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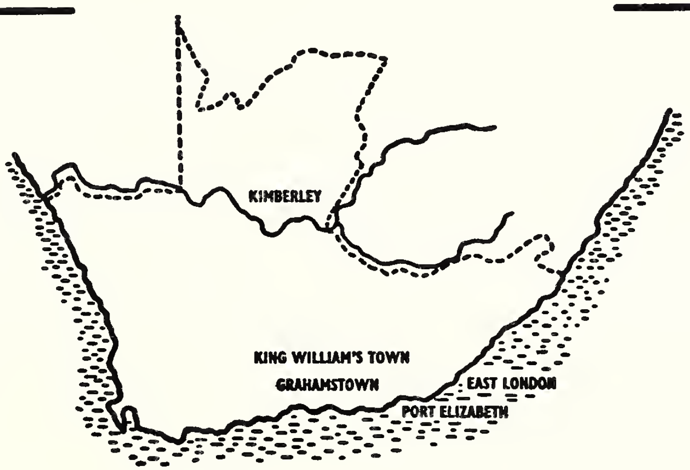

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Some aspects of an ethological study of the aculeate wasps and the bees of a karroid area in the vicinity of Grahamstown, South Africa

by

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CONTENTS

ABSTRACT

The present paper is based upon a survey of the aculeate wasps and the bees of a karroid area in the Eastern Cape Province of South Africa. The location, topography, geology, climate and vegetation of the study area are outlined. An annotated list of 241 species arranged on the basis of their ethology is given.

There follows a discussion of the nesting behaviour of the community as a whole showing how the diversity of the ethology of such a large number of sympatric species results in their ecological displacement and giving some indication of the phylogenetic pattern leading to this diversity.

From a dissertation approved for the degree of Doctor of Philosophy, Rhodes University.

INTRODUCTION

During the eleven year period 1970–1980, the aculeate Hymenoptera occurring at Hilton, a farm situated near Grahamstown, South Africa, were the subjects of extensive study by the author and his wife and frequent co-author, S. K. Gess.

The choice of Hilton for the study followed the sampling of insect populations in areas of various differing vegetation types in the vicinity of Grahamstown. From this survey it was concluded that a karroid area showed the greatest promise with respect to potentially interesting species.

Fieldwork at Hilton embraced the formation of extensive collections in the form of frequent samples taken of the populations associated with various ecological situations. Methods of sampling, besides the use of hand nets, included the use of Malaise traps and trap-nests. Concomitant with the sampling of the populations, field studies of the nesting of many individual species belonging to a range of families of both wasps and bees were pursued. An outcome of this work was the publication between 1974 and 1980 of a number of papers dealing with the ethology of certain species of solitary wasps (Gess, 1978, 1980a and 1980b; Gess and Gess, 1974, 1975, 1976a, 1976b, 1980a, 1980b, 1980c and 1980d). Further publications of a similar nature are in preparation.

Among the species already reported upon in the above listed publications are two species of *Dichragenia, D. pulchricoma* (Arnold) and *D. neavei* (Kohl) which are of particular interest as, in the Pompilidae, they bridge the gap between fossorial nesters and mud-using aerial nesters. Similarly, in two species of *Bembecinus, B. cinguliger* (Smith) and *B. oxydorcus* (Handlirsch), the use of water in the excavation of the nest and the construction of a mud entrance turret appears to represent a nest type previously unknown in the Sphecidae. *Parachilus insignis* (Saussure) is shown to sub-divide the cell into an egg compartment and a pantry compartment in which way it differs in behaviour from other species of Eumenidae. The ethological account of the three species of *Ceramius* (Masaridae) clarifies some uncertainties and serious misconceptions, most notably showing that *C. lichtensteinii* (Klug) is a mass provisioner and not as was previously believed a progressive provisioner. The accounts of the nesting of *Parachilus insignis* (Saussure) (Eumenidae), *Jugurtia confusa* Richards (Masaridae) and *Kohliella alaris* Brauns (Sphecidae) are the first for the three genera to which these species belong. That of *Holotachysphex turneri* (Arnold) (Sphecidae) greatly augments what little was previously known of the ethology of its genus. Of particular interest with respect to *Dasyproctus westermanni* (Dahlbom) (Sphecidae) is the orientation of the pupae which appears to be governed by gravity rather than by the position of the nest entrance which is usually the rule. For the genus *Cerceris* (Sphecidae) twelve new prey associations give weight to the author's hypothesis that *Cerceris* is an Old World genus, that its original prey was hymenopterous and that the taking of Coleoptera is derived.

The present paper represents the hitherto unpublished portion of a dissertation submitted to Rhodes University and approved for the degree of Doctor of Philosophy. Other than in the omission of the above listed previously published papers as well as three further papers of a supporting nature (all bound into the dissertation) the present paper deviates from the dissertation only in the following respects: in the substitution of an abstract for the original summary; in the present expanded introduction; in the modified list of references (omitting references listed in and pertaining to the published papers); in the omission of an appendix listing plant species characterizing the vegetation communities of Hilton.

The study is the first attempt in southern Africa to consider an entire community of aculeate wasps and bees and their interactions with their environment as manifested by their ethology. As far as the author has been able to ascertain it is in fact the most comprehensive of its kind to have been undertaken anywhere. The only comparable account, that of Evans (1970), is more restricted in its scope as it is mainly concerned with fossorial species and their associates. It moreover deals with a fauna already fairly well known whereas the present study deals with a fauna which is largely unstudied ethologically. By its nature, the present paper serves also to place in correct context within the community of which they are members those species concerning which ethological studies have already been published and provides a matrix within which the subjects of further, yet to be published, ethological studies may be fitted.

All the material, including voucher specimens, amassed during the course of the study is housed in the collection of the Albany Museum, Grahamstown, in which institution are deposited also all relevant fieldnotes.

ASPECTS OF THE ECOLOGY OF THE STUDY AREA

Location and topography

The farm Hilton, the site of the present study, is situated 18 kilometres WNW of Grahamstown (33° 19′S., 26° 32′E.) in the Albany Division of the Eastern Cape Province of South Africa very close to the midpoint of a straight line connecting the village of Riebeek East and Grahamstown (Figs 1 and 2).

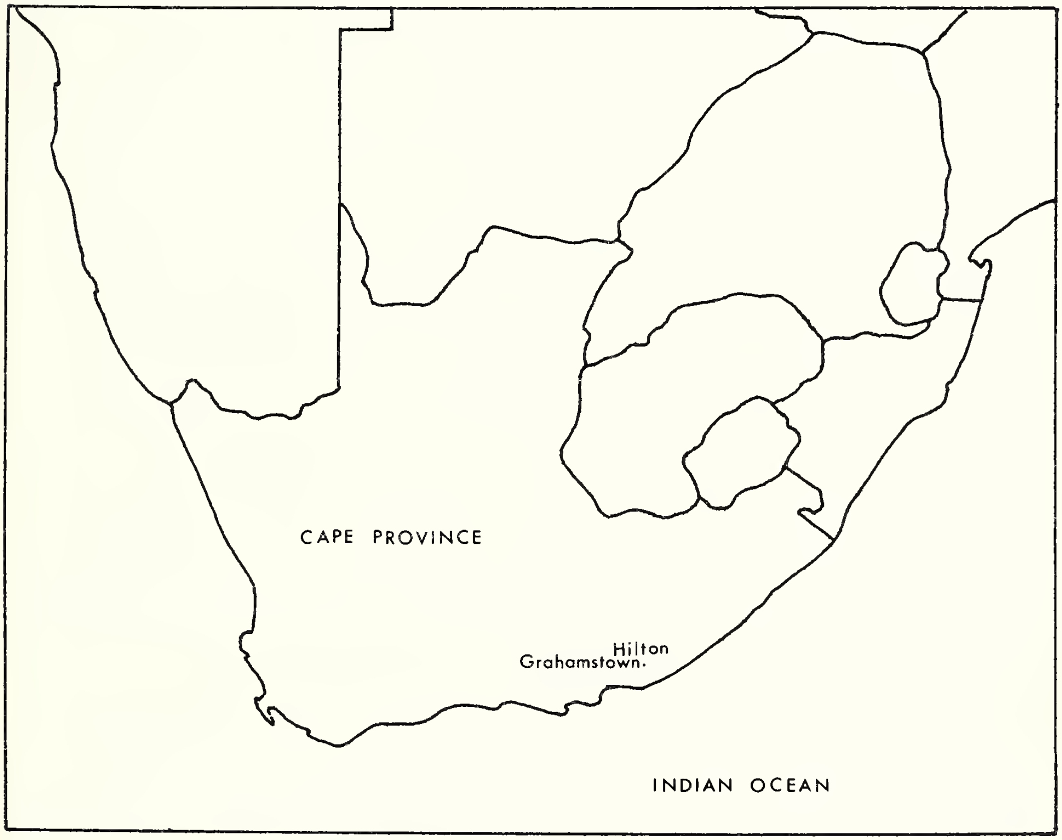

Fig. 1. Map of southern Africa showing position of study area.

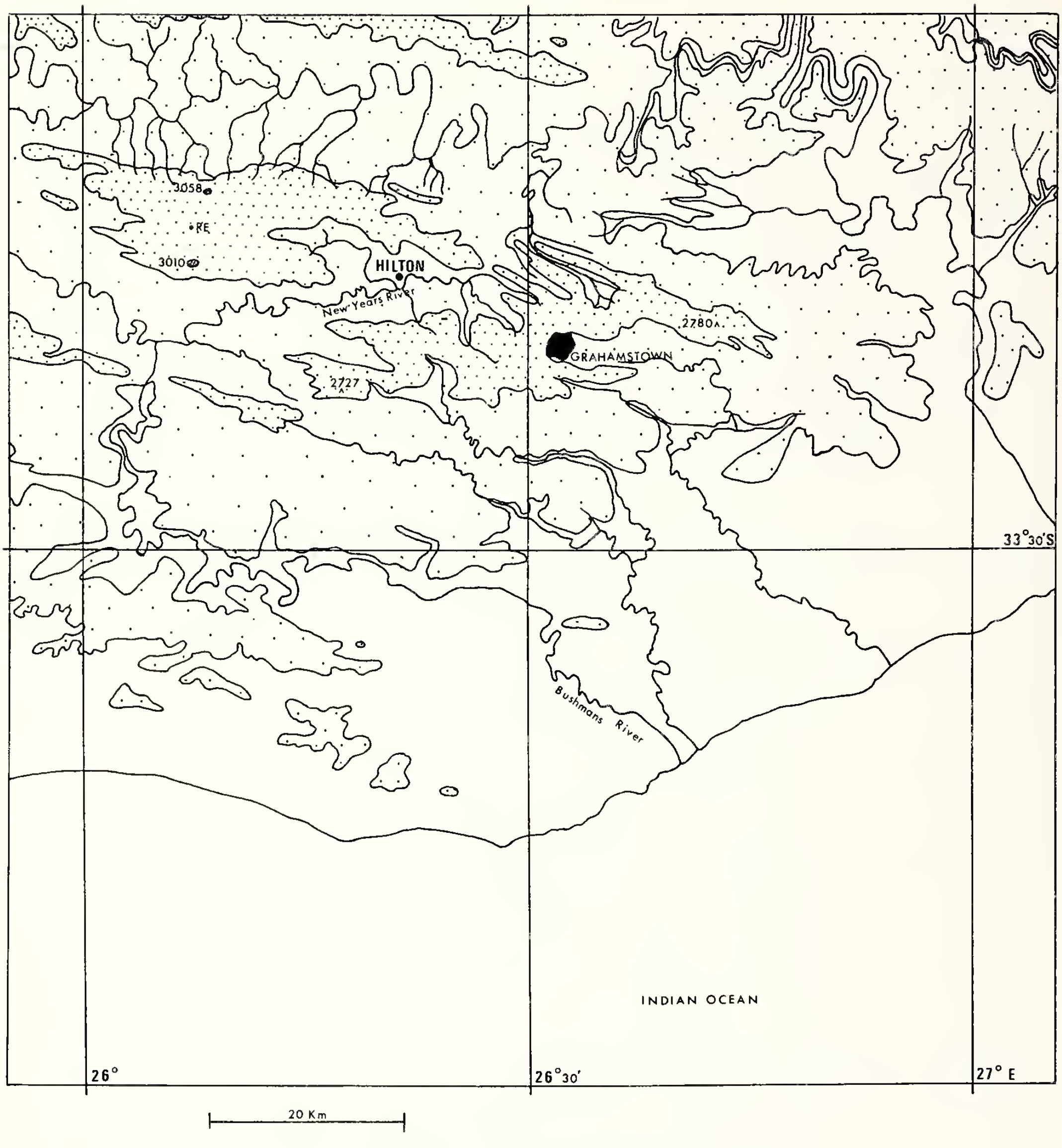

Fig. 2. Topographical map showing position of study area.

Situated on the course of the New Year's River, Hilton at a minimum altitude of 1 550 –1 650 feet (472–503 m) above sea level occupies low-lying land more or less surrounded by rising ground forming the lower slopes of a series of sub-parallel mountain ranges running roughly ESE. Within a radius of 25 kilometres of Hilton these ranges consist of an unnamed range passing through the trigonometrical point Grootfontein at 3 058 feet (932 m) just to the north of Riebeek East; another range, the Swartwatersberg, just south of Riebeek East which rises to a height of 3 010 feet (917 m) at the beacon Riebeek; a third which passes just south of Grahamstown and which, near Highlands at a point roughly 13 kilometres SSW of Hilton, attains 2 727 feet (831 m) and finally Botha's Hill ridge to the north of Grahamstown which rises to 2 780 feet (847 m) at Driver's Hill. South of the range through Highlands the topography consists of a series of dissected peneplains gradually dropping in elevation southwards towards the coast, 58 kilometres due S of Hilton. As will be shown below, the climate of Hilton and especially the rainfall is influenced to a marked extent by the surrounding topography, the ranges immediately to the south being of particular importance.

At Hilton itself the altitude of the study area varies from a minimum of just less than 1 550 feet (472 m) in the river bed at the foot of the cliff to the west to a maximum of about 1 850 feet (564 m) on the slopes of the E-W ridge to the south. Most of the study area, however, is situated at an altitude of between 1 550 and 1 650 feet (472 and 503 m) (Fig. 3.)

The New Year's River which rises just north of Grahamstown enters the study area from the north-east and after a markedly meandering course across the low-lying flat area of Hilton leaves the study area in the south-west shortly before winding through precipitous gorges on its way to Alicedale where it joins the Bushman's River. Along its course through Hilton the river is impounded at two points by stone weirs with the result that upstream from these weirs water is present at all seasons in two reaches of considerable length (1 300–1 500 m). Below the weirs the river breaks up into isolated pools during the dry seasons. Several small seasonal tributaries in wide shallow valleys join the New Year's River along its course through Hilton. Of particular importance with respect to the present study is a tributary, marked as the Iron Put River on the Geological Survey Cape Sheet No. 9, which enters the study area from the south-east, flows more or less parallel to the rising ground in the south and joins the river about 450 m upstream of the lower weir. Arising in the mountains (the third range listed above) and draining an area S to SE of Hilton in the vicinity of Atherstone, this tributory (the Iron Put R.) falls in altitude by 700 feet (213 m) over the distance of about 8 kilometres from its sources to its confluence with the New Year's River at the point indicated above. After an initial rapid rate of descent the rate decreases progressively and over the last 2½ kilometres before the confluence the fall is of the order of 90 feet (27 m). In the study area its course is over only very slightly sloping ground and is in the form of shallowly incised meanders cut into its flood plain. Frequently it is completely dry or at most holds a few pools but following heavy rain in its catchment area comes down in flood, overflowing its banks and spreading over its floodplain. About 2 kilometres above its confluence with the New Year's River a dam across the course of this tributary provides water for a furrow running below the 1 600 foot contour across the central part of the study area.

Also in this part of the study area is a shallow earth dam fed after rain by run-off from slightly sloping ground to the east and partly by water overflowing from a break in the above furrow, the lower course of which passes immediately to the north of the dam. In both the dam and the furrow water is seasonal and temporary. Water generally flows in the furrow for some time after good rains have fallen in the catchment area but as the dry season advances the water shrinks to stagnant pools and then dries up completely.

Geology and soil types

Geologically Hilton is situated upon three conformable strata: from south to north these are the Lower Witteberg Quartzites, the Upper Witteberg Shales (both belonging to the Cape Supergroup) and Dwyka Tillite (the oldest stratum of the overlying Karroo Supergroup).

The contact between the strata of the Cape and the Karroo Supergroups is situated immediately outside the study area to the north more or less in line with the road to Riebeek

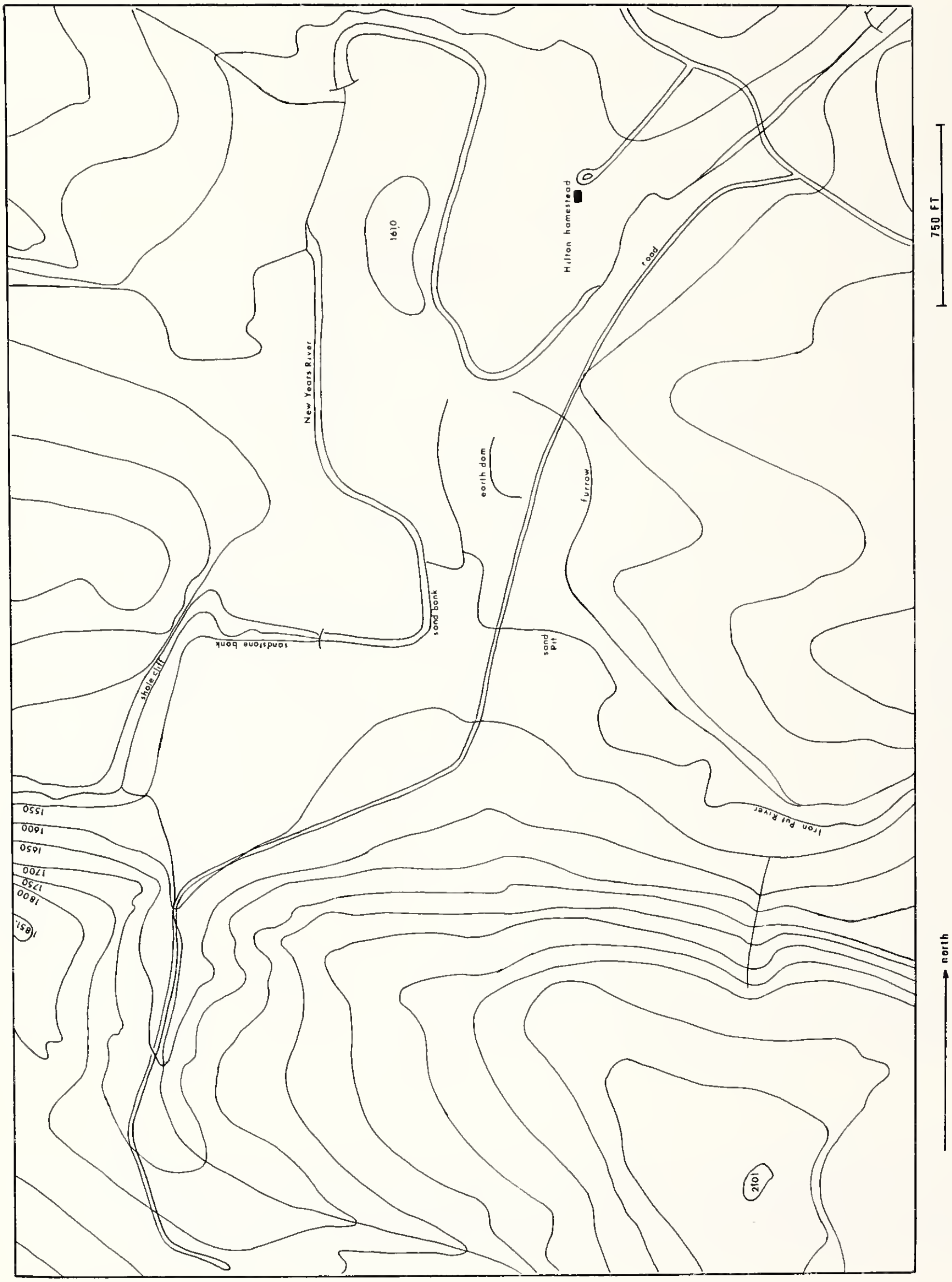

Fig. 3. Map of study area.

East where this passes the turn-off to the Hilton homestead. Strata within the study area are thus limited to the two Witteberg formations.

The pale grey Witteberg Quartzites form the ridge at the south of the study area and indeed are the materials of the entire series of previously listed sub-parallel mountain ranges of which the ridge is a part.

The rather dark coloured Witteberg Shales on the other hand form the lower-lying land between the ridge in the south and the Dwyka Tillite in the north. The cliff at the west of the study area is cut across this shale formation (Fig. 9) which is exposed also in the river bed below the lower weir and at a point where the farm road crosses the 1 600 foot contour on the rise north of the earth dam. On this rise are also found blocks of a dark sandstone derived from a band of this material in the shale.

Upon weathering the Witteberg Quartzites give rise to a light grey sandy soil whereas the Witteberg Shales (as also the Dwyka Tillite) give rise to brownish and reddish clayey soils.

As the entire study area, excepting the ridge in the south, is situated upon Witteberg Shales it follows that the reddish clayey soil derived from this formation is basically the dominant soil of the area. Whereas the clayey soil is somewhat thin in places on slopes such as those of the rising ground north-east and east of the earth dam where the bedrock may be barely covered, considerable thicknesses of this soil are present in lower-lying areas such as that below the 1 600 foot contour east of the earth dam (Fig. 6) At this juncture it may be noted that in describing the clayey soil of this particular locality within the study areas Gess and Gess (1974: 192 and 1975: 24) stated that it was derived from the Dwyka Series. This identification was consequent upon the use of the older geological classification which regarded the shales in question as belonging to the Lower Dwyka rather than to the Upper Witteberg.

In the southern half of the study area light coloured sandy soil occurs overlying the clayey soil and is in places intermixed with it. This sandy soil derived from the weathering of the Witteberg Quartzite has two separate origins. On the higher ground in the south of the study area the overlying sand is derived from the ridge and has been transported downhill by sheet erosion. In thickness this sand tails off downslope (i.e. northwards). On the lower ground below the 1 600 foot contour a wide band of similar sand but of alluvial origin has been deposited upon its flood plain by the tributary of the New Year's River previously referred to as the Iron Put River. Near the middle of the flood plain near the present incised course of the tributary the depth of alluvial sand is of the order of several feet, sufficiently deep for the establishment of a pit (Fig. 5) for the removal of building sand and for the excavation by aardvarks *(Orycteropus afer)* of their deep burrows.

Climate

The Albany Division, situated between the winter and summer rainfall regions, receives rain in moderate amounts throughout the year, the wettest periods being spring and autumn, the driest mid-winter.

The overall rainfall pattern for the region has been indicated by Dyer (1937: 33–34) who showed the marked effect of topography upon precipitation. That author showed that rain clouds from the coast on coming into contact with higher altitudes precipitate moisture either in the form of rain or mist but that they pass uninterruptedly over lower valley levels which are therefore drier. Specifically, regions of greater rainfall were shown to be the previously described series of sub-parallel ESE running mountain ranges and further north the Fish River Rand whereas the low, broad Fish River Valley, situated between these two belts of higher ground, was shown to be a region of low rainfall.

The distribution of rainfall at Hilton and its more immediate surroundings fits well into the overall pattern. This may be illustrated by means of average annual rainfall figures for several localities in the area concerned. At Clifton at 1 276 feet (389 m) above sea level on the peneplain near Seven Fountains, 22 km S of Hilton on the coastal side of the ESE ranges the average annual rainfall is 575 mm (22,6″) (Weather Bureau, 1965). Proceeding northwards the rainfall figures rise with increasing altitude till the crest of the ESE range is reached where it is assumed the rainfall is highest. Unfortunately records for the crest are mostly unobtainable for, as Dyer (1937) has pointed out, homesteads, the site of most rainfall stations, are generally placed in more protected positions. Thus of four recording stations on the relevant part of the range only one, Faraway near Coldsprings, is on the crest whereas the other three are below the crest on the inland (drier) side.

Proceeding along the range from west to east, Atherstone at 2 263 feet (690 m) has an average annual rainfall of 573 mm (22,55″) (Dyer, 1937); Slaaikraal at 1 949 feet (594 m) has 652 mm (25,7″) (Weather Bureau, 1965): Faraway at slightly above 2 400 feet (732 m) has circa 864 mm (34″) (pers. comm. C. F. Jacot Guillarmod, Oct., 1978), and Grahamstown at 1 768 feet (539 m) has 688 mm (27,1″) (Weather Bureau, 1965).

The average annual rainfall figure for Hilton: circa 356 mm (14″) (pers. comm. T. C. White, Febr., 1973) is in marked contrast to the above rainfall figures for localities on the ranges. The low rainfall at Hilton is clearly attributable to the nature of the topography for at 1 600 feet (488 m) the study area lies 700–1 100 feet (213–335 m) below the crests of the ESE ranges only 7–12 kilometres distant to the SW, S and SE and is therefore situated in a rain shadow area similar to that of the Fish River Valley to the north.

The low rainfall in the rain shadow at Hilton raises to considerable ecological importance the fact that the catchment areas of the water courses passing through the study area are in regions of greater rainfall on higher ground. The introduction of water from outside the rain shadow area results in the presence of semi-permanent to permanent water (apart from impounded water such as in the earth dam) even when the study area itself is very dry.

Vegetation

From a consideration of "Veld Types of South Africa" (Acocks, 1953) and the accompanying map the study area is seen to lie on the tongue of False Karroid Broken Veld which extends eastwards towards Grahamstown, principally along the valley of the New Year's River. As the land rises to the north and south there is a transition to Valley Bushveld merging into Eastern Province Thornveld in the south-east. False Macchia is present in the highest areas.

The study area is characterized by dwarf karroo scrub with, where sufficient water and bare earth are available, an addition of thorn scrub and along the river banks an admixture of small trees. The sandy foot of the E-W ridge in the south is characterized by grassveld which gives way to scattered succulents, notably *Aloe ferox*, and xerophytic bushes on the dry, rocky north-facing slope (Fig. 13). To the west of the study area the valleys become narrower and steeper and are characterized by Valley Bushveld which gives way as the land rises in the south-west to False Macchia. Further to the south-east and rising from the low-lying study area there is a transition to Eastern Province Thornveld.

The dwarf karroo scrub may be divided into three main communities. These are:

1. *Pentzia incana* Scrub which characterizes clayey soil which has not been disturbed by cultivation (Gess, 1980b: Fig. 1).
2. *Pentzia incana*—*Chrysocoma tenuifolia* Scrub which characterizes previously cultivated clayey soils in the area extending from above the furrow to the New Year's River below the earth dam (Fig. 6).
3. *Chrysocoma tenuifolia* Scrub which characterizes the previously cultivated sand flats of the flood plain of the Iron Put River and extends across to its confluence with the New Year's River (Fig. 5).

All three of these communities are subject to trampling and grazing by sheep and cattle.

The thorn scrub which is characterized by *Acacia karroo* occurs within the dwarf karroo scrub area in places where the soil has been exposed and where in addition the available amount of water in the soil is greater than elsewhere in the area (Fig. 12). Such sites are those where there is seepage from the furrow and earth dam and where the water run-off over eroded land causes the formation of temporary standing water in erosion gullies and low-lying areas.

The rivers represent older and more permanent water erosion gullies and their banks therefore support the same species as are present in the thorn scrub community except that the conditions being more favourable the vegetation no longer falls into the classification of scrub but rather of small trees (Fig. 8 and Gess and Gess, 1975: Plate 3).

Along the New Year's River where permanent and semi-permanent water bodies occur in natural pools and for considerable reaches above the two weirs the water is fringed by beds of *Phragmites australis*, "Common Reed" (Fig. 14). These reeds are also present in the earth dam immediately within the retaining wall (Fig. 15). Sedges which characterize marshy ground are present in clumps along the river banks, along the course of the furrow and fringe and earth dam (Gess and Gess, 1974: Plate 2).

Forage plants

A large number of flowering plants in the study area are visited by aculeate wasps and by bees of both sexes for the purpose of obtaining their own nutriment. Little specificity is shown, the requirement generally appearing to be the availability of nectar, short tubed or open flowers being favoured. Nearness to nesting sites is also of importance, suitable flowering plants growing at any considerable distance from nesting sites not being visited.

Particularly attractive to a large number of species are the flowers of *Maytenus linearis* (Celastraceae) and flowers and sticky young growth of *Acacia karroo* (Leguminosae). However, many species visiting these plants will also forage on low-growing plants, for example *Selago corymbosa* (Selaginaceae), *Melolobium candicans* (Leguminosae), *Senecio* spp. and *Lasiospermum bipinnatum* (both Compositae). Composites are often favoured at the beginning of the summer when *Acacia karroo* and *Maytenus linearis* are not yet in flower.

When plants are used as a source of provision for the young, or as a source of nesting materials, or their tissue is used as a subtrate in which to excavate a nesting gallery more specificity is shown. These associations are given in the annotated list.

Seasonal cycles of wasps and bees

The majority of the aculeate wasps and the bees of the study area show marked seasons of activity and quiescence. In these species the period of quiescence extends from the end of the nesting season in the summer until the following spring or summer when activity recommences with the emergence of the adults from the nests in which they have remained in the pre-pupal or pupal stage throughout the cold, usually dry winter months. In most of these species there appears to be one generation per year but in some species such as *Ampulex* sp. near *cyanura* there may be two generations—a non-diapausing first generation and a diapausing second generation.

The minority of species such as the carpenter bees and the social wasps (Vespidae) which emerge as adults before the end of the summer overwinter as adults (both males and females in the bees, fertilized females in the vespids) and may show a certain limited activity on warm days during the winter months.

A CLASSIFICATION OF THE ACULEATE WASPS AND OF THE BEES OF THE STUDY AREA ON THE BASIS OF THEIR ETHOLOGY

The aculeate wasps and the bees collected in the study area are grouped on the basis of three ethological characters, situation of the nest (I, II, III, IV) subdivided into IN and ON

(A, B), nature of substrate (a, b, c) and degree of participation in construction of nest (i, ii, iii) (Fig. 4). This grouping results in the formation of twenty-seven categories numbered 1, 2, 3 . . . 27.

- I. NESTING IN THE GROUND (Figs 5 and 6)
  - (a) *In non-friable soils.* (Typically compacted clayey soils.)
    - (i) In nest constructed entirely by the nester. 1
    - (ii) In pre-existing cavity modified by the nester. 2
    - (iii) In pre-existing cavity *not* modified by the nester. 3
  - (b) *In friable soils.* (Typically sandy soils, exceptionally disturbed and therefore non-compacted clayey soils.)
    - (i) In nest constructed entirely by the nester. 4
    - (ii) In pre-existing cavity modified by the nester. 5
    - (iii) In pre-existing cavity *not* modified by the nester. 6

- II. NESTING IN OR ON VERTICAL BANKS (Figs 7, 8 and 9)
  - A. IN VERTICAL BANKS
    - (i) In nest constructed entirely by the nester. 7
    - (ii) In pre-existing cavity modified by the nester. 8
    - (iii) In pre-existing cavity *not* modified by the nester. 9
  - B. ON VERTICAL BANKS
    - (i) In nest constructed entirely by the nester. 10
    - (ii) In pre-existing cavity modified by the nester. 11
    - (iii) In pre-existing cavity *not* modified by the nester. 12

- III. NESTING ON STONES (Figs 10 and 11)
  - (i) In nest constructed entirely by the nester. 13
  - (ii) In pre-existing cavity modified by the nester. 14
  - (iii) In pre-existing cavity *not* modified by the nester. 15

- IV. NESTING IN OR ON PLANTS (Figs 12, 13, 14 and 15)
  - A. IN PLANTS
    - (a) *Within woody stems.*
      - (i) In nest constructed entirely by the nester. 16
      - (ii) In pre-existing cavity modified by the nester. 17
      - (iii) In pre-existing cavity *not* modified by the nester. 18
    - (b) *Within pithy stems.*
      - (i) In nest constructed entirely by the nester. 19
      - (ii) In pre-existing cavity modified by the nester. 20
      - (iii) In pre-existing cavity *not* modified by the nester. 21
    - (c) *Within hollow stems.*
      - (i) In nest constructed entirely by the nester. 22
      - (ii) In pre-existing cavity modified by the nester. 23
      - (iii) In pre-existing cavity *not* modified by the nester. 24
  - B. ON PLANTS (Irrespective of whether plants are woody, pithy or hollow-stemmed.)
    - (i) In nest constructed entirely by the nester. 25
    - (ii) In pre-existing cavity modified by the nester. 26
    - (iii) In pre-existing cavity *not* modified by the nester. 27

In the annotated list which follows those species for which nesting was definately confirmed are listed with the symbol***.

Those species which were observed searching for nesting sites or transporting nesting materials or nest provision but for which no nests were discovered are listed with the symbol**.

The remaining species listed with the symbol* have been allocated on the basis of where they were collected in conjunction with morphological features and known biology of related species.

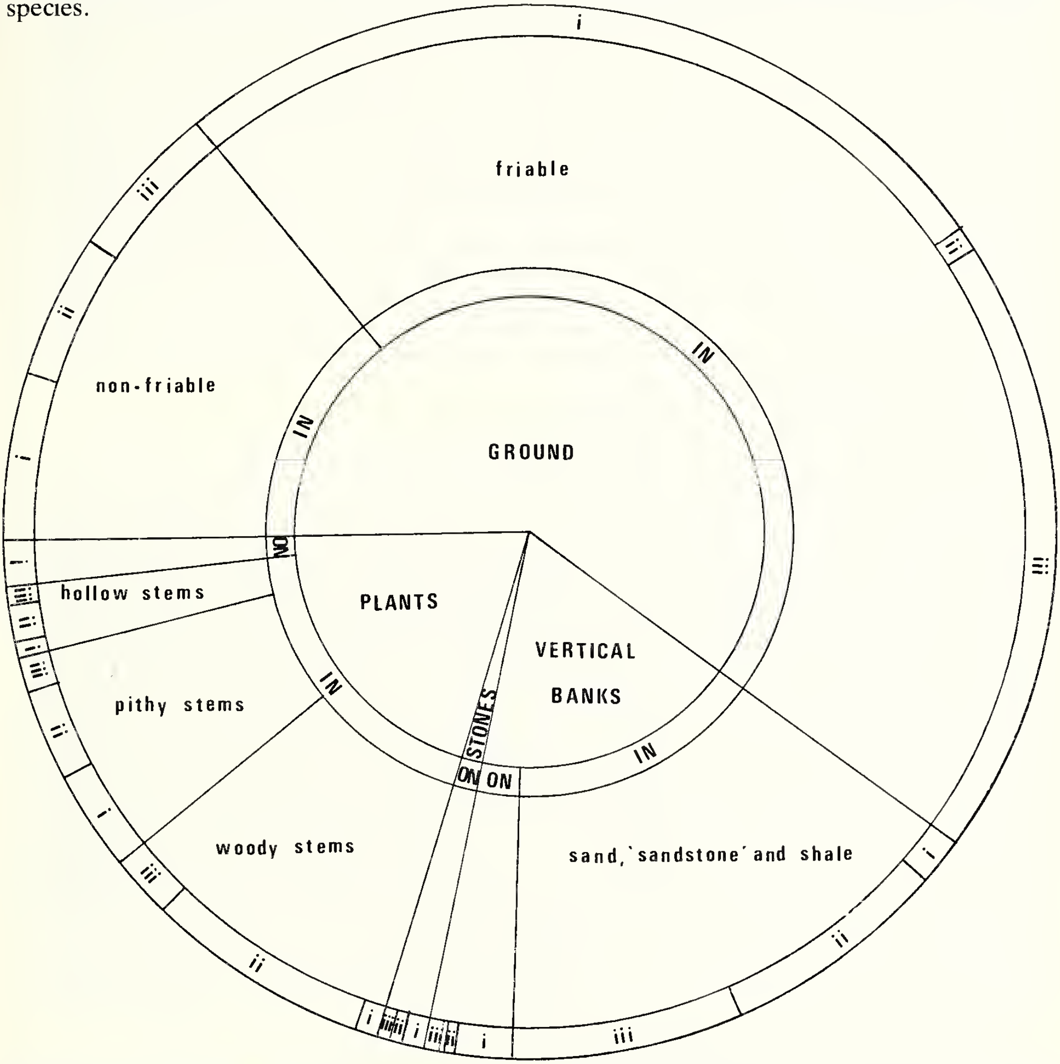

Fig. 4. Diagrammatic representation of the classification of the aculeate wasps and the bees of the study area on the basis of their ethology. The numbers (i, ii, iii) in the outermost ring correspond to the same numbers in the classification. (i) In nest constructed entirely by the nester. (ii) In pre-existing cavity modified by the nester. (iii) In pre-existing cavity *not* modified by the nester. The magnitude of the segments is in proportion to the number of species involved.

Fig. 5. Area of friable soil: the sandpit

Fig. 6. Area of non-friable soil: below furrow

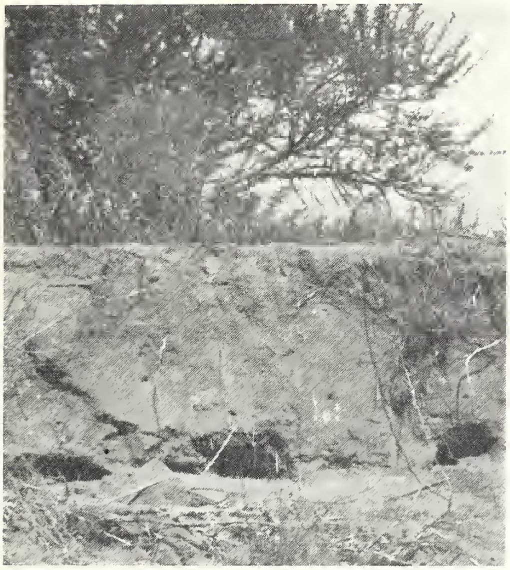

Fig. 7

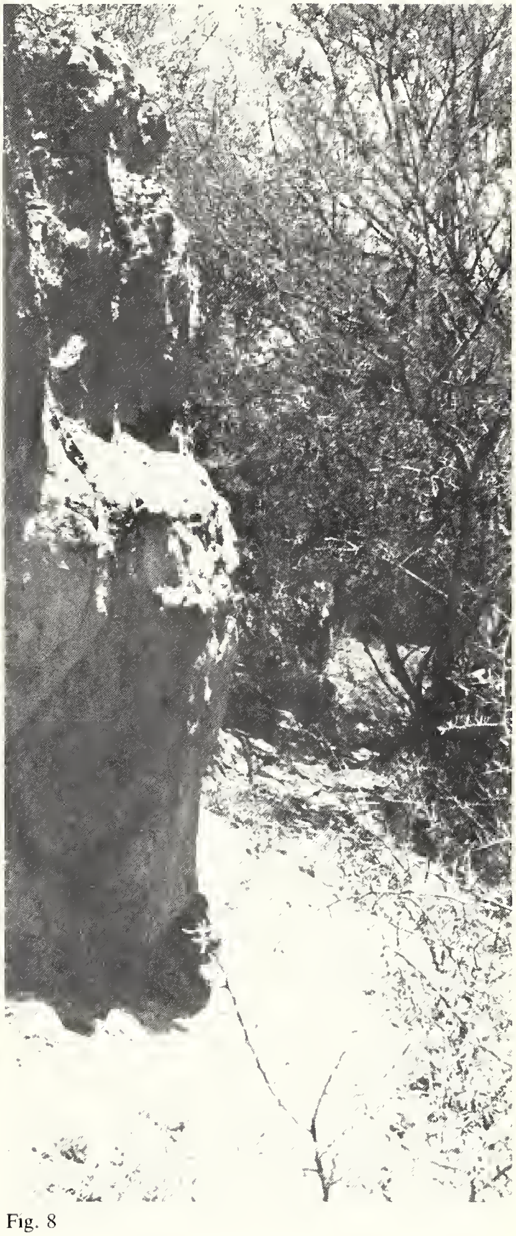

Fig. 9

Fig. 8

Figs 7, 8 and 9. Vertical banks along course of New Year's River: sand (Fig. 7), "sandstone" (Fig. 8) and shale (Fig. 9).

Fig. 10. Stone lying loose on ground and bearing nest of *Auplopus rossi*.

Fig. 11. Stone embedded in ground and bearing nest of *Hoplitis jansei*.

Fig. 12. Woody stemmed plant: *Acacia karroo* on bank of watercourse.

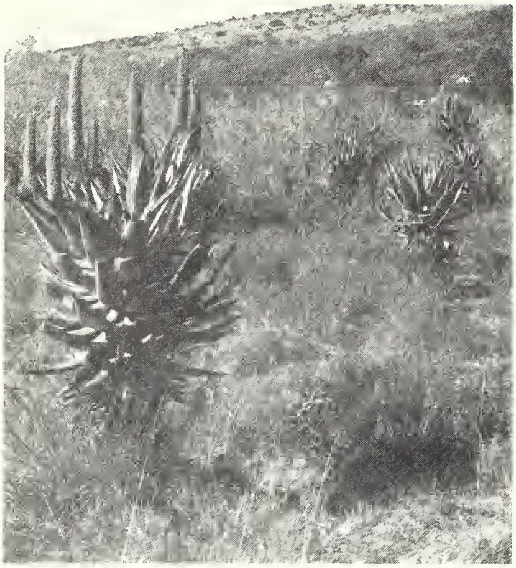

Fig. 13. Pithy stemmed plant: *Aloe ferox* on north-facing slope.

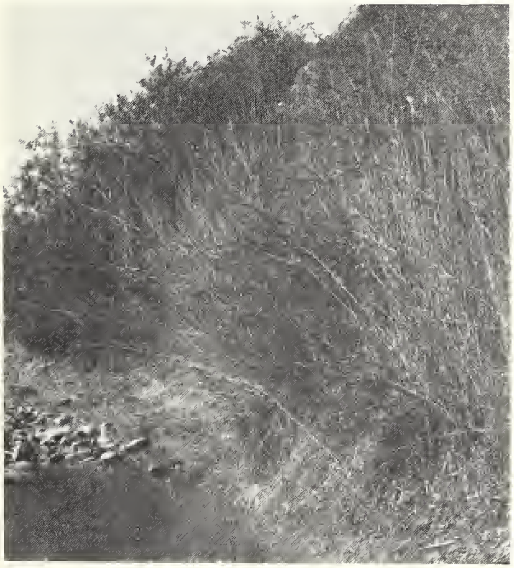

Fig. 14

Fig. 15

Figs 14 and 15. Hollow stemmed plant: *Phragmites australis* fringing New Year's River (Fig. 14), in earth dam (Fig. 15).

ANNOTATED LIST OF THE ACULEATE WASPS AND OF THE BEES OF THE STUDY AREA, ARRANGED ACCORDING TO THE CLASSIFICATION BASED ON THEIR ETHOLOGY.

Category 1.

I. NESTING IN THE GROUND
(a) *In non-friable soils.*
(i) In nest constructed entirely by the nester.

POMPILIDAE

*** *Dichragenia neavei* (Kohl). Uncommon. Nov.–Apr. Constructs turreted multicellular nest; each cell provisioned with a single lycosid or sparassid spider. Nesting described by Gess and Gess (1976b).

*** *Dichragenia pulchricoma* (Arnold). Common. Oct.–Apr. Constructs turreted multicellular nest; each cell provisioned with a single lycosid, pisaurid, sparassid or salticid spider. Nesting described by Gess and Gess (1974).

EUMENIDAE

*** *Antepipona scutellaris* G. Soika. Common. Oct.–March. Constructs turreted one- or two-celled nest; each cell provisioned with about 12 small pyralidid caterpillars.

*** *Parachilus insignis* (Saussure). Common. Oct.–Febr. Constructs one- or two-celled nest; each cell provisioned with 8–17 psychid caterpillars. Nesting described by Gess and Gess (1976a).

*** *Parachilus capensis* (Saussure). Rare. Oct.–Jan. Constructs turreted one- or two-celled nest; each cell provisioned with about 11 psychid caterpillars.

*** *Pseudepipona erythrospila* (Cameron). Rare. Oct.–March. Constructs collared one-celled nest; cell provisioned with pyralidid caterpillars.

*** Eumenid sp. G. Rare. Jan. Constructs turreted one-(? or two-) celled nest; cell provisioned with chrysomelid larvae.

*** Eumenid sp. (minute, black). Rare.

MASARIDAE

*** *Ceramius capicola* Brauns. Common. Nov.–March. Constructs turreted multicellular nest; each cell provisioned with a mixture of pollen and nectar derived from Mesembryanthemaceae.

*** *Ceramius lichtensteinii* (Klug). Common. Oct.–April. Constructs turreted multicellular nest; each cell provisioned with a mixture of pollen and nectar derived from Mesembryanthemaceae. Nests perennial.

*** *Ceramius linearis* (Klug). Rare. Oct.–Jan. Constructs turreted multicellular nest; each cell provisioned with a mixture of pollen and nectar derived from Mesembryanthemaceae.

* *Jugurtia braunsiella* (von Schulthess). Rare. Sept.–Dec.

*** *Jugurtia confusa* (Richards). Common. Sept.–Febr. Constructs turreted multicellular nest; each cell provisioned with a mixture of pollen and nectar derived from Mesembryanthemaceae.

Nesting of above Masaridae described by Gess & Gess (1980c).

SPHECIDAE

*** *Bembecinus cinguliger* (Smith). Very common. Nov.–March. Constructs turreted one- or two-celled nest; each cell provisioned with numerous Cicadellidae (and also Fulgoroidea). Nesting described by Gess & Gess (1975).

*** *Bembecinus oxydorous* (Handlirsch). Common. Jan.–Apr. Constructs turreted one- or two-celled nest; each cell provisioned with numerous Cicadellidae. Nesting described by Gess & Gess (1975).

Category 2.

I. NESTING IN THE GROUND

(a) *In non-friable soils.*

(ii) In pre-existing cavity modified by the nester.

EUMENIDAE

*** Eumenid sp. Very rare. March. One record. Curved, lacy turret constructed surmounting turret of empty burrow of *Bembecinus oxydorcus*. (Gess & Gess, 1975: 40).

SPHECIDAE

* *Ampulex mutilloides* Kohl. Very rare. Jan. One record. Circumstantial evidence suggests that nesting may be in ground burrow of cockroach, *Pilema* sp.

*** *Prionyx kirbii* (Van der Linden). Common. Nov.–May. Nesting in old or abandoned burrows of *Parachilus insignis* (Fig. 24). Single cell provisioned with 1–2 grasshoppers (Acrididae: *Acrotylus, Aiolopus, Anaeolopus, Calliptamulus* and other genera).

* *Tachysphex modestus* Arnold. Rare. Dec.

*** *Tachysphex* sp. near *modestus* Arnold. Rare. Dec.–Jan. Nesting in old or abandoned burrows of *Parachilus insignis* (Fig. 25). Single cell provisioned with 2 grasshoppers (Lentulidae).

** *Pison allonymum* Schultz. Rare. Oct.–May. Strong circumstantial evidence suggesting that nesting is in old or abandoned burrows of *Bembecinus cinguliger* and *B. oxydorcus*. Prey consists of small spiders (e.g. Salticidae). In Gess & Gess (1975: 40) incorrectly referred to as *Pison ?montanum* Cam.

MEGACHILIDAE

** *Megachile (Eutricharaea) aliceae* Cockerell. Rare. Oct.–Dec. Nesting in old burrows of *Parachilus insignis*. Cells constructed of ?leaves. (Gess & Gess, 1976a: 98).

*** *Megachile (Eutricharaea) meadewaldoi* Brauns. Uncommon. Sept.–March. Nesting in old or abandoned burrows of *Bembecinus oxydorcus, Parachilus insignis* and *Antepipona scutellaris*. Cells constructed of petals from low-growing flowers (*Oxalis* sp., *Wahlenbergia* sp.). (Gess & Gess, 1975: 40 and 1976a: 98).

** *Megachile (Eutricharaea) semiflava* Cockerell. Common. Sept.–March. Nesting in old or abandoned burrows of *Parachilus insignis*. Cells constructed of leaves. (Gess & Gess, 1976a: 98).

*** *Megachile (Eutricharaea) stellarum* Cockerell. Common. Sept.–March. Nesting in old or abandoned burrows of *Dichragenia pulchricoma, Parachilus insignis* and *Ceramius lichtensteinii*. Cells constructed of leaves. (Gess & Gess, 1974: 204–206, Fig. 8; 1976a: 98; 1980c: 78).

*** *Creightoniella dorsata* (Smith). Common. Nov.–March. Nesting in old or abandoned burrows of *Parachilus insignis*. Cells constructed of leaves. (Gess & Gess, 1976a: 98).

ANTHOPHORIDAE

* *Tetralonia minuta* Friese. Uncommon. Nov.–Dec. Nesting in old or abandoned burrows of *Bembecinus cinguliger* and *Parachilus insignis*. (Gess & Gess, 1975: 40 and 1976a: 98). For account of nesting see also Rozen (1969a).

Category 3.

I. NESTING IN THE GROUND

(a) *In non-friable soils.*

(iii) In pre-existing cavity *not* modified by the nester.

CHRYSIDIDAE

*** *Allocoelia bidens* Edney. Common. Nov. Parasitic in the nests of *Jugurtia confusa*. (Gess & Gess, 1980c: 76)

Allocoelia capensis Smith. Not yet recorded from Hilton but *highly likely* to occur there. Parasitic in the nests of *Ceramius lichtensteinii*. (Gess & Gess, 1980c: 76).

Allocoelia latinota Edney. Not yet recorded from Hilton but *highly likely* to occur there. Parasitic in the nests of *Ceramius capicola and Ceramius linearis*. (Gess & Gess, 1980c: 76).

*** *Octochrysis vansoni* (Brauns). Common. Nov.–Jan. Parasitic in the nests of *Parachilus insignis*. (Gess & Gess, 1976a: 97).

*** *Pseudospinolia ardens* (Mocsary). Uncommon. Nov.–Dec. Parasitic in the nests of *Parachilus insignis*. (Gess & Gess, 1976a: 97).

MUTILLIDAE

* *Brachymutilla gynandromorpha* André. Rare. Oct. Found in nesting area of *Jugurtia confusa.*

* *Dasylabris stimulatrix* (Smith). Rare. Nov.–Febr. Found in nesting areas of *Jugurtia confusa* and *Parachilus insignis*. (Also found in association with friable soils.)

*** *Dasylabroides caffra* (Kohl). Common. Oct.–May. Found in nesting areas of *Dichragenia pulchricoma, Parachilus insignis, Bembecinus oxydorcus, Jugurtia confusa* and *Ceramius lichtensteinii*. Reared from the cells of *C. lichtensteinii* in which parasitic. (Gess & Gess, 1980c: 76).
(Rarely found in association with friable soils and vertical banks.)

* *Glossotilla speculatrix* (Smith). Rare. March. Found in nesting area of *Bembecinus oxydorcus*. (*Very commonly* found in association with friable soils.)

* *Mutilla scabrofoveolata* Sichel & Radoszkowski. Rare. Nov.–April. Found in nesting areas of *Dichragenia pulchricoma* and *Parachilus insignis*. (Also rarely found in association with vertical banks.)

* *Smicromyrme* sp. Rare. Found in nesting area of *Jugurtia confusa*.

* *Smicromyrme hecuba* (Péringuey). Common. Dec.–April. Found in nesting areas of *Parachilus insignis* and *Bembecinus cinguliger* and *B. oxydorcus*. Circumstantial evidence strongly indicates that parasitic in the nests of *Bembecinus* spp. (Common also in association with friable soils.)

POMPILIDAE

*** *Ceropales punctulatus* Cameron. Rare. Nov.–March. Parasitic in the nests of *Dichragenia pulchricoma*. (Gess & Gess, 1974: 202, 204.)

MEGACHILIDAE

** *Coelioxys (Liothyrapis) lativentroides* Brauns. Rare. Dec. Circumstantial evidence very strongly indicates that this species is parasitic in the nests of Megachilidae (*Megachile* and *Creightoniella* spp.) nesting in old or abandoned burrows of *Parachilus insignis*.

Category 4.

I. NESTING IN THE GROUND

(b) *In friable soils.*

(i) In nest constructed entirely by the nester.

POMPILIDAE

** *Batozonellus fuliginosus sepulchralis* (Smith). Uncommon. Nov.–Apr. Observed searching for prey on *Acacia karroo* and dragging prey, *Caerostris* sp., across sandpit. Known to dig shallow, sloping one-celled nest and to provision cell with a single large argiopid spider. *Araneus* sp. or *Caerostris* sp. (Gess & Gess, 1980b).

** *Cyphononyx flavicornis antennatus* Smith. Common. Nov.–Mar. Observed dragging prey, *Palystes* sp. (Sparassidae) across ground.

* *Tachypompilus ignitus* (Smith). Uncommon. Nov.–Febr. Known to dig nest in dry sand in sheltered situation and to provision cell with a single large sparassid spider, *Palystes natalius* Karsch (Gess & Gess, 1980b).

SPHECIDAE

*** *Prionyx kirbii* (Van der Linden). Common. Nov.–May. In friable soils this species appears to dig its own nest. (In non-friable soils nests in old or abandoned burrows of *Parachilus insignis.*)

*** *Podalonia canescens* (Dahlbom). Common. Aug.–May. Digs simple one-celled nest; cell provisioned with a single hairless caterpillar of the cutworm type (Noctuidae).

*** *Ammophila beniniensis* (Palisot de Beauvois). Common. Oct.–Apr. Nesting in disturbed, loose and crumbly clayey soil.

* *Ammophila bonaespei* Lepeletier. Rare. Dec., Mar. Known to provision with hairless caterpillars (Geometridae).

* *Ammophila conifera* (Arnold). Uncommon. Nov.–Mar.

*** *Ammophila ferrugineipes* Lepeletier. Very common. Oct.–May. Nesting in fine but consolidated sand. Digs a simple burrow terminating in single cell; cell provisioned with several hairless caterpillars (Geometridae) carried to nest in flight. Parasitized by Stylopidae (Strepsiptera).

* *Ammophila insignis litoralis* (Arnold). Uncommon. Febr.–Apr.

* *Ammophila vulcania* du Buysson. Rare. Nov. and Dec.

* *Diodontus* sp. Rare. Oct. and Nov. Species of this genus are known to nest in soil and to provision with aphids. (Bohart & Menke, 1976: 178).

*** *Astata fuscistigma* Cameron. Rare. Nov.–Apr. Nesting in compacted sand. *Astata* species are known to provision with bugs, especially Pentatomidae (Bohart & Menke, 1976: 211–212).

* *Dryudella flavoundata* (Arnold). Rare. Dec. Prey known to be a "small heteropteran" (Arnold, 1924: 38).

* *Liris* spp. (Some species may belong here, others may belong in category 2). Known to provision with crickets (Gryllidae).

* *Tachytella aureopilosa* Brauns. Rare. Jan. Only species in genus; biology unknown. Presence in female of foretarsal rake and of pygidial plate indicative of sand-nesting. Provisioning likely to be with Orthoptera *(sensu lato)*.

* *Tachysphex aethiopicus* Arnold. Rare. Jan.

*** *Tachysphex albocinctus* (Lucas). Common. Dec.–Mar. Digs simple one- or two-celled nest, each cell provisioned with 1–3 mantids (Mantidae), usually nymphs.

*** *Tachysphex fugax* (Radoszkowski). Common. Sept.–May. Digs simple two-celled nest; each cell provisioned with several grasshoppers (Lentulidae), adults and nymphs.

* *Tachysphex karroensis* Arnold. Uncommon. Dec.–Febr.

*** *Tachysphex panzeri pentheri* Cameron. (= *caliban* Arnold). Common. Oct.–Mar. Digs simple two-celled nest; sealed cell examined contained two prey; grasshopper nymphs (Acrididae).

* *Tachysphex schoenlandi* Cameron. Common. Dec.–Mar. Known to provision with nymphal mantids (Mantidae).

* *Tachysphex sericeus* (Smith). Uncommon. Nov.–May.

* *Parapiagetia vernalis* Brauns. Rare. Nov. Biology of genus largely unknown. Presence in female of foretarsal rake and of pygidial plate indicative of sand-nesting. Immature Acrydiidae recorded as prey of the Madagascan *P. longicornis* Arnold (Arnold, 1945: 94).

*** *Kohliella alaris* Brauns. Common. Dec.–Mar. Digs shallow nest with one to several cells; each cell provisioned with several nymphs of the Tree Cricket, *Oecanthus capensis* Saussure (Gryllidae: Oecanthinae). Nesting described by Gess & Gess (1980a).

*** *Palarus latifrons* Kohl. Common. Nov.–Mar. Unicellular nest dug in firm sand overlain by a layer of loose sand. Provisions with honey bees, *Apis mellifera* L. (Apidae). Brauns (1911: 117) in addition to honey bees recorded the following prey:
Mesa ♂ (cited as *Elis*) (Tiphiidae), *Ceramius capicola* Brauns (Masaridae) and small bees. In South Africa known as the Banded Bee Pirate and is a nuisance to beekeepers (Mally, 1908: 206–213; Brain, 1929: 396; Taylor, 1939: 103; and Smit, 1964: 356).

* *Palarus oneili* Brauns. Rare. Jan. and Febr. Prey known to include *Meria* ♀ (cited as *Myzine*) (Tiphiidae) and small bees (Brauns, 1911: 117).

* *Oxybelus acutissimus propinquus* Arnold. Rare. Nov.–Mar.

* *Oxybelus aethiopicus* Cameron. Rare. Jan.

* *Oxybelus imperialis* Gerstaecker. Rare. Nov.

*** *Oxybelus lingula* Gerstaecker. Common. Nov.–Mar. Nesting in loose sand. Like all *Oxybelus* spp. provisions with adult Diptera. Prey recorded at Hilton: *Stomorhina lunata* (F.) (Calliphoridae) and *Musca* sp. (Muscidae). Other prey known for this species: *Sarcophaga* sp. (Calliphoridae).

* *Oxybelus peringueyi* Saussure. Rare. Oct., Nov. and Mar.

* *Oxybelus rubrocaudatus* Arnold. Uncommon. Oct.–Jan.

* *Oxybelus ruficaudis* Cameron. Uncommon. Oct., Nov. and Jan.

* *Dienoplus vicarius karrooensis* (Brauns). Uncommon. Nov.–Mar. Species of the genus are known to dig simple nests in sandy soil. There may be from 2–15 cells per nest; cells are provisioned with Cicadellidae and Cercopidae (Bohart & Menke, 1976: 495).

* *Oryttus kraepelini* (Brauns). Uncommon. Dec. and Mar. The well developed foretarsal rake in the female is indicative of nesting in friable soil. Species of the genus are known to provision with Cicadellidae and Fulgoridae (Bohart & Menke, 1976: 507).

** *Hoplisoides aglaia* (Handlirsch). Uncommon. Oct.–Mar. Associated with sandy soil. Provisions with Membracidae.

* *Hoplisoides thalia* (Handlirsch). Uncommon. Dec., Jan. and Apr.

* *Stizus imperialis* Handlirsch. Rare. Dec., Jan. *Stizus* species are known to provision mostly with grasshoppers.

*** *Bembecinus braunsii* (Handlirsch). Very common. Oct.–Apr. Nesting in loose dry fine sand. Digs one- or two-celled nest; each cell provisioned with numerous Cicadellidae (incl. *Macropsis octopunctatus* China and *Macropsis chinai* Metcalf), exceptionally with one or two Fulgoroidea in addition.

* *Bembecinus dentiventris* (Handlirsch). Very rare. Nov., Dec.

*** *Bembecinus haemorrhoidalis* (Handlirsch). Very common. Oct.–Apr. Nesting in loose dry fine sand. Digs one- or two-celled nest; each cell provisioned with numerous Cicadellidae (incl. *Coloborrhis corticina* Germar, *Exitianus nanus* (Distant), *Macropsis octopunctata* China, *Macropsis chinai* Metcalf, *Macropsis* sp. nov., *Idioscopus* sp. and *Batracomorphus subolivaceus* (Stal)), exceptionally with one or two Fulgoroidea or Membracidae in addition.

*** *Bembix albofasciata* Smith. Common. Nov.–Febr. Digs a one-celled nest in sandy soil; cell provisioned progressively with adult Diptera belonging to the following families:
Stratiomyidae, Tabanidae (*Chrysops obliquefasciata* Macq.), Bombyliidae (several spp., incl. *Lomatia pictipennis* Wied.), Asilidae (several spp. incl. *Stenopogon dilutus* Walker), Conopidae (*Conops* sp.), Muscidae (2 spp. incl. *Musca lusoria* Wied.), Calliphoridae (incl. *Sarcophaga* sp. and *Chrysomyia* sp.) and Tachinidae.

* *Bembix cameronis* Handlirsch. Uncommon. Nov.–Jan.

* *Bembix capensis* Lepeletier. Uncommon. Dec., Jan. Single prey obtained was an adult fly (Tachinidae).

* *Bembix fusciipennis* Lepeletier. Rare. Mar.

*** *Bembix melanopa* Handlirsch. Uncommon. Dec.–Febr. Both nests located were in steeply sloping firm and compacted sand. Known to provision with adult Diptera (incl. Muscidae).

* *Bembix sibilans* Handlirsch. Uncommon. Nov.–Mar.

* *Philanthus loefflingi* Dahlbom. Rare. Nov., Dec.

*** *Philanthus triangulum* Fabricius. Uncommon. Oct.–Jan. Nesting in clayey yet friable soil. Provisioning with honey bees, *Apis mellifera* L. (Apidae) captured at their foraging flowers.

*** *Cerceris* sp. A. Rare. Dec. Nest excavated in disturbed clayey soil. Shallow multicellular nest; each cell provisioned with numerous Pteromalidae.

* *Cerceris amakosa* Brauns. Rare. Dec.–Mar. Associated with sandy soil.

* *Cerceris armaticeps caffrariae* Empey. Very rare. Febr.

* *Cerceris diodonta diodonta* Schletterer. Rare. Dec.

* *Cerceris discrepans discrepans* Brauns. Very rare. Nov.

* *Cerceris dominicana* Brauns. Very rare. Nov., Dec.

* *Cerceris erythrosoma* Schletterer. Very rare. Dec. Associated with sandy soil. Known to provision with Curculionidae.

*** *Cerceris holconota holconota* Cameron. Common. Nov.–Apr. Nesting in sandy soil; provisioning cells with Hymenoptera of various families (Braconidae, Bethylidae, Tiphiidae, Mutillidae, Formicidae and Halictidae).

* *Cerceris hypocritica* Brauns. Rare. Dec.–Febr. Associated with sandy soil.

*** *Cerceris languida languida* Cameron. Very common. Oct.–Apr. Nesting in sandy soil; provisioning cells with Phalacridae (*Olibrus* sp.).

*** *Cerceris latifrons latifrons* Bingham. Very common. Nov.–Mar. Nesting in sandy soil in very deep nests; provisioning cells with Scarabaeidae (Melolonthinae: Hopliini).

*** *Cerceris lunigera* Dahlbom. Uncommon. Dec.–Mar. Nest excavated in disturbed clayey soil; provisioning cells with Halictidae.

* *Cerceris nasidens obscura* Schletterer. Uncommon. Nov., Dec., Mar. and Apr. Associated with sandy soil. Known to provision its cells with Scarabaeidae (Melolonthinae).

* *Cerceris nigrifrons nigrifrons* Smith. Uncommon. Nov.–Febr. Associated with sandy soil. Known to provision its cells with Buprestidae (Brauns, 1926a: 320).

*** *Cerceris oraniensis* Brauns. Uncommon. Dec.–Mar. Nesting in sandy soil in deep nests; provisioning with Curculionidae (*Protostrophus* sp.) (Fig. 17).

* *Cerceris pearstonensis pearstonensis* Cameron. Common. Dec.–Apr. Nest excavated in disturbed clayey soil. Known to provision its cells with Curculionidae.

* *Cerceris pictifacies* Brauns. Rare. Dec.

*** *Cerceris ruficauda ruficauda* Cameron. Uncommon. Oct.–Apr. Nesting in disturbed clayey soil; provisioning with Chrysomelidae.

*** *Cerceris rufocincta polychroma* Gribodo. Very common. Nov.–Apr. Nesting in sandy soil; provisioning with Tiphiidae and Mutillidae.

*** *Cerceris spinicaudata spinicaudata* Cameron. Common. Nov.–Mar. Nesting in sandy soil; provisioning with Halictidae.

Ethological notes concerning above *Cerceris* spp. given in Gess (1980a).

COLLETIDAE

* *Colletes* sp. Uncommon.

HALICTIDAE

* *Halictus* sp. A. Common. Oct.–Apr. Associated with sandy soils.
* *Halictus* sp. B. Common. Nov.–Mar. Associated with sandy soils.
* *Lasioglossum* spp. Uncommon. Associated with sandy soils.
*** *Nomiodes ?halictoides* Blüthgen. Common. Oct.–Mar. Nesting in sandy soil.
*** *Nomia* sp. Common. Nov.–Febr. Nesting in sandy soil.

Category 5.

I. NESTING IN THE GROUND
(b) *In friable soils.*
(ii) In pre-existing cavity modified by the nester.

SPHECIDAE

* *Liris* sp. Uncommon. May belong here or in category 4. Known to provision with crickets (Gryllidae).

*** *Megachile (Eutricharaea) semiflava* Cockerell. Common. Sept.–Mar. Frequently seen flying low over the ground in the sandpit carrying green leaf-discs; on several occasions seen to be nesting in holes on the floor of the sandpit. Identity of original excavator of holes not established.

Category 6.

I. NESTING IN THE GROUND
(b) *In friable soils.*
(iii) In pre-existing cavity *not* modified by nester.

CHRYSIDIDAE

A total of seven species was recorded in association with sandy soils—in the sandpit. Of these, six species (*Chrysidea africana* Mocsary, *Hedychrum coelestinum* Spinola, *H. gonomaculatum* Edney, *Octochrysis laminata* (Mocsary), *O. mucronifera* (Mocsary) and *Pyriachrysis stilboides* (Spinola)) were rare and were mostly more commonly found associated with vertical banks.

One species, however, was both restricted to and common in the sandpit, namely:

Hedychrum sp. (near *comptum* Edney). Nov.–Mar. Associated with the nests of *Bembecinus braunsii* and *B. haemorrhoidalis* and believed to be parasitic in them.

TIPHIIDAE

A total of seventeen species was recorded in areas of friable, mostly sandy soil in and around the sandpit. Sixteen of these species (*Anthobosca* sp., *Meria* spp. (10), *Mesa* spp. (2) and *Tiphia* spp. (3)) are believed to be predaceous upon soil-inhabiting larvae of Scarabaeidae. The remaining species was:

Methocha mosutoana Péringuey. Rare. Jan. *Methocha* spp. are known to be predaceous upon the burrow-inhabiting larvae of tiger-beetles (Cicindelidae). The prey of the present species is certain to be *Cicindela brevicollis* Wied., adults of which are present in very large numbers in the sandpit throughout the summer months and well into the autumn or even early winter.

MUTILLIDAE

Fourteen species of Mutillidae were collected in association with the friable sandy soil of the sandpit. The most common species by far was *Glossotilla speculatrix* (Smith) (46 females and 67 males collected) followed by *Smicromyrme hecuba* (Péringuey) (29 females and 11 males collected), *Mimecomutilla renominanda* Bischoff, *Dasylabris* sp. nr. *danae* (Péringuey) and *Dasylabris mephitis* (Smith). Also recorded but uncommon were *Antennotilla phoebe* (Péringuey), *Dasylabris* sp. nr. *bassutorum* (André), *Dasylabris* sp. nr. *cryentocincta* André, *Dasylabris stimulatrix* (Smith), *Dasylabris thais* (Péringuey), *Dasylabroides caffra* (Kohl), *Labidomutilla tauriceps* (Kohl), *Psammotherma flabellata* (Fabricius) and *Viereckia* sp.

With the exception of *Dasylabroides caffra* which is a species characteristic of clayey rather than sandy areas and *Smicromyrme hecuba* which is common in both sandy and clayey areas, all the above listed species, with the exception of *Antennotilla phoebe*, were more common in the sandy areas than elsewhere and many appeared restricted to such areas.

Glossotilla speculatrix is highly characteristic of the sandy areas and in contrast to the larger numbers caught in the sandpit only two specimens were collected in bare patches in clayey areas. Though not reared from any nests circumstantial evidence indicates that the species is parasitic in the nests of *Bembecinus* species though other species nesting in the same situations are doubtless also parasitized. Its flight period is from December to April.

Smicromyrme hecuba appears like *Glossotilla speculatrix* to be associated with *Bembecinus* species and the two species of mutillid are usually found together within the areas occupied by *Bembecinus* pseudocolonies in the sandpit. Its flight period is similarly from December to April.

SCOLIIDAE

Eleven species of Scoliidae, believed to be associated with friable soils, were collected, many on flowers. By far the most common species was *Cathimeris capensis* (Saussure) (28 males and 13 females collected) which was present in the sandpit from September to May. Less common or rare were *Campsomeriella* sp., *Micromeriella* spp. (2), and *Scolia* spp. (7). All are believed to be predaceous upon soil-inhabiting larvae of Scarabaeidae.

SPHECIDAE

* *Nysson braunsi* Handlirsch. Rare. Nov.–Jan. Species of *Nysson* are known to be cleptoparasitic in the nests of various gorytin genera including *Oryttus*, *Dienoplus* and *Hoplisoides* (Bohart & Menke, 1976: 468). Representatives of these genera associated with friable soils at Hilton are *O. kraepelini*, *D. vicarius karrooensis*, *H. thalia* and *H. aglaia* and it may be assumed that the present species of *Nysson* is associated with one or more of these potential host species.

HALICTIDAE

*** *Sphecodes* sp. Common. Sept.–Febr. In the sandpit frequently observed inspecting holes in the ground and entering them. Found associated with *Nomia* sp. which species is believed to have been the excavator of the nests concerned and thus to be the host of this *Sphecodes* sp. The genus *Sphecodes* is known to be cleptoparasitic in the nests of other Halictidae *(Halictus* and *Lasioglossum)* (Michener, 1944: 250) and also certain Andrenidae and Colletidae (Krombein *et. al.* 1979: 1974).

MEGACHILIDAE

* *Coelioxys (Lyothyrapis) bruneipes* Pasteels. Very rare. Jan. Possibly parasitic in the nests of *Megachile (Eutricharaea) semiflava* Cockerell.

ANTHOPHORIDAE

* *Epeolus amabilis* Gerstaecker. Uncommon. Oct.–Apr. The species of *Epeolus* are known to be parasitic in the nests of *Colletes* (Michener, 1944: 279) and of *Tetralonia* and *Colletes* (Arnold, 1947: 218). Mostly collected in the sandpit where it probably parasitizes the *Colletes* sp.

* *Thyreus* sp. A. Uncommon in sandpit, more usually found associated with "sandstone" bank. In sandpit female observed inspecting holes in the ground.

Category 7.

II. NESTING IN OR ON VERTICAL BANKS
A. IN VERTICAL BANKS
(i) In nest constructed entirely by the nester.

POMPILIDAE

** *Dichragenia jacob* (Arnold). Uncommon. Apr.–May. Nine females, three with prey caught, at the "sandstone" bank with which this species, which was not found elsewhere, was definately associated. No nests located but females seemed to be coming and going to and from a small cave so situated on the bank that it could not be reached by the author. Assumed to construct its nest itself as do other *Dichragenia* species. Prey: lycosid spiders.

SPHECIDAE

*** *Chalybion (Hemichalybion) spinolae* (Lepeletier). Rare. Nov.–May. Nesting in the "sandstone" bank, circumstantial evidence indicates that the wasp excavates cavities itself, rather than utilizing pre-existing ones. Nesting cavity mud-lined. Prey: known to be small spiders.

MEGACHILIDAE

*** *Hoplitis anthodemnion* Michener. Common. Nov.–Feb. Nesting in the "sandstone" bank. Nest consists of excavated inclined burrow terminated by a single excavated cell containing a cell constructed from discs cut from petals (including those of *Barleria pungens*). Nest closure, occupying space between provisioned cell and nest entrance, consists of tightly packed sand.
Nesting described in detail by Michener (1968).

ANTHOPHORIDAE

*** *Anthophora* sp. Common. Oct., Nov. and Mar. Nesting in sand bank and "sandstone" bank. Probably the most common species at the "sandstone" bank, and its old and abandoned nests are probably those used most often by species nesting in this situation in pre-existing cavities (that is species of category 8).

Category 8.

II. NESTING IN OR ON VERTICAL BANKS
A. IN VERTICAL BANKS
(ii) In pre-existing cavity modified by the nester.

POMPILIDAE

* *Auplopus carinigena* Cameron. Rare. Apr.–May.

* *Auplopus ferruginea* (Magretti). Rare. Apr.–May.

** *Auplopus personata ornaticollis* (Cameron). Uncommon. Apr. Prey known to consist of errant spiders of the families Clubionidae, Salticidae and Sparassidae.

All three species were collected on the face of the "sandstone" bank. *A. personata* was observed hunting, boldly entering and searching crevices containing spider-spinnings, at times pushing its way through veils of spinnings at the entrance of the spiders' lairs; a prey-carrying female was furthermore seen entering a pre-existing cavity and it is consequently believed that this species (and the other two) may nest in such cavities. Support for this belief comes from Taylor (1968:72) who recorded *Auplopus mazoensis* (Arnold) nesting in a trap-nest and using mud to form cell partitions.

EUMENIDAE

A number of species, collected in association with vertical banks, is included in the present section, some having been observed nesting in pre-existing cavities, others being suspected of doing so. The species include:

*** Eumenid A. Uncommon. Nov. Nesting in pre-existing cavities in the "sandstone" bank, in cracks within and between the layers of the near-horizontally bedded shale of the shale bank, and in trap-nests inserted into larger crevices in the latter. Nest entrance furnished with a lacy downturned mud turret, nest a linear series of cells separated by mud partitions, each cell provisioned with numerous small bright green caterpillars (Pyralididae).

* *Anterhynchium natalense* (Saussure). Rare. At "sandstone" bank.

* *Antodynerus radialis oogaster* (Gribodo). Rare. Feb.–Apr. At "sandstone" bank.

* *Euodynerus euryspilus* (Cameron). Rare. Nov.–Feb. At "sandstone" bank. Recorded in a later category (17) nesting in trap-nests tied to *Acacia karroo*.

*** *Rynchium marginellum sabulosum* (Saussure). Uncommon. Feb. Nesting in trap-nests inserted into crevices in the "sandstone" bank and thus highly likely to be nesting in pre-existing cavities in the bank itself. Nest a linear series of cells separated by mud partitions; each cell provisioned with several (4–13) caterpillars (Pyralididae). Known in Grahamstown to nest in cut culms of *Arundo donax* used for vegetable frames.

*** *Tricarinodynerus guerinii* (Saussure). Uncommon. Jan. and Feb. Nesting in pre-existing cavities in sandbank, "sandstone" bank and shale bank as also in a trap-nest inserted into a larger crevice in the latter. Nest entrance furnished with a downturned mud turret (Fig. 28), nest a linear series of cells separated by mud partitions; each cell provisioned with several caterpillars, probably Tortricidae. *Anthrax ?tetraspilus* Hesse (Bombyliidae) reared from cells.

SPHECIDAE

* *Chalybion (Chalybion) tibiale* (Fabricius). Rare. Nov.–Apr. Circumstantial evidence strong that this species nests in pre-existing cavities in the "sandstone" bank. Nesting described in a later category (17).

* *Pison allonymum* Schultz. Uncommon. Dec.–May. Nesting recorded and described in previous category (2).

* *Pison montanum* Cameron. Rare. Oct.–Mar. Nesting recorded and described in a later category (17).

* *Trypoxylon* sp. Rare. Oct.–Mar. Nesting recorded and described in later category (17).

MEGACHILIDAE

*** *Anthidiellum (Pygnanthidiellum) kimberleyanum* Friese. Uncommon. Oct. and Nov. Nesting in "sandstone" bank.

*** *Branthidium braunsii* (Friese). Uncommon. Oct., Nov. and Apr. Nesting in "sandstone" bank.

*** *Chalicodoma (Pseudomegachile) schulthessi* (Friese). Uncommon. Sept. and Oct. Nesting in "sandstone" bank. Nest entrance furnished with a small mud collar, nest a linear series of cells separated by mud partitions, final closure also of mud.

* *Heriades ?freygessneri* Schletterer. Uncommon. Nov., Dec., Apr. and May. Thought to nest in "sandstone" bank. *H. freygessneri* is known to nest readily in trap-nests (Taylor, 1962b, 1965 and 1968).

*** *Immanthidium junodi* (Friese). Common. Nov.–Apr. Nesting in "sandstone" bank. A carder bee. Nesting described by Michener (1968), Skaife (1950) and Taylor (1962a).

*** *Megachile (Eutricharaea) gratiosa* Gerstaecker. Uncommon. Oct.–Mar. Nesting in trap-nests inserted into crevices in the shale bank and presumably also in cracks within and between layers of the shale. Nest a linear series of cells constructed of pieces cut from green leaves. Parasitized by *Zonitoschema eborina* (Fabr.) (Meloidae). Nesting described by Taylor (1963, 1965 and 1968).

*** *Megachile (Paracella) spinarum* Cockerell. Uncommon. Oct.–Apr. Nesting in "sandstone" bank and also in trap-nest inserted into crevice in the above. Nest a linear series of cells constructed of pieces cut from green leaves of *Maytenus heterophylla.*

Category 9.

II. NESTING IN OR ON VERTICAL BANKS
A. IN VERTICAL BANKS
(iii) In pre-existing cavity *not* modified by the nester.

CHRYSIDIDAE

Seven of the eight species of cuckoo wasps collected on the vertical banks are believed to be associated with wasps nesting in the banks. The seven species, none of which was common, are: *Chrysidea africana* (Mocsary), *Chrysidea ghiliani* Gribodo, *Chrysis antiqua* Brauns, *Chrysis capitalis* Dahlbom, *Hedychrum coelestinum* Spinola, *Octochrysis laminata* (Mocsary), and *Octochrysis mucronifera* (Mocsary). Hosts are known for two species:

* *Chrysidea africana* Mocsary. Known to be parasitic in the nests of *Trypoxylon* (see category 18).

*** *Octochrysis laminata* (Mocsary). Reared from the nests of *Tricarinodynerus guerinii* (Saussure) (2 specimens).

MUTILLIDAE

Six species of Mutillidae were collected on the vertical banks, namely *Antennotilla phoebe* (Péringuey), *Dasylabroides caffra* (Kohl), *Mimecomutilla renominanda* Bischoff, *Mutilla scabrofoveolata* Sichel & Radoszkowski, *Ronisia trispilota* (Radoszkowski) and *Stenomutilla* sp. No species was common and no species can be said to be typical of this situation. One species only was definitely associated with a wasp nesting in the bank, namely

*** *Stenomutilla* sp. Reared from the nest of Eumenid A. constructed within open crack in shale bank. (1 specimen).

SAPYGIDAE

* *Sapyga (Sapygina) simillima* Arnold. Uncommon. Oct., Nov. and Apr. Known to be parasitic in the nests of *Heriades* sp. (see category 18. Possibly to be associated with *Heriades ?freygessneri* Schletterer nesting in "sandstone" bank.

* *Sapyga (Sapygina) undulata* Gerst. Rare. Apr.

MEGACHILIDAE

** *Euaspis abdominalis* (Fabricius). Very rare. Nov. Circumstantial evidence indicates that this parasitic bee may be associated with the nests of *Chalicodoma schulthessi* (Friese) in the "sandstone" bank.

* *Coelioxys (Coelioxys) lucidicauda* Cockerell. Very rare. Febr.

* *Coelioxys (Lyothyrapis) bruneipes* Pasteels. Very rare. Nov. Possibly parasitic in the nests of *Megachile (Paracella) spinarum* Cockerell.

** *Coelioxys (Lyothyrapis) lativentris* Friese. Rare. Oct., Nov. Recorded as associated with an *Anthophora* sp. and as probably parasitic in its nest (Rozen, 1969b: 55). In the present community thus probably also associated with *Anthophora.*

** *Coelioxys (Lyothyrapis) lativentroides* Brauns. Rare. Oct.–Dec. Seen entering and leaving nests of *Chalicodoma schulthessi* (Friese) and therefore believed to be parasitic in the nests of this species. Supporting evidence for this belief supplied by Brauns (1930) who recorded this species as a parasite of *Chalicodoma latitarsis* Friese.

ANTHOPHORIDAE

* *Thyreus* sp. Common. Nov.–May. A species of *Thyreus* was recorded as parasitic in the nests of an *Anthophora* species (Rozen, 1969b) and the same association may exist in the present community.

Category 10.

II NESTING IN OR ON VERTICAL BANKS
B. ON VERTICAL BANKS
(i) In nest constructed entirely by the nester.

EUMENIDAE

* *Synagris abyssinica* Guérin. Rare. Feb. and Apr. Flying about in front of "sandstone" bank. Known to make aerial nests of mud and to provision with caterpillars.

* *Synagris analis* H. de Saussure. Rare. Mar. and Apr. As above.

*** *Eumenes lucasius* Saussure. Rare. Dec. & Apr. Urn-shaped mud cells found in sheltered positions on shale bank. Prey: caterpillars. Parasite: *Osprynchotus violator* (Thunberg) (Ichneumonidae).

VESPIDAE

*** *Ropalidia* sp. A. Rare. One nest with foundress female found (Jan.) in a fist-sized cavity in the sand bank. Nest aerial, constructed of wood pulp ("wasp paper") and in the form of a naked paper comb suspended from the roof of the cavity by a short pedicel. Social species: larvae fed directly on macerated insects and nectar.

SPHECIDAE

*** *Sceliphron spirifex* (L.) One nest with female found (Apr.) in a fist-sized cavity in the "sandstone" bank and several found on shale bank. Nest aerial, constructed of mud and consisting of several cells arranged parallel to one another and covered with a common envelope of mud applied after the last cell has been sealed. Each cell provisioned with numerous small spiders. Parasite: *Osprynchotus violator* (Thunberg) (Ichneumonidae).

Category 11.

II. NESTING IN OR ON VERTICAL BANKS
B. ON VERTICAL BANKS
(ii) In pre-existing cavity modified by the nester.

EUMENIDAE

*** *Eumenid* A. Rare. Nov. Nesting in old urn-shaped mud cells of *Eumenes lucasius* Saussure found in sheltered positions on the shale bank. Prey: Pyralididae (caterpillars).

Category 12.

II. NESTING IN OR ON VERTICAL BANKS
B. ON VERTICAL BANKS
(iii) In pre-existing cavity *not* modified by the nester.

CHRYSIDIDAE

*** *Chrysis* sp. One specimen reared from the urn-shaped mud cell of *Eumenes lucasius* Saussure found in a sheltered position on the shale bank.

MUTILLIDAE

* *Stenomutilla* sp. Rare. Known to be parasitic in the nests of Eumenid A. (see category 9).

Category 13.

III. NESTING ON STONES

(i) In nest constructed entirely by the nester.

POMPILIDAE

*** *Auplopus rossi nigricornis* (Arnold). Rare. One nest was found, consisting of nine contiguous mud cells attached to the underside of a large flat stone where there was a shallow space between it and the ground on which it rested. One of the cells when opened was found to have been provisioned with a single spider of the family Lycosidae. Two male wasps and a female emerged from the cells during Sept.-Oct.

MEGACHILIDAE

*** *Hoplitis jansei* (Brauns). Uncommon. Nests constructed upon the exposed portions of partially buried quartzite stones and boulders. Nests consist of independent cells closely grouped together and constructed of small, irregularly shaped pebbles of quartzite cemented in a matrix of resin. Emergence of adult bees from Aug.-Nov. Brauns (1926b: 220) recorded the species foraging on low composites at Willowmore.

Category 14.

III. NESTING ON STONES

(ii) In pre-existing cavity modified by the nester.

MEGACHILIDAE

*** *Megachile (Eutricharaea) gratiosa* Gerstaecker. On one occasion was found to have utilized old open cells of *Hoplitis jansei* (Brauns) for purposes of nesting. Old *Hoplitis* cells each contained a single *M. gratiosa* cell constructed of pieces cut from green leaves. A male reared from such a cell emerged during Nov. *M. gratiosa* nests more commonly in pre-existing cavities associated with vertical banks and with woody plants (categories 8 & 17).

Category 15.

III. NESTING ON STONES

(iii) In pre-existing cavity *not* modified by the nester.

MUTILLIDAE

*** *Antennotilla phoebe* (Péringuey). Rare. Parasitoids in the cells of *Auplopus rossi nigricornis* (Arnold). Three males reared from these cells emerged during early November.

Category 16.

IV. NESTING IN OR ON PLANTS
A. IN PLANTS
(a) *Within woody stems.*
(i) In nest constructed entirely by the nester.

ANTHOPHORIDAE

* *Xylocopa caffra* L. Rare and all sightings confined to the riverine bush. Old abandoned galleries found in dead trunks and branches of *Rhus* and *Pinus* located in the riverine bush believed to have been those of this species. Known to nest in dead branches and structural timbers of *Pinus* spp.

* *Xylocopa divisa* Klug. Rare and all sightings confined to riverine bush. Known to nest in dead branches.

Category 17.

IV. NESTING IN OR ON PLANTS
A. IN PLANTS
(a) *Within woody stems.*
(ii) In pre-existing cavity modified by the nester.

EUMENIDAE

*** *Euodynerus euryspilus* (Cameron). Rare. Found nesting (Nov., Febr.) in four trap-nests tied to *Acacia karroo*. Nest a linear series of cells, cell partitions and closing plug composed of mud. Each cell provisioned with 7–13 caterpillars of family Pyralididae, in two nests *Loxostege frustalis* Zeller, the Karroo Caterpillar, a pest of *Pentzia incana*.

SPHECIDAE

*** *Ampulex* sp. (near *cyanura* Kohl) (Fig. 36). Uncommon. Found nesting (Nov.–March) in thirty trap-nests tied to *Acacia karroo*. Examination of dead finger-thick branches of this shrub or small tree revealed that the natural pre-existing cavities used by this wasp were abandoned larval galleries of *Ceroplesis hottentota* (Fabricius) (Cerambycidae, Coleoptera) (Fig. 35). In both natural and artificial nesting cavities nest consists of a single cell plugged with loosely compacted detritus. Each cell provisioned with a single large nymph or apterous female of *Bantua dispar* (Burmeister) (Blattidae) (Fig. 36).

*** *Ampulex denticollis* Cameron. Rare. Found nesting (Febr.) in one trap-nest tied to *Acacia karroo*. Nest single-celled, plugged with detritus and provisioned with a single blattid nymph.

*** *Chalybion (Chalybion) tibiale* (Fabricius). Rare. Found nesting (Jan. and Febr.) in three trap-nests tied to dead tree-stump in riverine bush. Nest a linear series of cells; cell partitions and closing plug composed of mud; outer surfaces of partitions and closing plug whitened with uric acid from bird droppings. Each cell provisioned with 14–34 small spiders of the families Argiopidae *(Araneus, Argiope, Caerostris, Cyclosa, Isoxya* and *Nephila)*, Thiridiidae *(Rhomphaea)* and Zodariidae. Nesting described by Gess & Gess (1980d).

*** *Isodontia pelopoeiformis* (Dahlbom). Common. Found nesting (Jan.–Feb.) in over eighty trap-nests tied to *Acacia karroo, Maytenus linearis* and *Rhus lancea* in thorn scrub and riverine bush. Nest a linear series of cells; cell partitions constructed of plant "fluff" derived from fruiting inflorescences of *Lasiospermum bipinnatum* and *Senecio* spp.; preliminary plugs and closing plugs of the above materials as well as clods of earth and debris (Fig. 32). Each cell provisioned with several katydids—Tettigoniidae: Phaneropterinae (*Terpnistria zebrata* nymphs, *Eurycorypha prasinata* nymphs, and *Phaneroptera* spp.—nymphs and adults). Nesting of this species in Rhodesia described in Smithers (1958).

* *Isodontia simoni* (du Buysson). Rare. Nov. & Dec. Not found nesting.

*** *Isodontia stanleyi* (Kohl). Uncommon. Found nesting (Dec.–Febr.) in eighteen trap-nests similarly situated to those of *I. pelopoeiformis*. Nest a linear series of cells; cell partitions constructed of short lengths of grass leaf blades transversely arranged; preliminary plugs and closing plugs of grass inflorescences, transversely coiled and longitudinally arranged respectively (Fig. 33). Grasses used: *Danthonia curva, Diplachne fusca, Eragrostis* sp. (probably *E. curvula*), *Melica racemosa* and *Sporobolus* sp. (probably *S. fimbriatus*). Each cell provisioned with several katydids, apparently the same species taken by *I. pelopoeiformis* but smaller (younger) individuals. One cell in addition contained two tree crickets (*Oecanthus capensis* Saussure (Gryllidae: Oecanthinae)).

*** *Holotachysphex turneri* (Arnold). Rare. Found nesting (Dec.–Febr.) in five trap-nests tied to *Acacia karroo* and *Salix mucronata*. Nest a linear series of cells; cell partitions constructed of coarse detritus and clayey earth; closing plug of coarse detritus. Each cell provisioned with a variable number (4–32) of *?Pyrgomorphella* sp. nymphs (Pyrgomorphidae, Acridoidea). Nesting described by Gess (1978).

*** *Pison montanum* Cameron. Rare. Found nesting (Dec.–Febr.) in eight trap-nests tied to *Acacia karroo* and *Maytenus linearis*. Nest a linear series of cells; cell partitions and closing plug constructed of mud. Each cell provisioned with a variable number (7–47) of small spiders of the family Argiopidae.

*** *Trypoxylon* sp. Common. Found nesting (Oct.–Febr.) in twenty-five trap-nests tied to *Acacia karroo* and *Rhus lancea*. Nest a linear series of cells; cell partitions and closing plug constructed of mud. Each cell provisioned with a variable number (5–11) of small spiders of the following families: Lycosidae (incl. *Hippasa* sp.), Pisauridae (*Euphrosthenops* sp.), and Argiopidae (incl. *Araneus* spp., *Larinia* sp.).

COLLETIDAE

*** *Hylaeus braunsi* (Alfken). Rare. Dec. Found nesting in two trap-nests tied to *Acacia karroo*. Nest a linear series of cells; cell partitions and nest closure of very shiny and thin transparent "cellophane"-like material.

* *Hylaeus* spp. (at least two others).

MEGACHILIDAE

*** *Immanthidium junodi* (Friese). Common. Nov.–May. Commonly found nesting in trap-nests tied to *Acacia karroo*. A carder bee constructing cell partitions and closing plug of cottonwool-like material. Nesting of this species described or commented upon by Skaife (1950), Taylor (1962a) and Michener (1968).

*** *Heriades* sp. Rare. Oct. Found nesting in one trap-nest tied to *Maytenus linearis*.

*** *Chalicodoma (Pseudomegachile) fulva* (Smith). Rare. Found nesting (Dec.) in two trap-nests tied to *Acacia karroo*. Nest a linear series of mud cells.

*** *Chalicodoma (Pseudomegachile) sinuata* (Friese). Rare. Found nesting (Jan., Febr.) in three trap-nests tied to *Acacia karroo*. Nest a linear series of mud cells. Parasitized by *Zonitoschema eborina* (Fabr.) (Meloidae).

*** *Megachile (Eutricharaea) gratiosa* Gerst. Common. Found nesting (Dec.–Feb.) in trap-nests tied to *Acacia karroo*. Nest a linear series of cells constructed of pieces cut from green leaves. Parasitized by *Zonitoschema eborina* (Fabr.) (Meloidae).

*** *Megachile (Paracella) spinarum* Cockerell. Common. Found nesting in many trap-nests tied to *Acacia karroo*. Nest a linear series of cells constructed of pieces cut from green leaves of *Maytenus heterophylla*.

Category 18.

IV. NESTING IN OR ON PLANTS
A. IN PLANTS
(a) *Within woody stems.*
(iii) In pre-existing cavity *not* modified by the nester.

CHRYSIDIDAE

*** *Chrysidea africana* Mocsary. Uncommon. Parasitic in the nests of *Trypoxylon* sp. nesting in trap-nests. (Seven females reared.)

*** *Chrysis* sp. (near *purpuripyga* Edney). Uncommon. Parasitic in the nests of *Trypoxylon* sp. nesting in trap-nests. (Nine individuals reared.)

*** *Chrysis inops* Gribodo. Rare. Parasitic in the nests of *Pison montanum* Cameron nesting in trap-nests. (Three males and a female reared.) Previously recorded as parasitic in the nests of *Pison transvaalensis* Cameron in Natal (Taylor, 1968).

*** *Octochrysis hoplites* (Mocsary). Rare. Parasitic in the nests of *Euodynerus euryspilus* (Cameron) nesting in trap-nests. (Six individuals reared.)

SAPYGIDAE

*** *Sapyga (Sapygina) simillima* Arnold. Rare. Parasitic in the nest of *Heriades* sp. nesting in a trap-nest. (One individual reared.)

MEGACHILIDAE

*** *Coelioxys (Coelioxys) penetratrix* Smith. Rare. Parasitic in the nests of *Megachile (Paracella) spinarum* Cockerell nesting in trap-nests. (2 females and one male reared.)

Category 19.

IV. NESTING IN OR ON PLANTS
A. IN PLANTS
(b) *Within pithy stems.*
(i) In nest constructed entirely by the nester.

EUMENIDAE

* *Raphiglossa natalensis* Smith. Very rare. March. Not found nesting. Recorded at Willowmore (as *R. flavo-ornata* Cameron) as excavating its cells in dry pithy stems (chiefly those of Liliaceae) and provisioning its cells with small caterpillars (Lepidoptera) (Meade–Waldo, 1913: 45 and Bequaert, 1918: 29–30).

SPHECIDAE

* *Dasyproctus bipunctatus* Lep. & Brullé (incl. the colour forms *bipunctatus* Lep., *lugubris* (Arnold) and *simillimus* (Smith)). Flight period: Oct.–March. Common. Known to nest in the inflorescence stems of Amaryllidaceae, Iridaceae and Liliaceae (Bowden, 1964: 425–437) and to provision with adult Diptera.

* *Dasyproctus dubiosus* (Arnold). Very rare. Dec., Jan.

* *Dasyproctus immitis* (Saussure). Rare. Oct.–March.

* *Dasyproctus ruficaudis* (Arnold). Rare. Dec.–Febr.

*** *Dasyproctus westermanni* (Dahlbom). Common. Oct.–March. Found nesting during Dec. and Jan. in inflorescence stems of *Urginea altissima* (Liliaceae); nest a linear series of cells in an ascending and a descending gallery; cells provisioned with numerous small adult Diptera (Simuliidae, Stratiomyidae, Bombyliidae, Empididae, Syrphidae, Otitidae, Chamaemyiidae). Parasites: *Perilampus* sp. (Perilampidae, Chalcidoidea, Hymenoptera) and Phoridae (Diptera). Evidence of nesting by *Dasyproctus* spp. (unidentified) also in inflorescence stems of *Gasteria* spp. (Liliaceae) and in stems of *Berkheya decurrens* Compositae).

Nesting of *Dasyproctus* spp. (especially *D. westermanni*) described by Gess (1980b).

ANTHOPHORIDAE

*** *Xylocopa (Gnathoxylocopa) sicheli* Vachal. Common. At Hilton found nesting exclusively in dry but still attached inflorescence stems of *Aloe ferox* (Liliaceae) (Fig. 30). Nest consists of a descending gallery and an ascending gallery, both unbranched and subdivided serially into a number of cells each sealed with a pithy plug made of material rasped from the gallery walls. Bees are present throughout the year; nesting takes place during the summer. Parasite: *Coelopencyrtus* sp. (Encyrtidae, Chalcidoidea). Cleptoparasites: *Gasteruption robustum* Kieffer (Gasteruptionidae) and *Synhoria hottentota* Péringuey (Meloidae).

*** *Ceratina* sp. A. Common. Commonly found nesting in the thinner branches of dry but still attached inflorescence stems of *Aloe ferox* (Liliaceae), less commonly nesting in the stems of *Gasteria* spp. (Liliaceae) and infrequently in stems of *Datura stramonium* (Solanaceae). Nest plan like that of *X. sicheli* but all dimensions much smaller. Bees are present throughout the year; nesting takes place during the summer.

*** *Ceratina* sp. B. Eleven further species known to occur at Hilton. *C.* sp. B found nesting in inflorescence stem of *Aloe ferox* (1 nest); One male of *C.* sp. C found sheltering in bored dry stem of *Berkheya decurrens* (Compositae); one female and two males of *C.* sp. D. found sheltering in bored dry inflorescence stem of *Apicra* sp. (Liliaceae).

Category 20.

IV. NESTING IN OR ON PLANTS
A. IN PLANTS
(b) *Within pithy stems.*
(ii) In pre-existing cavity modified by the nester.

SPHECIDAE

*** *Isodontia stanleyi* (Kohl). Three nests found within old galleries of *Xylocopa sicheli* in inflorescence stems of *Aloe ferox* (Fig. 38). (For details of nesting of this wasp see previous entry for this species in category 17.)

*** *Trypoxylon* sp. Nests found within old galleries of *Ceratina* sp. A. in inflorescence stems of *Aloe ferox*, within old galleries of *Ceratina* and *Dasyproctus* spp. in inflorescence stems of *Gasteria* sp., and within galleries of *Dasyproctus westermanni* in inflorescence stems of *Urginea altissima* (Gess, 1980b). (For details of nesting of *Trypoxylon* see previous entry for *Trypoxylon* sp. in category 17.)

ANTHOPHORIDAE

*** *Allodape rufogastra* Lep. & Serv. OR *Allodape exoloma* Strand. Nests found within old galleries of *Dasyproctus* sp. in stems of *Berkheya decurrens*. Bee nest characterized by lack of cell partitions and by the eggs being cemented to the gallery wall.

MEGACHILIDAE

*** *Capanthidium capicola* (Friese). Two nests found within old galleries of *Ceratina* sp. A. in inflorescence stem of *Aloe ferox*. A carder bee constructing cell partitions of cotton-wool-like material.

*** *Immanthidium junodi* (Friese). Nests found within old galleries of *Ceratina* sp. A. in inflorescence stems of *Aloe ferox*, within old galleries of *Ceratina* and *Dasyproctus* spp. in inflorescence stems of *Gasteria* sp., and within old galleries of *Ceratina* sp. in stems of *Datura* sp. (For details of nesting of this bee see previous entry for this species in category 17.)

*** *Heriades spiniscutis* (Cameron). Two nests found within old galleries of (?) *Dasyproctus* sp. in stems of *Berkheya decurrens* and one nest found within old gallery of *Dasyproctus* sp. in inflorescence stem of *Gasteria* sp. Nest in linear series of cells; cell partitions (when present) and closing plug of dark resin-like substance. Cell provisioned with bright yellow, rather dry pollen. The nesting of *H. spiniscutis* has been described in detail by Michener (1968).

*** *Chalicodoma (Pseudomegachile) sinuata* (Friese). Six nests found within old abandoned galleries of *Xylocopa sicheli* in inflorescence stems of *Aloe ferox* (Fig. 40). Nest in linear series of mud cells.

*** *Megachile (Paracella) spinarum* Cockerell. Six nests found within old abandoned galleries of *Xylocopa sicheli* in inflorescence stems of *Aloe ferox* (Fig. 39). Nest a linear series of cells constructed of pieces cut from green leaves of *Maytenus heterophylla*. Parasites: *Leucospis africana* Cameron (Leucospidae) (three females reared from above nests) and a species of Cleridae (?*Trichodes aulicus* Klug) (one larva found in one of the above nests). Also *Coelioxys (Coelioxys) penetratrix* Smith (see below).

Category 21.

IV. NESTING IN OR ON PLANTS
A. IN PLANTS
(b) *Within pithy stems.*
(iii) In pre-existing cavity *not* modified by the nester.

No species were recorded in this category from the above nests within pithy stems and branches of non-woody plants. However, parasites recorded from the nests of species nesting in trap-nests may be expected to occur also in the nests of the same host species nesting in pithy stems and branches. The following species are thus listed on the strength of this assumption:

CHRYSIDIDAE

Chrysidea africana Mocsary. Parasitic in the nests of *Trypoxylon* sp.

Chrysis sp. (near *purpuripyga* Edney). As above.

MEGACHILIDAE

Coelioxys (Coelioxys) penetratrix Smith. Parasitic in the nests of *Megachile (Paracella) spinarum* Cockerell.

Category 22.

IV. NESTING IN OR ON PLANTS
A. IN PLANTS
(c) *Within hollow stems.*
(i) In nest constructed entirely by the nester.

ANTHOPHORIDAE

*** *Xylocopa caffrariae* Enderlein. Common. Nesting exclusively in dry but still attached hollow culms of *Phragmites australis* (Gramineae), "Common Reed", growing along the course of the New Year's River and immediately within the retaining wall of the earthen dam. Nest consists of a descending and an ascending gallery subdivided serially into a number of cells each sealed with a pithy plug made of material rasped from the gallery walls. Access to the hollow internode is through an entrance hole cut by the bee through the 1 mm thick side wall of the culm (Fig. 31). Bees are present throughout the year; nesting takes place during the summer. Cleptoparasite: *Gasteruption robustum* Kieffer (Gasteruptionidae).

Category 23.

IV. NESTING IN OR ON PLANTS
A. IN PLANTS
(c) *Within hollow stems.*
(ii) In pre-existing cavity modified by the nester.

SPHECIDAE

*** *Isodontia stanleyi* (Kohl.) Two nests found within old galleries of *Xylocopa caffrariae* in bored hollow culms of *OHHRAGMITES AUSTRALIS*. (For details of nesting of this wasp see previous entry for this species in category 17).

*** *Holotachysphex turneri* (Arnold). Two nests found within old galleries of *Xylocopa caffrariae* in bored hollow culms oe *Phragmites australis*. (For details of nesting of this wasp see previous entry for this species in category 17, Gess (1978) and Gess & Gess (1980a: 52)).

*** *Trypoxylon* sp. A few nests found within old galleries of *Xylocopa caffrariae* in bored hollow culms of *Phragmites australis*, a few others found in hollow culms of the same plant bored by lepidopterous larvae. (For details of nesting of *Trypoxylon* see previous entry for *Trypoxylon* sp. in category 17).

MEGACHILIDAE

*** *Chalicodoma (Pseudomegachile) sinuata* (Friese). One nest found within old gallery of *Xylocopa caffrariae* in bored hollow culm of *Phragmites australis*. Nest a linear series of mud cells.

Category 24.

IV. NESTING IN OR ON PLANTS
A. IN PLANTS
(c) *Within hollow stems.*
(iii) In pre-existing cavity *not* modified by the nester.

No species were recorded in this category from the above nests within hollow stems of hollow-stemmed plants. However, parasites recorded from the nests of species nesting in trap-nests may be expected to occur also in the nests of the same host species nesting in hollow stems. The following species are thus listed on the strength of this assumption:

CHRYSIDIDAE

Chrysidea africana Mocsary. Parasitic in the nests of *Trypoxylon*.
Chrysis sp. (near *purpuripyga* Edney). As above.

Category 25.

IV. NESTING IN OR ON PLANTS
B. ON PLANTS (Irrespective of whether woody, pithy or hollow-stemmed).
(i) In nest constructed entirely by the nester.

EUMENIDAE

*** *Eumenes lucasius* Saussure. Rare. Urn-shaped aerial mud cell found under loose bark of fallen tree. Provisioned with caterpillars. A few other aerial mud nests constructed by Eumenidae were found but in all cases they were old, the wasps having already emerged, and identification of the species involved was not possible.

MASARIDAE

* *Celonites capensis* Brauns. A rare species at Hilton; not found nesting. Known to construct small aerial mud cells. Provisions with a mixture of pollen and nectar.

VESPIDAE

*** *Polistes smithii* Saussure. One nest (with foundress female) found (Nov.) attached to branches of *Lycium* overhanging "sandstone" bank. Nest aerial, constructed of wood pulp ("wasp paper") and in the form of a naked paper comb suspended from the branch by a short pedicel. Social species; larvae fed directly on macerated insects and nectar. Adult males occasionally stylopized.

*** *Ropalidia* sp. B. One nest (with foundress female) found (Nov.) attached to branches of *Cadaba aphylla* overhanging "sandstone" bank. Form of nest similar to that of *Polistes smithii*. Adult males likewise occasionally stylopized.

SPHECIDAE

* *Sceliphron quartinae* (Gribodo). Rare. Nov., Febr. Not found nesting at Hilton. Known to construct its cells of cow dung or clayey mud and to attach them singly or in twos to grass culms or other plant stems at some height above the ground. Provisioning is with small spiders. (Brauns, 1911: 119 and Jacot Guillarmod, *pers.comm.*) At Hilton found at puddles, presumably collecting mud for nest-building purposes.

Category 26.

IV. NESTING IN OR ON PLANTS
B. ON PLANTS (Irrespective of whether woody, pithy or hollow-stemmed.)
(ii) In pre-existing cavity modified by the nester.

No representatives recorded for this category.

Category 27.

IV. NESTING IN OR ON PLANTS
B. ON PLANTS (Irrespective of whether woody, pithy or hollow-stemmed.)
(iii) In pre-existing cavity *not* modified by the nester.

No representatives recorded for this category.

DISCUSSION

Evaluation of the completeness and representativeness of the sample

The classification of the aculeate wasps and of the bees of the study area on the basis of their ethology encompasses an annotated list of a total of 241 species. The strengths of the specific representation of the families involved are shown in Table 1.

Table 1.

The strengths of the specific representation of the families included in the annotated list.

Family	No. of spp.	Family	No. of spp.
Chrysididae	19	Vespidae	3
Tiphiidae	17	Pompilidae	11
Mutillidae	20	Sphecidae	91
Scoliidae	11	Colletidae	3
Sapygidae	2	Halictidae	6
Masaridae	6	Megachilidae	25
Eumenidae	16	Anthophoridae	11

It is inevitable that in a survey of the present kind not all the species present in a given area (in the present instance, the farm Hilton) will be collected and identified and that it will not be possible to allocate to any particular nesting association those species for which ethological information is lacking.

It is axiomatic, however, that in any area, the most common species are the most likely to be noticed and recorded—that is most likely to be collected and most likely to be found nesting or at least intimately associated with a particular nesting association (e.g. a particular type of soil) in which nesting may be assumed to take place. It may therefore be expected that the present account of the ethology of the aculeate wasps and the bees of Hilton includes amongst the 241 species listed most if not all of the common and therefore most important species occurring there. Judged on the basis of the inclusion in the sample of these common and important species the sample may therefore be considered as representative of the entire community of the above defined insects.

Although further study of the whole area of Hilton would undoubtedly swell the lists of some if not all the various categories of the present classification with further species, it is believed that this quantitative change would not be accompanied by a qualitative change of any real importance.

For some families at least it is possible to obtain some indication of how representative the number of species listed above is of the total number of species occurring at Hilton. For example, with respect to the Sphecidae, the predominant family of the sample, the 91 species listed are believed to represent 80–90% of the total number of species of the family present at Hilton, and the five and six species listed respectively for the Vespidae and the Masaridae are believed to represent 60% and 100% of their total numbers, however, the nineteen listed species of Chrysididae are believed to represent only 45% of their total number.

An evaluation of the classification of the aculeate wasps and the bees of the study area on the basis of their ethology.

In the classification of the aculeate wasps and the bees of the study area on the basis of their ethology 27 categories are recognized. When the 241 species are allocated to these categories it is found that 209 species occur in only one category each and 32 in more than one category each. If, however, those species which construct their nests entirely by themselves are considered, it is found that of the 118 species in this category only one (0,85%) occurs in two categories, both of which offer the species in question, *Eumenes lucasius*, an aerial nester, a support for its nest.

The species which modify pre-existing cavities and therefore do not have to excavate their cavities themselves show, as one would expect, less specificity. Of the 44 species involved 13 species (29,5%) occur in more than one category. Of these 13 species 10 nest only above the ground either in vertical banks or in plants and of these three were restricted to plants. One species, *Megachile semiflava*, was restricted to cavities in the ground regardless of the nature of the soil.

Of the 79 species which nest in pre-existing cavities which they do not themselves modify 17 (21,5%) occur in more than one category, however, these species, belonging to the Chrysididae, Mutillidae, Sapygidae and Megachilidae such as *Coelioxys*, are "parasitic" in one way or another and the categories in which they occur are therefore determined by those of their hosts. These species are therefore 100% restricted on the basis of host.

It is clear that each community determined by habitat is characterized by those species which construct their nests entirely by themselves but that there is, not surprisingly, overlap in species using pre-existing cavities and a resultant overlap in species which are hosted by the latter.

Having established the validity of the ethological classification nesting in the four main habitat categories; ground, vertical banks, stones and plants; will be discussed.

Discussion of nesting in the four main habitat categories.

The Ground

Soils may be divided into two different types—friable and non-friable. By definition, the word "friable" means easily crumbled and a friable soil therefore is one in which it is easy to dig, the individual particles being relatively loosely aggregated and not difficult to part from one another. "Non-friable" means not easily crumbled and a non-friable soil is therefore one in which it is difficult to dig, the individual soil particles being closely aggregated and difficult to part from one another. The character of a non-friable soil may, however, vary greatly with the amount of moisture which it contains, a wet non-friable soil being more easily worked than a dry one.

At Hilton the friable soil is mostly sandy in nature and is derived from the weathering of Witteberg Quartzite and the non-friable soil is clayey in nature and is derived from the weathering of Witteberg Shale. In certain small areas recent disturbance during farming activities has broken down the structure of the clayey soil and has temporarily rendered it partially friable.

At Hilton, the number of species recorded as nesting in the ground exceeds the number recorded from the three other situations combined: 167 species as against 74. Of the 167 species recorded from the ground, 126 (75,5%) were associated only with friable soil, 35 (21%) were associated only with non-friable soil and 6 (3,5%) were associated with both friable and non-friable soils.

On account of the species which were recorded in both soil types, the number of species/substrate associations exceeds the actual number of species by 6 and therefore totals 173. An analysis of this figure according to the degree of participation of species of wasps and of bees in the construction of their nests is given in Table 2 and is shown graphically and in greater detail in the Pie-diagram (Fig. 16).

TABLE 2.

Number of species of aculeate wasps and of bees nesting in the ground.

	In nests constructed entirely by the nesters themselves	In modified pre-existing cavities	In unmodified pre-existing cavities
In non-friable soils	15	12	14
In friable soils	76	2	54

It may be seen immediately that with respect to those species which excavate their nests themselves there are many more (76 as against 15) that do so in friable soils than in non-friable soils. It should be noted that this marked difference in the numbers of species nesting in the two soil types is not a reflection of the extent of the availability of these soils for nesting, the density of nesting in areas of friable soil being far greater than in areas of non-friable soil with readily available water sources. Furthermore this discrepancy is not a peculiarity of the Hilton population but bears out the picture which emerges from a consideration of ground-nesting aculeate wasps as a whole.

It can be clearly seen from the Pie-diagram (Fig. 16) that, at Hilton, at the family level the composition of the communities of species which construct their nests themselves are strikingly different in friable and non-friable soils. Whereas in friable soils the vast majority of species, 67 (88%), are members of the family Sphecidae in non-friable soils this family is only represented by two (13%) of the species. The majority of species, 11 (74%), in non-friable soils are members of the Vespoidea, five species of Masaridae and six species of Eumenidae. There are no representatives of the Vespoidea nesting in friable soils. Species of Pompilidae excavate their nests in both soil types. Whereas the two species of *Dichragenia* appear to be the only pompilids associated in this way with non-friable soils, the number of species, 3, recorded for friable soils is in all probability too low. Bees represented, albeit poorly, amongst the nest excavators in friable soil are absent amongst those in non-friable soil.

The construction of nests in the two very different soil types clearly demands different excavation techniques and therefore differences in the structure and behaviour of the wasps involved.

Characteristic of the species excavating nests in friable soil is that there is no modification of the physical nature of the substrate by the addition of water. Excavation of the nests is by digging, the organs involved being the mandibles, the fore-legs and in some species the pygidium.

Initial loosening of the soil at the working face of the excavation is frequently done with the mandibles. These may be used simply to bite away the soil but in some species nesting in compacted soil they are aided in their work by the wasp's manipulation of its flight mechanisms which produces vibrations transmitted by the mandibles to the substrate. Evidence of this method of loosening the soil was the very noticeable buzzing sound that could frequently be heard being made by excavating females of the sphecids *Podalonia canescens* and *Ammophila ferrugineipes*. Frequently this buzzing sound emanating from the ground was the first indication that nest excavation by one of these species was under way in the immediate vicinity.

Removal of the loosened soil may be effected in several ways, on the basis of which Olberg (1959) divided the digger wasps into "rakers", "pullers", "carriers" and "pushers". A

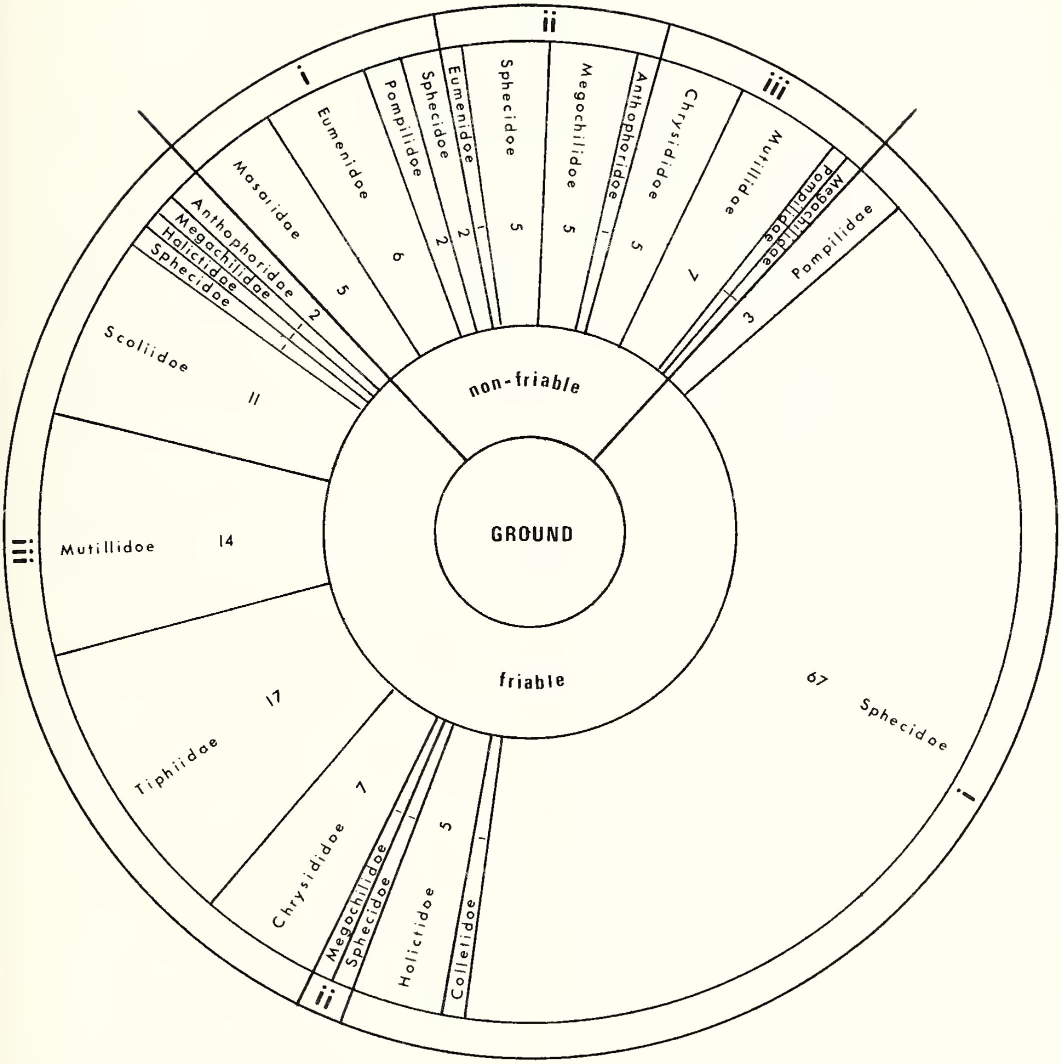

Fig. 16. Diagram showing the structure of the communities of the aculeate wasps and the bees nesting in the ground in the study area. Numbers accompanying the family names represent numbers of species. The numbers (i, ii, iii) in the outermost ring correspond to the same numbers in the classification of the aculeate wasps and the bees of the study area on the basis of their ethology. (i) In nest constructed entirely by the nester. (ii) In pre-existing cavity modified by the nester. (iii) In pre-existing cavity *not* modified by the nester.

good account of the different modes of digging based upon the above division is given by Evans and Eberhard (1970) and will only be briefly outlined here, with the addition of examples drawn from the present study.

The "rakers", constituting the majority of the fossorial wasps, are characterized by having a strongly developed series of stout spines on the front tarsus, forming the so-called "tarsal comb" or "sandrake". In digging, the fore tarsi which are bent towards the midline of the body are moved repeatedly backwards and forward, each backstroke throwing back a load of soil which passes beneath the upheld abdomen to behind the body. By walking backwards whilst so raking, loose soil can rapidly be swept from the excavation. Many of the species observed nesting in friable soil at Hilton are included in the "rakers", for example *Batozonellus fuliginosus* (Pompilidae) (Gess and Gess, 1980b), *Tachyphex* spp., *Kohliella alaris* (Gess and Gess, 1980a), *Palarus latifrons, Bembecinus braunsii, Bembecinus haemorrhoidalis* and *Bembix albofaciata* (Sphecidae). In some species the two front legs move alternately (e.g. *Batozonellus*), in other species synchronously (e.g. *Bembix*). By virtue of the fact that it is not possible to rake or sweep loose sand vertically upwards, all the burrows of "rakers" examined at Hilton were found to be inclined, often at a fairly small angle with the horizontal (for example see nest plans of *Kohliella alaris*—Gess and Gess, 1980a: Figs 4 and 5).

The "pullers" like the "rakers" use the fore legs to remove the loosened soil from the excavation. However, instead of raking out the soil, the latter is gathered together to form a load held between the underside of the head and prothorax and the basal parts of the fore legs and, the wasp walking backwards, this soil is then pulled out of the excavation and deposited at its entrance. At Hilton a common "puller" is *Podalonia canescens*. However, this wasp does also act as a "raker" for the small heap of excavated soil pulled to the nest entrance is from time to time dispersed by raking. Raking of soil is also practised in nest closure. Soil pulling unlike soil raking does not necessarily require the burrow to be inclined and the burrow of *Podalonia canescens* is frequently subvertical, at least initially.

The "carriers" are like the "pullers" in their mode of removing the loosened soil from the excavation. However, unlike the "pullers" they do not deposit the soil at the nest entrance but drop it at a distance from the nest entrance, having transported it there either on foot or in flight. At Hilton the most common carrier nesting in friable soil is *Ammophila ferrugineipes* which carries the soil to a distance of 1–1,5 m from the nest before dropping it. Generally each load of soil is dropped in the same area, mostly into a low bush. Despite the fact that each load is dropped in the same place, the discarded sand is not noticeable for, being dropped from a height into a bush by a wasp which is moving in flight, it is well scattered and concealed. Like the burrow of *Podalonia canescens*, the burrow of *Ammophila ferrugineipes* is initially subvertical. The "pushers" differ from the "rakers", "pullers" and "carriers" in their use of the end of the abdomen in clearing soil from their excavations. Soil loosened by the mandibles and fore legs is moved back by the legs to behind the wasp which then backs up its burrow pushing the soil before it, in an action comparable to that of a piston in its cylinder. The common "pushers" in friable soil at Hilton are the many species of *Cerceris* which for the purpose of pushing soil with the end of the abdomen have a well developed pygidial plate. Characteristic of *Cerceris* burrows is that they are vertical or subvertical and that the excavated soil in the form of "sand sausages" forms a conical heap surrounding and surmounting the nest entrance (Fig. 17). The length of the "sand sausage" indicates that this method of nest excavation allows a great amount of loosened material to be brought to the surface at any one time—more than can be moved at any one time by a "puller". It is therefore an efficient and time-saving method of excavation and allows the construction of nests of great depth. At Hilton, *Cerceris latifrons*, for example, constructs a burrow far deeper than that of any other species examined there—at a depth of 600 mm, the reach of the excavator's arm, the burrow still continues downwards.

Characteristic of those species constructing original nests in non-friable soils is that excavation of the nest is affected by the use of water used to soften the soil thus rendering it workable. The water, collected by the nesting female from a water source, usually a pool or

Fig. 17. Nest entrance of *Cerceris oraniensis* showing excavated soil in the form of "sand sausages". (× 1)

puddle in the vicinity of the chosen nesting site, is carried to the nesting site in the crop. The mechanics of excavation consist of the regurgitation of a droplet of water from the crop onto the working face of the excavation, the working of this water into the soil by the mandibles, and the formation of the resultant mud into a pellet which is carried from the excavation by means of the mouthparts. Several such pellets may be formed from a single crop-full of water: when the supply is depleted the wasp returns to the water source for a further crop-full. Whilst the above outlined method of softening the soil is unique to those wasps nesting in non-friable soils, the use of the mandibles for carrying out the pellets of mud from the excavation involves the same behaviour as shown by many nesters in friable soils which may use their mandibles for carrying out pebbles and other objects from their excavations though their digging is otherwise done by raking or pulling the soil. Another facet of behaviour shared by certain excavators in both friable and non-friable soils is the use of vibrations generated by the manipulation of the flight mechanisms and transmitted by the mandibles to the substrate for the purpose of loosening the latter. Recorded above with respect to the sphecids *Podalonia canescens* and *Ammophila ferrugineipes* ("pullers" and "carriers" respectively), it is a feature also of the excavating behaviour of the sphecid *Bembecinus cinguliger* (and probably also *Bembecinus oxydorcus)*.

The use of water for nest excavation has been described in detail for several species of wasps nesting in clayey soils at Hilton: *Dichragenia pulchricoma* (Arnold) (Gess and Gess, 1974) and *Dichragenia neavei* (Kohl) (Gess and Gess, 1976b) (both Pompilidae); *Parachilus insignis* (Saussure) (Gess and Gess, 1976a) (Eumenidae); *Ceramius capicola* Brauns, *Ceramius lichtensteinii* (Klug), *Ceramius linearis* Klug and *Jurgurtia confusa* Richards (Gess and Gess, 1980c) (all Masaridae); *Bembecinus cinguliger* (Smith) and *Bembecinus oxydorcus*

(Handlirsch) (Gess and Gess, 1975) (both Sphecidae). In addition to these species a further five species, all Eumenidae, have been recorded using this method of nest excavation: included are *Antepipona scutellaris* Giordani Soika, *Parachilus capensis* (Saussure) and *Pseudepipona erythrospila* (Cameron).

The above species, in marked contrast to those excavating their nests in friable soils, make no use of the fore-legs in manipulating the nesting substrate and these limbs are consequently devoid of any modifications such as "sandrakes" used for digging. This is particularly striking with respect to the sphecid genus *Bembecinus*, represented at Hilton by four very common species, *B. braunsii* and *B. haemorrhoidalis* nesting in friable soil (in the sandpit) and *B. cinguliger* and *B. oxydorcus* nesting in non-friable, clayey soil. Typically the members of this large cosmopolitan genus are sand-raking and have the fore-tarsi furnished with long spines for this purpose as in *B. braunsii* and *B. haemorrhoidalis*. In *B. cinguliger* and *B. oxydorcus*, by contrast, these spines forming the "sandrake" are totally absent, the fore-tarsi having instead a dense row of short spines (Figs 18 and 19).

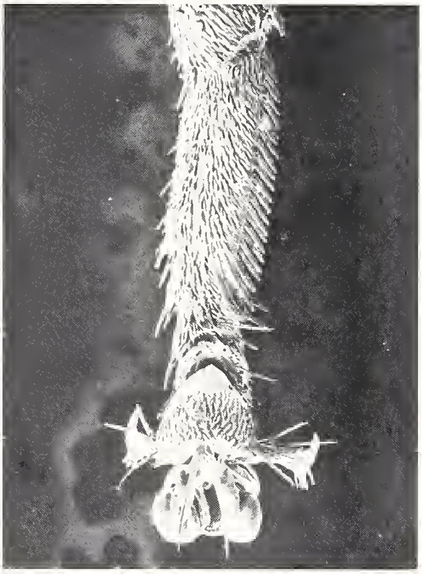

Fig. 18. Left fore-tarsus of *Bembecinus cinguliger* showing dense row of short spines. (× 32)

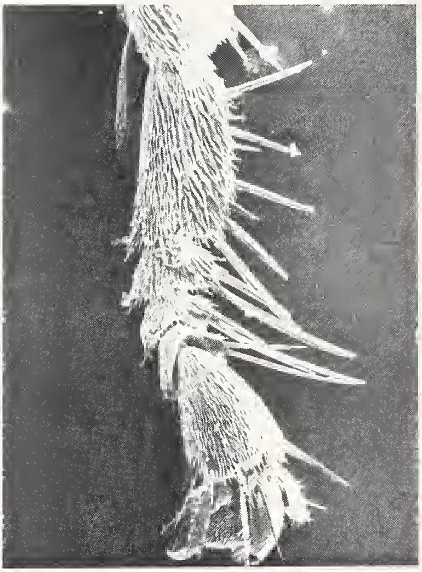

Fig. 19. Left fore-tarsus of *Bembecinus haemorrhoidalis* showing long spines forming "sandrake". (× 32)

Within the Pompilidae, the unmodified fore-tarsi of the two species of *Dichragenia* nesting in non-friable soil may similarly be contrasted with the modified fore-tarsi of *Batozonellus fuliginosus* nesting in friable soil (Figs 20 & 21).

It might be expected with respect to the clay-nesters that as all work associated with the manipulation of the substrate and of the excavated material (mud pellets) is performed by the mouthparts, principally the mandibles, some modifications associated with these organs might be present. This does indeed appear to be the case in the two *Dichragenia* species, females of which possess a brush of long, stiff, forwardly directed bristles emitted from the base of the

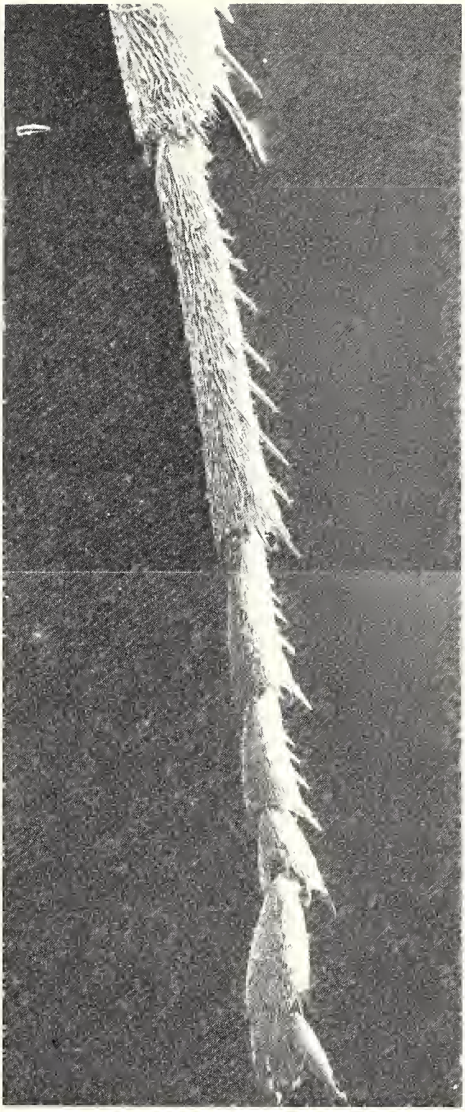

Fig. 20. Left fore-tarsus of *Dichragenia pulchricoma* showing very short spines not forming a "sandrake". (× 28)

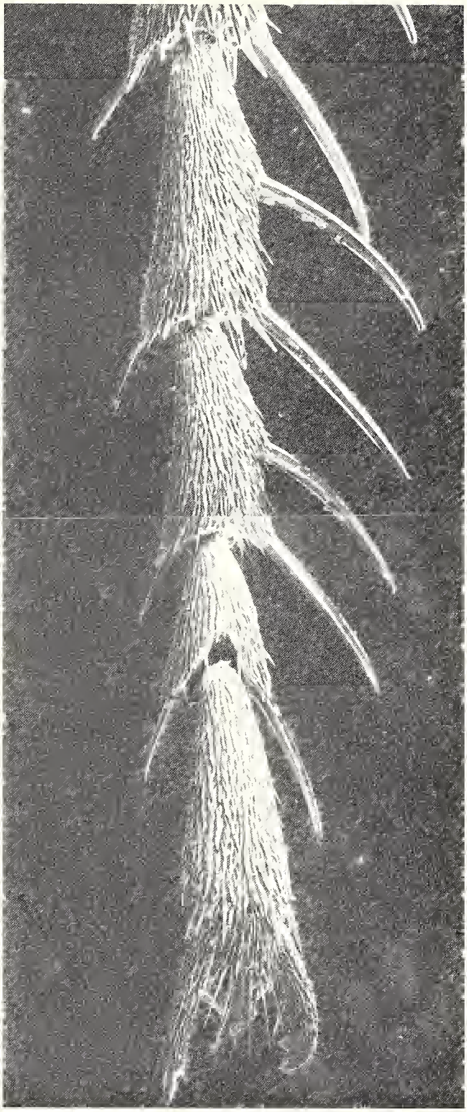

Fig. 21. Left fore-tarsus (distal four joints only) of *Batozonellus fuliginosus* showing long spines forming "sandrake". (× 24)

mentum (Figs 22 & 23 and Arnold, 1934: Figs 1, 1a). It is believed that these bristles may by supporting it from below aid the mandibles in holding and manipulating a mud pellet. Support for this belief may be drawn from two auplopodine genera closely allied to *Dichragenia—Phanagenia* and *Auplopus* which possess similar brushes of mental bristles and which use mud pellets to construct aerial mud cells.

Fig. 22. Underside of head of *Dichragenia pulchricoma* showing stiff, forwardly directed bristles emitted from the base of the mentum. (× 56)

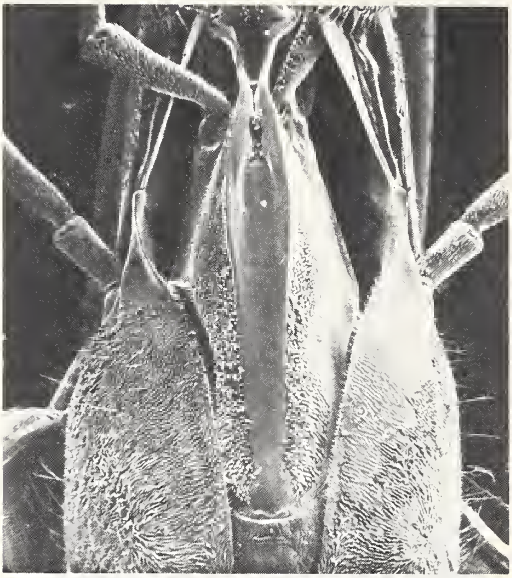

Fig. 23. Underside of head of *Batozonellus fuliginosus* showing absence of forwardly directed bristles. (× 24)

In the brief outline given above of the excavating methods used by nesters in friable soils, it was shown that whereas soil raking allowed the construction only of inclined burrows, soil pulling and the development of soil pulling—soil carrying—allowed the construction of vertical burrows. As the species excavating their nests in non-friable soils all remove the excavation spoils in the form of mud pellets held by the mandiblss it follows that they may be considered soil carriers and it is not surprising that the nests excavated are without exception vertical or subvertical (Gess and Gess, 1974: Figs 2–5; 1975: Figs 10–17; 1976a: Figs 1–4; 1976b: Figs 1–2; 1980c: Figs 1–5). The genus *Bembecinus* may once again be used as an illustration, in this instance to show the differences in the nest plan resulting from different excavation techniques employed in the two substrates. Thus, whereas the nest of several sandraking species has been described by Evans (1966: 137–138) as being without exception oblique, a description also fitting the nests of *B. braunsii* and *B. haemorrhoidalis*, the nest of the mud pelletcarrying *B. cinguliger* and *B. oxydorcus* is vertical or subvertical. The distinction can be clearly seen by comparison between Evans (1966: Fig. 76) and Gess and Gess (1975: Figs 10–17). The same picture emerges from a comparison of the nest plan of *Batozonellus fuliginosus* (Gess and Gess, 1980b: 5) with those of the two *Dichragenia* species.

Characteristic of all the species recorded excavating their nests in non-friable clayey soil is that at least some of the excavated material—in the form of mud pellets—is used to build an aerial superstructure encircling and surmounting the nest entrance. Among the species involved, the two *Dichragenia* species are unique in that all the pellets removed from their burrows are added to the superstructures. All other species stop adding pellets to the superstructure once this has attained a certain size, and further pellets are discarded at varying distances from the nest, depending upon the species.

Each species builds a superstructure of definite form so that the identity of the builder may readily be established from the style of its architecture.

The largest and most striking superstructures are constructed by the two Pompilidae: that of *Dichragenia pulchricoma* is retort-shaped (Gess and Gess, 1974: 195–196, Pls 5–8 and 1976b: Fig. 3) whereas that of *D. neavei* is funnel-shaped (Gess and Gess, 1976b: Pl. 1 and Figs 1 and 2).

The nest superstructures of the Eumenidae are all of a single basic type or developments thereof: a low collar encircling the nest entrance in *Parachilus insignis* (Gess and Gess, 1976a: 88, Fig. 1 and Pls 3–8) and in *Pseudepipona erythrospila*; a very low turret with a downwardly recurved lip in Eumenid sp. G; a short vertical flared tube in *Antepipona scutellaris*; and a vertical funnel-shaped turret in *Parachilus capensis*.

The four Masaridae studied all construct nest superstructures in the form of cylindrical turrets. That of *Jugurtia confusa* is characteristically very short (Gess and Gess, 1980c: 66, Figs 1 and 7) whereas those of the three species of *Ceramius* are longer: those of *C. linearis* (Gess and Gess, 1980c: 66, Fig. 3) and *C. lichtensteinii* (Gess, 1973: 117, Pl. 2; and Gess and Gess, 1980c: 66, Figs 4, 5 and 9) are initially vertical or subvertical but may, if of any considerable length, curve over and that of *C. capicola* (Gess, 1973: 117, Pl. 1; and Gess and Gess, 1980c: 66, Figs 2 and 8) is always downcurved and may continue in a horizontal plane close to the ground but always free from it.

The nest superstructures of the two Specidae though superficially very different are on closer examination clearly of similar plan and may readily be homologized (Gess and Gess, 1975: 33): that of *Bembecinus cinguliger* is elongated and is applied to the surface of the ground (Gess and Gess, 1975: Figs 6–9 and Pls 5 and 6) whereas that of *B. oxydorcus* is shortened and raised above the ground (Gess and Gess, 1975: Figs 2–5 and Pls 7–13).

A feature common to the nest superstructures of the Pompilidae, Eumenidae and Masaridae enumerated above is that of radial symmetry, at least in the initial stages of their construction. Whereas radial symmetry is characteristic of the completed superstructures of all the Eumenidae and of *Jugurtia confusa* as well as of large superstructures of *Dichragenia neavei*, it is lost in those of the *Ceramius* species and in large superstructures of *D. pulchricoma*. The nest superstructures of the two species of *Bembecinus* (Sphecidae), however, are never radially symmetrical even initially.

In *Ceramius lichtensteinii* at least, it has been established (Gess, 1973: 117) that experimental removal of a completed nest turret is followed by its replacement by the nesting wasp with a new one of similar design to and size as the first. The response by *D. pulchricoma* to a damaged nest superstructure is different and has been described in detail by Gess and Gess (1974: 196).

That the possession of an aerial superstructure surmounting the nest entrance is of survival value to species excavating their nests in non-friable clayey soils is evident by the fact that all the species listed as belonging to this category of ground nesters construct such superstructures. This is all the more striking when it is considered that the species involved belong to four different families and that the technique of nesting in clay has evolved independently in the Pompilidae, Eumenidae-Masaridae, and Sphecidae. Ways in which these superstructures may be of value to the wasps constructing them will be discussed later.

All the species of wasps excavating their nests in the ground exhibit the same behavioural elements. Differences in the nesting behaviour result from differences in the sequence in which these behavioural elements are performed and from the repetition in some species of the performance of one or more of the behavioural elements within the sequence.

The basic and most primitive ethological type found in nest-excavating wasps is characterized by the sequence:

Hunting—Paralysis of the prey (by stinging)—*Transportation of the prey—Excavation of* *the nest* (consisting of an entrance burrow and a cell)—*Oviposition—Closing of the cell and of the nest.*

This basic type is found amongst species excavating their nests in friable soils and is typical of the vast majority of Pompilidae, examples at Hilton being *Batozonellus fuliginosus* and probably *Tachypompilus ignitus* (Gess and Gess, 1980b). A few Sphecidae such as the noctuid-caterpillar-hunting *Podalonia canescens* also exhibit this primitive nesting type.

The wasp after transporting the prey into the vicinity of the chosen nesting site, often close to the point of prey capture, is forced temporarily to deposit the former on the ground or in some place of concealment—frequently under a leaf or in a small weed—while a shallow burrow for its reception is rapidly excavated. Despite the fact that the wasp may frequently interrupt her digging to check upon the prey, the latter is subject to misadventure and may either be carried away by other insects such as ants or may be oviposited upon by cleptoparasitic insects such as the pompilid *Ceropales.*

Excavation of the cell having been completed the wasp retrieves the prey, transports it into the cell, oviposits upon it and then closes the cell by filling the burrow leading to it with some of the previously excavated soil.

In the behaviour of the wasps belonging to this basic ethological type characterized by the fact that hunting precedes nest excavation there is never any repetition of a behavioural element within a single sequence and it therefore follows that not only is a cell provisioned with only a single prey but each nest consists of only a single cell. With the closure of the cell the association with the nest is ended and capture of a further prey by the wasp is followed by the excavation of a new nest.

More specialized ethological types found amongst species excavating their nests in the ground are all characterized by the fact that hunting and nest excavation have been transposed in the sequence in which the behavioural elements are performed—that is nest excavation now precedes hunting. Of immediate benefit to all wasps having this more advanced sequence is that the prey may be taken directly into the cell with greatly reduced risks of its being stolen or furnished with an egg by a cleptoparasite.

Nest excavation preceding hunting is the sequence common to the majority of those wasps recorded at Hilton as excavating their nests in friable soil and is characteristic of all those species excavating their nests in the non-friable clayey soil.

As has been noted above, wasps which hunt before excavating nests construct these close to the site of capture of the prey. With the adoption of the new sequence of nest excavation before hunting, the nest site is not chosen as a matter of expediency but on the basis of its overall suitability and as a consequence there is a tendency for successive nests excavated by a wasp to be localized in one area which may moreover be removed from the hunting area.

The grouping by a wasp of successive nests in the same nesting area is clearly pre-adaptive for a labour and time saving shortcut in which there is a substitution of a smaller number of nests with two or more cells for a larger number of nests each with a single cell. This change from single-celled to two-celled or multi-celled nests is brought about within the new sequence of nest excavation before hunting by a delay in carrying out the final element of the sequence—that of nest closure (as opposed to cell closure) and by a repetition after cell closure of all the preceding elements in the sequence other than the initial one—the excavation of the entrance burrow.

The amended sequence may be expressed as:

Excavation of the nest entrance burrow—[Excavation of the cell—Hunting—Paralysis of the prey—Transportation of the prey—Oviposition—Cell closure]^n *—Nest closure.*

(The portion of the sequence in square brackets is that subject to repetition "n" times.)

At Hilton, examples of wasps belonging to this ethological type are the two pompilids excavating their nests in clayey soils—*Dichragenia pulchricoma* and *D. neavei* (Gess and Gess, 1974 and 1976b, respectively). In both these species the final nest closure has never been found to occur and it therefore seems that it is not only delayed but is omitted altogether.

The sequence of nest excavation preceding hunting is pre-adaptive for the substitution in the provisioning of a cell of several smaller prey for a single large one. This is clearly of advantage with respect to prey transport, it being easier to transport several small prey, one at a time, than a single large prey. The advantage can easily be seen with respect to wasps provisioning their cells with spiders (Table 3). Like all Pompilidae, *Batozonellus fuliginosus* and *Tachypompilus ignitus* (Gess and Gess, 1980b) provision each cell with a single spider, which on account of its weight relative to that of the wasp transporting it—up to around eight times—cannot be transported other than by being dragged laboriously over the ground. Frequently the wasp has difficulty in overcoming the obstacles on the way to the nest. By contrast, in the Sphecidae *Chalybion tibiale* (Gess and Gess, 1980d) and *Pison montanum* provision each cell with numerous small spiders, which on account of their light weight—for each individual a mere fraction (about one-third) of that of the wasp—are able to be transported effortlessly, rapidly and directly to the nest by the wasp in flight.

TABLE 3

The relationship for some species of Pompilidae and Sphecidae between the weight of the spider or spiders forming the provision of a cell and the weight of the female wasp provisioning the cell.

Wasp family & species	Size of sample	No. of prey/cell (range)	No. of prey/cell (average)	Provision weight / wasp wt. (range)	Provision weight / wasp wt. (average)	Individual prey wt. / wasp wt. (average)
POMPILIDAE						
Batozonellus fuliginosus	2	1	1	2,25–7,61	4,93	4,93
Tachypompilus ignitus	16	1	1	1,00–8,52	4,2	4,2
SPHECIDAE						
Chalybion tibiale	3	15–21	17,4	4,65–6,52	5,87	0,37
Pison montanum	20	7–23	14,5	2,5–7,0	4,9	0,33

The substitution of several smaller prey for a single large one, like the substitution of two-celled or multi-celled nests for single-celled nests discussed above, is achieved by repetition of some of the elements of the behavioural sequence—in this case the elements concerned with hunting, paralysis of the prey, and transport of the latter to the nest.

It is clear that though the number of prey introduced as provision into a single cell may be increased from one to several or many, oviposition within the cell must be limited to a single egg and cannot automatically follow the introduction of each prey into the cell. However, whereas multiple oviposition is universally suppressed, there is variation in the point in time during the provisioning of a cell when oviposition of the single egg occurs. Oviposition may be fixed to be either on the first prey to be introduced into the cell or may be on the last (as in *Cerceris* species) or it may not be determined by order of prey introduction at all but rather by the size or some other particular attribute of one of the prey. This appears to be the case in the sand-nesting sphecid *Kohliella alaris* for which size of prey appears to be a factor in the determination of the prey chosen for oviposition (Gess and Gess, 1980a: 52).

Oviposition upon the first prey to be introduced into a cell may be followed by two distinct forms of provisioning differing in the time span during which the subsequent provisioning (that is introduction of additional prey) is performed. Thus, if rapidly performed, the cell may be fully provisioned and sealed before the larva hatches from the egg (= mass provisioning). However, if subsequent provisioning is delayed, the larva may hatch before provisioning is completed. Whereas this may be the consequence of a shortage of prey or of weather unfavourable for hunting, some wasps habitually practise delayed provisioning even under optimal conditions. In this case, introduction of the second prey into the cell is delayed until the young larva has at least partially consumed the first (on which the egg was laid) and subsequent prey are similarly introduced only when the larva is ready to consume them (= progressive provisioning). Such is the case in the nesting of *Bembix albofasciata*, at Hilton excavating its one-celled nests in sandy soil.

Whereas oviposition in all the ethological types hitherto discussed has been upon the provision and has thus followed the introduction of one or more prey into the cell, some of the more specialized wasps exhibit transposition of hunting and oviposition and oviposit into an empty cell.

This behaviour is uncommon in the Sphecidae but is known in the genus *Bembecinus*, amongst others, and at Hilton has been described for *B. cinguliger* and *B. oxydorcus* (Gess and Gess, 1975). Oviposition into an empty cell is, however, typical of all Vespoidea and amongst the ground nesting wasps of Hilton has been described for the eumenid *Parachilus insignis* (Gess and Gess, 1976a) and for masarids of the genera *Jugurtia* and *Ceramius* (Gess and Gess, 1980c).

Oviposition into an empty cell, like oviposition onto the first prey to be introduced into a cell, allows either mass or progressive provisioning. Both options are shown by the above wasps. The two *Bembecinus* species practise progressive provisioning at least initially (Gess and Gess, 1975: 38–39) whereas *Parachilus insignis* practises mass provisioning. Mass provisioning is the method used by the Masaridae studied. The contrary belief held by some authors in the past that one of these species *(Ceramius lichtensteinii)* practises progressive provisioning has been exhaustively discussed and shown (Gess and Gess, 1980c: 80–81) to have been based upon incorrect interpretation of delayed provisioning due to external causes. In passing it may be mentioned that the Masaridae are unique amongst the wasps in that (with the exception of one genus) all provision not with insect or spider prey but with a mixture of pollen and nectar. In this facet of their behaviour the Masaridae therefore parallel the bees.

The nesting of the solitary bees recorded excavating their nests in the ground: *Colletes* (Colletidae), *Halictus, Lasioglossum, Nomioides* and *Nomia* (Halictidae) is similar in many respects to that of the more specialized wasps and follows a sequence of behaviour found also amongst the latter. Nesting is initiated by the excavation of an entrance burrow and of a cell. Provisioning of the cell (with a mixture of pollen and nectar) follows and is completed before oviposition on or near the provision takes place; thereafter the cell is sealed and the next cell is excavated. It will be noted that the relative order of provisioning and ovipositioning in these bees and in the pollen and nectar provisioning wasps (Masaridae) is reversed.

When the nesting of the relevant species of wasps recorded at Hilton is considered with respect to the foregoing account of the ethological types represented in the nesting of the wasps and bees excavating original nests in the soil, an interesting distinction between those species associated with friable and non-friable soils may be discerned. Whereas a wide range of ethological types from the most basic (hunting before nest excavation) to the most advanced is found amongst those species associated with friable soils, only the more advanced types are found amongst those species associated with non-friable soils. Illustrative of this is that in all the species associated with non-friable soils hunting is preceded by nest excavation and that two-celled or multi-celled nests are the rule (though *Bembecinus* and *Parachilus* may occasionally fail to excavate the second cell). Furthermore that in all the species, with the exception of the two *Dichragenia* species, provisioning of each cell is with numerous prey and that oviposition in the empty cell is practised.

It must therefore be postulated that, amongst the wasps and bees excavating their nests in the soil, the association with friable soil is the original one and is primitive and that the association with non-friable soil is secondary and is derived and advanced.

Certainly, the difficulties attendant upon the excavation of nests in non-friable soil precludes those species doing so from possessing the sequence of behavioural elements (hunting before nest excavation) characteristic of the basic or primitive ethological nesting type. On the other hand, the more advanced ethological nesting types seen amongst the species nesting in friable soil are pre-adaptive in overcoming the difficulties imposed by nesting in non-friable soil.

With respect to the relative sequence in which hunting and nest excavation are performed, the primitive sequence (hunting preceding nest excavation) is possible only if the delay in the introduction into the nest of the prey, already at hand and waiting, can be kept to a minimum. This is possible if the nest is being excavated in friable soil in which digging is easy and therefore rapid. However, in non-friable soil where excavation is difficult and therefore slow and furthermore involves the periodic absence of the wasp from the site when fetching water the prey would be exposed for a longer period which would increase the possibility of desiccation, theft or parasitism. Nest excavation preceding hunting is therefore a prerequisite for nesting in non-friable soils.

The change from single-celled to two-celled or multi-celled nests sharing a single entrance burrow common to both or all the cells, though in terms of saved energy and time advantageous to nesters in friable soils, is of even greater advantage to nesters in the more difficult non-friable soils, and must be considered pre-adaptive to nesting in the latter substrate.

Similarly, the substitution in the provisioning of each cell of several smaller prey for a single large one, besides being of importance with respect to ease of transport, must be seen as bringing about a saving in energy and time expended in nest excavation in that the bore of the entrance burrow and the overall size of the cell can thereby be reduced. This again is of greatest advantage to excavators in non-friable soil and can be seen as pre-adaptive to nesting in this substrate.

A comparative reduction in the bore of the entrance burrow and in the size of the excavated cell is achieved also by the two species of *Dichragenia* despite the fact that, like in all Pompilidae, provisioning of each cell is with but a single large spider. In this case reduction of the dimensions of the nest is made possible by the amputation of the legs of the prey. This habit of amputation of the legs of the prey, characteristic of the pompilid tribe Auplopodini, like the change seen in more highly evolved wasps from a single large prey to several smaller ones per provisioned cell, probably serves the primary purpose of greater ease of prey transport but is also pre-adaptive for nesting in non-friable soils.

A prime requisite for the nesting of all nest-excavating wasps, whether nesting in friable or non-friable soils, is the presence of areas of soil partially or totally denuded of plant cover. Thus, at Hilton the most favoured areas for ground-nesting are those which have been modified by man's activities and take the form of paths, car-tracks, a sand-pit, and tracts once denuded of their original plant cover (by ploughing and cultivation) and subsequently only partially covered by mostly pioneer species.

Over the decade during which the nesting of wasps and bees has been studied at Hilton, it has been noticeable that available nesting sites both in friable and in non-friable soils have shrunk due to an increase of plant cover, a trend which, if it continues, will eventually lead to a marked reduction in the size of the nesting communities.

It is obvious that the nest-excavating species associated with friable, sandy soil are able to excavate their nests in this substrate where ever bare patches of it occur within a given area. Species associated with non-friable, clayey soil, however, have no such freedom but are restricted to bare patches of this substrate in those parts of a given area that lie within a certain maximum distance of a source of water required for soil softening. This distance, which may vary from one species to another, is determined by how far it is economical, in terms of expenditure of energy and time, for a wasp to have to fly to collect this water. In effect, it has been observed at Hilton to limit the nesting areas of the species concerned to tracts of clayey soil in fairly close proximity to water sources (Gess and Gess, 1974: 192; 1975: 24; 1976a: 86; 1976b: 131; 1980c: 64). Other tracts of bare clayey soil, apparently identical in all respects to the above but further removed from water sources are notable for the absence of any nesting wasps.

The water sources most commonly used at Hilton by excavators in non-friable clayey soils are temporary in nature and consist of pools formed after rain in small depressions, in erosion gullies and in a man-made furrow flanking the chief nesting area (Gess and Gess, 1974: Pls 1–4). Infrequent use is made of small puddles left in the river bed but the larger and more permanent water bodies, the dams, are unused. It follows therefore that nesting is dependent upon the occurrence of rain and of run-off filled water holes and that it can continue only for as long as the water supply lasts. In contrast therefore to those wasps excavating their nests in friable sandy soil, which as a community may be found in any one year to nest continuously over a long period, from early spring to late autumn, the wasps excavating their nests in non-friable clayey soil and requiring water for nest excavation are as a community in any one year frequently restricted to a very much shorter nesting period, or have an interrupted nesting period, determined by the time and abundance of rainfall and by the availability of water in temporary pools. Though these wasps individually and as a community have the potential for a long nesting period, like that seen in the sand nesters, it is frequently not realized and in several summer seasons it has been seen to have been arrested at or near its height by the failure of the water supply. This is particularly noticeable with respect to *Bembecinus cinguliger*.

In the light of the physical difficulties attendant upon the excavation of nests in non-friable clayey soils and the spatial and temporal restrictions imposed upon nesting in such soils due to the requirement that water be available to the wasps where and when nesting is undertaken, it must be asked what led certain groups of wasps to leave a friable substrate in favour of a non-friable one.

The answer must be postulated to lie on the one hand in a response to the pressure of interspecific competition for available nesting sites and prey with respect to one substrate and on the other hand in a response to the existence of another, unexploited substrate with its associated community of unexploited potential prey species.

The ability of certain wasps to adapt to excavating nests in the previously unexploited non-friable clayey soils allowed the spread of ground-nesting wasps into tracts of country which had such soils and from which the latter had hitherto been debarred. Moreover, in situations as at Hilton where both soil types occur in close proximity a given area including both soil types can support a greater number of soil-excavating species than could the same area if only one soil type were included.

The presence at Hilton of both soil types must be seen as the key to the co-existence there of large nesting populations of four species of *Bembecinus*, two, *B. cinguliger* and *B. oxydorcus*, associated with non-friable soil and two, *B. braunsii* and *B. haemorrhoidalis*, associated with friable soils. Whereas it is immediately apparent that there is no competition between the two pairs of species for nesting sites, there is likewise no competition for prey. Examination of the prey recovered from the cells of the four wasps shows that whereas provisioning by all the species is with numerous species of (mostly) Cicadellidae and that both nymphs and adults, males and females, large and small individuals are utilized, the specific composition of the prey of the two pairs of *Bembecinus* species is completely different though within a pair of species it is similar. This situation is a reflection of the observed fact that the two soil types support different plant communities which in turn have feeding upon them different complexes of Cicadellidae and furthermore that the *Bembecinus* species do not hunt at any great distance from their nests and therefore exploit those prey found on vegetation growing on the soil type to which they (the wasps) are themselves restricted.

Whereas the use for nest excavation of non-friable soils appears to have been adopted only very rarely and sporadically by the Pompilidae and the Sphecidae, it is typical of almost all the ground-nesting Eumenidae and of all the ground-nesting species of the allied Masaridae. This has in effect freed the Vespoidea from competing with the vast majority of the Pompilidae and Sphecidae for nesting sites in the ground.

Of interest are those Eumenidae which, atypically, do excavate their nests in friable, sandy soil—species of *Pterocheilus*, divided by Bohart (1940) into a number of subgenera. These sand-nesting Eumenidae, unlike the sand-nesting Pompilidae and Specidae, do not possess sandrakes on the fore-legs, which limbs do not differ in structure from those of the clay-nesting and water-utilizing *Parachilus insignis*. Instead, for the removal from the burrow of the sandy material loosened by the mandibles, the wasp possesses a "sand basket" formed by long hairs fringing the outer edges of the mandibles and by others fringing the second and third segments of the long pendulous labial palps (Evans and Eberhard, 1970: Fig. 55).

It must be postulated that the Vespoidea evolved from forms associated with friable soils, that at an early stage in their evolution they forsook nesting in that soil type in favour of nesting in non-friable soil and that forms such as *Pterocheilus* now found nesting in friable soil secondarily returned to that substrate. However, the Eumenidae having as a group earlier lost any fore-tarsal digging organs, removal of excavation spoils by the sand-nesting species is by means of the mouthparts as in the pellet-carrying, water-utilizing, clay-nesting species from which the sand-nesters are probably derived.

It has been shown above that the substitution in the provisioning of each cell of several smaller prey for a single large one was advantageous in terms of greater ease of transport of the prey and greater economy of labour consequent upon the construction of nests of smaller dimensions. However, a disadvantage introduced with the substitution is that cell closure has to be delayed until after the last of several or many prey has been placed in the cell and that the partially provisioned cell is left unattended by the wasp during the time the latter is away hunting for additional prey. During this time, the open, partially provisioned cell is in danger of attention by parasites of one sort or another unless some means are employed to exclude them.

This exclusion of at least a certain proportion of parasites is effected by many of the species excavating their nests within friable soil by the maintenance of a temporary closure at the nest entrance. In the present study, this is described for the sphecid *Kohliella alaris* (Gess and Gess, 1980a: 52) which rakes sand respectively into or out of the nest entrance each time it leaves or returns to the nest.

So easy and quick a way of closing and opening a nest is clearly possible only in friable soil and it must be asked how those wasps nesting in non-friable soil have solved the matter of the exclusion of parasites. The answer may be sought in a comparative study of certain aspects of the nesting of a genus including both sand- and clay-nesters—in the present instance the genus *Bembecinus*.

All four species of *Bembecinus* studied at Hilton construct temporary nest closures but the frequency with which these are fashioned differs between the sand-nesting and clay-nesting species.

In the sand-nesting *B. braunsii* and *B. haemorrhoidalis* temporary nest closures are maintained throughout the wasps' working day whenever the wasps are not within their nests. In the clay-nesting *B. cinguliger* and *B. oxydorcus*, however, temporary closures, in the form of mud plugs sited in the entrance shafts (and in *B. oxydorcus* at the turret opening as well) (Gess and Gess, 1975: Figs 11 and 16), are constructed only at the end of each working day and the first action by the wasps on returning to the nesting sites at the beginning of the following working day is to remove these mud plugs. Therefore, whereas the nests of *B. braunsii* and *B. haemorrhoidalis* are open only for short periods during which the wasps are introducing prey, those of *B. cinguliger* and *B. oxydorcus* are open for the full duration of the wasps' working day, whether the wasps are present in the nests or not. As it is not an unreasonable assumption that parasite pressure on *Bembecinus* should be similar in the two nesting substrates—indeed at Hilton species of Mutillidae, notably *Smicromyrme hecuba*, are commonly found associated with all four species—the lack of a temporary closure during the working day of *B. cinguliger* and *B. oxydorcus* must be compensated for by some other factor. In the absence at the time of cell provisioning of any other behavioural difference between the two pairs of species, the factor can only be an additional difference in the physical nature of the nest, namely the presence in those species omitting the temporary closure of the mud superstructures surmounting the nest entrances. The hypothesis is therefore put forward that in *Bembecinus* at least, the mud superstructures serve as a protection against the entry of parasites into the nest.

Possibly a similar rôle may be assigned to the nest superstructures built by at least some of the other species. Oldroyd (1964: 132) has pointed out that Bombyliidae seen hovering close to the ground are not always looking for flowers but may be actively egg laying, the egg being dropped near the burrow of a solitary bee or wasp. Furthermore, Painter (1932, as reported by Clausen, 1940: 377) recorded experiments in inducing oviposition by a hombyliid, *Villa* sp., which develops in the cells of solitary bees. The eggs were reported to be "readily projected into glass vials buried in the soil to simulate the nest openings of the host". It would appear that the stimulus to oviposit by the hovering fly is visual and consists of the sight of a small, dark, round hole in the ground. It does not seem unreasonable therefore to suggest that the removal of the stimulus to oviposit by the concealment of the dark hole in the ground would be of survival value to those wasps which leave their nest entrances open—that is, those wasps that nest in clayey soils. In many of these wasps concealment from above of the burrow entrances is effectively achieved by covering them with curved turrets and it is therefore postulated that these superstructures are a defence against parasitization by Bombyliidae. It is perhaps significant that the only bombyliid larva found during the course of the excavation of very many nests of a variety of species nesting in clayey soils was in a cell of *Parachilus insignis* (Gess and Gess, 1976a: 97), a species which surmounts its nest entrance not with a curved turret but with a low collar which does not conceal the "dark, round hole".

In addition to the probable value of at least some nest superstructures in excluding certain categories of parasites, it is certain that all superstructures, even those consisting only of a low collar surrounding the nest entrance serve to prevent loose, powdery clay soil and other fine wind-blown debris from entering the nest shafts. This may well be of value to wasps which lack both the physical equipment (tarsal sand rakes) and the behaviour requisite for the removal of fine, loose material from their burrows.

Finally, the more extensive of the superstructures covering nest entrances serve to protect the nests against flooding for upon being well wetted by rain or surface run-off the superstructures collapse upon the nest entrances, effectively blocking them. The nest collar of *Parachilus insignis* is clearly too small to serve this function. However, as described in detail by Gess and Gess (1976a: 99) the wasp nevertheless protects its nest from flooding by blocking the nest shaft with its own body and by allowing a plug of water-borne mud to form above it.

Among the 167 species of ground-nesting wasps and bees recorded during the survey at Hilton, thirteen species were found to nest not in burrows of their own excavation but in pre-existing cavities which they, however, modify by the construction within them of a cell or cells. The thirteen species concerned are listed in the annotated list of species under categories

2 and 5. Four families were represented: Eumenidae (1 species), Sphecidae (6 species), Megachilidae (5 species) and Anthophoridae (1 species).

A necessary pre-condition for the nesting of these species is the presence in the ground of pre-existing cavities of a bore suited to their individual requirements. The pre-existing cavities most often used are burrows excavated for nesting purposes by other, nest excavating, aculeates. Usually these burrows are no longer being used by their excavators but are newly excavated burrows that have been abandoned for some reason or another (such as the death of the builder) or are old burrows, excavated in a previous nesting season, from which the wasps that developed within them have emerged. There is very little evidence that competition for burrows occurs between the original burrow excavators and the users of pre-existing cavities—that is, burrows do not appear to be usurped if still in use.

It will be seen from Table 2 and from the Pie-diagram (Fig. 16) that, whereas in non-friable soil the number of species nesting in modified pre-existing cavities approximates the number of species excavating original nests, in friable soil the number nesting in modified pre-existing cavities is very low indeed. This is all the more striking on account of the far greater number of species excavating original nests in friable soil than in non-friable soil.

The reason for the difference which is clearly substrate-determined is probably due largely to the fact that a burrow excavated in non-friable clayey soil is stable and long-lasting whereas one excavated in friable sandy soil tends if it is not maintained to collapse or fill with loose material after even a short time. This is of particular relevance to old burrows from which wasps or bees have emerged. With respect to newly excavated but abandoned burrows, it must be remembered that wasps excavating in friable soil frequently maintain a temporary closure at the nest entrance which would render such burrows inaccessible to seekers of pre-existing cavities even when the original "owners" of such nests had suffered some misadventure during hunting or foraging. The opposite would pertain to burrows excavated in non-friable soil particularly where the clay next superstructures are incomplete or broken.

It appears that the thirteen species recorded as making use of pre-existing cavities (burrows) in the ground may be divided into those for which such behaviour is obligatory and those for which it is facultative.

Among the former are the five megachilid bees belonging to the genera *Megashile* and *Creightoniella.* One of these bees, *Megachile semiflava,* has been recorded as making use of pre-existing burrows in both the non-friable clayey soil and the friable sandy soil and there seems no reason why the other species should not show a similar lack of restriction to a particular soil type. All five species construct their cells within the pre-existing cavities with foreign materials—green leaves or in the case of *M. meadewaldoi* the petals of low-growing flowers.

Other species for which nesting in pre-existing cavities is obligatory are the sphecid *Pison allonymum* and an unidentified eumenid known only by its turret which it had constructed surmounting that of *Bembecinus oxydorcus*, the burrow of which species it was using. Both species are probably derived from forms which used water to excavate nests in non-friable soils. Though the ability to excavate nests has been lost, both species remain associated with clayey soils due to their use of mud in modifying the burrows in which they nest.

The nesting of all the above species involves the modification of the chosen pre-existing cavities by the introduction into them of foreign materials for cell construction prior to the gathering and introduction of provision.

Very primitive in comparison is the presumed nesting behaviour of *Ampulex mutilloides* which though not actually found nesting is included in the present category on considerable circumstantial evidence.

Ferruginous and metallic blue and thus atypical in colouration, this *Ampulex* looks very mutillid-like (as attested by its specific epithet), a similarity that is enhanced by the fact that in the experience of those who have seen the species in the field (the present author and the late C. F. Jacot-Guillarmod—*pers. com.*) it is only met with on the ground. The fact that the Hilton specimen, a freshly emerged female, had clayey soil adhering to her head strengthens the view that this species nests in the ground. Probable prey is *Pilema thoracica*, a cockroach excavating burrows in clayey soils in the area in which the wasp was found walking on the ground.

In common with other species of *Ampulex*, nesting would be commenced with hunting which would be followed by the introduction of the single prey into an unmodified pre-existing cavity which would then be closed with detritus. If the above interpretation of the nesting of *A. mutilloides* is correct, this wasp would be restricted to nesting in clayey soils as it is there that its prey occurs. Furthermore, it is possible that the pre-existing cavities used by the wasp are the burrows excavated in the soil by the cockroach.

Species for which nesting in pre-existing cavities in the ground appears to be facultative and determined by the nature of the substrate are *Prionyx kirbii, Tachysphex* sp. near *modestus* and possibly *Tachysphex modestus* itself (all Sphecidae) and *Tetralonia minuta* (Anthophoridae).

Prionyx kirbii and *Tachysphex* sp. near *modestus* both have well developed tarsal sand rakes and may therefore be expected to excavate original burrows in friable soil. This indeed is the case with the common *P. kirbii* which has been observed at Hilton to excavate original burrows in the sandpit. *Tetralonia minuta* also is probably capable of excavating original burrows. Though this is not actually stated it may be inferred from the account of the nesting of this bee given by Rozen (1969a).

What are these species doing then in pre-existing cavities? The only explanation is that these species have some plasticity of behaviour and that, in non-friable soil, burrow excavation is intitiated not at the surface of the soil but at the bottom of a pre-existing cavity: the old or abandoned burrows of *Parachilus insignis* in the case of *P. kirbii* and *T.* sp. near *modestus*; the old or abandoned burrows of *Parachilus insignis* or of *Bembecinus cinguliger* in the case of *T. minuta*. In some instances at least (as with *P. kirbii* and *T.* sp. near *modestus*) the pre-existing cavity may already approximate in dimensions the burrow excavated in friable soil so that little additional excavation need be done. With respect to *T. minuta* which appears to make deeper and more complex nests than do the two sphecids it is probable that the initial use of a pre-existing cavity enables the bee to start its own excavation at a depth at which the soil may be moister and consequently softer and where it is therefore easier to excavate.

In all cases, the use of pre-existing cavities as a starting point for nest excavation allows these species to extend their distribution into areas of non-friable soil where nesting in the manner normal to them would be precluded or would at best be very difficult. That the use of pre-existing cavities by these species is simply a short cut in nest excavation adopted in hard clayey soil and does not represent any radical change of behaviour is shown by the fact that both *P. kirbii* and *T.* sp. near *modestus* do remove considerable quantities of soil from the bottom of the pre-existing cavity. *P. kirbii* arranges the material removed from the cavity in a circle around the burrow opening (Fig. 24); *T.* sp. near *modestus* places it only to one side of the opening (Fig. 25). Both species prepare the burrow before hunting and *P. kirbii* carefully positions three or four small clods of earth as a temporary closure at the entrance of the modified pre-existing cavity before she leaves to hunt.

Sixty-four of the 167 species of ground-nesting wasps and bees recorded during the survey at Hilton are listed, under categories 3 and 6, as developing within pre-existing cavities which they do not themselves modify. Ten species were recorded from non-friable soils, 50 species were recorded from friable soils and four species, all Mutillidae, were recorded from both friable and non-friable soils. It must be pointed out, however, that the above figures pertaining to the two soil types are not directly comparable for, whereas all 14 species listed for non-

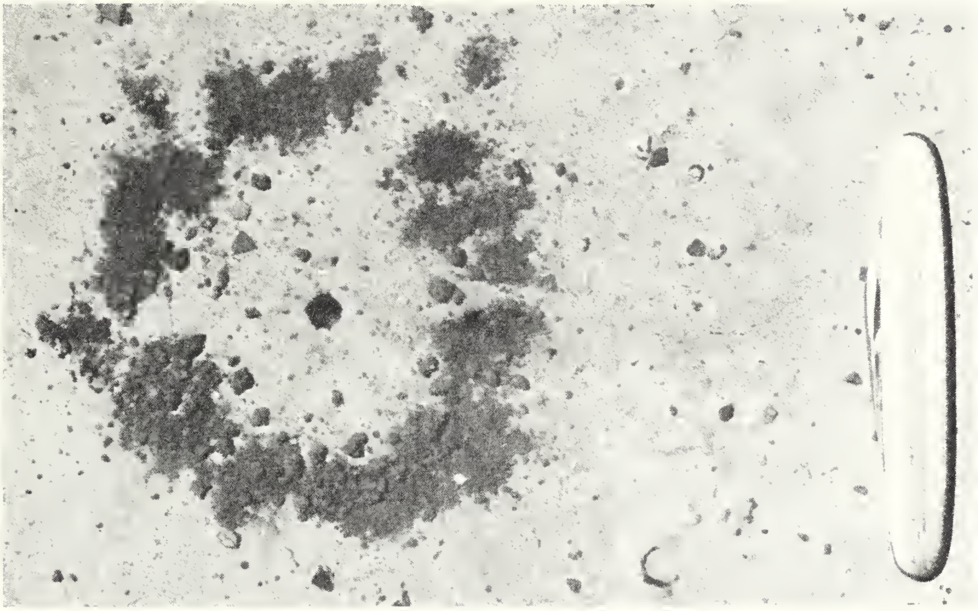

Fig. 24

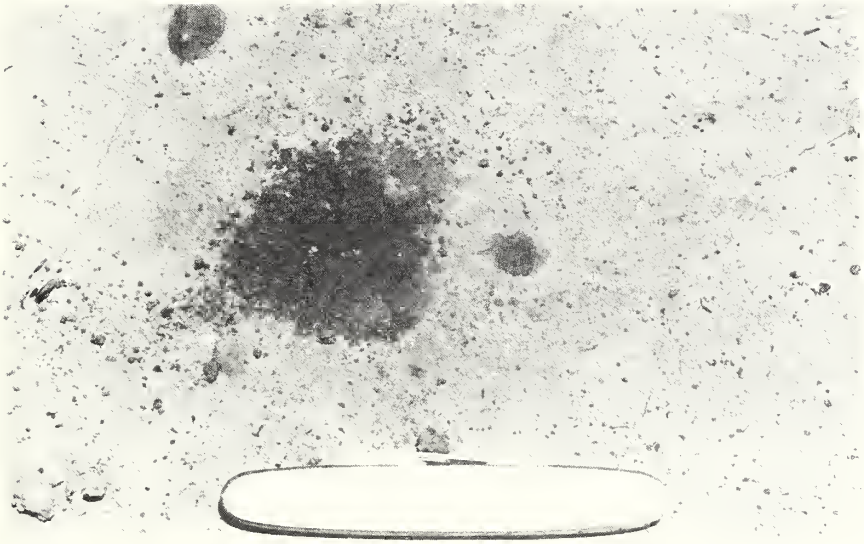

Fig. 25

Figs 24 and 25. Entrances of old burrows of *Parachilus insignis* used for nesting by *Prionyx kirbii* (Fig. 24) and by *Tachysphex* sp. near *modestus* (Fig. 25), showing arrangement of material removed from the pre-existing cavities by these wasps. (× 0,7) friable soils are "parasitic" in one way or another in what are to them pre-existing cavities—cells constructed and provisioned by other wasps and bees and occupied by the eggs or immature stages of these species, this is true of only 26 of the 54 species listed for friable soils. The remaining 28 species listed for friable soils are associated with the larvae of Coleoptera, with one exception *(Methocha mosutoana)* those of Scarabaeidae, which are sought for and attacked in their burrows, often deep in the ground, where, after they have been oviposited upon, they are usually left *in situ*.

Those species which are "parasitic" in the cells of other aculeate Hymenoptera and are therefore dependent upon the occurrence of the latter for their own presence belong primarily to the families Chrysididae (12 species) and Mutillidae (17 species). A few other families are represented as well, namely Pompilidae *(Ceropales punctulatus)*, Sphecidae *(Nysson braunsi)*, Halictidae (*Sphedes* sp.), Megachilidae *(Coelioxys bruneipes* and *C. lativentroides)* and Anthophoridae (*Epeolus amabilis* and *Thyreus* sp.).

TABLE 4.

Secondarily cleptoparasitic ground-nesting species and their established or presumed hosts. (For authorities see annotated list.)

CLEPTOPARASITE		HOST	
Genus & Species	Family	Genus & Species	Family
Ceropales punctulatus	Pompilidae	*Dichragenia pulchricoma*	Pompilidae
Nysson braunsi	Sphecidae Nyssoninae	*Oryttus kraepelini* OR *Dienoplus vicarius karrooensis* OR *Hoplisoides aglaia* OR *Hoplisoides thalia*	Sphecidae Nyssoninae Specidae Nyssoninae Sphecidae Nyssoninae Sphecidae Nyssoninae
Sphecodes sp.	Halictidae	*Nomia* sp.	Halictidae
Coelioxys bruneipes	Megachilidae	*Megachile semiflava*	Megachilidae
Coelioxys lativentroides	Megachilidae	*Megachile* sp. OR *Creightoniella* sp.	Megachilidae Megachilidae
Epeolus amabilis	Anthophoridae	*Colletes* sp.	Colletidae
Thyreus sp.	Anthophoridae	?	?

Ethologically the species belonging to families other than Chrysididae and Mutillidae are possibly the most interesting for all are derived from non-parasitic forms and the cleptoparasitism now practised by them is therefore secondary or derived. As may be seen from Table 4 most of the species are related to their hosts and in each case host and cleptoparasite must therefore have a common origin.

In all cases the cleptoparasitic way of nesting has been arrived at by a reduction in the number of elements in the behavioural sequence performed by the parasite, the "missing" elements being supplied by the host. For example, the pompilid *Ceropales punctulatus*, recorded as cleptoparasitic in the nests of *Dichragenia pulchricoma* (Gess & Gess, 1974: 202, 204) and assumed to behave like other species of its genus, restricts its nesting activity to hunting and oviposition. Hunting, however, is not for a free active spider but for one already captured and stung by the host pompilid and oviposition (inside the booklungs) takes place before the host has installed the spider in its cell. There the *Ceropales* egg hatches before that of its host and the young foreign larva after destroying the latter feeds upon the spider. In the case of *Ceropales* most of the labour involved with nesting is therefore supplied by its host, *Dichragenia*, namely construction of the cell, hunting of the spider prey, stinging of the prey, transport of the prey to the cell, and closure of the cell.

The cleptoparasitic bees behave similarly in so far that all the labour involved in nest construction and provisioning is supplied by their hosts. Concomitant with the adoption of a cleptoparasitic way of life has been the secondary loss of the pollen-collecting apparatus and therefore the ability to provision cells. The search for cells already provisioned with a mixture of pollen and nectar by the host bees therefore replaces the search for flowers from which to obtain these substances and flower-visiting by cleptoparasitic bees is therefore restricted to the purpose of obtaining their own nutriment.

In contrast to the above discussed species, the species of Chrysididae and Mutillidae, all of which are "parasitic", are not related to their hosts.

The Chrysididae show similarities in their ethology to the cleptoparasitic Pompilidae, Sphecidae and Apoidea in so far that the majority of species develop on the provision stored by their hosts, the egg being introduced into the cell while this is being provisioned. Such appears to be the case with respect to *Octochrysis vansoni* which was recorded (Gess & Gess, 1976a: 97) as attending the open nests of *Parachilus insignis*, inspecting these when they were left unguarded and occasionally entering them, presumably in order to oviposit in the cells. In behaviour *O. vansoni* is therefore clearly cleptoparasitic.

The Mutillidae on the other hand do not develop on the stored provision but limit their attack to fully fed, diapausing larvae or pupae, the female mutillid breaking into a cell containing a cocoon into which she introduces her egg. Feeding upon the host within its cocoon is followed by the mutillid larva spinning its own cocoon within that of its host, as recorded (Gess & Gess, 1980c: 76) for *Dasylabroides caffra* in the cells of *Ceramius lichtensteinii*. In behaviour *D. caffra*, like other Mutillidae, is therefore clearly a parasitoid. This term has been used (Evans & Eberhard, 1970: 9) with respect to a species which cannot be considered a true parasite (because it kills its host) nor a true predator (because it is confined to a single prey individual).

The remaining 28 species listed as developing within pre-existing cavities which they do not themselves modify are species of Tiphiidae and Scoliidae. As already stated all are associated with the larvae of Coleoptera, the majority with those of Scarabaeidae. All were found in association with friable soil for it is only in such soil that the beetle larvae and the female wasps hunting them are able to dig. In no case was the nesting investigated and only one species was associated with its prey: *Methocha mosutoana* (Tiphiidae) with *Cicindela brevicollis* (Cicindelidae).

Vertical banks

The vertical banks studied at Hilton are situated at the sandpit and in places along the course of the New Year's River. At the former locality the banks are man-made and constitute the actual walls of the sandpit whereas in the other localities they have been cut by the river and constitute the banks thereof. Mostly the latter are situated at a height above the river bed reached by water only during times of flood.

The banks of the sandpit and a section of the river bank near the confluence of the Iron Put River with the New Year's River are composed of firmly compacted very fine sand. Going downstream along the course of the latter river the physical nature of the banks changes, increasing amounts of clay being mixed with the sand. In places the mixture of sand and clay has apparently been affected by recent mineralization and has assumed the character of a weak and crumbly sandstone-like material. Still further downstream the western bank of the river is formed by the face of a low cliff cutting across roughly horizontally bedded shale.

Though the sand and shale banks clearly constitute very different substrates, those banks composed of mixtures of sand and clay and including both mineralized and unmineralized portions, cannot, on account of their variability, be placed in a single class. It seems preferable therefore not to attempt to further classify the banks on the basis of the physical nature of the materials of which they are composed but to deal with all banks together. However, where it is relevant, attention will be drawn to substrate-determined differences in the nesting of the wasps and bees concerned.

Wasps and bees which nest in association with vertical banks may be divided into those which nest within the banks and those which nest on the banks and use the latter solely as a raised support to which to attach their aerial nests.

At Hilton the number of species recorded as nesting in association with vertical banks totals 51, made up of 43 species nesting within the banks, 6 nesting in aerial nests on the banks and 2 nesting both in the banks and in aerial nests on the banks. On account of the latter species the number of species/substrate associations exceeds the actual number of species by 2 and therefore stands at 53. An analysis of this figure according to the degree of participation of species of wasps and of bees in the construction of their nests is given in Table 5 and is shown graphically in the Pie-diagram (Fig. 26).

TABLE 5.

Number of species of aculeate wasps and of bees nesting in or on vertical banks.

	In nests constructed entirely by the nesters themselves	In modified pre-existing cavities	In unmodified pre-existing cavities
In vertical banks	4	20	21
On vertical banks	5	1	2

With regard to the nesting of wasps and bees a vertical bank resembles level ground with respect to the nature of the substrate which it offers but differs with respect to the angle at which this substrate is presented.

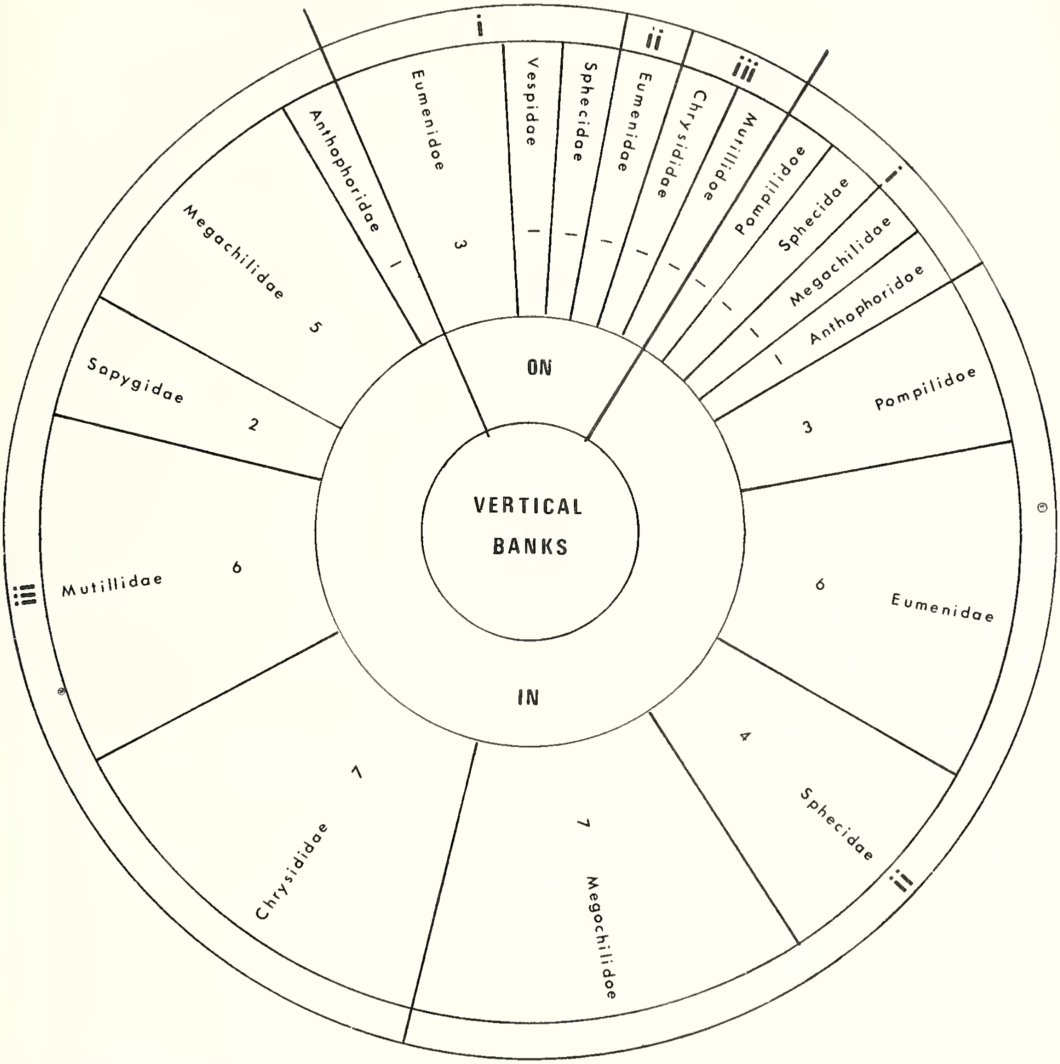

Fig. 26. Diagram showing the structure of the communities of the aculeate wasps and the bees nesting in or on vertical banks in the study area. Numbers accompanying the family names represent numbers of species. The numbers (i, ii, iii) in the outermost ring correspond to the same numbers in the classification of the aculeate wasps and the bees of the study area on the basis of their ethology. (i) In nest constructed entirely by the nester. (ii) In pre-existing cavity modified by the nester. (iii) In pre-existing cavity *not* modified by the nester.

The difference in the angle of presentation of the soil surface—vertical as opposed to horizontal—has a very profound influence upon nesting. Illustrative of this is that, with the possible exception of *Pison allonymum*, there is no sharing of species between level ground and vertical banks. Indeed, both nesting situations are characterized by communities of species unique to themselves. It is furthermore very noticeable that in the two nesting situations there is a marked difference between the proportion of species excavating their nests and those modifying pre-existing cavities. In level ground as has already been shown, nest excavators greatly outnumber nest modifiers (91 as against 14) whereas in vertical banks the opposite is true, nest excavators being outnumbered by nest modifiers (4 as against 20).

In view of the great dissimilarity between the communities nesting in vertical banks and in level ground, it is of interest that some points of similarity exist between the former community and that nesting within plant tissue, at least with respect to those species which do not excavate or hollow out their nests themselves but modify pre-existing cavities. Thus at Hilton at least seven species nesting in pre-existing cavities are shared between vertical banks and plant tissue, namely *Euodynerus euryspilus* (Eumenidae), *Chalybion (Chalybion) tibiale, Pison montanum* and *Trypoxylon* sp. (Sphecidae), and *Immanthidium junodi, Megachile gratiosa* and *Megachile spinarum* (Megachilidae). *Rynchium marginellum sabulosum* (Eumenidae) at Hilton found nesting in trap-nests inserted into crevices in the "sandstone" bank but known in Grahamstown to nest in cut culms of the reed *Arundo donax* used for vegetable frames may probably be added to the above listed species.

Furthermore, the preponderance of nest-modifiers over nest excavators characteristic of the vertical banks is evident also with respect to plant tissue.

Characteristic of the community nesting within the vertical banks studied is the dominant rôle played by bees, both in terms of number of species and number of individuals. Thus, of the four species of wasps and bees listed as excavating their nests in the vertical banks, only the two bees, *Hoplitis anthodemnion* (Megachilidae) and *Anthophora* sp. (Anthophoridae) are of any real importance. Common to the degree of being by far the most noticeable species, their presence is fundamental to the existance of a large part of the rest of the community as a whole, for it is their abandoned galleries that constitute the pre-existing cavities which are sought for and modified by a much larger number of diverse species of wasps and bees which do not excavate their nests themselves (Fig. 27). Furthermore, among the latter cavity-

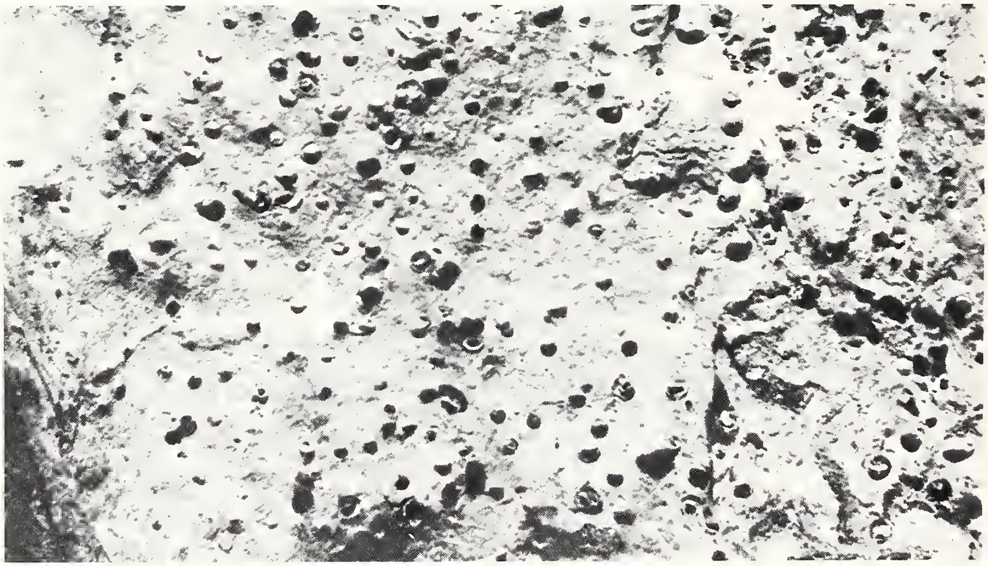

Fig. 27. Small portion of the surface of the "sandstone" bank showing the abundance of old nesting galleries available to nesters in pre-existing cavities.

modifying species, twenty in number, the Megachilidae with seven species is the best represented family. Involved are *Anthidiellum kimberleyanum, Branthidium braunsii, Chalicodoma schulthessi, Heriades ?freygessneri, Immanthidium junodi, Megachile gratiosa* and *M. spinarum*. Though in terms of numbers almost equally by the Eumenidae the bee family nevertheless considerably surpasses the latter in number of individuals. Bees are well represented also amongst those species which nest parasitically in the nests of other species, five Megachilidae, namely *Euaspis abdominalis, Coelioxys lucidicauda, C. bruneipes, C. lativentris* and *C. lativentroides*, and one species of Anthophoridae, *Thyreus* sp., being listed.

Taken altogether, bees represent 33% (15 out of 45) of the total number of species listed as nesting within vertical banks. Comparative figures for nesters within level ground and within plant tissue are 10% (17 out of 167) and 46% (18 out of 39) respectively. It may be seen that, gauged with respect to the relative numerical representation of species of bees and wasps in the different nesting substrates, vertical banks once again appear to have more in common with plant tissue than with level ground.

With regard to the different substrates offered by vertical banks at Hilton, that consisting of recently mineralized mixtures of sand and clay and referred to as "sandstone" supports the largest community, both in terms of number of species and number of individuals. This is on account of the fact that it is in this sandstone-like material that the principal nest excavators, *Anthophora* sp. and *Hoplitis anthodemnion*, are most active; indeed *H. anthodemnion* appears to be restricted to this substrate. *Anthophora* sp. on the other hand also nests in sand banks but not as commonly. Clearly no nest-excavators are able to nest in the shale bank.

Whereas many of the wasps and bees nesting in modified pre-existing cavities are restricted to the sand and in particular to the "sandstone" banks, probably on account of their dependence upon the presence of old abandoned galleries of the above two nest-excavating bees, a few species have in addition colonized the shale bank where they make use of pre-existing cavities in the form of open cracks between and within individual layers of the shale. Such is the case with respect to Eumenid A and *Tricarinodynerus guerinii* (both Eumenidae) and probably also *Megachile gratiosa*. At Hilton *T. guernii* has been found nesting in vertical banks presenting all three major substrates and is possibly the most characteristic species of vertical banks (Fig. 28). Its nest which is furnished with a downturned mud turret is invariably sited in a protected situation such as under an overhang where it is protected from the weather and particularly from rain.

Protected situations are sought also by those species which nest not within banks but construct aerial nests upon them, as was demonstrated by the location of recorded nests: a naked comb made of "wasp paper" by *Ropalidia* sp. A. was sited in a fist-sized cavity in a sand bank; a mud nest of *Sceliphron spirifex* was built in a similarly sized cavity in the "sandstone" bank; and urn-shaped mud cells of *Eumenes lucasius* were found attached to the face of the shale bank under overhangs.

On stones lying upon the ground

At Hilton, stones lying upon the ground were found to represent the least used of all four nesting situations with only four of the 241 species included in the annotated list associated with it. It is clear therefore that this nesting situation is of very little importance with respect to the nesting of the community as a whole. However, it must be taken into consideration that all nests associated with stones are aerial in nature and that a true assessment of the status of this nesting situation can therefore only be arrived at by comparison with the status of aerial nesting associated with other nesting situations. Thus it may be seen that the number of species (2) constructing original nests on stones though smaller is nevertheless comparable to the numbers of species constructing original nests on vertical banks (5) and on plants (5).

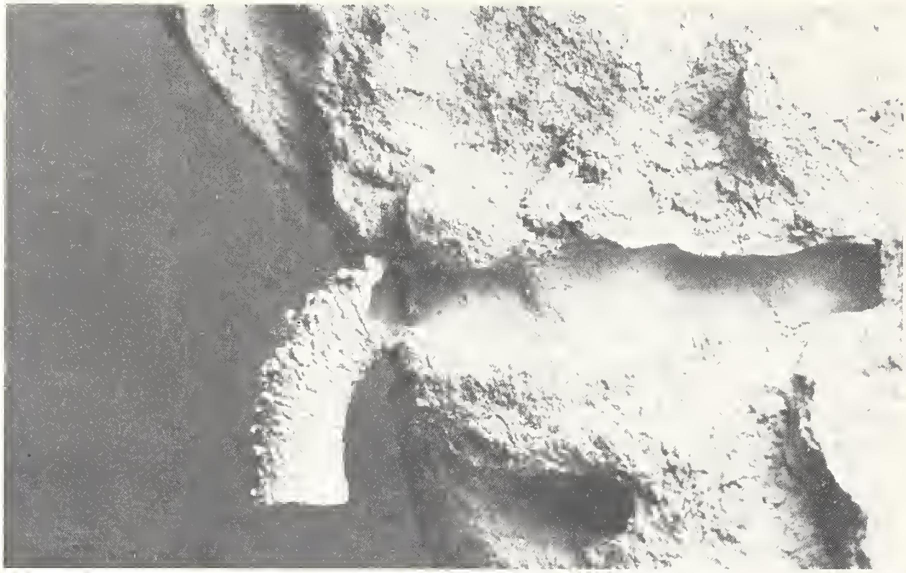

Fig. 28. Section through "sandstone" bank showing pre-existing cavity modified for nesting and furnished with a down-turned mud turret by *Tricarinodynerus guerinii*. (× 1,6)

The two species constructing original nests on stones differ in the placement of their cells. Whereas *Auplopus rossi* (Pompilidae) builds its cells in a sheltered position on the underside of large stones lying loose upon the ground (Fig. 10), *Hoplitis jansei* (Megachilidae) builds its cells fully exposed on the upper surface of partially buried stones and boulders (Fig. 11). In the case of the former species a sheltered position for the placement of the cells is essential as these are made of dried mud, are thin-walled and fragile, and would consequently melt and collapse if exposed to rain. The cells of *Hoplitis*, by contrast, are made of plant resin in which are set numerous small pebbles and are consequently waterproof and of great mechanical strength.

The cells of *Hoplitis* being fully exposed on the upper surface of stones and boulders, are clearly potentially subject to extremes of temperature, both high and low, which might well be detrimental to the bee young within them. There may therefore be a good reason with respect to survival why the bee builds only on those stones which are partially buried in the ground for these stones by virtue of the fact that heat can be exchanged between them and the ground would not become as hot or as cold as similar stones lying loose upon the ground with as a consequence a reduced capacity for heat exchange.

The nesting of *Auplopus rossi* in aerial mud cells which though separate are built in close proximity to one another is of the most advanced and specialized ethological type exhibited by the Pompilidae. It has been shown by Evans (1953: 161) that this ethological type may be derived from that exhibited by those ground-nesting Pompilidae which prepare the cell before hunting. This advanced sequence of behaviour has already been discussed with reference to the two turret-constructing, clay-soil nesting *Dichragenia* species occurring at Hilton. The mastery of the technique of using water to work clayey soils shown by species such as the latter may be seen as presaging the eventual abandonment by some species of the ground as a nesting substrate in favour of nesting aerially. There is thus a change from mud being merely a by-product of nest excavation to be used in turret construction to mud being purposively mixed to provide the material used for cell construction.

Only one species was found to modify pre-existing cavities associated with stones on the ground: *Megachile gratiosa* (Megachilidae) which constructed its own cells, made of pieces of leaves, within old, abandoned and therefore open resin and pebble cells of *Hoplitis jansei.*

Antennotilla phoebe (Mutillidae), a parasite, was reared from the unmodified cells of its host, *Auplopus rossi.*

Plants

Wasps and bees which nest in association with plants may be divided into those which nest within plants, in galleries within plant tissue, and those which nest on plants and use the latter solely as a raised support to which to attach their aerial nests.

With respect to those species which nest within plant tissue, it is necessary that the parts of the plants concerned should be thick enough to contain the nesting galleries and that the hollow parts should retain their physical structure for at least as long as it takes the species nesting within them to complete their development from egg to adult and to emerge from the nest. Parts of plants fulfilling these requirements are certain stems and, in the case of larger shrubs and trees, branches.

Just as soils are divisible on the basis of whether they are sandy or clayey, so plant stems may be divided on the basis of their internal cellular development and may be classified as woody, pithy or hollow. The nature of each stem determines which species may be able to prepare galleries within it and each of the three stem types therefore has associated with it species peculiar to itself. The internal nature of a stem or branch, however, has no direct bearing upon those wasps and bees using plants merely as sites to which to attach aerial nests. Therefore, whereas the nesting of those species nesting within plant tissue is dealt with with reference to the nature of the stems, the nesting of those species attaching aerial nests onto plants is dealt with irrespective of the natures of the plants concerned.

At Hilton, the number of species recorded as nesting in or on plants totals 44, made up of 39 nesting within plant tissue and 5 nesting in aerial nests on plants. Of those nesting within plant tissue, 17 (43,5%) were associated only with woody stems, 12 (31%) were associated only with pithy stems, and 1 (2,5%) was associated only with hollow stems. Nine species (23%) were associated with two or all three stem types.

On account of the species which were recorded in two or three stem types, the number of species/substrate associations exceeds the actual number of species by 14. The number of species/substrate associations with respect to those species nesting in plant tissue is therefore 53 and the total number of species/substrate associations for both those species nesting within and on plants is 58. An analysis of this figure according to the degree of participation of species of wasps and of bees in the construction of their nests is given in Table 6 and is shown graphically in the Pie-diagram (Fig. 29).

With respect to those species which themselves prepare galleries in plant stems there is complete specificity as regards stem type. Pithy stems are by far the most commonly utilized and the number of species recorded (nine) could probably be more than doubled. Besides the two species of *Ceratina* listed, approximately another ten species belonging to the genus are known to occur at Hilton.

Species preparing their galleries themselves belong chiefly to the Anthophoridae (*Xylocopa* and *Ceratina*; large and small carpenter bees, respectively) and the Sphecidae *(Dasyproctus). Raphiglossa natalensis* of the Eumenidae, known to occur at Hilton but to date not found nesting, is included among the gallery-excavators on the authority of Meade-Waldo (1913) and Bequaert (1918).

TABLE 6.

Number of species of aculeate wasps and of bees nesting in or on plants.

	In nests constructed entirely by the nesters themselves	In modified pre-existing cavities	In unmodified pre-existing cavities
In woody stems	2	18	6
In pithy stems	9	8	3
In hollow stems	1	4	2
On plants	5	—	—

In their choice of nesting substrates it appears that these bees and wasps exhibit marked ecological displacement. In the present study this can best be illustrated with reference to the nesting of the four species of large carpenter bees recorded at Hilton: *Xylocopa caffra, X. caffrariae, X. divisa* and *X. sicheli.*

X. caffra and *X. divisa* have been observed to be confined to thick riverine bush where as far as can be established they make their nests in dead, dry, woody branches of the trees occurring in that situation. As the two species are very different in size it is likely that each is confined for its nesting to branches of a certain thickness and interspecific competition between the two for nesting sites is therefore unlikely despite the fact that they occur in the same habitat.

X. caffrariae is also a riverine species but occurs not in thick bush but in open tracts along the banks of permanent and semi-permanent water bodies where it nests exclusively in the dry culms of *Phragmites australis*, a reed forming beds in such situation (Figs 14 & 15).

X. sicheli, by contrast is found only in open country and is associated with *Aloe ferox* growing on higher ground, especially on the north facing slope of the E–W ridge to the south of the study area. Nesting is restricted to the old, dry but still attached, inflorescence stems of this plant (Figs 13 & 30).

The small carpenter bees, *Ceratina* species, appear also to show considerable ecological displacement. One of these species, *Ceratina* sp. A. is most commonly found nesting with *X. sicheli* in *Aloe ferox* inflorescence stems. Though galleries of both bees frequently occur in the same inflorescence stems they never occupy the same parts: *X. sicheli* galleries are restricted to the thicker basal parts above and below the point where the inflorescence branches whereas *Ceratina* sp. A. galleries are restricted to the thinner terminal portions of the branches themselves. Maximum use is therefore made of the nesting substrate offered by the inflorescence stem without any interspecific competition for gallery space arising.

With respect to species of *Dasyproctus* it may be seen from the review of their known ethology (Gess, 1980b) that considerable specificity exists in their choice of pithy stems in which to nest. At Hilton *D. westermanni* was found to nest exclusively in galleries hollowed out within green inflorescence stems of *Urginea altissima*, which stems were, however, not utilized by any of the other four *Dasyproctus* species. Evidence of the nesting of the latter was, however, found in the form of old galleries in inflorescence stems of *Gasteria* species and in stems of *Berkheya decurrens* (Gess, 1980b).

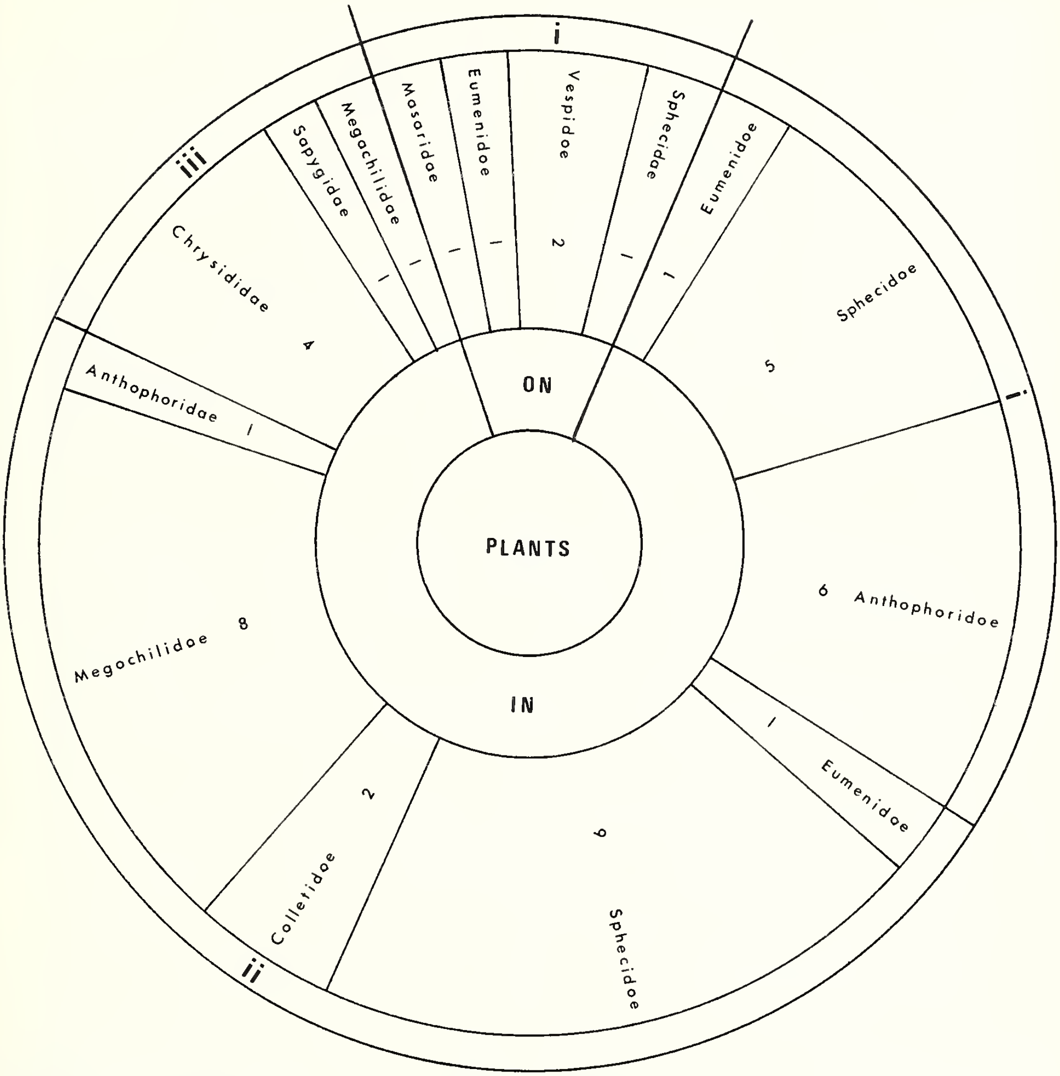

Fig. 29. Diagram showing the structure of the communities of the aculeate wasps and the bees nesting in or on plants in the study area. Numbers accompanying the family names represent numbers of species. The numbers (i, ii. iii) in the outermost ring correspond to the same numbers in the classification of the aculeate wasps and the bees of the study area on the basis of their ethology. (i) In nest constructed entirely by the nester. (ii) In pre-existing cavity modified by the nester. (iii) In pre-existing cavity *not* modified by the nester.

Xylocopa, Ceratina and *Dasyproctus* share certain characteristics with respect to their nesting: all initiate nesting with the preparation of galleries within plant tissue, all construct multicellular nests the cells of which are serially arranged and mass provisoned, and all construct the cell partitions of materials derived from within the plant stem—plant tissue rasped from the walls of the gallery. In no case is foreign nesting material introduced into a gallery from without.

Xylocopa caffrariae differs from the other species in that it does not itself hollow out a nesting gallery but makes use of the naturally formed hollow internode of *Phragmites*. The bee must nevertheless be classed with the nest constructors and not the tube renters in that it does not seek out broken off reeds in order to enter the internodes at an open end but habitually cuts an entrance hole through the hard wall of the culm and thus gains access to an intact internode from the side (Fig. 31). Once through the culm wall, however, it is spared the trouble of hollowing out a gallery as this already exists due to the natural breakdown and disappearance of the pith concurrent with the maturing of the culm.

The nesting by the genera *Xylocopa, Ceratina* and *Dasyproctus* in galleries constructed by themselves within plant tissue must be seen as advanced and derived from nesting in the ground. Supporting this view is the fact that most nest-constructing (that is, non-parasitic) Anthophoridae are ground-nesting (Krombein *et alia*, 1979: 2082) as are many of the more primitive genera of the Crabronini (the sphecid tribe of which *Dasyproctus* is an advanced genus) (Bohart and Menke, 1976: 371). These genera therefore substituted the excavation of galleries in plant tissue for the more basic excavation of burrows in friable soil, thereby both freeing themselves from competition for nesting sites in the soil and, more importantly, gaining the ability to invade previously unutilized habitats.

Dasyproctus differs from the Anthophoridae in so far that it hollows out its galleries in green plant tissue whereas this is not the case with respect to the two genera of bees. The statement by Brauns (1913: 117–118) repeated by Hurd and Moure (1963: 15 and 185) and by Hurd (1978: 1) to the effect that *Xylocopa sicheli* excavates its galleries in *Aloe* inflorescences which are still green and juicy could not be substantiated by the field work of the present author and must be recognized as being incorrect.

A danger inherent in nesting in green plant stems is that these stems with any nests contained within them may be ingested by browsing herbivores. The ways in which the nests of several *Dasyproctus* species, including that of *D. westermanni* in *Urginea altissima*, are protected by physiological or morphological attributes of the stems or by the protected habitats of the latter is discussed by Gess (1980b: 105).

Among the 39 species recorded at Hilton as nesting within plant tissue, 21 were found to nest not in galleries of their own excavation but in pre-existing cavities which they, however, modified by the construction within them of a cell or cells. The species concerned are listed in the annotated list of species under categories 17, 20 and 23. Four families were represented: Eumenidae (1 species), Sphecidae (9 species), Colletidae (2 species) and Megachilidae (9 species).

There seems little restriction by these insects to any one particular stem type, three of the species *(Holotachysphex turneri, Immanthidium junodi* and *Megachile spinarum)* having been recorded in two stem types each and another three species *(Isodontia stanleyi, Trypoxylon* sp. and *Chalicodoma sinuata)* in all three stem types each. Further field work would doubtless augment the number of species recorded in more than one stem type, all the more so as many of these species are not even restricted to plant stems but are found nesting also in pre-existing cavities in vertical banks *(Euodynerus euryspilus, Chalybion tibiale, Pison montanum, Trypoxylon* sp., *Immanthidium junodi, Megachile gratiosa* and *Megachile spinarum)*.

Due to the catholicity which these wasps and bees exhibit with respect to the nature of the material in which the pre-existing cavities utilized by them occur, it is not surprising that they should readily accept trap-nests of the types described by Krombein (1967 and 1970).

With the exception of one species *(Isodontia simoni)*, all the wasps and bees listed in category 17 as nesting in woody stems were in fact nesting in trap-nests tied to woody branches of trees such as *Acacia karroo, Maytenus linearis* and *Rhus lancea*. The fact that these trap-

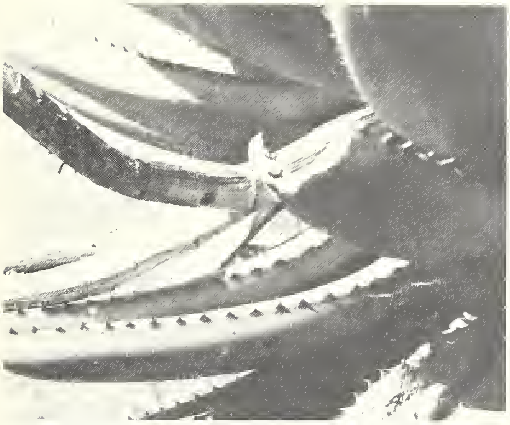

Fig. 30. Downcurved dry inflorescence stem of *Aloe ferox* showing nest entrance hole cut by *Xylocopa sicheli*.

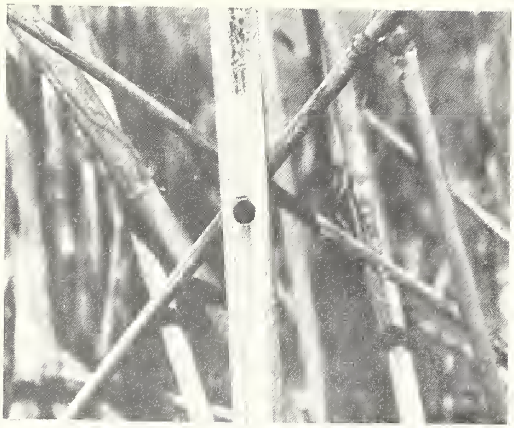

Fig. 31. Dry culm of *Phragmites australis* showing nest entrance hole cut by *Xylocopa caffrariae*.

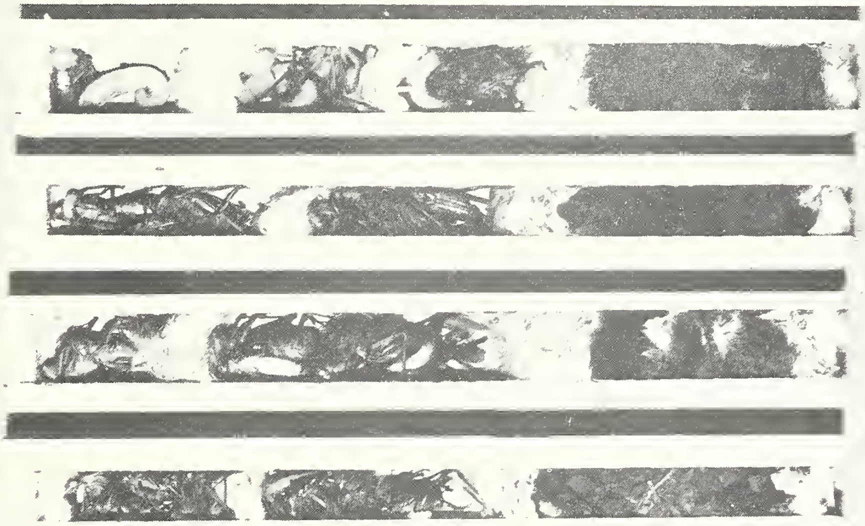

Fig. 32. Completed nests of *Isodontia pelopoeiformis* in trap-nests, showing prey, nesting materials and immature stages of wasp. (× 0,65)

Fig. 33. Completed nest of *Isodontia stanleyi* in trap-nest, showing prey, nesting materials and immature stages of wasp. (× 0,52)

nests were so readily and frequently made use of (for example, over a period of three summer seasons 85 trap-nests were occupied by *Isodontia pelopoeiformis* alone) shows that the woody branches to which they were attached were in fact being carefully searched for the presence of pre-existing cavities by the wasps and bees concerned. The inclusion of the trap-nests as extensions of the trees themselves is therefore validated. Further proof of the validity of the approach is furnished by the nesting of *Ampulex* sp. near *cyanura*. It having been noticed that the wasp nested only in those trap-nests tied to *Acacia karroo*, a careful physical investigation was made of this tree species which culminated in the discovery within its branches of nests constructed within naturally occurring pre-existing cavities.

All nests consisting of cells built within pre-existing cavities may immediately be recognized as such and may readily be distinguished from nests consisting of cells built within a gallery prepared by the nesting wasp or bee itself. This is possible due to the fact that all users of pre-existing cavities in plant tissue introduce foreign materials into the former for the construction of cell partitions and nest closures, whereas, as already noted above, species hollowing out galleries themselves utilize materials rasped from the gallery walls.

Of all the species nesting in pre-existing cavities in plant tissue at Hilton, the two species of *Ampulex*, *A.* sp. near *cyanura* and *A. denticollis* exhibit the most primitive behaviour. Nesting in both species is commenced with hunting. After the introduction of the single large prey (a cockroach) into the pre-existing cavity, oviposition onto the prey takes place after which the cavity is sealed with detritus. It follows that neither *Ampulex* ever introduces foreign nesting material into a cavity prior to the introduction of the prey. Preliminary plugs, as found at or near the blind ends of cavities used for nesting by many of the behaviourally more advanced wasps, are therefore unknown in the *Ampulex* nests. Furthermore, each nest consists of a single cell and where two or more cells are found within a single cavity these represent as many separate nests, not necessarily even made by the same female.

The great majority of species, however, are behaviourally advanced and commence nesting with the search for a suitable pre-existing cavity. Thereafter some foreign nesting material is frequently introduced in connection with cell construction. In the wasps, a preliminary plug at or near the inner end of the cavity may or may not be constructed to form the inner end-wall of the first cell as shown for *Holotachysphex turneri* (Gess, 1978: Fig. 1) and for *Chalybion tibiale* (Gess and Gess, 1980d: Fig. 1) and additional material may be used to form a temporary cell closure as in species of *Isodontia*. In at least some of the bees the introduced foreign materials may be used to fashion not merely an inner end-wall of a cell but a complete cylindrical cell within the walls of the cavity. Such is the case with the leaf-cutter bees, *Megachile gratiosa* and *M. spinarum*, and the mason-bees, *Chalicodoma fulva* and *C. sinuata*. Only after some form of cell preparation has been undertaken does provisioning commence.

If the pre-existing cavity is of a length that allows it, several serially arranged cells are constructed. Successive provisioned cells are separated one from another by partitions of foreign material, the outer end-wall (i.e. the cell closure) of one cell forming the inner end-wall of that immediately succeeding it. Frequently the nest is completed by the construction near the cavity opening of a closing plug as shown for *Holotachyphex turneri* (Gess, 1978: Fig. 1).

Exceptionally no foreign nesting materials are introduced into the pre-existing cavity and there is therefore a complete absence of any cell partitions. Such is the case in the nests of *Allodape* sp. (*rufogastra* or *exoloma*) found at Hilton within old *Dasyproctus* galleries in *Berkheya decurrens* stems. This bee is unusual also in that it practises progressive provisioning of the larvae whereas all the other bees recorded at Hilton as nesting in modified pre-existing cavities in plant tissue practise mass provisioning of the cells, an egg being laid on the provision of each cell prior to the closure of the latter. The biology of species of *Allodape* and of related genera has been reported in detail by Michener (1971b).

The nesting of the species modifying pre-existing cavities in plant tissue, like that of the species excavating original galleries in this substrate may be seen as being derived from nesting in the ground. At Hilton this derivation is clearly reflected in those species for which the foreign material introduced into the pre-existing cavities in plant tissue consists wholly or partially of earth. The earth used is in all cases of a clayey nature and may be introduced into the cavity either in the form of mud or in the form of dry clods. In the latter instance small pieces of twig, bark and other detritus found lying upon the surface of the ground are utilized in addition.

Such is the case with *Holotachysphex turneri*, found nesting both in trap-nests tied to woody trees (Gess, 1978: 209) and in old abandoned galleries of *Xylocopa caffrariae* in the dry culms of *Phragmites* (Gess and Gess, 1980a: 52), which, as has been discussed by Gess (1978: 212–214), may be considered to have developed from a *Tachysphex*-like form. The species differs ethologically from typical *Tachysphex* species in that excavation of a nest in friable soil has been abandoned in favour of the utilization for nesting of a pre-existing cavity in plant tissue. Concomitant with this ethological change has been the secondary loss of both the foretarsal rake and the pygidial plate.

The nesting of *Tachysphex* sp. near *modestus* in pre-existing cavities (abandoned wasp burrows) in non-friable clayey soil, discovered since the publication of the account of the nesting of *Holotachysphex turneri* but described in some detail earlier in the present discussion, may be seen to represent an intermediate but very important pre-adaptive step that will have had to have been taken by the progenitor of *H. turneri*. Clearly, once the basic change had been made from the excavation of a nest in friable soil to the facultative use of a pre-existing cavity in non-friable soil (as in *Tachysphex* sp. near *modestus*) the way was open to a change to obligatory use of such a pre-existing cavity in the ground and for its eventual abandonment in favour of a pre-existing cavity above the ground in plant tissue. The use by *Holotachysphex turneri* of dry clods of clayey earth and pieces of detritus collected on the ground must therefore be interpreted as relict behaviour envolved in response to nesting in pre-existing cavities in non-friable clayey soils.

Dry clods of clayey earth and pieces of detritus (including bits of stick, vetch burs, insect remains and small mammal droppings) picked up off the ground are also the main foreign nesting materials introduced into pre-existing cavities in plant tissue by *Isodontia pelopoeiformis*, according to Bohart and Menke (1976: 121) one of the more structurally primitive species of the genus *Isodontia*. The same interpretation as that given to the use of these nesting materials by *Holotachysphex turneri* may be applied to their use by *Isodontia pelopoeiformis* which therefore is seen similarly as having evolved from a nester in pre-existing cavities in non-friable soils. It is therefore of interest that amongst the nesting situations recorded for species of *Isodontia* by Bohart and Menke (1976: 121) there should be that of abandoned bee burrows in the ground.

Isodontia pelopoeiformis, however, in addition to the above foreign nesting materials uses "fluffy" plant material, at Hilton derived from the fruiting inflorescences of the Composites *Lasiospermum bipinnatum* and *Senecio* species (including *S. leptophyllus*) (Fig. 32). Cell partitions are almost exclusively constructed of this material whereas preliminary plugs and nest closing plugs are constructed of earth, detritus and "fluff" in distinct layers. The "fluffy" plant material which is collected directly from the plant inflorescences represents "new" nesting material as opposed to the earth and the detritus which as has been shown to represent "old" or "relict" materials. Presumeably pieces of this "fluff" were initially picked up off the ground like any other detritus but as the use of this particular nesting material became more established the wasp took to collecting it from its source.

Isodontia stanleyi, a structurally more advanced species, is also ethologically more advanced for it has abandoned the legacy of its past in the form of "old" or "relict" nesting materials and uses only "new" materials (Fig. 33). These consist of short lengths of grass leaf blades and longer lengths cut from grass inflorescences including lengths of unbranched culm and the branched portions including the flower heads. The cell partitions are constructed of short lengths of grass leaf blades, transversely arranged; preliminary plugs and the inner parts of the closing plugs are composed of the longer lengths of grass inflorescences, transversely coiled; and the outer parts of the closing plugs are formed of the latter material arranged longitudinally, the stems lying parallel and projecting from the nest entrance as a broom-like tuft.

That the use of grass by *I. stanleyi* is homologous with the use of Composite "fluff" by *I. pelopoeiformis* is evident from the very occasional and exceptional use of lengths of very soft grass leaf blades by the latter species when its usual "new" nesting material is not available.

An interesting piece of behaviour practised by both *I. pelopoeiformis* and *I. stanleyi* is that of "buzzing" in the nesting cavity in order to consolidate the introduced materials forming the preliminary plug and the cell partitions. The "buzzing" is the same as that already commented upon in connection with other Sphecidae, the ground-nesting *Padalonia canescens* and *Ammophila ferrugineipes* which use it to loosen soil in the course of the excavation of their burrows. This behaviour may be seen as additonal evidence for deriving the plant-nesting *Isodontia* species from ground-nesting, possibly nest-excavating, forms.

Earth in the form of mud for the construction of cell partitions and nest closures is introduced into pre-existing cavities in plant tissue by *Euodynerus euryspilus* (Eumenidae) and *Chalybion tibiale, Pison montanum* and *Trypoxylon* sp. (all Sphecidae).

The use of mud as the nesting material suggests that these wasps are derived from species which employed water to aid them in the excavation of original nests in non-friable clayey soils in the manner already described for other species of Eumenidae (*Parachilus, Pseudepipona* and *Antepipona*) and Sphecidae *(Bembecinus)*. From the excavation of original nests in the ground to the use of pre-existing cavities in plant tissue two changes of behaviour would have been required—firstly the abandonment of the excavation of an original nest in the ground in favour of the use of pre-existing cavity in the same substrate, secondly the abandonment of nesting in this pre-existing cavity in the ground in favour of nesting in a similar pre-existing cavity above ground in plant tissue (or for that matter in a vertical bank). The use of mud for cell partitions and nest closures, initially a consequence of using water in nest excavation, is retained by those species nesting in pre-existing cavities and provides a continuous thread linking the three nesting types.

The three nesting types outlined above as necessary to the derivation may all be found to occur within the genus *Pison*. Thus, excavation with the aid of regurgitated water of an original burrow in non-friable soil has been reported for the South American *Pison chilense* (Janvier, 1928, as reported by Bohart and Menke, 1976: 335). Use of pre-existing cavities (abandoned burrows of bees and wasps) in clayey soils has been reported for the Micronesian *Pison nigellum* (Krombein, 1950: 139) and is recorded in the present account for *Pison allonymum* at Hilton. Use of pre-existing cavities in plant tissue has been reported for several species (see Bohart and Menke, 1976: 335) and is the habit at Hilton of *Pison montanum*, one of the species presently being discussed.

Great specificity is shown in the nature of the foreign materials introduced into pre-existing cavities in plant tissue by various pollen-collecting (that is, non-parasitic) bees. In the family Megachilidae, *Megachile gratiosa* and *Megachile spinarum* construct their cells of pieces of green leaves cut to definite shapes and sizes and arranged overlappingly (Fig. 39). Leaves of only one plant species are used by these two bees at Hilton, namely those of *Maytenus heterophylla* (Celastraceae) which would appear therefore to be those best suited for the purpose at that locality. Elsewhere *M. gratiosa* has been found to use not only green leaves but, less commonly, flower petals also (Taylor, 1963, 1965 and 1968). Other bees of the same family, *Capanthidium capicola* and *Immanthidium junodi*, both so-called carder bees, use cotton wool-like plant down, *Heriades* species use plant resin, and *Chalicodoma fulva* and *Chalicodoma sinuata* use mud (Fig. 40).

Hylaeus species including *Hylaeus braunsi* (family Colletidae), by contrast, construct their cells not of materials which they have collected but of a cellophane-like material secreted by their salivary glands.

The construction by many of the bees of complete cells within the pre-existing nesting galleries as opposed to the construction only of cell end walls (that is cell partitions) as by the wasps is clearly linked to the nature of the provision. The damp nature of the pollen and nectar mixture clearly requires that it be protected not only from desiccation through loss of moisture to the nesting substrate but also that it be protected from contamination from the nesting substrate. The cell walls be they of leaves, plant down or mud thus serve to isolate the provision from the nesting substrate. This is of particular importance in the *Hylaeus* species the nectar-pollen mixture of which is very liquid and can only be protected and contained by the impermeability of the cellophane-like "bags" forming the cells. On the other hand the pollen stored by *Heriades* species, including *H. spiniscutis* at Hilton nesting in old *Dasyproctus* galleries in *Berkheya* and *Gasteria* stems, is very dry which may account for the fact that no cell walls are constructed and that the introduced nesting material, resin, is used only for the construction of cell partitions and nest closures.

It may be accepted that foreign materials for the construction of cells within pre-existing burrows were used already by the ground-nesting antecedents of the bees now nesting above ground and that the change in nesting situation was not accompanied by any change in the nature of the nesting materials. Certainly, there is no difference in the nature of the leaf cells constructed at Hilton by, on the one hand, the ground-nesting *Megachile semiflava* and *M. stellarum* and, on the other hand, the above-ground-nesting *M. gratiosa* and *M. spinarum*.

In passing it may be remarked that the apparently successful co-existence at Hilton of six species of *Megachile* must be due at least in part to the fact that the search for suitable pre-existing cavities in which to nest is not restricted to one situation but is divided between the ground *(M. aliceae, M. meadewaldoi, M. semiflava* and *M. stellarum)* and situations above the ground *(M. gratiosa* and *M. spinarum)*. Within each of the two major nesting situations competition is probably further reduced by the fact that the species concerned are of different sizes and therefore seek pre-existing cavities of commensurate bore. For example, with respect to the two species nesting above the ground and thus found also in trap-nests, the 8 mm long *M. gratiosa* was found to be restricted to small bore (6,4 mm) trap-nests whereas the 13 mm long *M. spinarum* was found to use mostly larger bore (9,5 and 12,7 mm) trap-nests.

Six of the thirty-nine species recorded at Hilton as nesting within plant tissue were found doing so in pre-existing cavities which they themselves had not in any way modified. All were reared from cells constructed by other aculeate Hymenoptera and all may be classed as cleptoparasites as they feed upon the provision stored by their hosts.

Three families were involved, namely Chrysididae, Sapygidae and Megachilidae. The four cuckoo wasps and their hosts were: *Chrysidea africana* and *Chrysis* sp. (near *purpuripyga*), both in the cells of *Trypoxylon; Chrysis inops* in the cells if *Pison montanum*; and *Octochrysis hoplites* in the cells of *Euodynerus euryspilus*. *Sapyga simillima* (Sapygidae) and *Coelioxys penetratrix* (Megachilidae) developed in the cells of *Heriades* sp. and *Megachile spinarum* respectively.

All the above cleptoparasitic species ahear to be highly host specific with regard to the nests in which they develop and their occurrence is therefore linked with that of their hosts. *Chrysidea africana*, besides being reared from *Trypoxylon* cells in trap-nests tied to bushes and trees, was found also in association with *Trypoxylon* nests in cavities in vertical banks. On the face of the latter the cuckoo wasp was frequently seen walking about inspecting holes, then flying up and settling elsewhere after which the inspection of holes was resumed.

With respect to the association of *Coelioxys* with *Megachile* it is of interest that the two genera are closely related. It appears that both are probably derived from the same nest-constructing and pollen-collecting forms and that the cleptoparasitic behaviour of *Coelioxys* is secondary and specialized, being arrived at by the abandonment by this genus of nest construction and pollen collection in favour of the utilization for nesting of the nest constructed and provisioned by *Megachile*.

Five species, all wasps, were listed at Hilton as constructing aerial nests on plants, namely *Eumenes lucasius* (Eumenidae), *Celonites capensis* (Masaridae), *Polistes smithii* and *Ropalidia* sp. B. (Vespidae), and *Sceliphron quartinae* (Sphecidae).

The nesting of all these species, like those species constructing nests above ground but within plant tissue, may be seen as derived from nesting in the ground. In contrast to those species which nest within plant tissue and which in their nesting therefore are subject to the constraints imposed either by the availability of plant tissue suitable for gallery excavation or by the availability of pre-existing cavities of suitable dimensions, the species nesting on plants are free of such limitations and for their nesting require only that the plant should offer mechanical support for the nest. Despite this freedom with regard to the surface to which the nest may be attached, the species cannot nest anywhere for all are dependent upon the presence of water for the construction of their cells.

With respect to the four Vespoidea, water, collected in the crop and regurgitated from there, is required to transform dry clayey earth into mud and dry rasped-off wood fibres into wood pulp, materials used for cell building by *Eumenes* and *Celonites* and by *Polistes* and *Ropalidia* respectively. *Sceliphron quartinae*, in contrast to the above two water-collecting, mud-mixing species, probably behaves like the mud-daubing *Sceliphron spirifex* and related species which gather already existing mud from beside pools and puddles.

Nesting is therefore restricted to within a certain distance of water, and furthermore, in the case of those species making mud cells, to areas of clayey soils. However, *Sceliphron quartinae*, which has been reported by Brauns (1911: 119) to make its cells either of clayey mud or cow dung, will by its use of the latter material (when fresh and wet) be able to nest in areas where mud suitable for cell construction is unavailable, either because the soil is not of a clayey nature or because pools and puddles are absent, or both.

With respect to wasps and bees nesting within plant tissue, two associations between some species and certain plants are of particular interest. These associations will be dealt with in further detail in order to illustrate the primary rôle played by the plant in question and to show the chains of dependence existing amongst the insects constituting a community upon such a plant. It is obvious that such chains of dependence within a community are not the monopoly of those species nesting within plant tissue but are a feature of all communities whatever their nesting substrates and nesting situations. The present two examples are chosen as they have the added interest of having as the nesting substrate an additional living organism, the plant.

The first example pertains to a complex of three insect species associated with and restricted to the shrub or small tree, *Acacia karroo*, and concerns the nesting of the sphecid, *Ampulex* sp. near *cyanura*, listed in category 17 of the annotated list as being a modifier of pre-existing cavities in woody stems. As will be seen in Fig. 34 in which the association under discussion is diagrammatically portrayed the other two insects concerned are *Ceroplesis hottentota* (Cerambycidae) and *Bantua dispar* (Blattidae) (Figs 35 & 36).

First in the three-linked chain is the beetle, *C. hottentota*, the larvae of which in the course of their feeding bore galleries in finger-thick branches of *A. karroo*. The consequences of the activity of these larvae are three-fold and make possible the existence of the other two species in the chain. Firstly, damage to the living branches of the tree results in a copious amount of

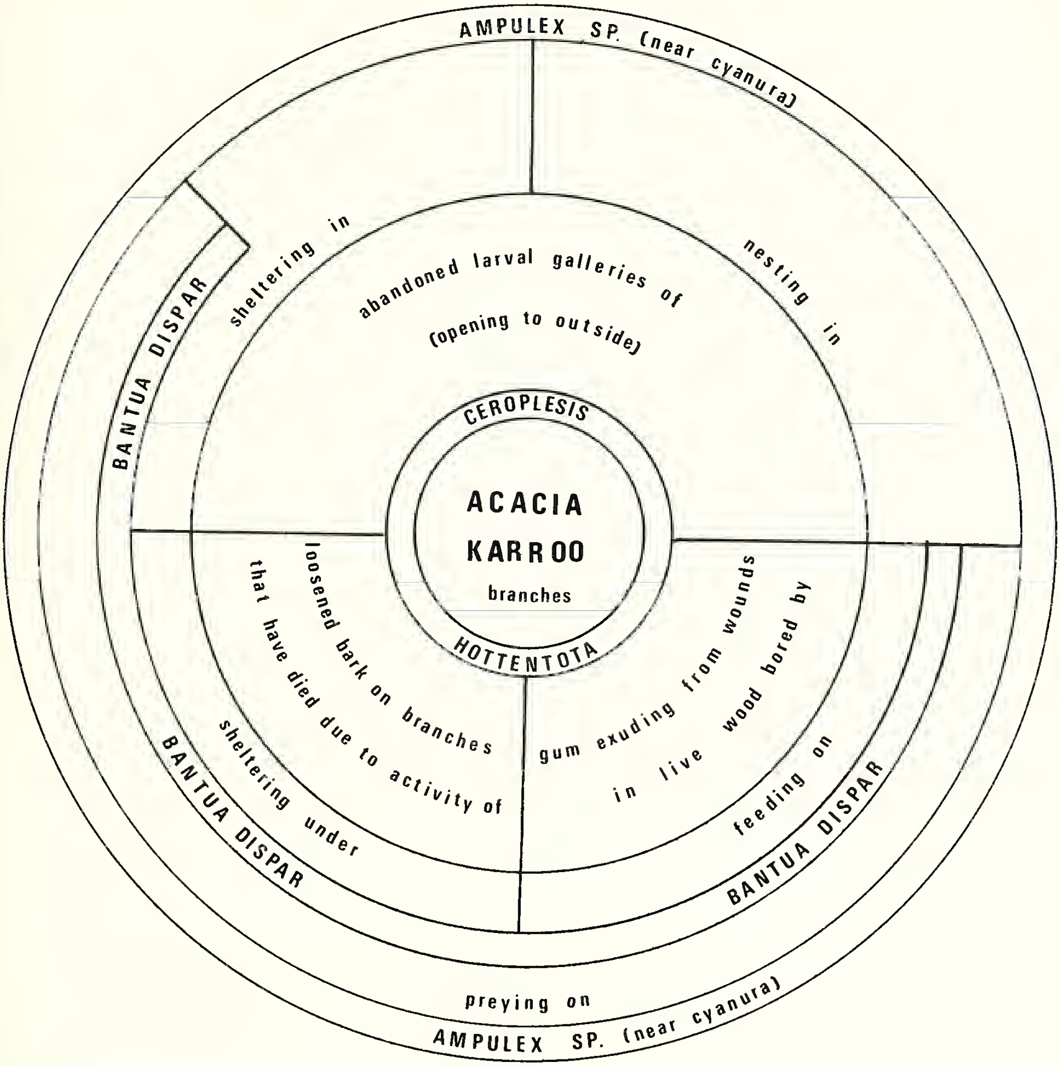

Fig. 34. Diagram showing the structure of a complex of three insect species, *Ceroplesis hottentota* (Cerambycidae), *Bantua dispar* (Blattidae) and *Ampulex* sp. near *cyanura* (Sphecidae) associated with and restricted to the shrub or small tree *Acacia karroo* (Leguminosae).

gum being exuded from the wounds. Secondly, and at a later stage, the bored branches die with the result that their bark separates from the wood. Thirdly, after the beetles have completed their larval feeding, have pupated and have metamorphosed into adults, they break out and abandon their galleries with the result that the latter become available for the use of other insects which cannot themselves hollow out such cavities.

Fig. 35. *Ceroplesis hottentota*, the larvae of which bore galleries in finger-thick branches of *Acacia karroo*. (× 3)

Fig. 36. *Bantua dispar* and *Ampulex* sp. near *cyanura*. The wasp having subdued the cockroach has cut off the end of an antenna (seen lying at bottom right-hand corner of photograph) and is malaxating prior to leading prey to nesting gallery. (× 3)

Second in the chain of species is the cockroach, *B. dispar*, which appears to be restricted to those *A. karroo* shrubs and trees harbouring *C. hottentota*. A nocturnal species, it spends the day in hiding in old abandoned beetle galleries and under the loosened bark of dead branches and comes out at night to feed upon the gum exuding from living branches being bored by the beetle.

Third and last in the chain is the wasp, *Ampulex* sp., which preys exclusively upon *B. dispar* for which it may be seen hunting on foot on the branches of the tree. Having flushed a *B. dispar* from its hiding place, the wasp stings it and then, holding the subdued cockroach by one of its antennae, leads it to an old *C. hottentota* gallery (Fig. 36). Once arrived there the wasp installs the cockroach within the cavity, oviposits on it and then seals the gallery with detritus collected on or immediately under the tree.

The existence of *Ampulex* sp. near *cyanura* within any locality is therefore inextricably linked with the presence of not only its prey but also with that of the beetle and ultimately with that of *Acacia karroo*. As the wasp was never collected anywhere other than on *A. karroo* it would appear that its entire life is spent on this plant.

The second example, presented diagrammatically in Fig. 37, pertains to a community of species referable to categories 19, 20 and 21 of the annotated list and associated with the dry inflorescence stems of *Aloe ferox*.

The community differs from the complex of three species concerned in the first example in that the species at the core of the community are hymenopterous, not coleopterous. Furthermore, species are included that exhibit all three degrees of participation in nest construction: those which construct their nests entirely by themselves, those which modify pre-existing cavities (Figs 38, 39 & 40) and those which nest parasitically in pre-existing cavities which they do not themselves modify.

Most strikingly different, however, is the far looser association with the plant, only the two gallery excavators at the core of the community, *Xylocopa sicheli* and *Ceratina* sp. A. being apparently restricted to the aloes. However, even these species are dependent upon these plants only in so far that they offer a suitable pithy substrate in which nesting galleries may be excavated and in areas where *A. ferox* does not occur, inflorescence stems of other species of *Aloe* are known to be used. Foraging for pollen and nectar with which to provision the cells within the galleries takes place on other plants for at the time of nesting the aloes are not in flower.

At the level of those species which modify pre-existing cavities and are recorded as using the abandoned borings of the two gallery excavating bees there is no dependence on the presence of aloes at all nor on the presence of the bees. As has been shown species like *Isodontia stanleyi, Trypoxylon* sp., *Megachile spinarum, Chalicodoma sinuata* and *Immanthidium junodi* will nest in a variety of pre-existing cavities provided these are situated up above the ground. It is clear, however, that if these species *are* to nest in *Aloe* inflorescence stems then they can do so only in the presence of old *Xylocopa* and *Ceratina* borings.

At the level of those species which do not modify pre-existing cavities but nest parasitically the association is clearly with their hosts only and the occurrence of these species is therefore determined by that of their hosts.

Communities of loosely associated species of wasps and bees, as exemplified by the community nesting in *Aloe ferox* inflorescences, may be seen to exist in all four nesting situations—the ground, vertical banks, stones and plants and in the subdivisions of these primary nesting situations. It may therefore be concluded that the picture that emerges of the interaction of species of wasps and bees in a community such as that described above is typical of the entire population of these insects at Hilton.

Within any community individual species, as exemplified by *Ampulex* sp. near *cyanura* of the community nesting in *Acacia karroo* stems, may be associated not with other species of

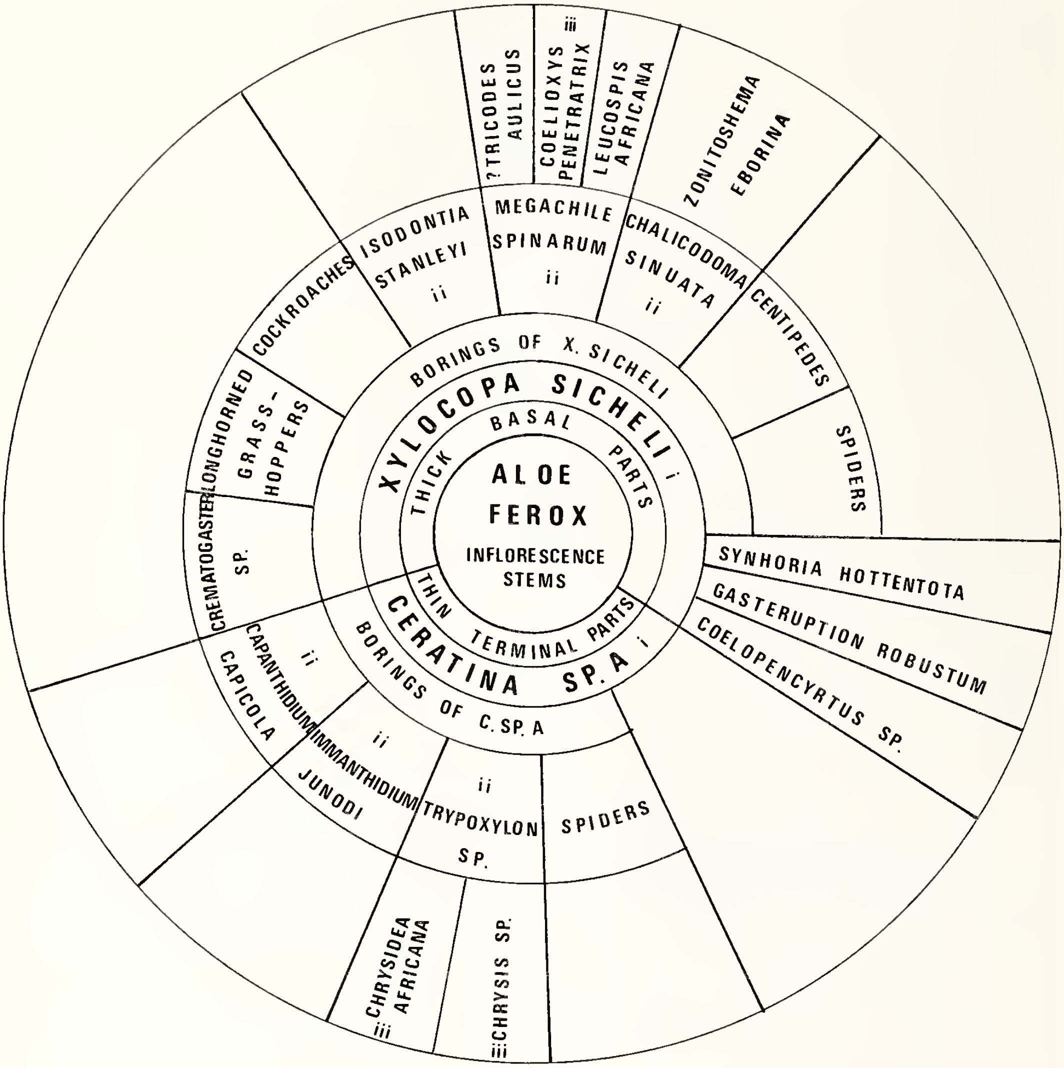

Fig. 37. Diagram showing the structure of a community of insects associated with the dry inflorescence stems of *Aloe ferox* (Liliaceae). With respect to the aculeate wasps and the bees the degree of participation in the construction of their nests is indicated by the numbers (i, ii, iii) as in the classification of these insects on the basis of their ethology. (i) In nest constructed entirely by the nester. (ii) In pre-existing cavity modified by the nester. (iii) In pre-existing cavity *not* modified by the nester.

Fig. 38

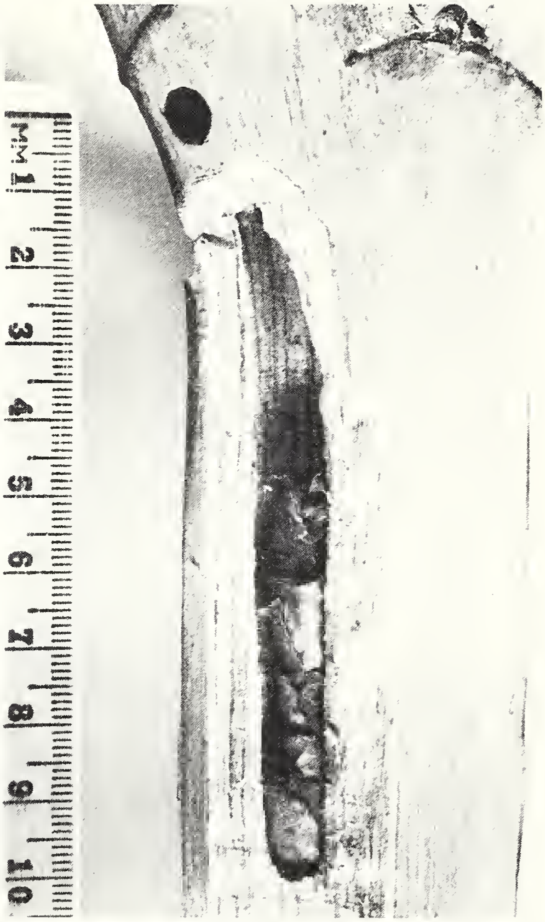

Fig. 39

Figs 38 and 39. Dry inflorescence stems of *Aloe ferox* cut longitudinally to show old galleries bored by *Xylocopa sicheli* and containing nests of *Isodontia stanleyi* (Fig. 38) and *Megachile spinarum* (Fig. 39).

wasps or with bees, except perhaps peripherally (e.g. in competition for pre-existing cavities), but may rather be part of the community by virtue of their association with non-hymenopterous species.

The circumscribed association of *Ampulex* sp. near *cyanura* with the beetle and the cockroach making up the three-species complex on *Acacia karroo* appears to be exceptional and no similar example was found during the course of the present study at Hilton.

Fig. 40. Dry inflorescence stem of *Aloe ferox* cut longitudinally to show old gallery bored by *Xylocopa sicheli* and containing nest of *Chalicodoma sinuata*.

The study of nesting ethology of the aculeate wasps and the bees of Hilton has apart from adding considerably to the knowledge of these groups in Africa provided a clear illustration of their remarkable propensity for behavioural adaptability which has led to the formation of communities of large numbers of sympatric species showing marked ecological displacement.

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