplained exceptions are as follows: On September 27 a nest was found with two clumps of larvae, each with a food mass. The lower group consisted of three large larvae; the egg remnants were at this level. The upper group consisted of nine larvae, some of them somewhat smaller; one might almost have been classed as middle sized. Can it be that if there are too many larvae to form one clump, in this case 12, the mother provides an adequate food mass for one (the lower) clump and then moves the remaining larvae to an upper clump? The adult could not reach the lower clump to replenish their food, but the supply that they had appeared to be adequate.

A nest found on September 28 contained a clump of four large larvae with no food supply, below which was one large larva that had finished feeding, and feces below it. Finally, near the bottom of the nest burrow, were two eggs. It would seem that in the absence of a food mass an adult can get past a clump of larvae and lay. It had not cleaned out the feces, however.

In three nests the oldest larvae, when no longer feeding, moved (or were moved) upward from the clump instead of downward. This was not always because of lack of space below the clump. In four nests taken in November feces were not removed in spite of the dissolution of the clump; each contained an adult bee and one contained three eggs.

***Allodapula dichroa* (Strand)**

Figures 65, 71, 73, 74

This species is even larger than *A. acutigera* on the average, from the vicinity of Knysna and Avontuur westward, but is smaller to the east. It ranges from the Cape to Zululand in Natal. Nests were found at two localities near sea level on the Cape Peninsula (Cape Nature Reserve; Kommetjie) but not at some of the localities that I studied most intensively in the Cape area, such as Hout Bay and the Kirstenbosch Botanical Garden. These localities are included in nesting

TABLE 27

STATISTICS ON EGGS AND YOUNG OF *Allodapula dichroa*. UPPER HALF, GRAHAMSTOWN, CAPE PROVINCE. LOWER HALF, VARIOUS LOCALITIES^a IN NATAL

	Eggs	Small Larvae	Medium Larvae	Large Larvae	Prepupae	Pupae
	Nov. 19 and Dec. 6 (44 nests; 106 eggs and young)					
1. % of nests containing each stage	36.4	18.2	6.8	6.8	4.5	9.1
2. % of eggs and young in each stage	50.0	17.0	10.4	7.5	5.7	9.4
3. Maximum no. of each stage in one nest	5	4	5	4	3	4
4. Mean no. of each stage in nests containing that stage	3.3	2.3	3.7	2.7	3.0	2.5
5. Mean no. of each stage for all nests	1.2	0.4	0.3	0.2	0.1	0.2
	Dec. 17-Feb. 23 (50 nests; 219 eggs and young)					
1. % of nests containing each stage	38.0	16.0	12.0	16.0	20.0	38.0
2. % of eggs and young in each stage	30.1	12.3	7.8	11.9	12.3	25.6
3. Maximum no. of each stage in one nest	7	4	5	6	5	6
4. Mean no. of each stage in nests containing that stage.	3.5	3.4	2.8	3.3	2.7	2.9
5. Mean no. of each stage for all nests	1.3	0.5	0.3	0.5	0.5	1.1

^aListed in text.

area 9 of Michener (1970a). The species was also found 40 miles east of Knysna; at Mossel Bay; and 3 miles south of Avontuur, 3500 feet altitude; Cape Province. In these localities and on the Cape Peninsula, nests were in Cape macchia, generally in the sun. The species also occurs in the somewhat marginal karoo areas at Worcester and 7 miles west of Robertson, Cape Province, where it nests in dead flowering stems of *Cotyledon paniculatum*, as described for nesting area 8 by Michener (1970a). To the east, nests were found in and near Grahamstown, Cape Province (nesting areas 6 and 7, Michener, 1970a), and at the following localities in Natal: Pietermaritzburg; 5 miles northwest of Pietermaritzburg; Nagle Dam, 17 miles east of Pietermaritzburg; Richmond, 2800 feet altitude; Salt Rock near Umhlali; 7 miles northeast of Kranskop; Umbumbulu; Scottburgh; 14 miles northeast of Bulwer; Balgovan, 25 miles northwest of Pietermaritzburg. Some of these localities were described as nesting areas 4 and 5 by Michener (1970a). *Allodapula dichroa* is thus widespread but in most places not very common.

SEASONAL CYCLE: From the 18 nests found on the Cape Peninsula in October, November, and February, no differences in the life cycle from that of *A. acutigera* could be noted except the earlier maturation of adults: four pupae were in the first nest found, October 1, and young adults

of both sexes were found in nests on October 29. As for *A. acutigera*, eggs were found in all three months; a new brood of eggs is sometimes laid about the time the first brood pupates, and worn and unworn females are found both in October and February.

Nests from Worcester and near Robertson, Cape Province, October 9 to 12, mostly contained pupae, suggesting that the season is ahead of that on the Cape Peninsula.

Series of nests from 40 miles east of Knysna (December), Mossel Bay (December), Grahamstown (November, December), and Natal (December, January) do not provide added seasonal information but merely verify the presence of all stages including both young and worn adults at all these seasons.

The statistics shown in table 27 do not indicate differences from *A. acutigera* (see table 23) greater than would be expected as a result of the seasonal and locality differences. The relatively uniform content of young of all ages in Natal is probably a reflection of the continuous presence of flowers in summer in this area of summer rains. The low frequency of large young in Grahamstown may reflect earlier local food shortages. The number of young (eggs to pupae) per nest reached a maximum of 14; means for all nests were 2.4 and 4.4 for Grahamstown and Natal respectively (dates and N's shown on table 27) and means for nests containing young were 3.2 and 4.8.

TABLE 28
STATISTICS ON EGGS AND YOUNG OF *Allodapula variegata* FROM NATAL^a

	Eggs	Small Larvae	Medium Larvae	Large Larvae	Prepupae	Pupae
Dec. 29–Feb. 27 (49 nests; 164 eggs and young)						
1. % of nests containing each stage	38.8	14.3	8.2	16.3	14.3	26.5
2. % of eggs and young in each stage	39.0	12.8	4.9	14.0	7.9	21.3
3. Maximum no. of each stage in one nest	9	5	3	7	4	5
4. Mean no. of each stage in nests containing that stage	3.4	3.0	2.0	2.9	1.9	2.7
5. Mean no. of each stage for all nests	1.3	0.4	0.2	0.5	0.3	0.7

^aLocalities listed in text.

These figures are in the general range shown for *A. acutigera* in table 23.

The ovarian cycle is similar to that of *A. acutigera* but ovarioles with two enlarging oocytes and ovaries with several large eggs at the same time are more common, approaching the situation in *A. melanopus*. The general shape of the ovaries is also more like that of *melanopus*.

INTERACTIONS AMONG ADULTS: *Allodapula dichroa* probably does not differ greatly from *A. acutigera* in this respect. Like the latter species, it is principally solitary. Out of a total of 150 nests taken at various localities, only 21 contained more than one adult female, the numbers varying from two to six. In most of these 21 nests, the extra females or some of them were callows, or if mature in coloration, were judged to be recently emerged adults on the basis of being unworn with slender (class E) ovaries in nests also containing pupae and callow adults. (All fully colored females had been fertilized.) There remain, however, four nests, each containing two adult females (both fertilized), suggestive of similar colonies of *A. acutigera*. One was taken on October 1, before emergence of adults on the Cape Peninsula, so the two bees had presumably overwintered together. In all four cases, one female had ovaries of class A or B, the other of class C or E, and the one with slender ovaries was smaller and had less worn wings than the other in three of the four nests.

IMMATURE STAGES: So far as known the account of *A. acutigera* would apply also to *A. dichroa* with few exceptions. Angles of egg axis to nest wall were estimated at 45 to 90 degrees but were most commonly 60 to 75 degrees. Masses of pollen on the nest walls were less commonly

seen than in nests of *acutigera*; in 50 nests from Natal such a pollen mass was seen only once. However, masses of dry pollen were seen in several nests from Cape Province. Three nests were opened in which small larvae had clear liquid food (nectar?). Such food was never observed in nests of *acutigera* but is seen occasionally in nests of *Braunsapis* and *Allodape* and perhaps all species feed their larvae occasionally in this way. The timing of larval defecation is as in *acutigera*. In one nest containing only a single larva, it was curved around a food mass as noted for isolated larvae of *acutigera*.

Allodapula variegata (Smith)

Figures 81–87

This is one of the common species of *Allodapula* with a red or largely red abdomen. It ranges from the Little Karroo in central and eastern Cape Province to Natal and Rhodesia, with two records for Tanzania, but is absent or exceedingly rare in the westernmost Cape region. Its nests were described by Brauns (1926). I found nests 16 miles northeast of Montagu, in Grahamstown, and 14 miles northwest of Grahamstown (total of 11 at all three places), Cape Province; and at the following localities in Natal (total of 49): Salt Rock near Umhlali; 7 miles northeast of Kranskop; Pietermaritzburg; Balgowan, 25 miles northwest of Pietermaritzburg; St. Lucia Estuary. The species was found common in Natal only at or near sea level; only one nest was found at Pietermaritzburg in spite of much collecting and one at Balgowan. The latter was the highest collecting locality for the species in Natal, 4500 feet altitude. Most of the nests found were at Salt Rock.

Habitats are described as nesting areas 4 to 7 by Michener (1970a).

Nests were taken in November and December in and near Grahamstown and from December to February in Natal; these were the only months when I was in the areas. Throughout this period young of all ages were taken. Table 28 shows the statistics on young for Natal, and the rather few nests from Grahamstown do not indicate different relative frequencies of young of various ages. Comparison of table 28 with the lower half of table 27 shows no obviously significant difference in development between *A. variegata* and *dichroa* in Natal.

Among the 10 nests taken in November, there were more young than later in the year (mean of 6.4 eggs and young for all nests, 7.5 per nest containing eggs or young), suggesting that there may be a spring season of reproductive activity greater than in summer. The maximum number of young (eggs to pupae) taken in a nest was 20, found in a November nest near Montagu that also contained six unworn adults (two males, four females). Another very productive nest, also taken in November but near Grahamstown, contained 19 young (eggs to pupae) and 11 unworn, more or less callow adults (five males, six females). In summer in Natal the maximum number of young was 17, means being 3.3 for all nests and 4.4 for nests containing eggs and young (N's shown in table 28), figures slightly less than the comparable ones for *A. dichroa*.

As in *A. acutigera*, young are produced in broods of individuals of approximately the same age in any one nest. After one brood reaches the prepupal stage the female may lay up to six eggs for a second brood; some of them might be contributed by other females rather than by the old mother.

Males were found in nests in moderate numbers; 20 males to 124 females among nests studied for which such data are reliable (i.e., nests taken on cool days or in the morning or evening).

A few nests containing only an adult female but no eggs or young and others containing a female with eggs or small larvae but no older young were found during each summer month. Presumably this indicates that new nests are established throughout the summer by the young females being produced. Occasionally, however, a lone female without or with only small young is an old, worn bee, probably one

whose first brood has entirely gone away or whose nest twig was destroyed so that she has begun a new nest. The meager evidence indicates that in this species, as in other allodapines, new nests are established by lone females.

The ovarian structure and apparent developmental sequence resemble those of *A. melanopus*.

INTERACTIONS AMONG ADULTS: The average number of adult females per nest is about the same from December to February and higher than in species discussed previously, about 2.3 (55 nests), the maximum being seven. Only slightly over one-third of the nests contained but one adult female. A high percentage of the adults, however, were recently emerged, and in most nests containing two or more, one could be recognized as fully colored, worn, and fertilized, whereas the others were at least slightly teneral in coloration, unworn, and unfertilized. It seems that attainment of full coloration requires some time and that at about the time when it is attained the females normally both mate and leave the parental nest. Out of nearly two-thirds of the nests found that contained two or more females, only 12 seemed to have two or more fully mature adults. Dissections and more careful study revealed that the extra females in eight of these were slightly teneral or at least were unworn, unfertilized, and with very regularly shaped ovaries of class E, oocytes not approaching the common oviduct and no white bodies in the ovaries or oviducts, and were therefore judged to be young adults that would probably soon have dispersed. The four remaining nests, or 7 per cent of the total number of nests, contained two or in one case three adults that are presumed to have lived together for extended periods. The conditions of the mature females (tenerals that were in some of these nests have been excluded) in these four nests are as follows (symbols as in table 14):

Nest 521: A+37, A-6. Nest 530: B+0, B+0

Nest 523: B+19, B+0. Nest 1530: C+5, C-8, E-3

In two nests, both females were fertilized; in the other two only one each was fertilized. Both unfertilized bees in nest 1530 had a few white bodies in the rather slender but irregular ovaries. The similarity in ovarian development among individuals of each nest suggests that there may be some mechanism to synchronize such development when two or more individuals live together. This would probably be necessary if

each were to lay eggs since when a large clump of larvae is present, adults presumably do not get past it, as indicated above for *A. acutigera*. In the latter species, however, there is no evidence of such synchronization.

IMMATURE STAGES: The sizes of nest populations of young of various stages have already been indicated. Masses of dry pollen on nest walls above larvae were found in only four nests, two from Grahamstown, Cape Province, and two from Natal. As with *A. dichroa* such masses were far rarer relative to the number of nests studied in Natal than in Cape Province.

The eggs are small, about 1.2 mm. long, as in other species of *Allodapula*, and attached by their posterior ends to the walls of the nest burrows. Unlike other species (except *A. rozeni*), the eggs are placed in a subvertical (i.e., nearly longitudinal), slightly spiral row, usually more vertical and more regular than the one shown by Brauns (1926). The middle parts of such rows vary from 2 to 10 cm. above the bottoms of the nests. Such a row may contain up to 11 eggs or may be short, with only two to four or six eggs, for second broods. The sequence in which eggs are laid is seemingly not consistent. In one nest the lowermost eggs had hatched before the nest was opened and hatching progressed upward during the next three days. This suggests that laying progressed from the bottom upward over a period of a few days. In another nest (1530), however, hatching was irregular; at the time the nest was opened (Feb. 27) young larvae (L) and eggs (E) were found in the row in the following sequence from top to bottom: L, E, L, E, E, L, L, L. (See comments on egg hatching of *A. rozeni*.) Only in one nest found were there two rows; it had six eggs in one row and on the opposite side of the nest burrow, three eggs in another row.

On hatching, as in other *Allodapula*, the larvae are ventral side up and the posterior end of each larva stays attached in the remains of the chorion, so that the larvae project into the lumen of the nest, as do the eggs. The young larvae are fed with masses of pollen moistened, presumably, with nectar. Occasionally a young larva has its own small pollen mass on its venter, but normally any pollen mass is utilized jointly by two or three larvae, which are sufficiently flexible so they can curve about to reach a shared mass. The three adjacent larvae in nest 1530, mentioned above, had a common food mass but each

of the isolated larvae had a small individual food mass on its venter. Of course a long row of young larvae is provided with several small pollen masses. As they grow, the larvae because of size, no longer look regularly arranged but along with the food form an irregular mass on one side of the burrow.

Larvae feed in the same manner, remaining attached at their posterior ends, sometimes until they are nearly half grown. Larger larvae, however, could not remain attached so close together and they form a clump like that of *A. acutigera* or *dichroa*, and are fed in the same way. The breakdown of the clump with larval maturation is also as in *acutigera*, the larvae that have stopped feeding and started defecating moving either below or above the feeding clump. A lone large larva, unable to support itself as in a clump, seemed to be fed as are such larvae of *acutigera*.

Larval feces are sometimes found in the bottom of the nest long after disintegration of the clump of larvae; adults are not very prompt to remove feces and may even lay eggs (second brood) almost among the droppings, below the prepupae and pupae.

One of the nests from Grahamstown and three from Salt Rock each contained a female of the parasitic allodapine bee, *Eucondylops konowi*.

***Allodapula rozeni* Michener**

Figures 88–90

Nests of this species, which are very similar to those of *A. variegata*, were found 16 miles north-east of Montagu, Cape Province. The habitat is described as area 8 by Michener (1970a).

The eggs were arranged in a single subvertical row, exactly as in *A. variegata*; the row of nine in the only nest with eggs and young spiraled through about one-fifth of the circumference of the burrow.

The varying sequence of egg hatching was noted above for *A. variegata*. Eggs in the single nest of *A. rozeni* evidently hatched from the top downward, since two weeks after the nest was collected and the larvae and adults removed, re-examination showed that the upper five eggs had hatched, the lower four still had not. I doubt if the downward sequence for this nest of *rozeni* is a specific character differentiating this species from the upward and mixed sequences noted for *variegata*; it seems more likely that there is much variation in this feature.

TABLE 29

STATISTICS ON EGGS AND YOUNG OF *Allodapula melanopus* AND *turneri* FROM THE ROBERTSON-WORCESTER AREA, CAPE PROVINCE

	Eggs	Small Larvae	Medium Larvae	Large Larvae	Prepupae	Pupae
October (35 nests; 320 eggs and young)						
1. % of nests containing each stage	48.6	2.9	20.0	34.3	20.0	71.4
2. % of eggs and young in each stage	24.1	0.9	5.3	9.7	4.1	55.9
3. Maximum no. of each stage in one nest	13	3	8	5	4	17
4. Mean no. of each stage in nests containing that stage	4.5	3.0	2.4	2.6	1.9	7.2
5. Mean no. of each stage for all nests	2.2	0.1	0.5	0.9	0.4	5.1
November (34 nests; 105 eggs and young)						
1. % of nests containing each stage	23.5	2.9	2.9	14.7	0	38.2
2. % of eggs and young in each stage	25.7	1.9	2.9	21.9	0	47.6
3. Maximum no. of each stage in one nest	6	2	3	8	0	8
4. Mean no. of each stage in nests containing that stage	3.4	2.0	3.0	4.6	0	3.8
5. Mean no. of each stage for all nests	0.8	0.1	0.1	0.7	0	1.5

Allodapula melanopus (Cameron) AND
A. turneri (Cockerell)

Figures 31–38, 75–80

Allodapula turneri is probably only a form of *A. melanopus* although the two occur sympatrically on the Cape Peninsula. There is nothing in the known biology of the two forms to indicate a difference and the four known nests of *turneri* are here treated with *melanopus*.

Allodapula melanopus in one sense replaces *A. variegata* in western South Africa. Although the two species overlap broadly, the first is common in the west, the second in the east. Nests of *A. melanopus* were found at the following localities, all in Cape Province: Cape Nature Reserve (with *turneri*); west side of Pakhuis Pass near Clanwilliam, 2500 feet altitude; 7 miles west of Robertson, 900 feet altitude; Worcester, 1000 feet altitude; 5 miles northeast of Worcester; 16 miles northeast of Montagu; Grahamstown; 12 miles west, 10 miles north, and 17 miles northwest of Grahamstown. The species occurs both in Cape macchia and in the karroo, habitats being described as nesting areas 6, 8, and 9 by Michener (1970a).

Nests were found in October, November, December, and February, 13 in October and November on the Cape Peninsula, five in February in the same area, 12 in and near Grahamstown in November and December; the only large group of nests was 69 from the

Robertson-Worcester-Montagu area taken in October and November. Young of widely different ages were found from October to February. Table 29 shows the frequencies of the various immature stages in the Robertson-Worcester-Montagu area in October and November. In this area there is a spring burst of reproductive activity shown by many pupae and young adults as well as younger stages in October. Young adults were found on October 1, when I first found nests of the species; how much earlier they may appear is not known. After this period of spring reproductive activity, November (and seemingly also December and February) is characterized by continued but less reproduction, as shown in table 29. Meager data for *A. variegata* suggest an active spring reproductive period for it, too, but later. In both the Cape Peninsula and the Robertson-Worcester area *A. melanopus* is ahead of other allodapines (except *A. turneri*) in its reproductive cycle. Can it be that larvae as well as adults of *melanopus* survive the winter in considerable numbers? Development in the Karroo is a few days ahead of that in the cool Cape Peninsula.

The maximum number of young (eggs to pupae) found in a nest was 32 (near Robertson, October 9), 13 eggs, four larvae, two prepupae, and 13 pupae. In addition it contained three young adults as well as one old female, who may or may not have produced all 35 offspring. Several other nests taken in October contained

more than 20 eggs and young but in November and the summer months the maximum was 17. In October the mean number of eggs and young per nest was 9.1; for those nests containing eggs and young it was 9.7. For November comparable figures are 3.1 and 4.8. (For N's, see table 29.) The means for October are higher than for any other species of *Allodapula*.

Production of young in separate broods is as in *A. variegata*, the only difference being that in October what appears to be a second batch of eggs may contain as many as 13 eggs. In November and summer nests, the maximum probable second batch was six but three or four are more common numbers.

Males were found in some nests throughout the period of study; 34 males to 216 females.

New nests may probably be started at various seasons by lone females. This is suggested by the few nests containing an adult female but no eggs or immature stages, or only eggs and young larvae. In October only three of 46 nests from western Cape Province were of this kind, and in November six of 34 nests lacked eggs and young as well as indications of prior use. (Six others taken in November that lacked eggs and young contained two or more young adults and sometimes also larval feces and presumably represented old nests that had produced a group of adults but in which egg-layers had died and no second batch of eggs had been laid.)

The ovaries differ from those of *A. acutigera* in their more slender form (figs. 31-37) and especially in that, when an egg is full size, its ovariole may contain two other enlarging oocytes, or a total of three. It appears that more eggs can be laid during a brief period by a female of *A. melanopus* (or *variegata*, which has similar ovaries) than by a female of *A. acutigera*, a conclusion supported by comparison of tables 23 and 29.

INTERACTIONS AMONG ADULTS: The average number of adult females per nest did not vary appreciably during the months of observation and was about 2.6 (103 nests), the maximum being 16. Forty-three out of 103 nests contained only one adult female each. In the remainder, containing two to 16 adult females, a considerable percentage was callow or could be recognized as young on dissection, as detailed for *A. variegata*. There is every intergradation between such young females and older ones that seem to have been in a nest, associated with one another or with an older female (mother?) for long

TABLE 30

CONDITIONS OF FEMALES IN COLONIES OF *Allodapula melanopus* AND *Allodapula turneri*^a

Nest No.	
488:	A+16, A+4, B+1, C+0, C+0, C-0, C-0, E-0
151:	A+12, B-1, F-3
228:	A+23, B+11, F+9, F-36
461:	B+25, F+24, B+22, F-16
225:	A+9, B+18, E+5, E-6
164:	A+13, C+5, F-0
421:	A+0, C+8 (<i>turneri</i>)
220:	A+19, C+25
222:	A+19, C?9, E-23
229:	B+12, C+12, F-25
235:	B+47, C+16, E+34, F-31
239:	A+29, C+11, E+37
240:	B+18, C+25
248:	B+23, C+0, E+5
459:	B+31, F+6
412:	A+20, E+21 (<i>turneri</i>)
231:	B+36, F+24
237:	A+6, E+19
241:	A+23, E+6
249:	C+14, C+4
475:	B+8, C-1, E-0
484:	A+19, C+0, C-0
487:	C+19, C+0, D+1, D+0, E+0, F+0
1302:	B+25, E-1, E-1, E-1, E-1, E-0
490:	E+34, E+0, E-0
437:	A+40, E-0
555:	A+9, E-0, E-0, E-0
468:	F+1, F+0, F+0
463:	E+0, E+0

^aEach colony consisted of two to eight fully colored females, information on which is separated by commas. Symbols as for table 14; see Methods. Colonies containing parasitized females are omitted. Teneral individuals that were in some of these nests have been excluded.

periods of time. Whereas for *variegata*, because of the rarity of such associations, it seemed reasonable to regard mature but unfertilized and unworn females as individuals that would soon disperse, in *A. melanopus* and *turneri* this assumption is untenable because of the frequency of groups of females that live together.

Populations of 41 nests that contained two or more fully colored (not callow) females were dissected. Of these, five were groups of not or scarcely worn, fertilized or unfertilized, bees with ovaries usually of class E or F, sometimes one individual of class C. Such groups doubtless

consist of sisters; they care for their younger sisters (larvae) when present, but do not give evidence for (or against) continued association. Sixteen other nests contained a fertilized female with enlarged ovaries and worn wings (probably the mother, legitimately called the queen) together with one or more not or scarcely worn females with ovaries of class E or F and usually unfertilized (probably daughters). Such individuals might disperse, but judging by the next group of nests, some would remain in the nest with the mother, or with one another after the mother dies. Twenty, or about half of the nests with more than one fully colored female, or one-fifth of all nests found, contained two or more old females as recognized by wing wear, white bodies in the ovaries or oviducts, or by enlarged ovaries.

Table 30 shows the diverse conditions of the females in these 20 nests and in a few other nests selected for comparison. Callow females also found in certain of the nests are omitted. The first 20 nests in the table (Nos. 488 to 249) are those containing two or more reasonably old females. Note that in some (488 to 225) there are two or three egg layers or bees ready to function as such (ovarian classes A and B), and in others (164 to 248) some ovarian enlargement (to class C) has occurred in an auxiliary or occasionally, as in 488 and 484, in a series of auxiliaries. Worker-like bees (slender ovaries but worn wings) are usually fertilized but some are much worn although unfertilized, as seen in nests 228, 461, 222, 229, and 235. The ovaries of such bees are usually elongate, irregular in shape, and with white bodies, quite unlike the similarly classified (E or F) ovaries of young females. In most colonies the bee with the largest ovaries is the most worn, presumably the oldest; such bees are listed at the left-hand side of the table and can tentatively be called queens. In some nests, however, workers (either fertilized or not) are much worn, sometimes more so than the egg layers. No seasonal differences were detectable in the attributes here discussed.

Recognizing 17 workers rather subjectively and omitting all little worn bees that might develop into egg layers, I found 11 (about 65 per cent) to be fertilized, six unfertilized. An independent calculation based on a larger and less strictly selected group of workers (table 5) showed 70 per cent fertilized, as good an agreement as could be expected.

TABLE 31

COMPARISON OF MEAN NUMBER OF OFFSPRING IN NESTS OF *Allodapula melanopus* AND *Allodapula turneri* CONTAINING TWO OR MORE WORN OR OVARIALLY DEVELOPED FEMALES^a WITH THAT IN NESTS CONTAINING LONE FEMALES

	No. of Colonies	Eggs and Small Larvae		Older Immatures	
		Groups	Lone ♀ ♀	Groups	Lone ♀ ♀
October	35	3.2	2.0	10.2	6.7
November	29	2.3	0.5	7.5	3.1

^aFirst 20 nests in table 30.

At the bottom of table 30 are included examples of certain other sorts of colonies, as follows: Auxiliaries having slightly enlarged ovaries which may indicate that some of them will remain in the parental nest (nest 475 to 487); auxiliaries fertilized even though unworn and with ovaries indicative of youth (487); "auxiliaries" with a little wear (one nick each) probably indicating nothing meaningful (1302); "auxiliaries" young, probably little different from the callows present in many nests (1302, 437, 555); groups of sisters without associated egg layers (468, 463).

There is no significant difference in mean head width or wing length between egg layers and workers or between fertilized and unfertilized workers.

To obtain an idea of the relative productivity of groups of females working together versus lone females, counts of eggs and young larvae and of older brood, including teneral adults were compared. The results appear in table 31. (Some of the nests listed under "lone ♀ ♀" contained teneral adults, counted as offspring. Various nests each containing an old female and one or more fully colored but unworn and not ovarially developed females were excluded from consideration in table 31 because the status of the supernumerary females was in doubt.) Eggs and young larvae had probably been produced by females found in the nests; older immatures might be offspring of females since deceased, but were fed and protected by whatever mature females were in the nest. Groups of adults clearly were associated with larger broods of immatures than lone adults; the difference in means in all cases was significant at the 0.01 level or better

(Kruskal-Wallis test). The number of colonies found was too small to differentiate productivity of groups containing different combinations of old females, e.g., two egg-layers versus one egg-layer and one worker, or different numbers of old females, especially considering that age and status of the females are subjectively determined. The very small mean number of offspring shown for lone females in November is partly a result of the increased frequency of nests with no offspring in that month, probably partly due to establishment of new nests by lone females that matured in October. When such nests are excluded, the means for lone females in November rise to 0.8 and 5.1, still significantly different from the means for groups of females. Mean group size (only females with five or more wing nicks or ovaries of class A or B were counted) was 2.7 in October, 3.0 in November. Nests with lone females were excluded from this calculation; see table 7 for figures including such nests.

At least in October it seems from these data that group behavior should be disadvantageous if all females were capable of living alone and doing as well as did observed lone individuals. More offspring could be reared to maturity by three bees living alone, for example, than by the same three bees in a group. Different selection at other seasons, suggested by November data, may counter this suggestion but probably more important is predation. Of course I never found the colonies that had been destroyed by predators, e.g., ants. Such destruction is more probable for lone females and their offspring than for groups.

IMMATURE STAGES: The sizes of nest populations of immatures have been indicated above. Extensive areas covered by pollen, which seems dry but sometimes caked, are common on nest walls. Typically such pollen is on one side of the nest burrow and may extend along it for as much as 2–3 centimeters; the pollen may be more than 0.5 mm. thick where thickest and at the margins thins out to a yellowish smear. Sometimes there are two or three areas covered with pollen in a single nest. Unlike other species of allodapines, such masses may be above, below, or in the midst of groups of young, and the older larvae may sometimes feed directly from them.

The eggs are small as in other *Allodapula* and attached by their posterior ends to the wall of the burrow, projecting downward into the lumen of the burrow as in other species of the genus. They are placed in one or more transverse rows, often

somewhat irregular, or occasionally one egg is isolated. A row may have from two to six eggs; the eggs are relatively close together so that instead of forming a ring around the nest burrow, as in *A. acutigera* and *dichroa*, a row is all on one side. There are often two or three rows of eggs in one nest; these may be close together, so that the eggs form a patch on one side of the burrow wall, or separated by as much as a centimeter or two. Eggs vary in position from almost the bottom of the burrow to only 2 cm. from the entrance. Even if not forming a patch, the eggs in any one burrow are not spread over more than 2 cm. of burrow length. Rarely is there gross irregularity in egg placement: one was found projecting sideways, at right angles to the axis of the nest, and another upward toward the nest entrance. Each was in a group of otherwise normally placed eggs.

On hatching, as is usual for the genus, the larvae are ventral side up. Their posterior ends remain attached to the remains of the chorion and thus to the nest wall until they are half grown. An isolated larva is fed with a mass of moistened pollen placed on its venter but groups feed from a common mass of food placed among them and supported by them as they feed from it, much as in *A. variegata*. There may be a single food mass for the larvae from a single patch or row of eggs, as the larvae can reach quite far, or there may be more than one. As the larvae grow they often curve around and largely obscure the food masses and look like an irregular group of larvae on the nest wall.

As with related species, large larvae become detached from the burrow wall. Sometimes they form distinct regular clumps filling the lumen of the burrow as in *A. acutigera* and other species, but often they are scattered along the burrow, isolated or in small groups that do not close the burrow and perhaps feed from the dry pollen on the burrow walls as suggested above. Irregularity in the behavior of large larvae is perhaps partly due to the frequent use of large and irregular burrows, for more than any other allodapine studied by me, *A. melanopus* utilizes such burrows made by other insects, often much larger in diameter than one would expect this small bee to make.

Even when a clump is formed, it is usually less regular and probably less long lasting than in species such as *A. acutigera*. In *A. melanopus*, eggs, young larvae being fed, adult bees, and pollen

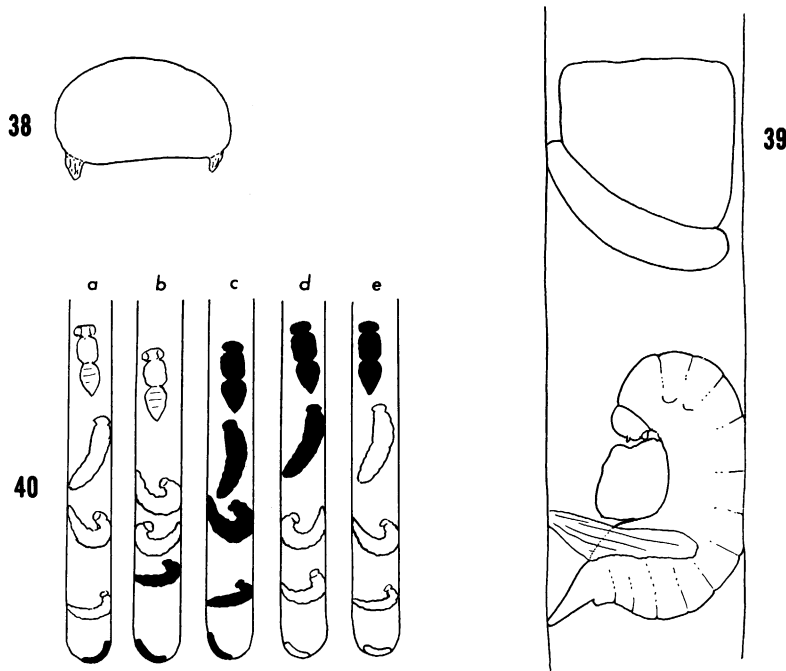


FIG. 38. Puparium-like larva or prepupa of *Allodapula melanopus* parasitized by *Xylencertus mumifex*. Pale, shriveled anterior and posterior extremities of host project downward at each end.

FIG. 39. Above: Egg of *Halterapis nigrinervis* supporting food mass. Below: Larva, feeding, supported by old chorion and its own apical projection.

FIG. 40. Diagrams of a sequence of nests of *Braunsapis facialis* parasitized by *Nasutapis straussorum*. Eggs and larvae of the former are shown as white, of the latter, black. In a, b, and c the *Nasutapis* female is present (not shown) along with one or more adult female *Braunsapis* (not shown). The *Braunsapis* brood is progressively replaced by *Nasutapis*. In d and e, the *Nasutapis* female has disappeared, the *Braunsapis* female again produces offspring, and progressively replaces *Nasutapis*.

are often found below or above such a clump or interspersed among large larvae scattered along the burrow. As in other species, the oldest or most mature individuals of a single brood may be either above or below the less mature ones, but in *melanopus* the whole matter seems erratic so that large larvae, prepupae, and pupae may be intermixed along a nest burrow. There seems to be more diversity in age of individuals in a brood than in related species. Sometimes eggs for a new brood have been laid when the smallest larva of the preceding brood is still only middle sized, although in such cases most members of the preceding brood are large larvae or prepupae.

All these irregularities may be related to the

frequency of colonies containing two or more mature, working females, but I have not been able to show that such irregularities occur more frequently in nests in which I found two or more such females than in nests containing only one.

As in related species, removal of larval feces seems erratic and eggs, larvae, pollen, etc., are often intermixed with feces from large larvae higher in the nest. In one case the bottom 2 cm. of an occupied nest was solidly filled with feces. Bits of pith and even feces of original borers are also not always removed.

Seventeen nests from the Robertson-Worcester-Montagu area contained adults or immature stages of *Eucondylops reducta*. Most of these nests were found in November and contained an adult

female of this parasitic bee, along with an apparently normal complement of *Allodapula*. In four nests, however, all taken in October, the identifiable immature stages were *Eucondylops* although adult *Allodapula* of varying ages and ovarian development were present. This indicates that, as in other parasitic allodapines, the female parasite destroys the host eggs or inhibits their laying over a considerable period during which she lives in the nest of the host. Meanwhile the female *Eucondylops* lays, and the resulting young are cared for by the *Allodapula*.

A puparium-like mature larva or prepupa of *A. melanopus*, parasitized by *Xylencyrtus mumifex*, is shown in figure 38. (See section on Associates and Parasites above.)

***Allodapula ornaticeps* Michener**

Two nests were found on the west slope of Pakhuis Pass, near Clanwilliam, Cape Province, at an altitude of 2500 feet on November 3, 1966. Each contained a single adult female, and one contained, in addition, a pupa and a prepupa.

***Allodapula xerica* Michener**

Figure 91

Six nests of this species were taken in stems of *Cotyledon paniculatum* 7 miles west of Robertson, 900 feet altitude, Cape Province, October 9, 1966. The habitat was described as nesting area 8 by Michener (1970a) where the species was misidentified as *A. pallipes*.

Each nest contained one mature female except for one with two such females and a callow male. Immature stages found were two eggs, two small larvae, three medium-sized larvae, and 10 pupae. Some nests with pupae also had eggs or small larvae, indicating a second batch of eggs as has been observed frequently for other species.

In the nest containing two small larvae and the one containing two eggs, these stages were attached to one side of the burrow with their axes about 90 degrees to one another, thus delimiting a quarter of a circle. In the nest containing three medium-sized larvae, however, the three egg remnants were arranged in a circle (i.e., with axes about 120 degrees to one another) as in *A. acutigera*. The three larvae formed a clump around a common food mass at the same level as the egg remnants, as in *A. acutigera*.

***Allodapula hessei* Michener**

Four nests were found on the west side of Pakhuis Pass, near Clanwilliam, Cape Province, at an altitude of 2500 feet on November 3, 1966. Each contained one mature female; immature stages present were eggs, prepupae, and pupae.

In one nest with five eggs and four pupae, the eggs, evidently representing second brood, were arranged as a horizontal row on half of the circumference of the burrow.

***Allodapula maculithorax* Michener**

Two nests of this species were found at Hout Bay, Cape Province, in September, 1966, in dead woody stems, one of *Protea*, the other an unknown small tree. This locality is included in nesting area 9 of Michener (1970a).

Each nest contained one adult female; one nest had four eggs, the other two eggs and two small larvae. The arrangement of eggs and the manner of feeding small larvae is like that of *A. acutigera*.

GENUS EXONEURULA

This is a small genus, widespread but rare in tropical and subtropical Africa and reaching the Arabian Peninsula. Nests of only one species have been found.

There is no evidence of a worker caste but one may exist in an occasional nest.

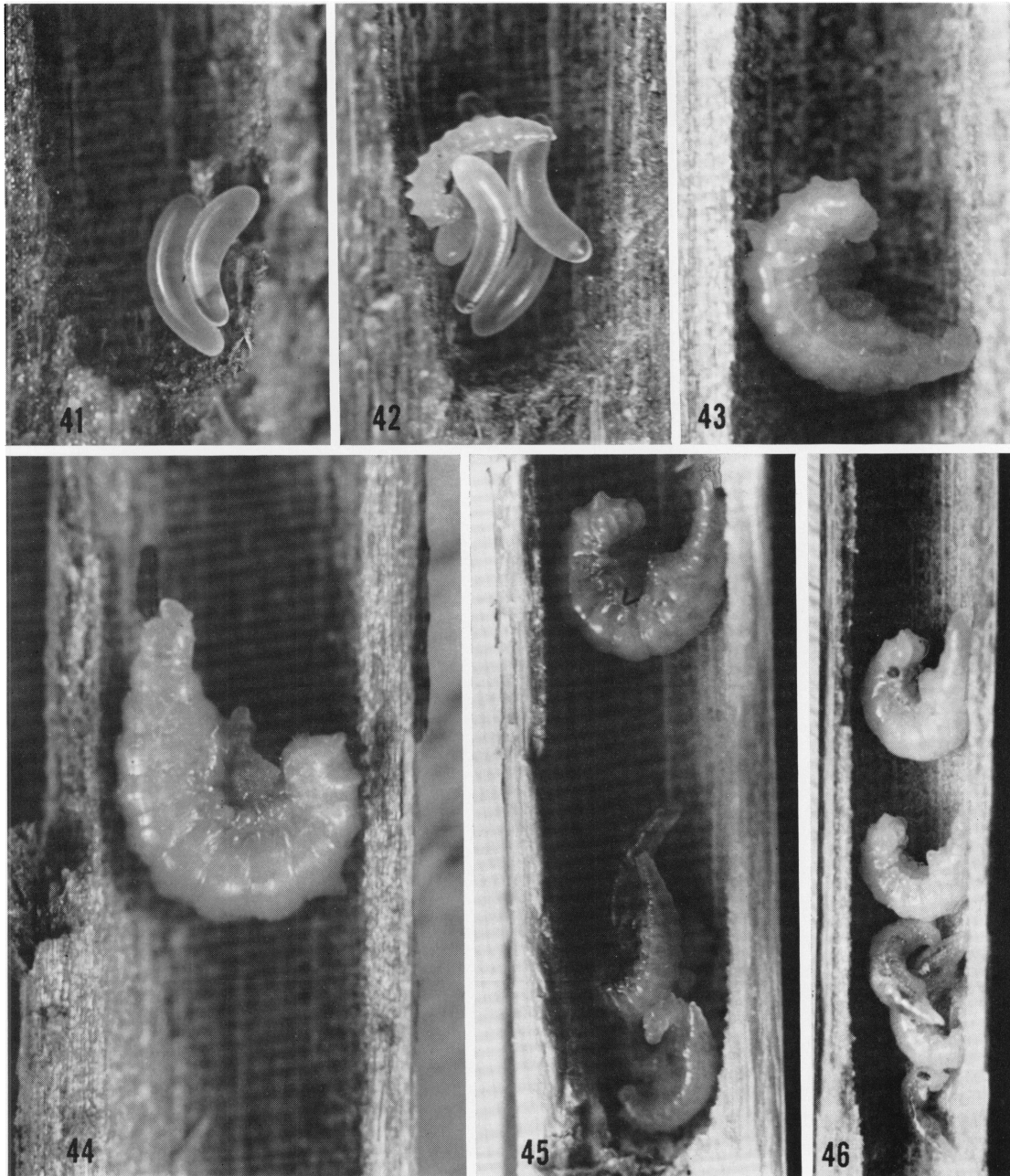
Eggs are attached by their posterior ends to the nest wall and the young larvae, like those of *Allodapula*, *Halterapis*, and *Macrogalea*, retain this position by not completely leaving the chorion, which is relatively tough. Older larvae seem to support themselves by pressing against the burrow walls, somewhat as do those of *Allodape* and *Braunsapis*. Food is provided individually and at least to young larvae, progressively. A middle-sized larva may get all the food needed for its future development in one mass similar to that of the mass-provisioning *Halterapis*. Food is placed on the venter of the larva.

The sequence of the immature stages in the nest burrow is irregular.

***Exoneurula stigmoides* Michener**

Figures 99–104

Ten nests of this species have been found, the only nests of the genus to have been studied. All were taken on May 11, 1967, from partially



FIGS. 41-46. Nests of *Allodape mucronata*. 41, 42, Eggs and a small larva. 43, Middle-sized larva with food. 44, Large larva with food, defecating. 45, Larvae too small to support themselves in burrow, and a larger larva above. 46, Larvae, positions perhaps somewhat disturbed in opening stem.

shaded stems of *Lantana camara* in Nairobi, Kenya, nesting area 2 of Michener (1970a).

Because so few nests are known, and the nesting biology is unique among known species of allo-

dapines, it seems worth giving the details of nest contents (table 32). The mean number of eggs and young per nest is 4.4, of eggs 1.4 for all nests or 2.3 for nests containing eggs. Young are

TABLE 32
CONTENTS OF NESTS OF *Exoneurula stigmoides*

Nest No.	Eggs	Small	Larvae Medium	Large	Prepupae	Pupae	Adult ♀ ♀
1681	3	—	1	1	2	2 ♀	1
1686	—	—	—	1	—	—	1
1690	1	—	—	—	—	—	1
1693	4	—	—	—	—	—	1
1694	1	1	—	2	2	—	2
1696	—	—	—	2	—	—	1
1697	—	1	1	—	—	—	1
1701	3	1	—	1	1	1 ♂, 3 ♀	2
1733	2	1	—	1	—	3 ♀	2
1742	—	1	—	1	—	—	1

distributed from eggs to pupae and there is no evidence of a major developmental gap in the brood in any of the nests.

Although three nests contained two adult females each, there is no evidence as to the interactions among them; one in each case could have been a young adult that would soon disperse.

IMMATURE STAGES: Eggs are about 1.40 mm. long, 0.58 mm. in maximum diameter, and attached by the somewhat tapered posterior end to the wall of the nest. They are not close together, but scattered along one side of the nest. The eggs (and small larvae), three or four in number, often form a vertical row about 10 mm. long, starting 4 to 9 cm. above the bottom of the burrow. On the other hand, the eggs may be rather irregularly placed. For example in nest 1681 the three eggs were 4, 7.5, and 7.8 cm. above the bottom of the nest, the upper two among pupae and prepupae, but all on one side and hence in a vertical row. The positioning of eggs is suggestive of that of *Halterapis* and *Macrogalea*, although the eggs are smaller in relation to the nest diameter than in those genera and project down rather than out into the lumen of the burrow. One egg was found loose in the bottom of a nest, but it may well have come loose when the nesting stem was snapped off by me.

In all three nests that had both eggs and small larvae (1694, 1701, 1733), it was the lowest egg that had hatched, indicating that laying is from the bottom upward, as in *Halterapis*.

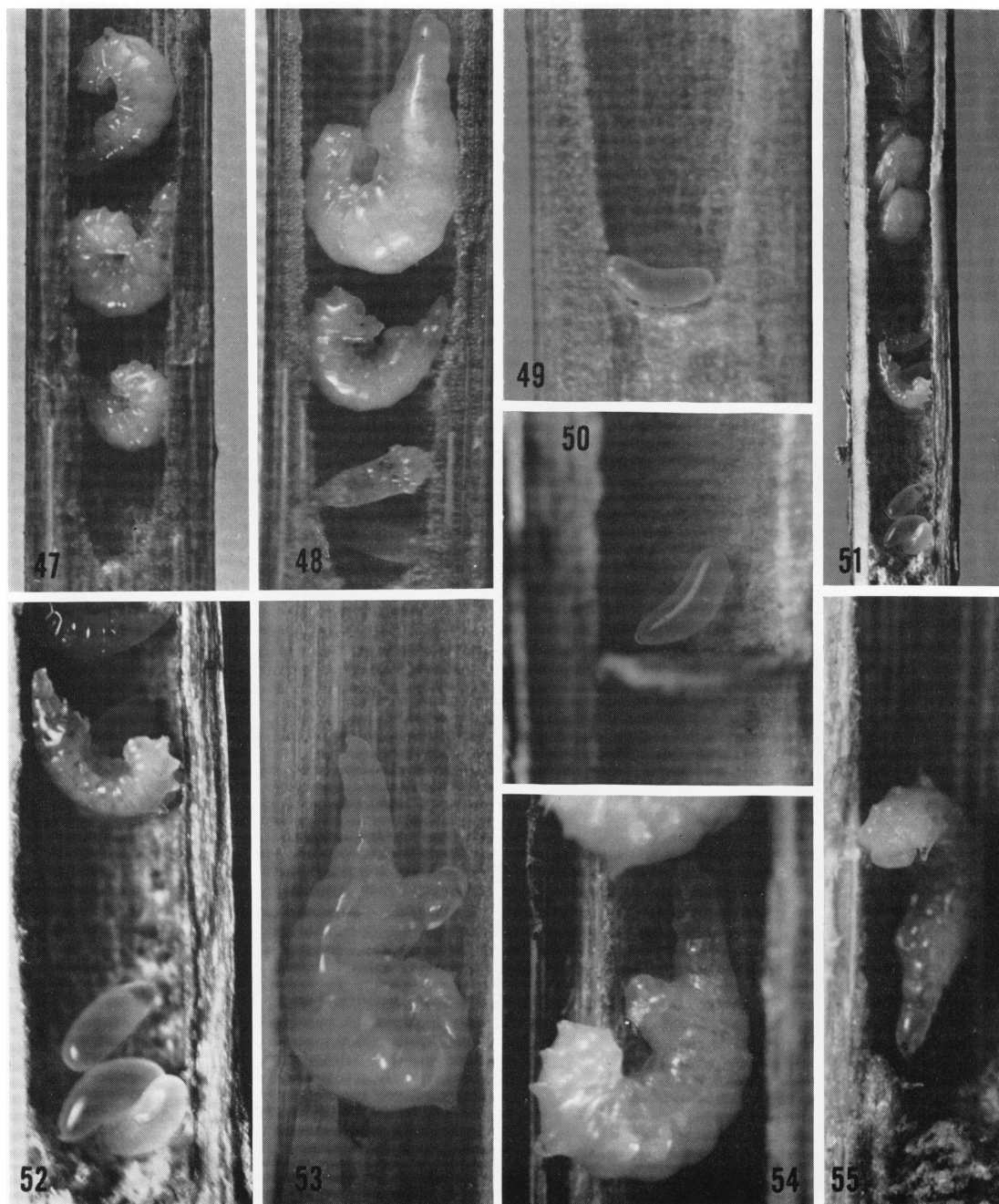
Small larvae retain their positions on the nest walls by leaving the posterior two-thirds of their bodies in the egg chorions. The larvae hatch

ventral side out or up, as in *Halterapis* and *Allo-dapula*. Two of the small larvae were being fed; one had a small amount of sticky pollen on its venter, the other had a larger mass, equivalent to about one-fourth of the volume of the larva.

As shown by table 32, only two middle-sized larvae were found. One (in nest 1681) had no food but the one in nest 1697 had a large food mass, 1.5 mm. high, 1.75 mm. in diameter, and shaped like food masses of *Halterapis* although smaller in relation to the burrow diameter. The larva was curled across the bottom of the food and was feeding just as do larvae of the same stage in *Halterapis*. The larva and food mass were not attached after I opened the nest but the larva could have been still attached by its posterior end to the egg chorion and thus supported in the burrow. It seems nearly certain, in this case, that adult bees could not pass the medium-sized larva and its food mass; the small larva in the nest was above it.

Older larvae seem to support themselves like larvae of *Braunsapis* or *Allodape*. They lie curled in the burrow, venter up, and by straightening the body could readily retain their positions. They lack, however, dorsal tubercles or hairs to help retain their positions. Sticky pollen is often found on the venters of such larvae in masses sometimes larger than usual for *Braunsapis* larvae of equal size. In one instance two large larvae were feeding from the same pollen mass.

The larger immature stages are rather irregularly arranged, as shown in the following lists of nest contents (bottom of nests to the left. Stages are E, egg; SL, small larva; ML, medium larva; LL, large larva; PP, prepupa; P, pupa.



FIGS. 47-55. Nests of *Allodape*. 47, Larvae of *A. mucronata*. 48, Egg and larvae of same. 49, Egg of *A. panurgoides*. 50, Egg of *A. friesei*. 51, Eggs, medium-sized larvae, and pupae of same. 52, Enlargement of above showing how larva of this size maintains its position in burrow. 53, 54, Large larvae of same. 55, Large larva of same probably not in usual position.

Individuals in the same parentheses were at about the same level).

Nest 1681: (E) (LL) (PP) (ML) (PP, E) (P, E) (P)

Nest 1694: (PP) (LL, E) (LL) (PP, E)

Nest 1701: (LL) (P) (P) (PP, SL) (P, E) (P, E) (E)

Nest 1733: (SL) (E) (E) (LL) (P) (P) (P)

TABLE 33
CONTENTS OF NESTS OF *Macrogalea candida*^a

Nest No.	Eggs	Small	Larvae Medium	Large	Prepupae	Pupae	Adult ♀ ♀
Nairobi							
1671	7	—	—	—	—	—	3
1725	—	—	—	2	—	1 ♀	1
1727	—	—	—	2	—	—	2
Malindi							
1781	4	1	—	3	1	2 ♀	4
1782	—	—	—	1	—	—	2
1785	—	2	—	—	—	—	1
1786	—	—	1	1	—	—	1
1787	3	1	—	—	—	—	1
1788	—	1	1	—	—	—	1
1789	—	—	—	—	—	1 ♀	1
1790	—	—	—	1	—	—	1
1793	—	—	—	—	1	—	1
1794	—	—	—	1	1	—	2
1795	—	—	—	2	—	—	1
1797	—	—	—	2	—	—	1
1801	1	—	—	—	—	1 ♀	1
1803	1	—	1	—	—	—	1
1805	—	1	1	—	—	—	1
1806	—	1	1	—	—	—	1
1807	—	—	1	—	—	—	1
1809	—	—	—	—	—	1 ♀	1
Mto Wa Mbu							
1854	4	2	2	7	—	2 ♀	7
Tororo							
1972	2	—	—	2	—	—	1

^aEight nests containing one adult and one to four eggs, and four nests containing an adult but no eggs or young are omitted.

It is clear that adults can ordinarily pass the immature stages in the nest, as in most allodapine genera, as shown by eggs and food on young in the lower parts of the nests and by the absence of feces in the nests.

GENUS MACROGALEA

This small genus consists of tropical African and Malagasy species which are unusually robust and hairy for allodapine bees.

There is inconclusive evidence of supernumerary, probably worker-like individuals in some nests.

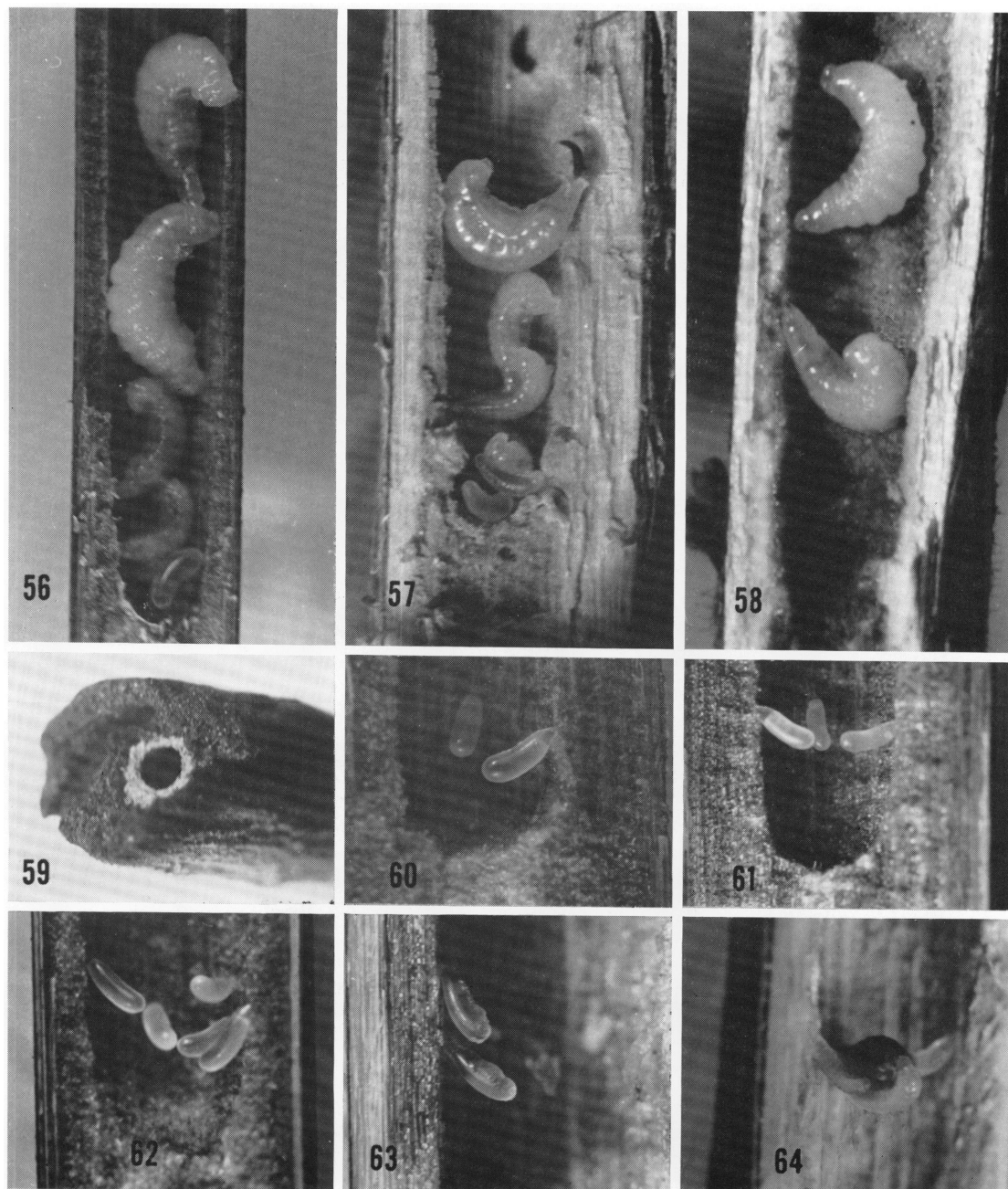
Eggs are attached to the nest walls by their posterior ends. Young larvae retain the positions of the eggs by leaving their posterior ends in the chorions, which are tough compared with those of *Allodape* and *Braunsapis*. Older larvae support themselves by curling in the burrow in such a

way that the hooked dorsal hairs cling to the rough burrow walls. Unfortunately none was found with food. They must be fed progressively but the way in which food is provided is unknown. The arrangement of immature stages in the nest burrow is rather irregular.

Macrogalea candida (Smith)

Figures 105–110

This is a widespread species in tropical Africa, from Angola to Tanzania and Ethiopia. It is a robust, hairy bee, quite unlike other Ceratinini in appearance. Thirty-five nests were found in partly shaded and in sunny stems at the localities listed below. *Kenya*: Nairobi (three nests, May); 13 miles south of Malindi (29 nests, May). *Tanzania*: Mto Wa Mbu, Lake Manyara (two nests, June). *Uganda*: 22 miles west of



FIGS. 56-64. Nests of *Allodape*, *Braunsapis*, and *Allodapula*. 56, Egg and larvae of *Allodape rufogastra*. Note irregular age sequence of larvae. 57, Egg and larvae of *B. facialis*. 58, Large larva and prepupa of *B. foveata*. 59, Nest entrance of *Allodapula acutigera* in charred stem; collar of white pith fragments contrasts with black stem. 60-62, Eggs, same species. 63, Eggs, same species, hatching. Common food mass and free larvae were removed. 64, Food mass and young larvae of same. Larva in center is free and on underside of food mass. Two smaller larvae, one at each side, are still largely in their chorions and support food mass and free larva, with help of the chorion from which the last emerged.

Tororo (one nest, June). The species is especially abundant along the Kenya coast but also occurs in the interior, even in the cool Kenya highlands. The Nairobi locality was described as nesting area 2 by Michener (1970a). Most of the nests from near Malindi were in twigs and stems of young bushes or small trees, *Ehretia petiolaris*, that had been killed by fire.

Because few nests are known and the biology is unique among known species of allodapines, details of nest contents are shown in table 33. The mean number of eggs and young per nest was 2.7 for all nests, 3.0 for the 31 nests containing eggs and young. The maximum number per nest was 17. The average number of eggs per nest was 1.2, but 2.8 for the nests containing eggs.

Obviously the number of progeny per nest is usually low, those nests containing but one adult female frequently having very few or no young. Some of those nests with only eggs or without eggs or young contained a worn female, showing that not all such nests are newly made by young adults.

Several nests contained more than one adult female. In nests 1781 and 1854 two females each had worn wings, suggesting that, as in many other allodapines, two or more females may live together forming a social unit. As usual, the nests with the largest numbers of adult females also had the largest numbers of eggs and young.

IMMATURE STAGES: Eggs measured 2.5–2.8 mm. long, 0.8 mm. in diameter, nearly straight, and are attached by their posterior ends to the wall of the nest. They project almost straight into the lumen of the burrow. They tend to be attached in a vertical or spiral row near the bottom of the nest, the eggs being several millimeters apart. However, the eggs in a row may be nearly touching. Two or more eggs may be at nearly the same level and projecting inward toward the center of the lumen of the nest. These arrangements are suggestive of patterns that appear regularly in different species of *Allodapula*. The eggs and small larvae in nest 1854 were all attached in a group on one side almost at the bottom of the nest. These may have belonged to the parasitic species, *M. mombasae* (see below), instead of to *M. candida*. When a twig is horizontal and the eggs in a row, the row was in at least one instance on the lower surface of the nest.

As in *Exoneurula* and *Halterapis*, laying is from

the lowest egg upward in a vertical row, to judge by the hatching sequence.

As in *Allodapula*, *Halterapis*, and *Exoneurula* small larvae retain their positions on the nest walls by leaving the posterior parts of their bodies in the egg chorions.

Older larvae retain their positions by curling around the burrow in a horizontal plane (if the nest is vertical). The entire dorsal surface of the larva is thus applied to the burrow wall. Since this part of the larva is covered with minute hooked hairs, which doubtless hook into the broken pith cell walls that form the burrow wall, the larva is securely held in position. Unlike other bees, even the prepupae remain similarly curled until just before ecdysis, when they straighten out.

The immature stages are rather irregularly arranged. Unfortunately eggs and young larvae in several of the nests from near Malindi became detached from the nest walls because of my snapping off the strong brittle stems in which the nests were made at that locality. Therefore placement of these stages is not always known accurately. However, the irregular arrangement of developmental stages is shown by the following lists of the contents of three nests (explanation as for *Exoneurula*):

Nest 1725: (P) (LL) (LL)

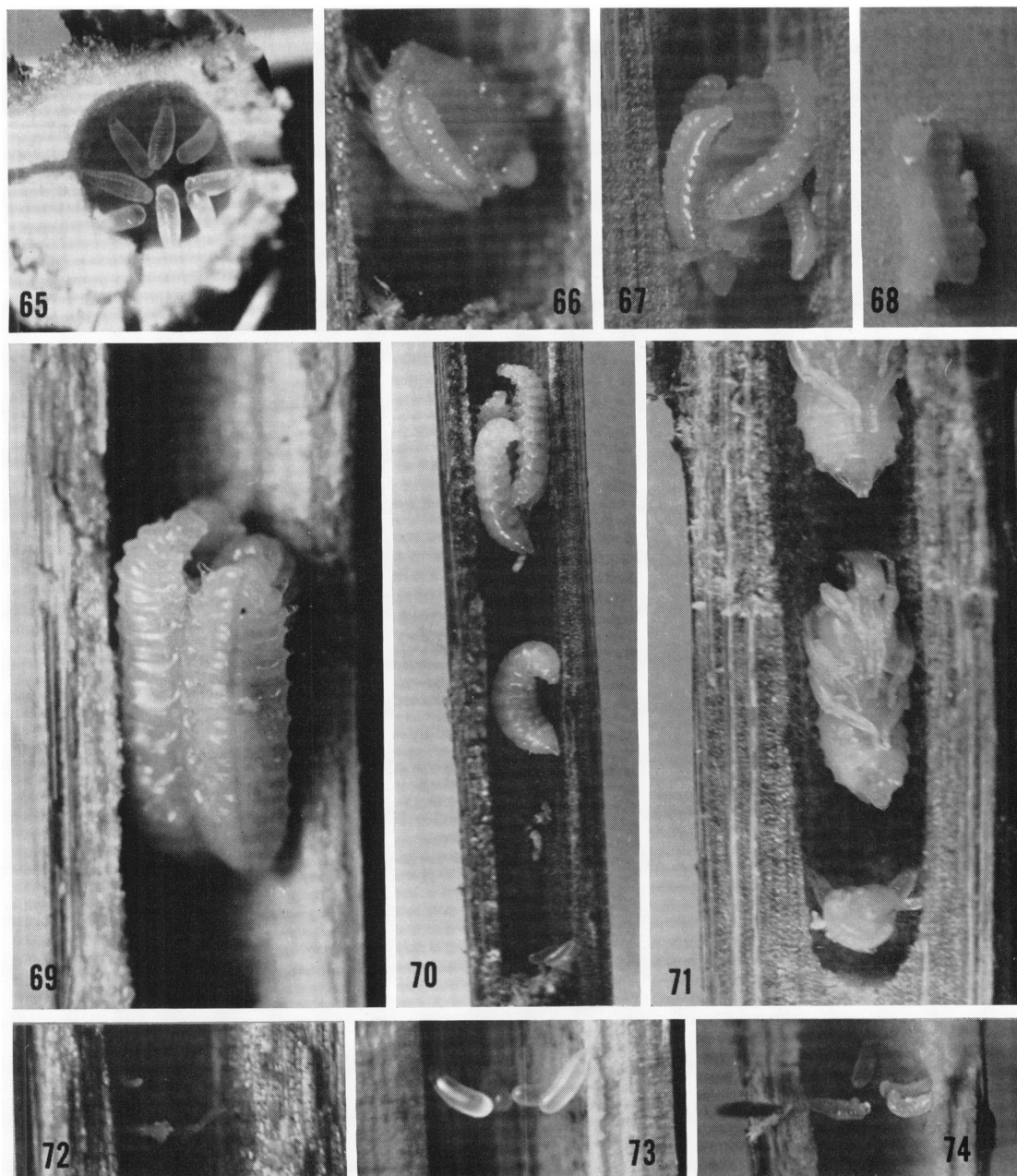
Nest 1781: (LL) (LL) (LL) (PP) (P) (P)

Nest 1854: (4E, 2SL) (ML, ML) (P) (P) (LL) (LL) (LL) (LL) (LL) (LL)

Since eggs and growing larvae are often below large larvae, prepupae, and pupae, it is evident that adults can pass the immature stages in the nest, as in most allodapine genera. Also, lack of feces in nests shows that adults remove them from below the larvae.

Unfortunately, in all the nests studied, not a single larva had food material on its body; we therefore do not know how larvae are fed. It is tempting to suggest that this means that food is supplied in small quantities and promptly eaten. However, it should be noted that a vast number of *Braunsapis* nests that lack food have been opened, yet others do contain visible and sometimes rather large supplies on the venters of some of the larvae. I suspect that the same would be found sometimes in nests of *Macrogalea*.

Nest 1854 contained, in addition to seven adult females of *M. candida*, a single adult female of *M. mombasae*, a parasitic species. As noted



FIGS. 65-74. Nests of *Allodapula*. 65, Eggs and small larvae in a nest burrow of *A. dichroa* that has been cut. Eggs alternate with young larvae, showing sequence of laying. 66, Small larvae of *A. acutigera* on a food mass supported by egg chorions. 67, Middle-sized larvae of same. Old chorions can be seen connecting food mass and burrow walls below; larvae are now big enough to support growing food mass by pressure against nest walls. 68, Large food mass of same. Facets are areas where larvae pressed against food. 69, A clump of large larvae of same. 70, Clump of large larvae, breaking up as they enter prepupal stage; two eggs at bottom. 71, Small food mass of *A. dichroa* (supported by small larvae and chorions) beneath pupae. 72, Remnants of chorions after removal of food mass and larvae of *A. acutigera*. 73, 74, Eggs and young larvae of *A. dichroa*. Eggs hatched after bees were removed from nest; hence no food was provided.

above, the eggs and small larvae in the nest may have belonged to that species. There is nothing about the large larvae and pupae to indicate that they do not belong to *M. candida*.

GENUS HALTERAPIS

This small genus which is restricted to southern Africa consists of species that morphologically closely resemble *Braunsapis*.

So far as known supernumerary mature adult females do not exist, but relatively few nests have been studied.

The large eggs are laid attached by their posterior ends to the nest wall. After an egg is laid, it is provided with a mass of provisions supported entirely by the egg and adequate for the whole growth of the larva. Thus, unlike other allodapines, this genus practices mass provisioning. After one egg is laid and provisions provided, another is laid above it and provisioned. The sequence of young in a nest is therefore from oldest below to youngest above, the reverse of the sequence of other allodapines with a regular arrangement of young but the same as that of *Ceratina* and other bees that provision young in series.

Halterapis nigrinervis (Cameron) Group

Figures 39, 92-98

As explained by Michener (MS), firm names for the species of this group, if more than one exists, must await collection of more male specimens and association of them with female type specimens. Five nests of the morph with the abdomen at least somewhat red were found 40 miles east of Knysna, Cape Province, December 4, 1966. Two nests of a form with black abdomen were found 10 miles north of Grahamstown, Cape Province, November 20, 1966; the only male reared had the hind femora simple, a condition otherwise seen only in field collected males from the Cape Peninsula. Eleven nests of the form with the abdomen black and the hind femora of the male toothed were found from December to February in Pietermaritzburg and 11 miles south of Pietermaritzburg, Natal. No seasonal differences were found, at least from November to January, among these nests nor were differences detected suggesting that the forms represent different species. Two of the habitats are described as nesting areas 5 and 6 by Michener (1970a).

Species of *Halterapis* differ from other allodapine bees in that they mass provision their nests. The nest is suggestive of that of *Ceratina*, but lacks partitions so that there are no separate cells. The young are arranged from oldest near the bottom of the nest to youngest near the entrance, as in *Ceratina* but the reverse of that of most allodapines.

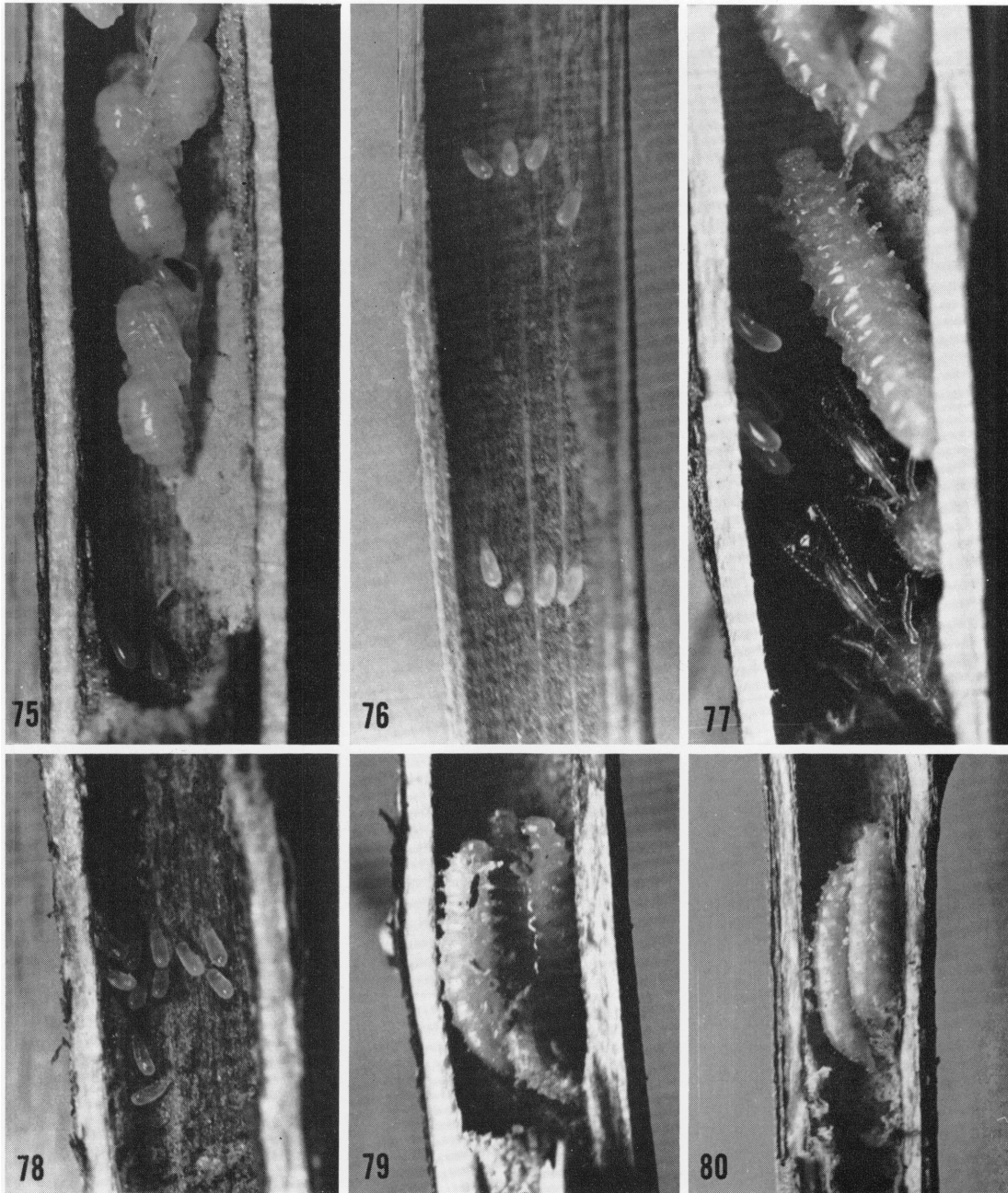
A considerable number of typical allodapine features exist in the nesting behavior, as follows: (a) the form of the nest including the constructed collar or constriction at the entrance and the lack of cells, (b) the ability of females when disturbed to block the nest entrance with the dorsal surfaces of the apical abdominal terga, (c) the survival of the mother through the growth of a brood of young so that she may be present in the nest with one or two female progeny, (d) probable ability of the mother to lay additional eggs after the young of one brood all reach the prepupal stage, and (e) the slow growth of the larva.

Perhaps because of the limitations presented by mass provisioning, the number of young in a nest averages far less than in forms that feed young progressively. The mean number (eggs to pupae) is 2.5 for all nests, 2.9 for nests containing immature stages, with a maximum of 8. The mean (and maximum) numbers of each stage per nest were as follows: eggs, 0.30 (2); small larvae, 0.04 (1); medium larvae, 0.17 (2); large larvae, 0.35 (2); prepupae, 0.35 (3); pupae, 1.30 (5).

The numbers of adult females per nest ranged from one to three, with a mean of 1.80. When there was more than one, there was usually only one that was fully colored, others being recognizably callow. Even when two fully colored individuals were present in a nest, only one was at all worn and there were invariably pupae or callow adults also present. From this evidence it seems likely that there is only one working adult per nest and that any others present are individuals that will soon disperse.

Probable new nests, i.e., nests containing no immature stages or none except eggs, were found in December and February, suggesting that young females may establish new nests in more or less any part of the warm season.

In four nests in which the uppermost young had finished feeding, a new egg or young larva was present with provisions near the bottom of the nest. This suggests that, after one series of



FIGS. 75-80. Nests of *Allodapula melanopus*. 75, Eggs below pupae. At right, above eggs, is a mass of dry pollen on burrow wall. 76, Eggs in two rows, an unusual arrangement. 77, Eggs in midst of prepupae and pupae. 78, Eggs. 79, 80, Clumps of mature larvae.

young has been produced, the mother bee waits for the time when she can get past the provisions and young, and then goes back to the bottom of the nest, cleans out the feces, and starts another

brood. In no case did the probable second brood consist of more than one egg or larva. The number of such nests studied was small and in each there were one or two young (mostly

callow) adult females present in addition to the older female. There is the remote possibility of egg laying by the young females, but none of them was dissected to determine ovarian development. In other allodapines, callow females never have enlarged ovaries, and I am strongly of the opinion that all such eggs are laid by the old mothers and represent second broods as found commonly in species that feed their young progressively.

Ovaries of this species were examined in only a few individuals but they seem similar to those of *Allodape panurgoides* or *Braunsapis facialis*.

Adult males were found in nests only in December; failure to find them in other months was doubtless owing to the small number of nests found. Only three adult males as compared to 41 females were taken from nests. Males are shown to constitute a small percentage of the production (see table 8).

IMMATURE STAGES: The eggs are 1.9 or 2 mm. long, i.e., they are large for bees of such small size. An egg is attached to the burrow wall by its posterior end and projects into and almost across the lumen of the burrow; the posterior part of the egg slopes downward, but because the egg is curved, the anterior part is nearly horizontal.

After an egg is laid, a mixture of pollen and nectar is placed on its upper (concave, morphologically ventral) surface. The food mass is cylindrical with a diameter only slightly less than that of the burrow (fig. 39). Thus in a burrow 2 mm. in diameter, the food mass was 1.7 mm. in diameter. Material is added to the top of the cylinder until it reaches a height of about 1.7 mm. but the surface is always smooth, the separate loads of pollen not being recognizable. The food mass is not in contact with the burrow walls, being supported entirely by the egg and separated from the walls on all sides by a distance of at least 0.1 mm. (fig. 39).

Having provided the provisions, the bee lays another egg 5 to 7 mm. or sometimes more above the first, and attached to the same side of the burrow wall. The process continues, but not rapidly, for one never finds more than two eggs in a nest.

Larval growth is slow. A half-grown larva required 10 days to finish its growth. In another case an egg taken on November 30 and undoubtedly laid earlier, as there was another fully provisioned egg above it, had become a medium-

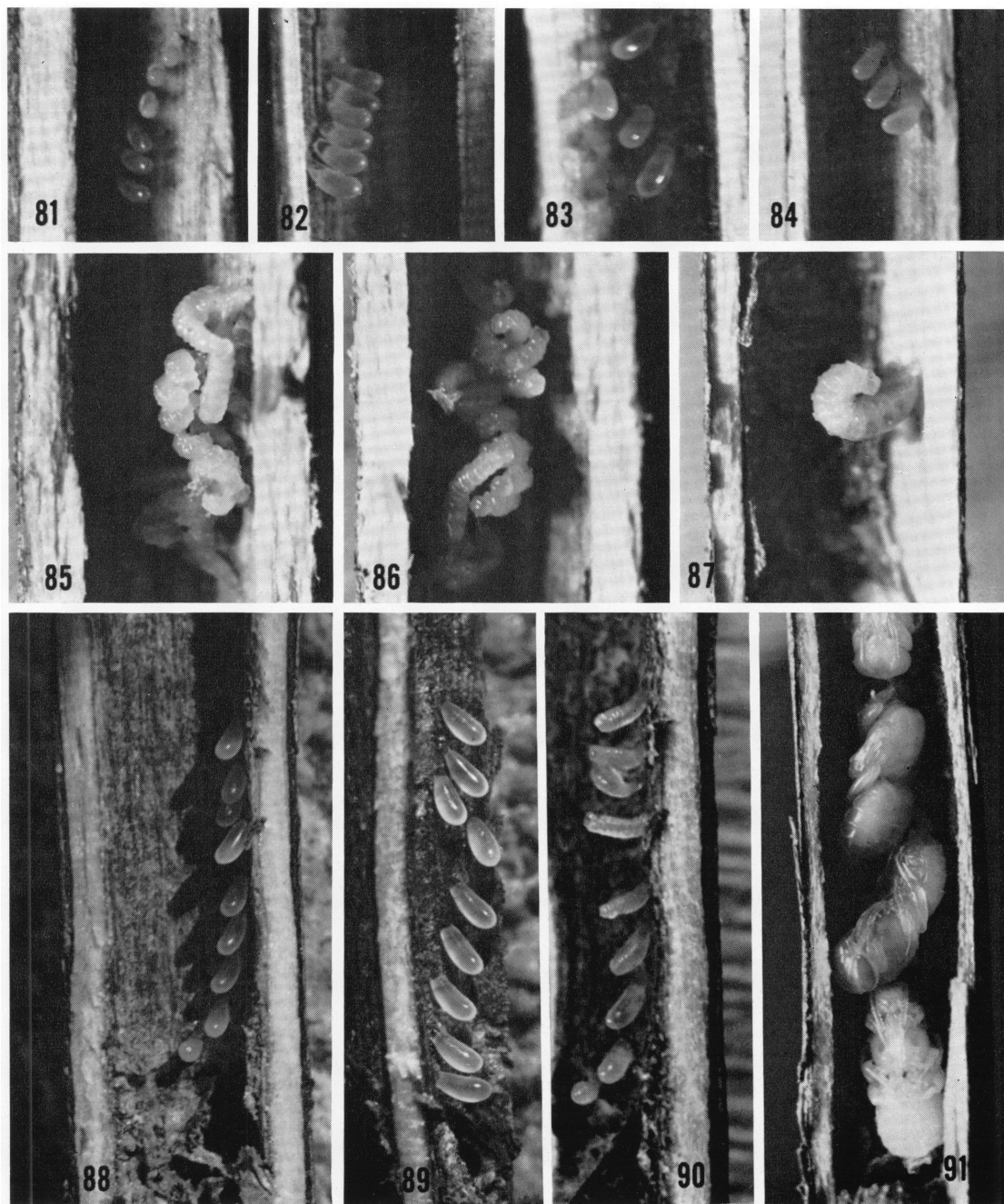
sized larva on December 4, a large larva but still with food on December 24, and had nearly finished feeding on December 30.

On hatching, the larva retains its connection with the egg chorion. It is ventral side up, its venter therefore against the food mass, and starts feeding upward on the side of the food mass opposite the egg attachment. As it grows, the larva eats around the food mass, which is supported by the larva. The pointed posterior end of the larva ultimately comes out of the chorion and serves as a brace, supporting the larva with the food mass, while the old chorion is still attached to and supports the bottom of the food mass and is stuck to the larva slightly in front of its posterior extremity (fig. 39). Thus throughout its feeding period the larva remains fixed to the nest wall, and it is quite impossible for an adult bee to pass it and get into the lower part of the nest.

Pale brown, dry fecal pellets about 0.75 mm. long are produced, starting when the larva is more than half grown but before the food supply is exhausted. They drop down the nest, falling to the bottom or sometimes lodging around prepupae or pupae below. The attachment of the larva to the nest wall is maintained through the prepupal stage in nests from which the adult has been removed or in parts of nests inaccessible to adults because of eggs or younger larvae above. Normally, however, the attachments are broken and the chorions disappear, along with larval feces, when the uppermost larva reaches the prepupal stage or slightly before. At this time, with prepupae and pupae stretched out and not curled like younger larvae, the adult can pass them and get into all parts of the nest. She doubtless moves them about somewhat as in other allodapines, and the nest looks much like that of a *Braunsapis* containing no immature stages younger than prepupae, except that the sequence of ages is reversed, the oldest near the bottom, the youngest above. There is sometimes irregularity in this, a prepupa being below a pupa, for example, presumably due to individual or sexual variations in growth rates.

As indicated above, once a female has renewed access to the bottom of the nest, she may remove some or all of the larval feces and lay and provision an egg there, so that one may then find an egg below prepupae or pupae.

In the one nest containing eight young, detachment of the youngest larva had occurred



FIGS. 81-91. Nests of *Allodapula*. 81-87, *A. variegata*. 88-90, *A. rozeni*. 91, *A. xerica*. 81-84, Eggs. 85, 86, Clusters of rather small larvae still anchored by their egg chorions. 87, A lone larva, middle-sized and still anchored to nest wall; this larva had pollen on its venter. Only other young in nest were already callow adults. 88-90, Different views of same set of eggs; upper ones hatched in 90. 91, Pupae, two of them reversed, facing downward.

before its feeding was completed, for a large larva, the uppermost young, was still curled around a small amount of pollen, yet was not attached. Two young adults had crowded past their pupal, prepupal, and larval siblings, and the mother (presumably) had laid an egg in the bottom of the nest and started provisioning. In nests with the usual numbers of young, however, emergence of adults in the lower part of the nest was seemingly later than attainment of the prepupal stage by the youngest larvae, and there was no evidence of either young adults or the mother passing feeding larvae.

As shown in table 3, nests are ordinarily shallow. There is no possibility of their being extended during the period of larval growth as occurs in many allodapines, and there is no evidence that they are deepened before the mother lays the egg of the second brood.

***Halterapis angustula* (Cockerell)**

Several nests of this species were found 40 miles east of Knysna, Cape Province, December 4, 1966, along with those of the *H. nigrinervis* group. No differences in behavior or life history between the two species of *Halterapis* were evident.

GENUS EXONEURELLA

In the interests of making the present paper as comprehensive as possible, comparative comments are included here on two nonparasitic genera not found in Africa. Data for *Exoneurella* are from Michener (1964). It is an Australian genus with only one known species.

Most nests contain only one mature adult female, although some young adults possibly have (temporary?) worker-like functions. In the few nests with two mature adults, they are equivalent in evidence of age and ovarian function, there being no worker-queen relationship.

The eggs lie loose in the bottom of the nest. The young are kept in the same regular sequence and fed as in *Allodape* and *Braunsapis* although larvae are morphologically very different from larvae of those genera.

GENUS EXONEURA

This second, extralimital genus contains many species. It is found in the southern half of Australia and Tasmania. Data are from Michener (1965) and contained references.

During the active season in species that have been adequately studied, roughly one-third of the nests contain one or more (rarely more) workers, much as in *Braunsapis*. *Braunsapis* and *Exoneura*, then, are the two most social genera of allodapine bees.

Eggs may be attached to the nest wall, projecting into the lumen of the burrow, as in *Allo-dapula*, *Exoneurula*, and the like, but in most species eggs are deposited loose and lie in a clump at the bottom of the burrow. As in *Allo-dapula* they are laid in rather large numbers during a short period of time, so that a number of young of about the same age are found in each nest. Also, as in *Allodapula*, the rather small egg size and the ovarian cycle make such behavior possible.

In species that attach their eggs, the young larvae are supported in the position of the egg by the chorion, as in *Allodapula* and some other genera. In species with free eggs the chorions seem to disappear early as in *Braunsapis* and *Allodape*. In such forms small larvae are in a cluster at the bottom of the nest; larger ones support themselves in the burrow.

Each larva is ordinarily fed progressively, with food placed on its venter. The young are kept roughly in order from youngest below to oldest above but irregularities are not rare so that, for example, pupae of various colors are often mixed instead of arranged from palest below to darkest above as is usual in *Braunsapis*.

PARASITIC SPECIES

Parasitic species have been treated taxonomically by Michener (1970b).

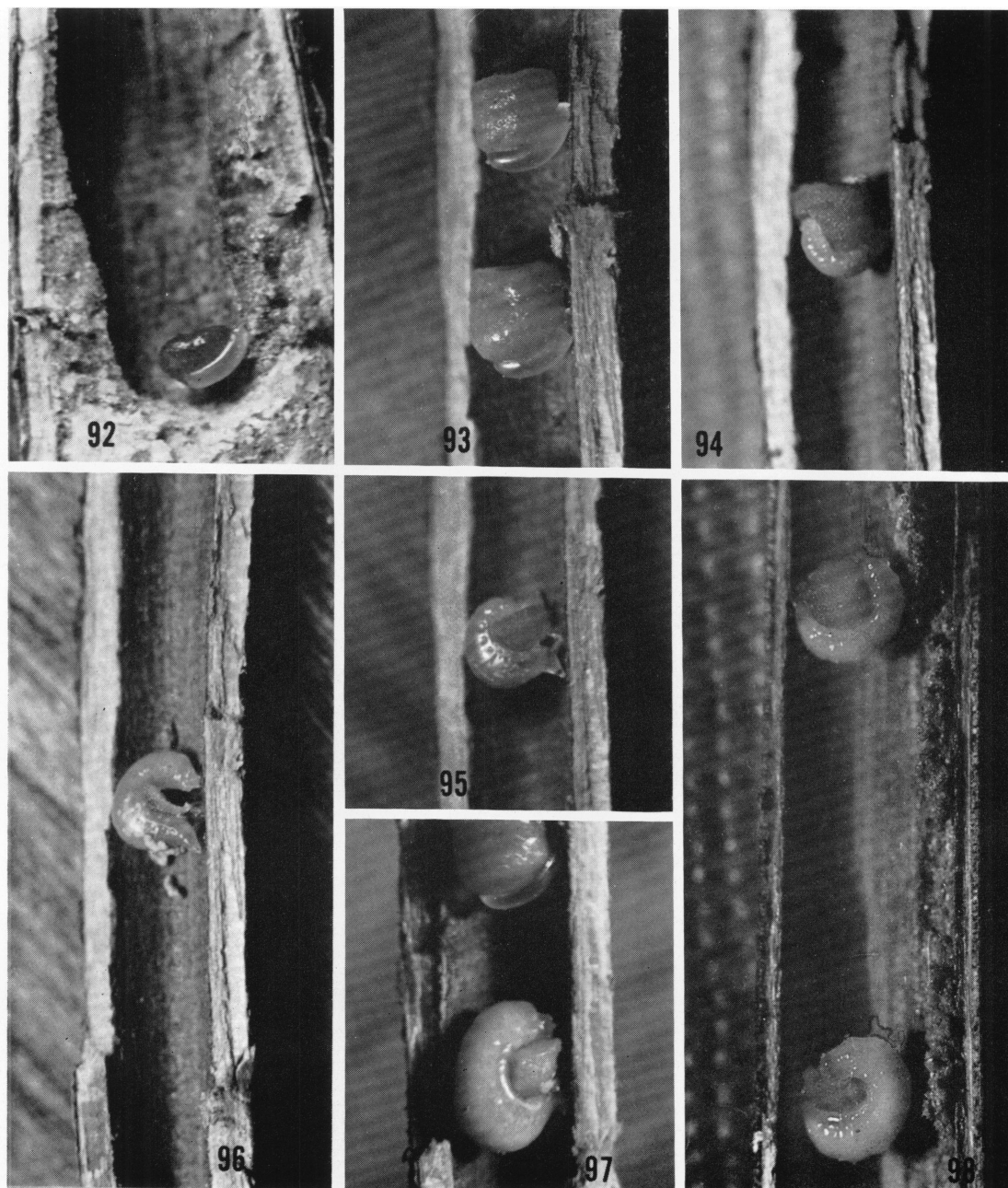
Comments on the relations of *Eucondylops* species to their hosts appear in the discussions of *Allodapula variegata* and *melanopus*. A similar note on *Macrogalea mombasae* appears under *M. candida*.

Braunsapis pallida, known from a single nest from Kasungu, Malawi, seems to be a parasitic species judging by its reduced scopa but was not associated with any host species (see Michener, MS).

Accounts of *Braunsapis natalica* and *Nasutapis straussorum* follow.

***Braunsapis natalica* Michener**

As explained by Michener (1970b, MS) females with both full and reduced scopas have



FIGS. 92-98. Nests of *Halterapis nigrinervis* group. 92, Egg and incomplete pollen mass (Pietermaritzburg). 93, Eggs supporting provisions (Grahamstown, Nov. 20). 94-96, Larva that hatched from lower egg in fig. 93 on Dec. 4, 24, and 30. Note continued attachment to nest wall. 97, Large larva with egg above (Grahamstown). 98, Feeding larvae (40 miles east of Knysna).

been taken associated with what appears to be a single species of male. Both types of female occur in Natal. In Malawi the few known females have

fully developed scopas but there are differences in the males that led me to term this form "*B. ?natalica*." The latter form is also known

from Angola. Some females in collections have probably not been recognized since those with scopas are sometimes not distinguishable from *B. facialis*.

The form with a reduced scopa (*natalica* proper, if two or more species are involved) must be a parasite; the others may or may not be. One slightly callow female and one male were taken at Salt Rock near Umhlali, Natal, with one egg and seven larvae (of ?*natalica*) in a nest containing a female of *B. leptozonia*. In this instance the *B. natalica* was seemingly a parasite of *leptozonia*. Two males, one reared from a pupa, were obtained from a nest of *B. facialis* at the same locality. Males of ?*natalica* were reared from two nests taken at Kasungu, Malawi. There is nothing to distinguish the associated females and larvae from *facialis* or to suggest parasitism.

At the Hluhluwe Reserve females of *B. natalica* with the scopa reduced were taken on flowers, indicating that, unlike *Nasutapis* and *Eucondylops*, but like *Macrogalea mombasae*, this species does visit flowers.

***Nasutapis straussorum* Michener**

Figure 40

This parasitic bee has greatly reduced mouth parts, lacks the pollen collecting scopa, and in spite of intensive collecting has never been taken on flowers. It presumably does not visit flowers but feeds exclusively on food brought to the host nest by females of the host species or on eggs of the host species. Wing margins are always intact or nearly so, supporting the view that these bees do very little flying.

Individuals of *Nasutapis* were found in 36 nests of *Braunsapis facialis* in a partly dead tree of *Schinus terebinthifolia* in a garden at Salt Rock near Umhlali, Natal, on December 29, 1966, and January 6 and February 27 to 29, 1967. Immature individuals of *Nasutapis* were present in 23 of these nests, with no seasonal changes in frequencies of the various immature stages from December to February. The total number of eggs and young (both *Nasutapis* and *Braunsapis*) per nest averaged 4.0, not greatly different from the 3.7 for unparasitized *Braunsapis* nests from Natal, but markedly above the 2.5 for the 45 unparasitized *Braunsapis* nests from Salt Rock. The latter figure may be low because of prior parasitization in some of the nests and because of a

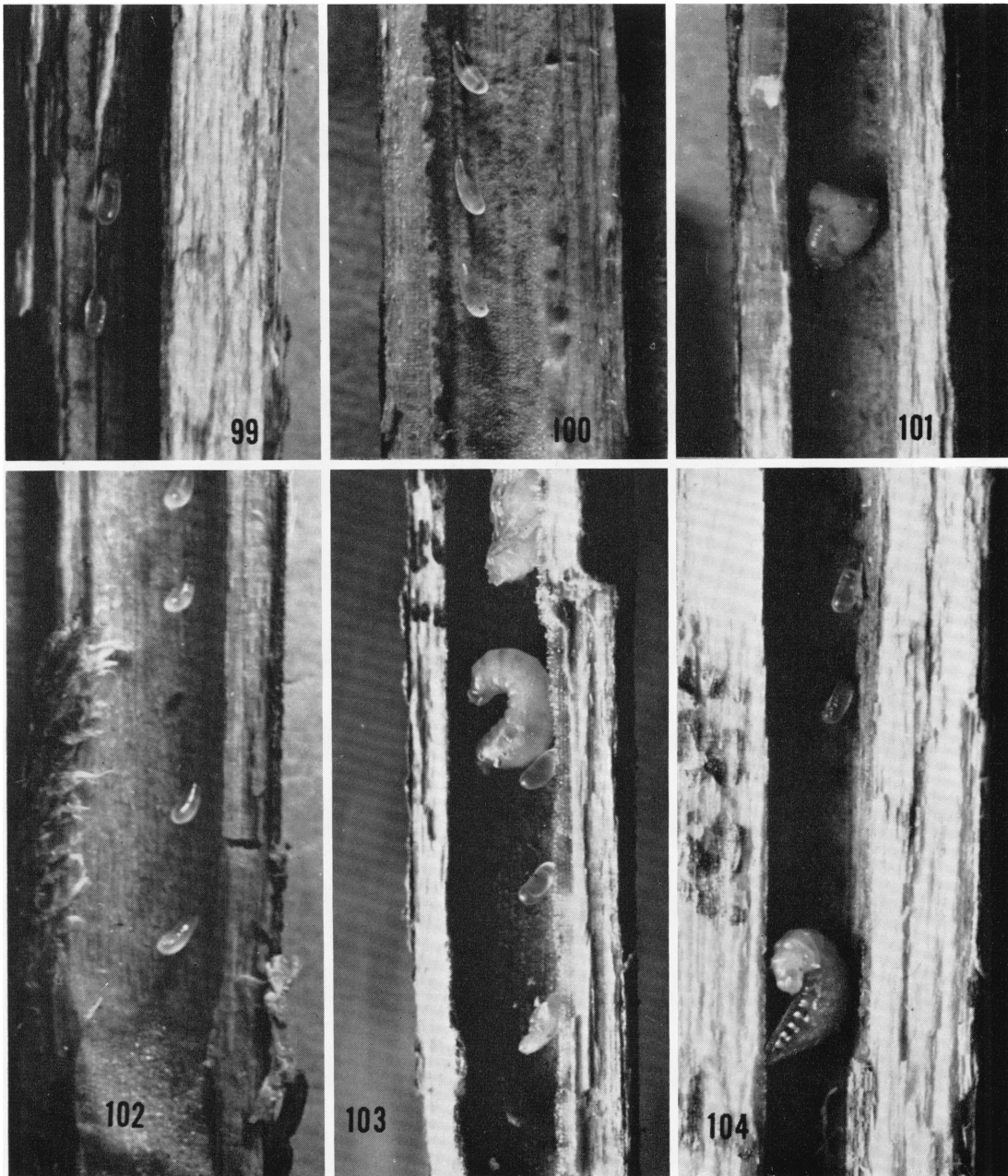
high number of new nests with only an egg or small larva. It is evident that parasitization may increase the total productivity of a nest, but it does so at the expense of *Braunsapis* productivity.

The age distribution of young clearly indicates that a female *Nasutapis* enters a host nest and stays there, replacing the host as an egg layer although one or more host females remain and serve as foragers. Fortunately all stages, egg to adult, are identifiable. Nests were found in all stages of parasitization (fig. 40). Some were perfectly normal *Braunsapis* nests except for the presence of an adult female *Nasutapis*. Others had a *Nasutapis* egg but all older young were *Braunsapis*. In still other cases the young *Nasutapis* were from egg to middle-sized larva, egg to prepupa, or even egg to white pupa, in each case with all older young being those of *Braunsapis*. It is therefore evident that the *Nasutapis* does not prevent rearing of *Braunsapis* already growing in the nest, but does prevent the production of additional individuals of *Braunsapis*. (I do not wish to imply that every such parasitized nest contained a *Nasutapis* egg; egg production is slow and sometimes there were neither eggs nor young larvae of either species present.)

The mechanism for preventing production of young *Braunsapis* could be either (1) the inhibition of laying, so that any adult female *Braunsapis* present would become essentially workers, or (2) destruction of *Braunsapis* eggs by the female *Nasutapis*. That the former is unlikely is shown by the enlarged ovaries of the female *Braunsapis*, which contain developing eggs as large as those of females not associated with *Nasutapis*. That the latter occurs is suggested by the presence, in two parasitized nests, of one *Braunsapis* egg in spite of older *Nasutapis* larvae. This is contrary to the findings of abrupt and complete cessation of *Braunsapis* production indicated in the preceding paragraph; I suggest that these eggs would soon have been destroyed, probably eaten, by the *Nasutapis*.

Occasionally a nest is found in which the adult female *Nasutapis* has disappeared, presumably died. In two such cases *Braunsapis* eggs or young were present, showing that the nest had reverted to its original function, but the older larvae and pupae of *Nasutapis* were being fed and cared for (fig. 40).

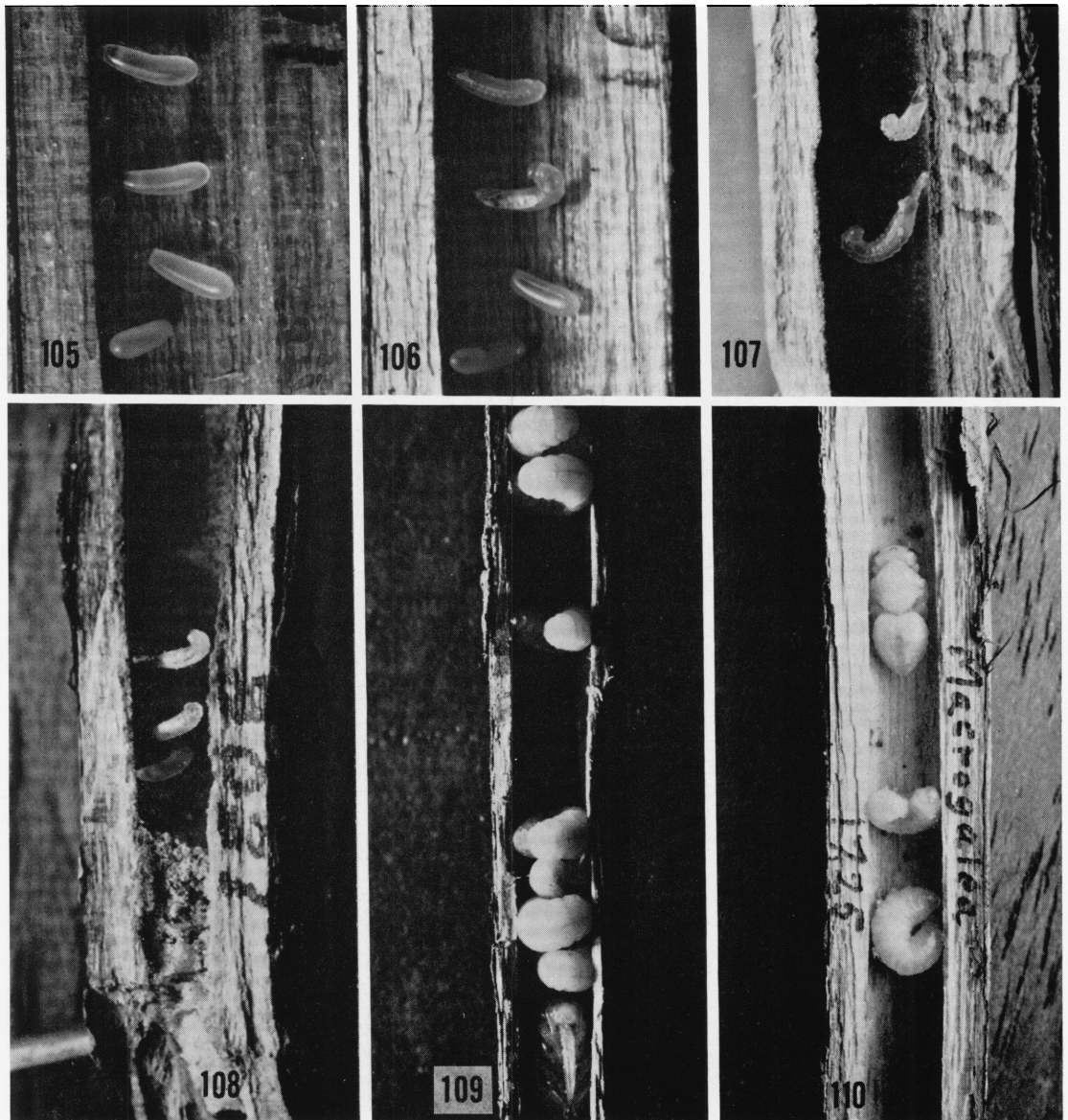
Of the 23 nests containing immature *Nasutapis*, nine contained no immature *Braunsapis*, 14 had



FIGS. 99-104. Nests of *Exoneurula stigmoides*. 99, 100, eggs, some of them beginning to hatch. 101, Larva feeding on provisions. 102, Eggs. 103, 104, Eggs and large larvae, pupa in 103.

young of both host and parasite. In the nine nests with no young *Braunsapis*, the number of young *Nasutapis* ranged from one to seven, with a mean of 3.8, approximately the same as for *Braunsapis* in unparasitized nests. In some cases

the young are more or less evenly scattered from egg to pupa, whereas in other cases there are large developmental gaps, as in one nest containing two eggs, four large larvae and a prepupa, all of *Nasutapis*.



FIGS. 105-110. Nests of *Macrogalea candida*. 105, Eggs. 106, Same, upper two eggs hatched. 107, 108, Young larvae attached to burrow walls by chorions. 109, 110, Large larvae, prepupae (which are still curled) and pupae.

***Inquilina excavata* (Cockerell)**

This Australian parasite of *Exoneura variabilis* has the same relation to its host as does *Nasutapis straussorum* to *Braunsapis facialis*. *Nasutapis* morphology is, however, more distinctive.

The evolutionary parallelism of the two parasitic genera (and presumably also the less well known genus *Eucondylops*) is noteworthy. In each case parasitism is dependent on the social tend-

encies of the host, for the female parasite replaces the host queen while the colony continues its existence, rearing parasites instead of hosts. Presumably this is also true for all allo-dapine parasites. The only counterparts among the bees are the relations of *Psithyrus* to *Bombus* and of *Bombus hyperboreus* to *B. polaris* (Richards, 1970). Other parasitic bees have entirely different relations to their hosts.

CONCLUSIONS

GENERAL CONCLUSIONS on allodapine biology derived from the present and previous studies are presented in the introductory sections of this paper, before the Species Accounts. General material on the parasitic allodapines is presented by Michener (1970b) and at the end of the section on parasitic species herein. Recapitulation of these materials seems unnecessary here.

The following paragraphs consist of an evaluation of various biological characters—tentative statements as to which character states are ancestral and which derived. They are based primarily on the character states found in related xylocopine bees.

1. EGG SIZE: Large is ancestral, being characteristic of *Xylocopa* and *Ceratina* as well as *Braunsapis* and *Halterapis*; small as in *Exoneura* and *Allodapula* must be derived and related to production of a number of eggs at about the same time.
2. TEXTURE OF CHORION: Delicate, as in nonparasitic bees generally including *Xylocopa*, *Ceratina*, *Allodape*, and *Braunsapis*, must be ancestral. Tougher chorions such as occur in allodapines like *Allodapula* must be derived.
3. EGG ATTACHMENT: *Xylocopa* and *Ceratina* eggs are attached to the nest wall by their posterior ends; this is presumably the ancestral condition, still found in various allodapines. Free eggs must be a derived character state.
4. EGG POSITION: Almost all other bees disperse eggs, one per cell. Dispersion of eggs in allodapines is presumably an ancestral character, seen not only in *Halterapis* but also in *Macrogalea* and *Exoneurula*. Close proximity of eggs, as seen sometimes, in *Macrogalea* and regularly in *Allodapula* and in forms with free eggs, is a derived state.
- 5, 6. EGG SHAPE: Those of *Xylocopa* and *Ceratina* are long and curved, as in some *Allodape*, *Braunsapis*, *Halterapis*, etc. Presumably both shortness (as in some *Braunsapis*) and straightness (as in *Macrogalea*) are derived states.
- 7, 8. OVARIAN DEVELOPMENT: Both *Xylocopa* and *Ceratina* lay at a slow rate, as cells are provisioned. Their ovaries show one mature egg at a time and only one conspicuous enlarging oocyte per ovariole, as is also true of some allodapines. The presence of larger numbers of mature eggs and of two or even three conspicuous oocytes per ovariole, reaching the extreme in *Exoneura* and *Allodapula*, are derived states. Production of young at intervals versus in batches is a corollary of these characters.
9. NEST ENTRANCE COLLAR: Lack of such a collar characterizes *Xylocopa* and *Ceratina*. Its absence in *Exoneurella* and weakness in *Allodape* may be ancestral, in contrast to full development in other allodapines.
10. FEEDING OF LARVAE: Mass provisioning of larvae characterizes nearly all bees, including *Xylocopa*, *Ceratina*, and *Halterapis*. Other allodapines have a derived character state, progressive feeding, with *Exoneurula* intermediate.
11. SEQUENCE OF YOUNG: In bees having linear nests like *Xylocopa*, *Ceratina*, and *Halterapis*, the oldest young must be at the bottom, the youngest at the top. A mixed arrangement as in *Macrogalea* and *Exoneurula* must be intermediate and the reversed sequence as in *Exoneurella*, *Allodape*, and *Braunsapis* should be the derived state.
12. FOOD MASSES: In nearly all bees there is one food mass provided to each growing larva. A common food mass for various larvae such as is used by *Allodapula* must be a derived character state.
13. SOCIAL LEVEL: Most bees, including *Xylocopa* and *Ceratina*, have only one working adult female per nest. Most allodapines have the potentiality for two or more mature adult females in a nest, and the increased frequency of such nests appears to represent progressively more derived states.
- 14, 15. FERTILIZATION AND OVARIAL DEVELOPMENT OF WORKERS: Extra mature adults may be similar to the bee that established the nest. Presumably this is the ancestral state—lack of social polymorphism—since such polymorphism is absent in related nonsocial bees. Behavioral and physiological polymorphism leads to increased percentages of unmated workers with slender ovaries, doubtless derived character states.
16. WORKER SIZE: Workers may be similar to queens in size or may average smaller. Presumably the latter is the derived character state, the ancestral one being lack of polymorphism as in related nonsocial bees.

The numerous and fascinating morphological characters of larvae, often related to behavioral attributes, will be treated in a paper now in preparation.

SUMMARY

A few allodapine bees (genus *Halterapis*) mass provision their nests, but most feed their larvae progressively. The structure and behavior of larvae and pupae enables them to maintain their positions in the hollow stems in which they live. In common genera such as *Braunsapis* and *Allo-dape*, the arrangement is from youngest below to oldest above. Each larva in these genera is fed by means of provisions placed on its venter by adult bees. In the genus *Allodapula*, however, larvae are together in a clump instead of one above another and feed from a common food mass. Such matters as positions of eggs, larvae, and pupae, and ways in which larvae are fed, are summarized in the preliminary account of each genus and in the section entitled Allodapine Biology. In the Conclusions are found comments on which of the physiological or behavior characteristics are ancestral and which derived.

Social behavior of allodapines is treated both in the Species Accounts and the section on Allodapine Biology. The allodapines are noteworthy for the small sizes of the populations of adults in their colonies and the failure of many nests, even of the more social species, to acquire workers at all. They range from simple subsocial

species in which each nest normally contains only a single bee and additional mature adult females are rare and seem almost accidental, to those in which nearly 40 per cent of the nests contain two or more mature adult females.

Even in the small and facultative groups of adult females, weak polymorphism arises. This is shown behaviorally in that certain females (workers) do most of the foraging, others (queens) do little foraging when workers are present. The workers often do not mate. Many workers, unlike queens, do not experience much ovarian development, although others do and probably lay some eggs. There is meager evidence that workers are short lived compared to queens. In some species the mean size of workers is less than that of queens. In all these features (except, of course, mating) intermediacy is common and many bees can be placed as to caste only arbitrarily.

In an Appendix preliminary descriptions are given for eleven new species falling in the genera *Allodape*, *Braunsapis*, *Allodapula*, and *Exoneurula* in order to validate names for forms on which biological information is presented.

APPENDIX

SEVERAL OF THE SPECIES discussed above have not been described, although a few of the names do appear in comments on habitats (Michener, 1970a). These forms are described and illustrated in a forthcoming taxonomic paper on African allodapine bees, but in order to avoid any nomenclatural confusion, brief descriptions are provided here.

Except as otherwise indicated, holotypes and allotypes will be placed in the American Museum of Natural History. Paratypes will be placed in the South African Museum, Cape Town; the Snow Entomological Museum, University of Kansas; and the British Museum (Natural History).

Allodape brachycephala, new species

DIAGNOSIS: This species differs from other tropical *Allodape*, such as *A. interrupta* Vachal, by its dark coloration and especially by the black tibial spurs (pale brown or testaceous in the other tropical species). An unusual feature, otherwise found only in certain South African species, is the tridentate mandible of the male.

DESCRIPTION: FEMALE: Length 7 mm.; wing length 6 mm. Black with the following parts pale yellow: median subapical clypeal dot in paratype only; streak along inner orbit, widest at level of tentorial pit, and tapering upward to point at level of or (in paratype) a little above antennal bases; narrow streak extending most of length of posterior orbit. Flagellum with underside dark brown. Tegula dark brown; median axillary sclerite brownish black. Small segments of tarsi rufescent; middle and hind tibial spurs black. Margins of metasomal sterna brown and in paratype discs of sterna partly red-brown but terga with margins almost as black as discs. Pubescence dull whitish; hairs of tibial brush (on outer side of tibia; not the scopa) coarse, sparse, black; pygidial fimbria golden. Marginal cell rounded or blunt, bent away from wing margin at apex. Gradulus of second tergum not extending past spiracle.

MALE: Size and coloration as in female, neither male specimen with red-brown on sternal discs; some infuscated hairs representing tibial brush on apical third or fourth of tibia. Mandible tridentate. First front tarsal segment about as long as others taken together, second about two-thirds as wide as long; teeth of hind trochanter of moderate length, apical one with

only a small, black, rounded head; hind femur with only a basal angle, not a tooth; hind tibia without long bristles such as are found in *A. interrupta* Vachal.

MATERIAL: Holotype female and allotype male: Lwiro River, 47 km. north of Bukavu, Congo, 1650 m. altitude, January 4, 1958 (E. S. Ross and R. E. Leech, California Academy of Sciences). One male paratype, same locality and collectors but labeled 1950 m. altitude, August 27, 1957. One female paratype, Kawanda, Kampala, Uganda, June 22, 1967, from nest no. 1958 (C. D. Michener). The paratypes are in the Snow Entomological Museum, the University of Kansas.

ETYMOLOGY: The specific name refers to the unusually short face.

Braunsapis draconis, new species

DIAGNOSIS: This is a small black species of the group of *B. leptozonia* (Vachal), from which it differs in the more reduced pale markings, the reduced hind trochanteral teeth of the male, the lack of the densely punctate and hairy upper genal area, and other characters listed below. Because of the reduced pale markings, including the T-shaped clypeal mark, the female is more similar to *B. luapulana* (Cockerell) than to *leptozonia*. It differs from *luapulana* in the usually nonhamate clypeal mark, the usually black pronotal lobes, and the scarcely convex median upper clypeal margin.

DESCRIPTION: MALE: Length 4–5 mm.; wing length 3.5–4 mm. Black, the following parts pale yellow: clypeus, labrum, often spot on mandible, lateral face mark not reaching much above tentorial pit (often limited to spot just below pit, sometimes absent, in paratypes), small pale area on pronotal lobe (commonly absent in paratypes). Tarsi black, small segments slightly brownish. Hind trochanter with teeth reduced to weak convexities; hind femur with concavity shorter than in *leptozonia*, not sharply margined on outer side, some rather long, nearly straight, and not or sparsely barbed hairs arising along inner margin.

FEMALE: Length 5–6 mm.; wing length 3–4 mm. Clypeal mark reduced, T-shaped, usually nonhamate; otherwise no yellow

markings (except occasionally small pale yellowish area on pronotal lobe); tegula translucent brown; median axillary sclerite brownish black. Small segments of tarsi infuscated. Upper genal area scarcely more hairy than rest of area (both sexes).

MATERIAL: Holotype male, allotype female, and 74 paratypes: Cathedral Peak Hotel, 28 miles south of Winterton, Natal, 4700 feet altitude, February 16, 1967 (C. D. Michener). Other localities from which paratypes are not designated, all in Natal: Umbumbulu; 14 miles northeast Bulwer, 3900 feet altitude; Hellahella, 13 miles southwest Richmond on Umkomaas River, 2400 feet altitude (all C. D. Michener).

ETYMOLOGY: The specific name, referring to a dragon, is based on the type locality in the Drakensberg, or dragon mountains.

***Braunsapis stuckenbergorum*, new species**

DIAGNOSIS: This is a small, black member of the group of *B. leptozonia* (Vachal) from which it differs in usually smaller size, more reduced pale markings, the lack of the densely punctate and hairy upper genal area, especially the enormous, basally directed hind femoral tooth of the male, and other features listed below. The females are similar to those of *B. draconis* which occurs in the same region, agreeing in the form of the clypeal mark and in the commonly dark pronotal tubercles. *Braunsapis stuckenbergorum* differs in its usually smaller size, the usually concave upper clypeal margin, the frequent presence of a pale spot on the tegula and the frequently pale outer part of the median axillary sclerite, and other features no one of which is completely diagnostic.

DESCRIPTION: MALE: Length nearly 4 mm.; wing length nearly 3 mm. Yellow limited to clypeus (lateral margins variably dark) and much of labrum. (Probably some have yellow on pronotal tubercle, tegula, and median axillary sclerite, but the three male specimens available have these areas dark.) Tarsi dark as in female. Malar area almost linear. Hind trochanter with the two teeth low and close together; hind femur with enormous, basally directed, median tooth; underside of hind tibia with hairs on apical half that are as long as tibial spurs and with long branches that are blunt tipped.

FEMALE: Length 4–4.5 mm.; wing length 3–3.5 mm. Clypeal mark reduced, T-shaped,

usually hamate; pronotal lobe yellow to black (even among individuals from one nest); outer half of median axillary sclerite usually yellow. Tegula transparent brown, usually with yellow spot.

MATERIAL: Holotype male, allotype female, and 13 female paratypes: 3 miles west of Pietermaritzburg, Natal, December 13 and 19, 1966, and January 12, 1967 (C. D. Michener). Two male and nine female paratypes: Richmond, Natal, 2800 feet altitude, December 26, 1966 (C. D. Michener).

Females apparently of this species, not listed among the paratypes for lack of associated males, are from the following additional localities: Hellahella, 13 miles southwest Richmond; 8 miles south Richmond; Nagle Dam, 17 miles east Pietermaritzburg; 11 miles south and 5 miles northwest and 5 miles west of Pietermaritzburg; all in Natal (C. D. Michener); Blantyre, Malawi (C. D. Michener).

ETYMOLOGY: This species is named for Mr. and Mrs. B. R. Stuckenberg of Pietermaritzburg in recognition of their interest in my work and the extensive help they gave me.

***Braunsapis simplicipes*, new species**

DIAGNOSIS: This small, black species has the size and most structural features of *B. gorillarum* (Cockerell) from which it differs in the more extensive yellow maculation, the strongly concave upper clypeal margin, the more slender dorsal metasomal hairs, and in details of the male genitalia.

DESCRIPTION: MALE: Length 4 mm.; wing length 3.5 mm. Black, the following parts yellow: clypeus, most of labrum, most of mandible, rim on paraocular area adjacent to lower half of clypeus (rarely extending up as far as tentorial pit), pronotal tubercle. Thoracic coloration as in female. Tarsi rather dark brown. Malar area almost linear, length much less than half width of scape. Middle flagellar segments slightly longer than broad (to as broad as long). Hind leg as in *B. natalica* Michener.

FEMALE: Length 4.5–5 mm.; wing length 3.5–4 mm. Black, the following parts yellow: most of upper half of clypeus and broad longitudinal band extending through lower half, sometimes spot at base or also at apex of underside of scape, pronotal lobe. Tegula translucent brown; wing base including median axillary sclerite light brown (to black). Basitibial plate

as in *B. facialis* (Gerstaecker). Hairs of terga 4–6 dusky, blunt, slender.

MATERIAL: Holotype male and allotype female: Nairobi, Kenya, July 5, 1967 (C. D. Michener); 132 paratypes from the same locality and Karen, a suburb of Nairobi, May 6 to July 5, 1967 (C. D. Michener). Other specimens, not paratypes, are from the following localities: 50 miles southeast Nairobi, Kenya; Kawanda, Kampala, Uganda; 2 miles south Blantyre and Kasungu, Central District, Malawi (all collected by C. D. Michener).

ETYMOLOGY: The specific name refers to the slender, untoothed hind femora and trochanters of the male.

***Braunsapis acuticauda*, new species**

DIAGNOSIS: This black species is similar to the sympatric *Braunsapis elizabethana* (Strand) from which it differs by the almost wholly densely punctate and hairy genal areas, the acutely pointed sixth sternum of the female, the more slender hind legs of the male, and other characters listed below. In contrast to most species pairs of *Braunsapis*, the females of *B. elizabethana* and *acuticauda* are relatively distinct and the males are difficult to distinguish.

DESCRIPTION: FEMALE: Length 4–6.5 (holotype) mm.; wing length 3–3.5 (holotype) mm. Clypeus usually wholly black, in holotype with small median anterior submarginal yellowish spot, in a few paratypes with narrow pale T; median axillary sclerite wholly brownish black. Genal area almost entirely densely punctured and covered with short plumose hairs. Apex of last sternum acutely pointed.

MALE: Length 4 mm.; wing length 3 mm. Clypeus sometimes (in one paratype) more extensively black than in *B. elizabethana*. Hind trochanter with two teeth separated by distinct concavity; hind femur less robust than in *elizabethana*; ventral hairs on these segments often much shorter than in *elizabethana*.

MATERIAL: Holotype female: Cape Nature Reserve, Cape Peninsula, Cape Province, October 1, 1966 (C. D. Michener). Allotype male: Same locality, October 15, 1966 (C. D. Michener). Thirty-one paratypes: Same data as for holotype or allotype, also October 29; Hout Bay, September 27, 1966; west side of Pakhuis Pass near Clanwilliam, 2500 feet altitude, November 3, 1966; all in Cape Province (C. D. Michener). Two female paratypes: Cape Town

(J. C. Bridwell, National Museum of Natural History, Washington).

ETYMOLOGY: The name refers to the acutely pointed apex of the metasoma of the female.

***Allodapula rozeni*, new species**

DIAGNOSIS: This species is similar to *A. variegata* (Smith) and may be a marginal isolate of that species, although no intergradation is known. It differs from *A. variegata* in the broken yellow pronotal band of the female, the absence of such a band in the male, the almost entirely red legs and metasoma, and other characters listed below.

DESCRIPTION: FEMALE: Length 6.5–7 mm.; wing length 5 mm. Similar to *variegata* (Smith) except for: Clypeal mark tapering and fading away below so that lower part of clypeus is all or largely black; pronotal band broken medially, labrum and mandible brown, heavily infuscated, without yellow; legs red except for black coxae, infuscated mid- and hind-trochanters and base of hind femur, and yellow on apical part of posterior surface of fore femur. Metasoma red, base of first tergum infuscated (both sexes). Upper margin of clypeus concave without median convexity.

MALE: Length 7 mm.; wing length 5 mm. Similar to *A. variegata* (Smith) except for: prothoracic yellow band absent; coloration of legs as in female; summit of clypeus about straight (true also of some males of *variegata*).

MATERIAL: Holotype female, allotype male, and four female paratypes (two of them callow) and one (headless) male paratype: 16 miles northeast of Montagu, Cape Province, November 12, 1966, from a nest (no. 483) in a dead flowering stem of *Cotyledon paniculatum* (C. D. Michener).

ETYMOLOGY: This species is named for Dr. Jerome G. Rozen, Jr., of the American Museum of Natural History in recognition of his excellent studies of bees. He was with me when the specimens of *A. rozeni* were collected.

***Allodapula ornaticeps*, new species**

DIAGNOSIS: In the extensive lateral face marks of the female this form differs from all other *Allodapula*, being approached only by *A. jucunda* (Smith). The yellow mandibular patch and proximity of the clypeus to the antennae are also unique features in the genus *Allodapula*. The yellow area on the apex of the front femur is

similar, not only in its presence but in its shape, in *A. variegata*, *rozeni*, *jucunda*, and *ornaticeps*. Other differences from the well-known *A. variegata* are indicated below.

DESCRIPTION: Female: Length 6 mm.; wing length 4.5 mm. Clypeal yellow mark a longitudinal band, not enlarged above, vaguely spreading below; broad bright yellow bands on paracocular areas and crescent below anterior ocellus; yellow of pronotal band joining with yellow on pronotal lobe. Labrum yellowish brown; mandible black with large yellow patch, reddish near apex. Legs yellowish red, coxae infuscated except at apices, middle of hind femur infuscated, posterior surface of front femur yellow apically as in *A. variegata*. Scape yellow beneath, yellow-brown above; flagellum brown above, pale brown beneath. Metasoma red with weak infuscation on first tergum and sides of second and of apical terga. Upper margin of clypeus concave; clypeoantennal distance equal to diameter of antennal socket.

MATERIAL: Holotype female and two female paratypes: West side of Pakhuis Pass near Clanwilliam, Cape Province, 2500 feet altitude, November 3, 1966 (C. D. Michener).

ETYMOLOGY: The specific name refers to the three yellow stripes and other yellow markings on the head.

***Allodapula xerica*, new species**

DIAGNOSIS: The only previously described close relative of this species is *A. palliceps* (Fries) from Willowmore, Cape Province, known only in the male. The male of *A. xerica* differs from that of *palliceps* in the yellow mandible, broken pronotal band, the linear malar area, the narrower face, and genitalic characters to be described later.

DESCRIPTION: FEMALE: Length 6–7 mm.; wing length 4.5 to nearly 5 mm. Black, the following parts pale yellow: broad band across upper part of clypeus extending downward medially as sharp point; large area on posterior pronotal lobe. Rest of pronotum black, or in some paratypes with transverse pale yellow streak on each dorsolateral angle, sometimes forming transverse pale yellow band, broken medially. Flagellum brown beneath. Tibiae and tarsi blackish brown or bases and apices of tibiae somewhat paler; anterior surface of anterior tibia brown to yellowish brown. Tegula translucent brown; median sclerite of wing base dark

brown, in some with yellow streak. Metasoma dark red-brown, much of first tergum and posterior and lateral margins of last two terga and posterior margins of all sterna infuscated. (In paratypes metasoma varies from largely red to reddish black.) Upper margin of clypeus distinctly concave (both sexes); clypeoantennal distance less than half diameter of antennal socket (both sexes). Malar area anteriorly less than half as long as diameter of scape. Dorsal hairs of terga 4–6 short, curved, thickened, blunt, longer on 4 than on 5 and 6, dusky on 4, usually pale but sometimes dusky on 5 and 6.

MALE: Length 6 mm.; wing length 5 mm. Black, the following parts bright yellow: clypeus, labrum, mandible except rufescent apex, paracocular area up to level of middle of antennal socket, scape, underside of antennal pedicel, broken pronotal band, pronotal lobe, and legs except coxae (or distal parts of coxae also yellow). Tegula transparent with yellow spot; median sclerite of wing base with yellow costal area, dark brown otherwise. Metasoma reddish brown, infuscated on segments 1 and 4–7.

MATERIAL: Holotype female, allotype male, and 14 female and one male paratypes: 7 miles west of Robertson, Cape Province, 900 feet altitude, in nests in dead flowering stems of *Cotyledon paniculatum*, October 9, 1965 (C. D. Michener). (The labels on the specimens do not specify the distance west of Robertson.)

ETYMOLOGY: The name *xerica* is proposed because of the xeric habitat of the species.

RELATIONSHIPS: *A. xerica*, *palliceps*, and the two species described below belong to *Allodapulodes*, a group best considered a subgenus of *Allodapula*. It is quite possible that *A. maculithorax*, *hessei*, and *xerica* are geographic variants of a single species. They are, however, quite different in spite of proximity of localities and are not known to intergrade. The only reasonable procedure at this time is to consider them separate species.

***Allodapula hessei*, new species**

DIAGNOSIS: This species is similar to *A. xerica* from which it differs by the extensive yellow areas on the scutum and scutellum of the male and the black or nearly black metasoma of the female, in addition to the other differences listed below.

DESCRIPTION: FEMALE: Yellow pronotal band unbroken or nearly so. Tibiae black or nearly so

except for brown anterior surface of front tibia. Median sclerite of wing base with costal part often broadly yellowish. Metasoma black, usually with dark red suffusion on second and third segments.

MALE (both specimens are teneral): Length 5 mm. Pronotal yellow band broad and unbroken, laterally reaching yellow of pronotal lobe. Scutum with yellow laterally, in one specimen extending full length of lateral margin, in the other limited to area in front of tegula; posterior margin of scutum with transverse yellow band, narrowed medially, or two yellow spots. Scutellum with broad transverse yellow band occupying anterior half or more. Coxae (as well as rest of legs) largely yellow; median parts of tibiae and streak on upper posterior side of hind femur darkened. (The mature coloration is not certain but presumably these areas become infuscated.) Median sclerite of wing base yellow with dark median streak. Infuscation of metasoma doubtful, perhaps absent.

MATERIAL: Holotype female, allotype male, and eight female and one male paratypes (some of them callow): West side of Pakhuis Pass near Clanwilliam, Cape Province, 2500 feet altitude, November 3, 1966 (C. D. Michener).

ETYMOLOGY: This species is named for Dr. A. J. Hesse of the South African Museum, Cape Town, in recognition of his extensive entomological work and the help he gave me.

***Allodapula maculithorax*, new species**

DIAGNOSIS: This species is similar to *A. xerica* from which it differs in the small, longitudinally elongate yellow scutellar spot in both sexes, the largely black rather than yellow legs of the male, and other characters as indicated below.

DESCRIPTION: FEMALE: Pronotum with medially broken pale yellow band (both sexes); scutellum with almost round or longitudinally elongate, median pale yellow spot (both sexes). Flagellum brownish black throughout. Tibiae and basitarsi black, small segments of tarsi brownish black. Median axillary sclerite black. Metasoma dark red, terga more infuscated medially, or fully red as in *xerica* in material from Cape Town.

MALE: Yellow areas pale yellow rather than bright yellow. Labrum infuscated laterally; mandible black with only small anterobasal yellow spot, distal half red-brown. Black extending down between upper margin of clypeus and yellow of paraocular area for some distance.

Scape yellow on underside only. Legs black with the following areas pale yellow: apical area on posterior surface of front femur (shaped as in *A. variegata*), streak on under surface of apical half of middle femur, outer apical areas on tibiae (that of front tibia extending basally nearly to middle of tibia), basitarsi. Small tarsal segments testaceous. Anterior sides of tibiae with red-brown, most extensive on fore tibia, least on hind. Tegula dark translucent brown. Metasoma reddish black (red in Cape Town specimens).

MATERIAL: Holotype female and two female paratypes: Hout Bay, Cape Peninsula, Cape Province, September 11, 1966 (C. D. Michener). Allotype male and one female paratype: Cape Nature Reserve, Cape Peninsula, October 29, 1966 and February 5, 1967, respectively (C. D. Michener). Twelve female and two male paratypes: Cape Town (J. C. Bridwell, National Museum of Natural History, Washington).

ETYMOLOGY: The specific name refers to the pale yellow spot on the scutellum.

***Exoneurula stigmoides*, new species**

DIAGNOSIS: This is a member of the group of *E. stigma* (Strand) and *E. harveyi* (Cockerell) and may be conspecific with them. Each of those species is based on a single specimen, one male (*stigma*) and one headless female (*harveyi*), and the new species is based on specimens from a single locality. It is quite possible that the differences will be found to be geographical variations in a single species rather than specific characters when adequate material is available. *Exoneurula stigmoides* lacks red on the metasoma, unlike *stigma* and *harveyi*. There are also striking differences in the yellow markings of the head and thorax.

DESCRIPTION: FEMALE: Length 5 mm. (varying to 4 mm.); wing length 4 mm. (varying to 3.5 mm.). Black (brown in teneral paratypes), the following parts yellow: clypeus except lower lateral parts, area on labrum, area on mandible (reddish yellow and sometimes absent), paraocular band along inner orbit not reaching level of summit of clypeus, lower surface of scape, broad band across pronotum reaching and including pronotal lobe, most of scutellum mesal to axillae except posterior margin. Terga 5 and 6 with broad, basal, pale yellow bands, not reaching sides of terga, posterior margins irregularly convex. Tegula transparent with

small yellow spot. Axillary sclerite testaceous (to yellow). The following parts red or reddish brown: lower lateral part of clypeus (sometimes black); labrum except for ill-defined yellow area (sometimes black except for yellow area); upper side of scape; underside of first two flagellar segments (sometimes blackish); legs, anterior coxa sometimes yellowish red, other coxae infuscated basally. Underside of metasoma dark reddish brown (sometimes largely black). Upper margin of clypeus uniformly strongly concave (both sexes); clypeoantennal distance less than diameter of antennal socket; malar area about one-third as long as diameter of scape. Discal and basal areas of wings almost hairless. Pubescence dull whitish, dorsal hairs of terga 4–6 robust, white, blunt, curved posteriorly.

MALE: Length 4.5 mm.; wing length 3.5 mm. Specimen somewhat callow, thorax and metasoma therefore brown, but coloration otherwise as described for female except labrum all yellow, mandible largely so, scutellum with a round

central yellow spot, yellow of metasoma limited to basal median transverse area on tergum 6 only; tegula translucent brownish without yellow spot; median axillary sclerite brown; posterior ventral surface of fore femur largely whitish but not in sharp contrast perhaps because of callosity (a mature specimen would probably show this area pale yellow against the reddish brown femoral background). Clypeoantennal distance equal to diameter of antennal socket; malar area less than one-third as long as diameter of scape. Hind legs simple, slender, ventral hairs of trochanter and femur very sparse, much shorter than diameters of these segments. Dorsal metasomal hairs much as in female.

MATERIAL: Holotype female, allotype male (on pin with teneral female from same nest), and 17 female paratypes: Nairobi, Kenya, May 11, 1967 (C. D. Michener).

ETYMOLOGY: The name *stigmoides* refers to the close resemblance of this species to *E. stigma* (Strand).

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