SOME ASPECTS OF AN ETHOLOGICAL STUDY OF THE ACULEATE WASPS AND THE BEES OF A KARROID AREA IN THE VICINITY OF GRAHAMSTOWN, SOUTH AFRICA

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CONTENTS

INTRODUCTION

The present 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 similar but more restricted account of this nature being that of Evans (1970) which is mainly concerned with fossorial species and their associates.

Before selecting a site for such a study the insect populations in areas of various differing vegetation types were sampled using Malaise traps and hand nets. A karroid area was selected as it showed greatest promise with respect to potentially interesting species.

ASPECTS OF THE ECOLOGY OF THE STUDY AREA

a) 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).

Situated on the course of the New Year's River, Hilton at a minimum altitude of 1550 - 1650 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 1550 feet (472 m) in the river bed at the foot of the cliff to the west to a maximum of about 1850 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 1550 and 1650 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

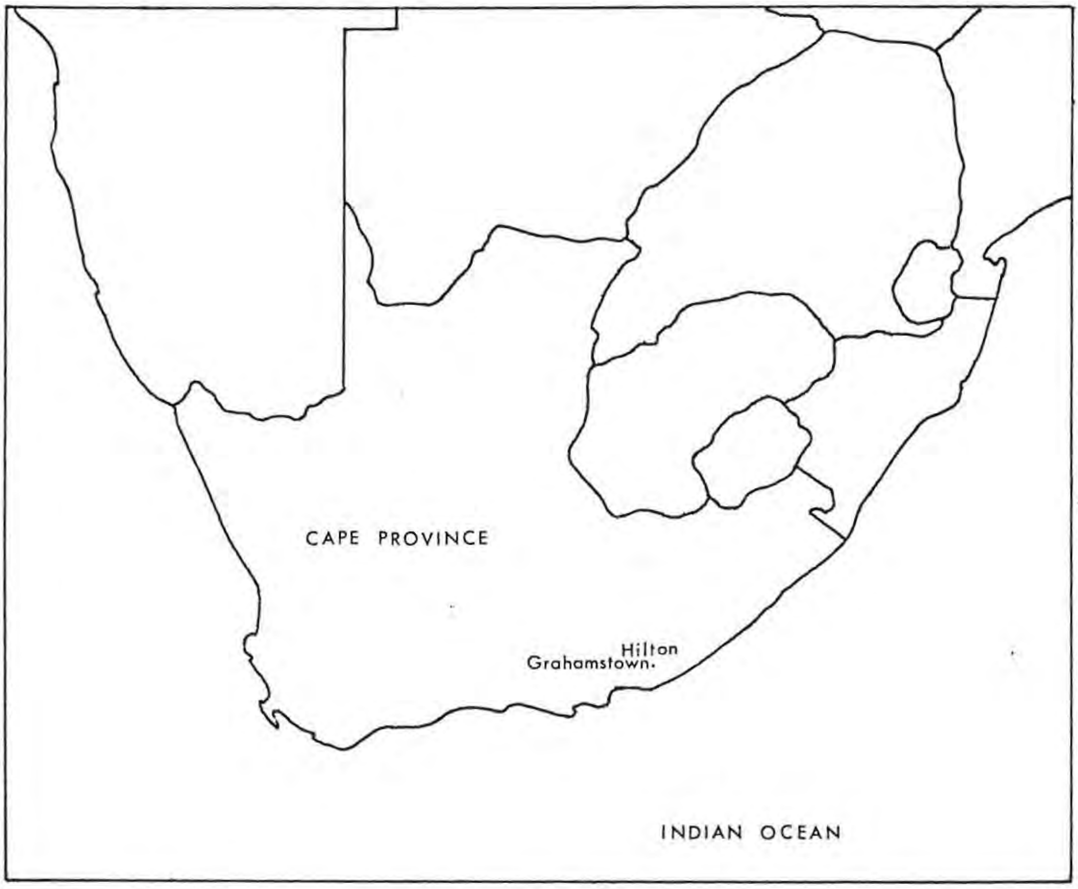

Fig.1

MAP OF SOUTHERN AFRICA SHOWING POSITION OF STUDY AREA

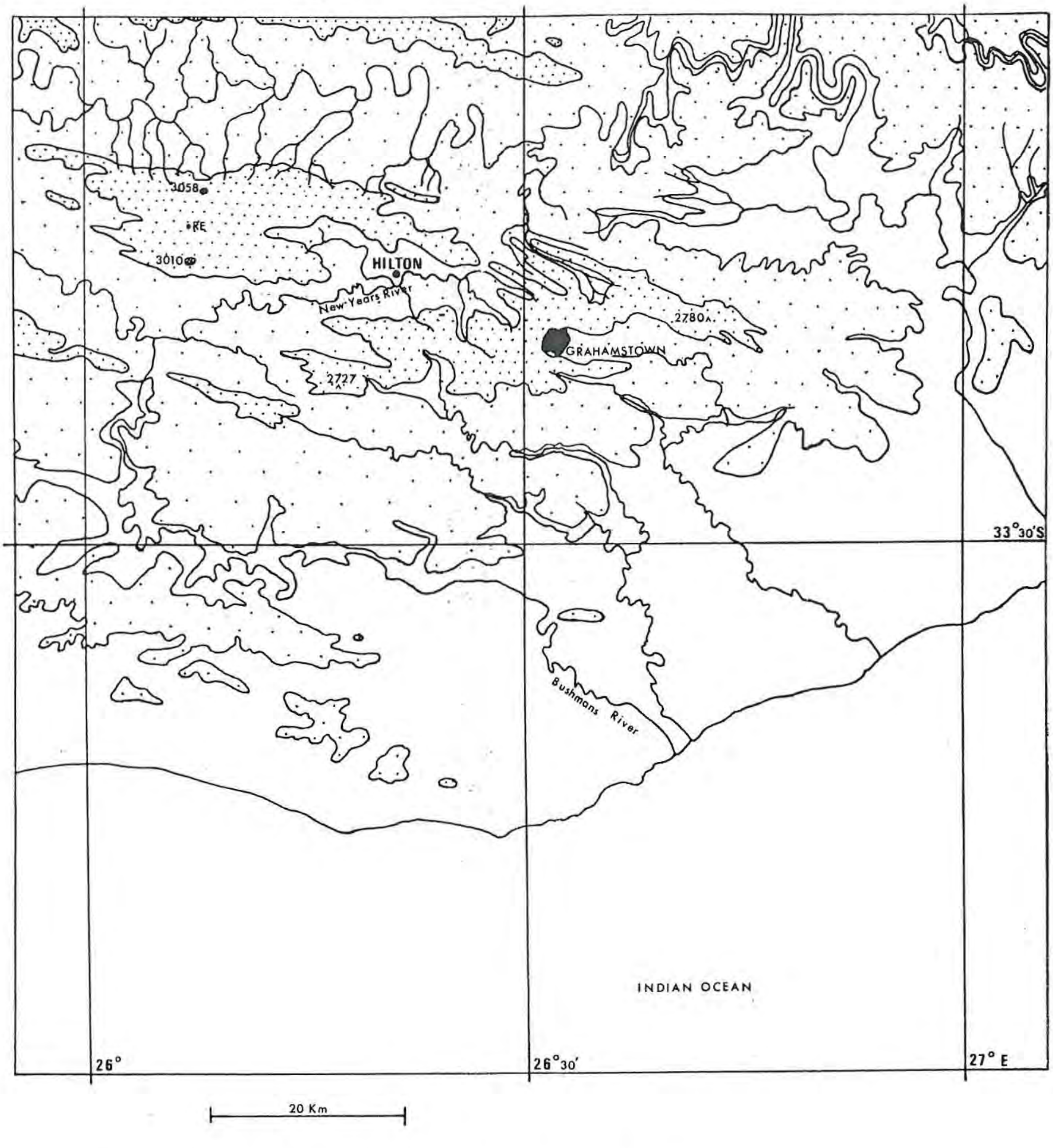

Fig. 2 TOPOGRAPHICAL MAP SHOWING POSITION OF STUDY AREA

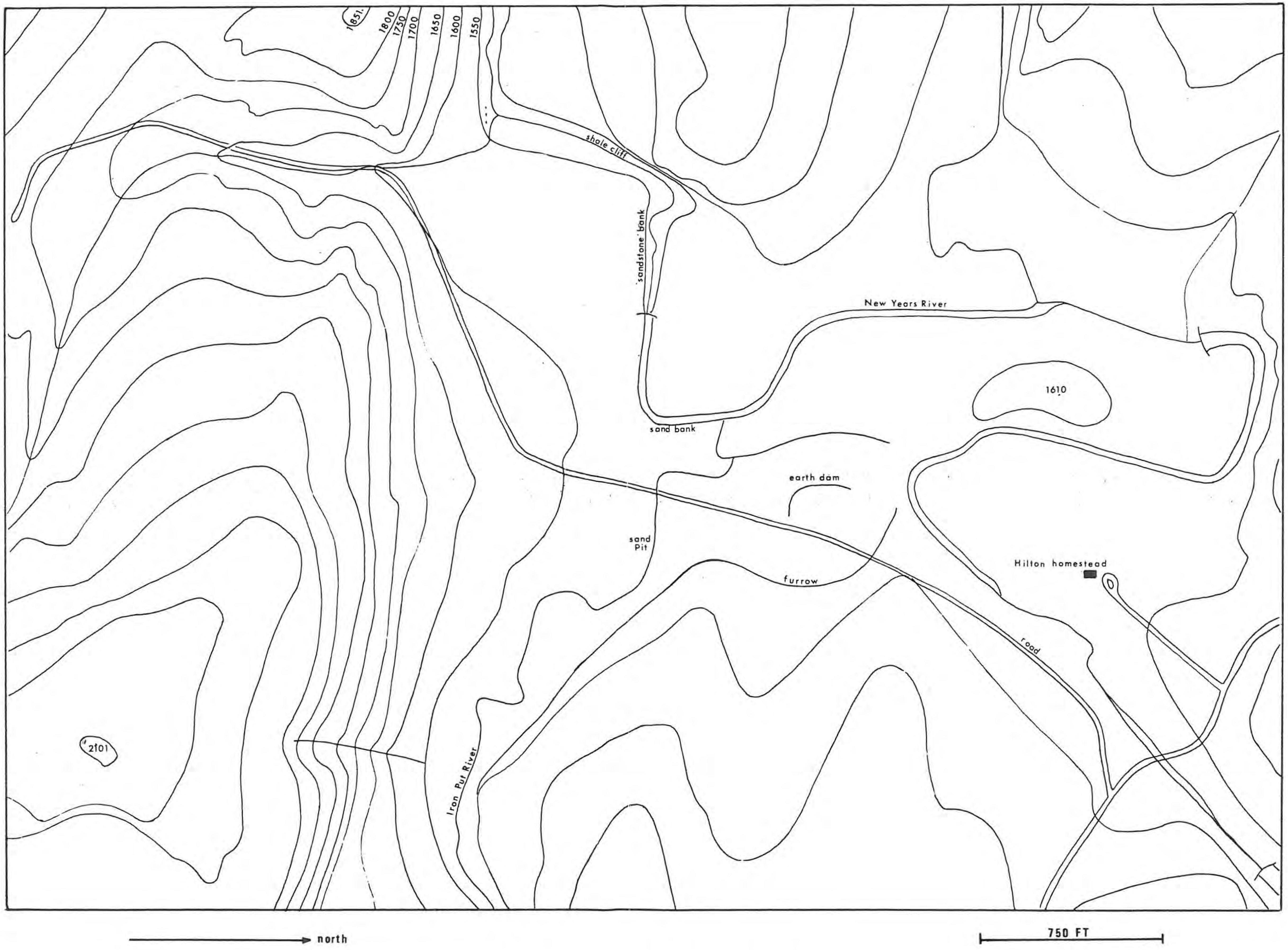

Fig.3 **MAP OF STUDY AREA**

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 (1300 - 1500 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 1600 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.

b) 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 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 1600 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 1600 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 area 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 1600 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.

c) 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 1276 feet (389 m) above sea level on the peneplain near Seven Fountains, 22km S. of Hilton on the coastal side of the ESE ranges the average annual rainfall is 575mm (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 2263 feet (690m) has an average annual rainfall of 573mm (22,55")(Dyer, 1937); Slaaikraal at 1949 feet (594m) has 652mm (25,7")(Weather Bureau, 1965): Faraway at slightly above 2400 feet (732m) has circa 864mm (34") (pers. comm. C.F. Jacot Guillarmod, Oct., 1978), and Grahamstown at 1768 feet (539m) has 688mm (27,1")(Weather Bureau, 1965).

The average annual rainfall figure for Hilton : circa 356mm (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 1600 feet (488m) the study area lies 700-1100 feet (213-335m) 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.

d) 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 the earth dam (Gess and Gess, 1974: Plate 2).

The plant species characterizing the above communities are listed in Appendix 1.

e) 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 substrate in which to excavate a nesting gallery more specificity is shown. These associations are given in the annotated list.

f) 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, fertilised 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.)
1 i) In nest constructed entirely by the nester.
2 ii) In pre-existing cavity modified by the nester.
3 iii) In pre-existing cavity not modified by the nester.
    (b) In friable soils. (Typically sandy soils, exceptionally disturbed and therefore non-compacted clayey soils.)
4 i) In nest constructed entirely by the nester.
5 ii) In pre-existing cavity modified by the nester.
6 iii) In pre-existing cavity not modified by the nester.

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

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

IV. NESTING IN OR ON PLANTS (Figs. 12, 13, 14 and 15)
    A. IN PLANTS

IV. NESTING IN OR ON PLANTS (Figs. 12, 13, 14 and 15)

A. IN PLANTS

(a) Within woody stems.

16 i) In nest constructed entirely by the nester.

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

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

(b) Within pithy stems.

19 i) In nest constructed entirely by the nester.

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

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

(c) Within hollow stems.

22 i) In nest constructed entirely by the nester.

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

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

B. ON PLANTS (Irrespective of whether plants are woody, pithy or hollow-stemmed.)

25 i) In nest constructed entirely by the nester.

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

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

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.

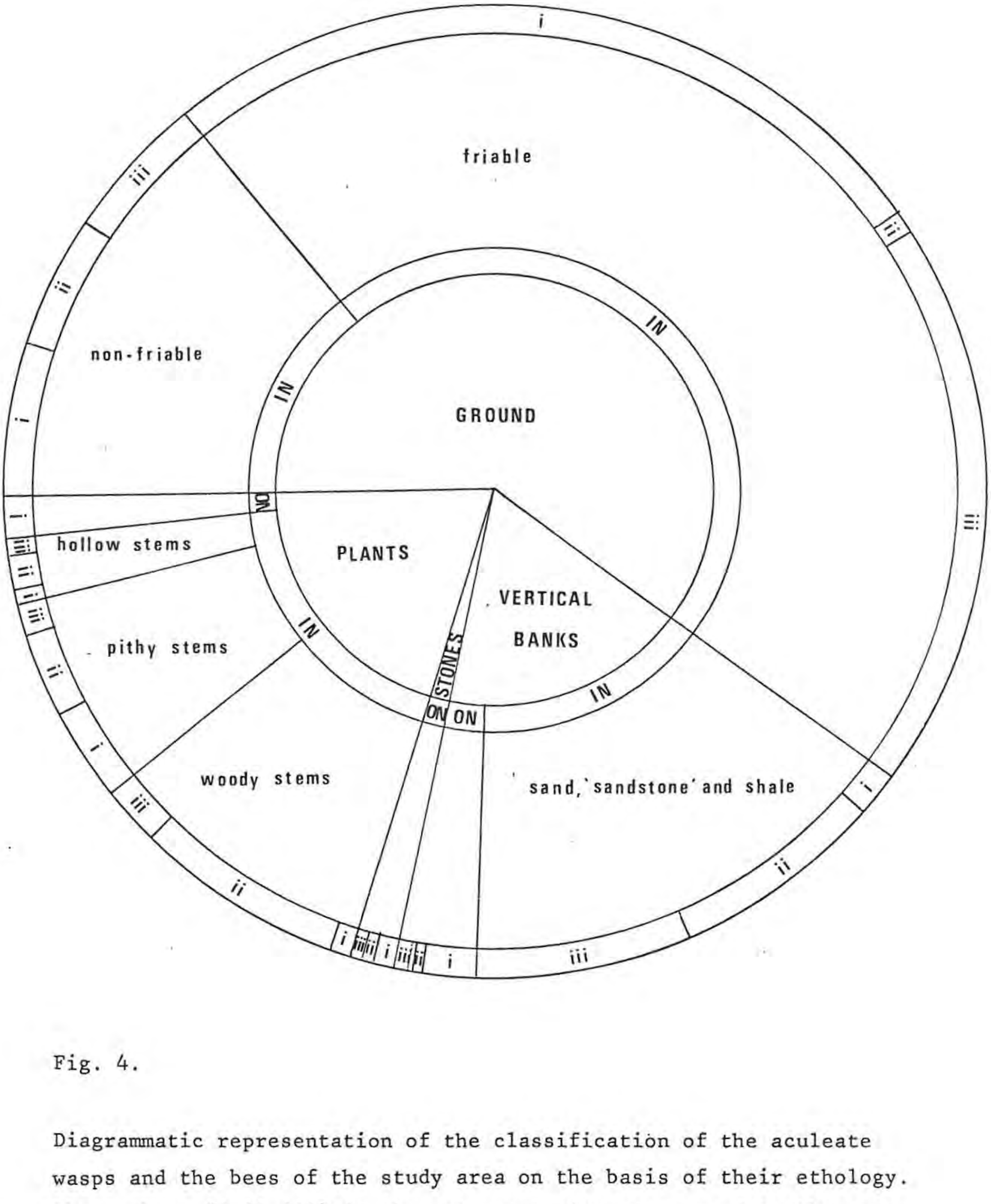

Fig. 4.

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 <u>not</u> modified by the nester.

The magnitude of the segments is in proportion to the number of species involved.

5

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9

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Fig.5. Area of friable soil: the sandpit.

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

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

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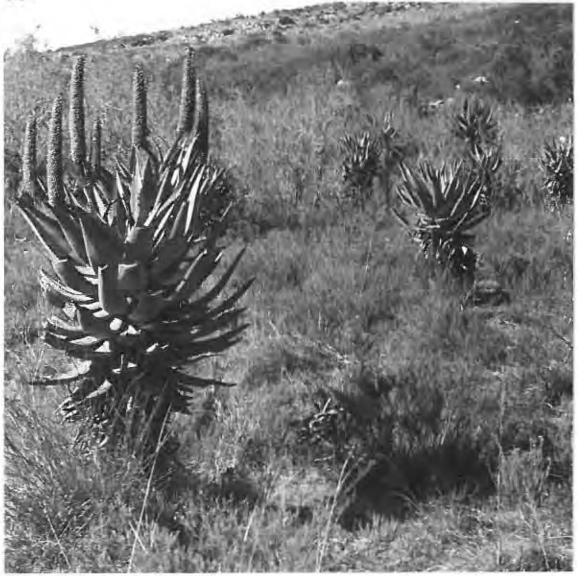

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Fig.10. Stone lying loose on ground bearing nest of Auplopus rossi.

Fig.11. Stone embedded in ground 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.

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.-Mar. 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 oxydorcus (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 Caerostis 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 Lepeltier. 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.

* Tachyspex 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)), excepttionally 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, 1926:320).

*** 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. Uncommom. 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 an 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 large 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 utilising 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 (Suassure). 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 definately 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 plud 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.

*** 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.)

CHRYSIDIDAE

*** 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 characterised 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 a 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 1mm 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 Phragmites 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 of 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. <u>ON</u> PLANTS (Irrespective of whether woody, pithy or hollow-stemmed.)

iii) In pre-existing cavity <u>not</u> modified by the nester.

No representatives recorded for this category.

AMPLIFIED ACCOUNTS OF THE ETHOLOGY OF SELECTED SPECIES, PRESENTED IN THE FORM OF BOUND-IN PUBLISHED PAPERS (in order of publication).

a) An ethological study of Dichragenia pulchricoma (Arnold) (Hymenoptera: Pompilidae), a southern African spider-hunting wasp which builds a turreted, subterranean nest.

b) Ethological studies of Bembecinus cinguliger (Smith) and B.oxydorcus (Handl.) (Hymenoptera:Sphecidae), two southern African turret-building wasps.

c) An ethological study of Parachilus insignis (Saussure) (Hymenoptera: Eumenidae) in the Eastern Cape Province of South Africa.

d) Ethological notes on Dichragenia neavei (Kohl) (Hymenoptera:Pompilidae), an African spider-hunting wasp building a turreted, subterranean nest.

e) Ethological notes on Holotachysphex turneri (Arnold) (Hymenoptera: Sphecidae:Larrinae) in the Eastern Cape Province of South Africa.

f) Ethological notes on Kohliella alaris (Hymenoptera:Sphecidae: Larrinae) in the Eastern Cape Province of South Africa.

g) Ethological studies of Jugurtia confusa Richards, Ceramius capicola Brauns, C.linearis Klug and C.lichtensteinii (Klug) (Hymenoptera: Masaridae) in the Eastern Cape Province of South Africa.

h) Prey and nesting sites of some sympatric species of Cerceris (Hymenoptera:Sphecidae) with a review and discussion of the prey diversity of the genus.

i) Some aspects of the ethology of Dasyproctus westermanni (Dahlbom) (Hymenoptera:Sphecidae:Crabroninae) in the Eastern Cape Province of South Africa.

j) Spider vanquishers: the nesting of Tachypompilus ignitus (Smith) and Batozonellus fuliginosus (Klug).

k) The whited sepulchre - the nesting of Chalybion tibiale (Fabr.).

An ethological study of Dichragenia pulchricoma (Arnold) (Hymenoptera: Pompilidae), a southern African spider-hunting wasp which builds a turreted, subterranean nest.

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CONTENTS

INTRODUCTION

It is estimated that at present between five hundred and six hundred species of the family Pompilidae have been described from the Ethiopian Region excluding Madagascar. As far as can be ascertained, not a single African species has been studied with respect to its ethology; indeed, the only published biological information pertaining to these nearly six hundred species appears to consist of about half a dozen prey records involving as many species of wasps, a list of species visiting a plant attractive to Hymenoptera, and a few other fragments in which the identity of the wasp concerned is not clearly stated.

Whatever the causes for this shocking hiatus in our knowledge of the African Pompilidae, it is patently obvious that a study of their biology is a potentially most rewarding field of endeavour, where virtually any observations made and recorded will be new.

An inherent difficulty associated with the gathering and recording of information of this nature, however, is the unpredictability in terms of time and place of the opportunity of observing this or that species doing something. The approach towards the study must be an opportunistic one in which whatever presents itself is followed up—an approach practised by the present authors. Thus, though the authors' curiosity had been aroused by the discovery on rare occasions in previous years of the nest turrets of *Dichragenia pulchricoma* (Arnold), the present study of the ethology of this wasp was not so much the outcome of a prior decision to investigate this species as of an unexpected opportunity which presented itself. This opportunity of making a relatively detailed study of what appeared to be a most unusual wasp arose from the chance discovery, during routine collecting in 1972, of two nesting sites, conveniently near Grahamstown, where this species occurred in large numbers.

As an understanding of the basic form of the nest of *D. pulchricoma* is required to appreciate fully not only the import of various statements made but also the relevance of techniques listed in the initial sections of this paper and as a detailed description of the nest follows only later, a brief statement concerning the nature of the latter is given at this juncture.

The nest of *D. pulchricoma* consists of two main sections—a subterranean portion consisting of a vertical burrow or shaft with at or near its end a variable number of cells and an aerial portion consisting of a mud turret of definite form surmounting the burrow entrance which latter is situated at ground level.

TECHNIQUES USED IN EXAMINING NESTS

After a nest turret had been located in the field, it was, if possible, covered with an inverted drinking glass, the aim being to capture the female nest-building wasp should she be in the nest at the time. Capture and subsequent examination of the female is essential, if verification of the species is required. The behaviour of the wasp is such that, having emerged from the nest on an outward-bound flight, it will only return to the nest after this has been carried out. Thus, if the wasp is in its burrow when a glass is placed over its turret, the wasp on emerging will be effectively trapped within the glass and can then be collected easily by introducing some ethyl-acetate impregnated cotton wool beneath the glass. A watch may be maintained at the covered turret until the wasp appears. If the wasp was away, when the glass was placed in position, the latter may be removed long enough to allow the wasp into its nest or an attempt may be made to capture the wasp then and there with a net. Sometimes the wasp remains in the nest until the turret is sprayed as described below, when it emerges very rapidly, and quick action must be taken to prevent its escape.

If, as in the present study, it is wished to preserve the nest turret which is of an extremely delicate and fragile nature, it is essential to impregnate the dried mud pellets of which it is made with a penetrating fluid which on drying hardens the individual pellets and glues neighbouring pellets together. In the present study an aerosol clear lacquer was found most effective. The lacquer was sprayed fairly liberally onto the turret and particularly onto the ground for a distance of about three to five centimetres around its base. After allowing the spray to dry (about $\frac{1}{4}$ hour in hot sunshine) the sprayed ground around the base of the turret was undercut with a strong penknife. The so-produced consolidated earthen disc bearing the turret itself was then lifted intact and placed on cotton wool in a small unit-tray in which it was readily incorporated into the collection.

As soon as the turret had been removed, the top of the vertical shaft then exposed was cleared of any material that might have blocked it, when the former was undercut and lifted. Flour was then blown down the shaft coating the walls with a white tracer which was indispensable in the subsequent excavation. In the present investigation a plastic mustard-dispenser as seen on the tables of some restaurants was used—the tip of the nozzle fitted to the screw-off top was directed into the shaft-opening and the container was then squeezed to blow out the flour.

In order to expose and draw the vertical shaft and the cells at or near its end, it was essential to excavate the nest from the side. A pit about fifteen centimetres deep and at least as long and wide was, therefore, dug to one side of the assumed position of the nest, the nearer side of the pit being about seven centimetres away from the shaft opening. As the ground was usually extremely hard, a geologist's pick was used to make this initial excavation. Working from the pit towards the nest, the ground was then carefully broken away using initially a cold chisel and club-hammer, later the point of a penknife. Final exposure of the shaft (marked with flour) and of the cells (if sealed not marked with flour) called for precise and careful work.

A plan was drawn and measurements of the nest taken as the latter was exposed, notes were taken of the nature of the cells, the prey and the wasp young. Prey and wasp young of each cell were individually collected in labelled glass vials or gelatin capsules and kept alive for subsequent closer examination.

SYSTEMATIC AND TAXONOMIC CONSIDERATIONS

In the key to genera and species of the tribe Macromerini (as subfamily Macromerinae) published by Arnold (1934: 289—95), the present species runs down easily to *Pseudagenia pulchricoma* Arnold, with the description of which (1934: 337—9) it agrees perfectly. No authoritatively determined specimens were available to confirm the identification but comparison with specimens of the subspecies *sordida* Arnold from Lesotho, identified as such by Arnold himself, supported the determination, allowance being made for the stated differences.

The present specimens are characteristically coloured: the greater part of the head and thorax (including the pronotum) is black, the wings are pale fuscous, while the abdomen is mostly ferruginous as are the legs with the exception of the coxae. In the female, the clypeus and antennae are ferruginous (the latter becoming gradually darker from the third or fourth joint onwards), the face, pro-mesonotum and scutellum have a pale greyish golden pubescence, while the second to fifth tergites are marked medially with black maculae which do not reach the posterior margins of the segments but which together give the impression of a somewhat diffuse, wide, median streak on the dorsum of the abdomen. This black streak on the otherwise ferruginous dorsum of the abdomen, taken in conjunction with the black thorax and fuscous wings readily identifies the wasp in the field. The male is similarly coloured but lacks the black streak on the abdomen.

Since the time of Arnold's revision of the Pompilidae of the Ethiopian Region (1932—7), the very large cosmopolitan genus *Pseudagenia* Kohl, 1884 (= *Auplopus* Spinola, 1841) has been split up into a number of smaller genera.

Banks (1934) in his account of the Psammocharidae of the Philippines removed from *Pseudagenia* (*senso lato*) one new subgenus and seven new genera, not all of which have been recognized by subsequent workers.

The present species, *pulchricoma* Arnold, would, according to the generic key given by Banks (1934: 39—40) be referable to the genus *Phanagenia* Banks (1933: 18). This genus, recognized as valid by subsequent workers, was erected "for certain American forms possessing spines on the underside of the last tarsal joint" (Banks, 1934: 78). The generic description (of the female only) of *Phanagenia* (type species: *Phanagenia osceola* Banks, 1933 = *bombycina* (Cresson), 1867) is short, but the characters indicated are all exhibited by the present species, *pulchricoma* Arnold.

In the key to the Nearctic genera of the Macromerini published by Townes (1957: 140) *pulchricoma* Arnold once more runs down to *Phanagenia* Banks, which genus according to Townes differs from *Auplopus* Spinola, 1841 (= *Pseudagenia* Kohl, 1884) and two other genera (*Ageniella* Banks and *Priocnemella* Banks) in the following combination of characters: (1) first tergite with a fine lateral crease that separates off the epipleuron; (2) propodeum without long erect hairs; (3) mentum of female with a brush of about 20 long stout bristles which are not divided into right and left groups; and (4) underside of last tarsal segment of female with preapical bristles.

The present species, *pulchricoma* Arnold, differs in having the mental bristles of the female rather sparse and in having the clypeus of the male simple (clypeus of male with specialized apical margin in *Phanagenia bombycina* (Cresson)). However, the same differences have been accepted as possibly merely specific ones by Townes (1957: 141), when considering the Madagascan *Agenia macula* Saussure as a possible Old World member of the genus *Phanagenia*.

Agenia macula Saussure has also been studied by Haupt who, however, named it as the type-species of *Dichragenia* (1950: 25 and 1957: 14), one of several new Ethiopian genera split off by him from *Pseudagenia* as understood by Arnold. *Dichragenia*, according to Haupt, is represented on the African continent itself by *pulchricoma* Arnold, the subject of this paper.

Without being able to compare the type-species of *Phanagenia* and *Dichragenia*, it is not possible to assess fully the morphological differences between the two, differences which undoubtedly are small.

While the ethology of *Dichragenia macula* (Saussure) is unfortunately unknown, that of *pulchricoma* Arnold differs in important aspects from that of *Phanagenia bombycina* (Cresson) and lends support to generic separation. In the present paper Haupt's view is adopted and the wasp is referred to as *Dichragenia pulchricoma* (Arnold).

Arnold (1934: 337—40) as well as describing *pulchricoma* (*senso stricto*) from "Southern Rhodesia and British East Africa", described two subspecies ("races" of Arnold): *sordida* from Harrismith (Orange Free State), Willowmore and Aliwal North (both Cape Province); *laeta* from Umtata (Cape Province), Delareyville ("De la Rey" of Arnold) and Lichtenburg (both Transvaal).

In the Albany Museum collection there are fair-sized series of both these "races"—9 females and 6 males of *sordida*, and 8 females and 15 males of *laeta*, the determinations being by Arnold himself. Unfortunately, all these specimens are from Lesotho, all but one from the same locality, Mamathes; months of capture for both are October—February/March, in quite a number of cases in the same year! From the above it is clear that *sordida* and *laeta* cannot both be considered as subspecies of *pulchricoma*.

Some aspects of the ethology of one species of "a certain group of spider hunters" in Lesotho have been observed by Jacot-Guillarmod (1945: 43). He refers to this species as "the Zimbabwe builder" and from personal discussions in 1972 it emerges that the wasp in question was *sordida*. As far as the information goes, no differences can be found with respect to the ethology of *pulchricoma* (*senso stricto*) as studied in Grahamstown. This together with the great general morphological similarity leads to the view that *pulchricoma* and *sordida* are indeed conspecific. On the other hand, despite the fact that *laeta* was more common than *sordida* in Lesotho, it was, unlike the latter, never observed nesting (Jacot-Guillarmod, pers. comm., 1972), leading to the belief that it may well do so in a different ecological situation. This taken in conjunction with the general morphological differences leads to the view that *laeta* is not conspecific with *pulchricoma* but is better regarded as a separate species. This view agrees with that expressed by Arnold in 1961 when, during discussions with Jacot-Guillarmod, his attention was drawn to the fact that *sordida* and *laeta* are sympatric in Lesotho (Jacot-Guillarmod, pers. comm., 1972).

GEOGRAPHIC DISTRIBUTION

Dichragenia pulchricoma (Arnold) appears to enjoy a very wide distribution in Africa. Published locality records indicate a distribution from the equator (Kisumu, Kenya, at the north-eastern extremity of Lake Victoria) to the southern parts of the Cape Province (33°S.), ranging through several major vegetational zones.

In addition to the localities given by Arnold (1934: 339—40)—namely, Rhodesia (where "a common species"), Kisumu ("British East Africa"), Harrismith (Orange Free State), Aliwal North and Willowmore (both Cape Province), the species has been recorded from a number of widely separated localities in Zaire (the former Belgian Congo) by de Saeger (1945: 99) and by Haupt (1957: 15).

The Albany Museum collection contains specimens from Lesotho (Mamathes, Teyateyaneng and Henley's Dam, Leribe) collected by C. F. Jacot-Guillarmod (October—February) and from the Eastern Cape Province (various localities near Grahamstown). A nest turret, now in the collection, obtained by R. A. Jubb at Kenton-on-Sea, 44 kilometres SSE of Grahamstown, indicates the species' presence there.

It is probable that the species occurs also in the western part of the Cape Province for a single female associated with a nest turret of typical form and believed to be *D. pulchricoma* was observed but not caught by one of the authors (F.W.G.) at the Olifants River between Klawer and Clanwilliam during October 1967.

LOCALITY AND DESCRIPTION OF NESTING SITES WITH PARTICULAR REFERENCE TO CLIMATE, NATURE OF VEGETATION, SOIL TYPE AND VICINITY OF WATER

Field observations in the present study were centred on Grahamstown (33° 19′ S, 26° 32′ E) in the Albany Division of the Eastern Cape Province of South Africa. The greater part of the field work, including the study of 55 nests was carried out at Hilton, a farm situated about 18 kilometres WNW of Grahamstown; a smaller number of nests (6) was studied at a second farm, Clifton, situated at about the same distance from the town but to the NW; one nest and its builder were studied in the authors' garden in Grahamstown itself. The greater part of the field work was spread over a period of six weeks from 26.x.1972 to 6.xii.1972; an additional three mornings' field work was carried out at Hilton later in the summer (9 and 14.ii.1973 and 1.iii.1973).

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 dryest mid-winter. Grahamstown itself has a mean annual rainfall of 697,2 mm (27,45 inches), however, the farms Hilton and Clifton, for reasons of topography, receive considerably less—at Hilton the mean annual rainfall is in the region of 356—381 mm (14 to 15 inches). During 1972, a drought year, Grahamstown received 532 mm (20,94 inches) and Hilton received only 229 mm (9 inches).

The vegetation of Hilton and Clifton is karroid in nature and consists largely of an open community of small shrubs, few of which are strongly succulent but many of which are xerophytic. *Acacia karroo* forms much of the taller scrub, and grasses have largely been eaten out by stock. In both localities there has been some erosion of the soil resulting in some localized denuded areas.

Nesting sites at both Hilton and Clifton as well as in Grahamstown itself are in low-lying situations (river valleys) in which the soil is derived from the Dwyka Series and is of a reddish-brown clayey nature.

All nests found during the present investigation were built in places where the ground had been disturbed and had been partially or completely denuded of vegetation as a direct or indirect result of Man's activities.

Thus at Hilton, nests were found on the slightly raised edges of a shallow earthen dam; on the raised bank of earth running parallel to a water furrow and derived from the excavation thereof; on the denuded ground on the opposite side of the furrow; on slightly sloping areas denuded of vegetation and topsoil by sheet erosion, and on the sides of small erosion gullies intersecting such bare areas (Plates 1—4). At Clifton nests were found in essentially similar situations; the nest found in Grahamstown was situated on bare earth fringing a vegetable bed.

Mud turrets surmounting the burrow entrances were sometimes found completely exposed in the middle of totally bare areas but were sometimes in somewhat more protected situations such as against small banks or steps in the ground level or next to the base of dwarf shrubs (Plates 5—8).

In all cases the nests were situated in close proximity to temporary sources of water. This water, a result of rain, had collected in muddy pools, erosion gullies, shallow furrows and, in the case of the garden, a concave cabbage leaf.

Similarly the previously mentioned nest turret observed at the Olifants River and believed to be that of *D. pulchricoma* was sited on a fairly steep, bare, sheet-eroded clayey slope situated not far from two water sources—the Olifants River itself, and, closer at hand, muddy pools below a leaking concrete irrigation furrow.

Turrets of nesting *D. pulchricoma* at Mamathes (Lesotho) were reported by Jacot-Guillarmod (pers. comm.) to have been built on denuded patches of black clay near a spring.

GENERAL COMMENTS CONCERNING NESTING AND AN ACCOUNT OF THE BEHAVIOUR ASSOCIATED WITH BURROW EXCAVATION AND TURRET CONSTRUCTION

Dichragenia pulchricoma (Arnold) appears, at least in the localities studied (around Grahamstown), to be an opportunist—emerging in response to rain and nesting during the short period during which standing water, essential for nest construction, is available in pools and puddles. However, it appears as if only a fraction of the total population responds to any one fall of rain, for during summer, that is during the period of October to March, each shower of rain substantial enough to wet the ground and to cause run-off to form puddles in depressions, is followed by a flush of wasps and a spate of nest-building. As the puddles dry up again, the number of wasps observed falls off and nesting ceases. Thus, the potential nesting season is divided up into a number of short nesting bouts by apparently successive waves of wasps; the period between the emergence of the wasps and the completion of their nesting is very short; and, at any one time, virtually all nests being worked upon are at a similar stage of development. Comparison, with respect to stage of development and size, of wasp young present in a number of nests examined on a day soon after the beginning of a nesting bout with young present in other nest samples examined on subsequent days (Fig. 1),

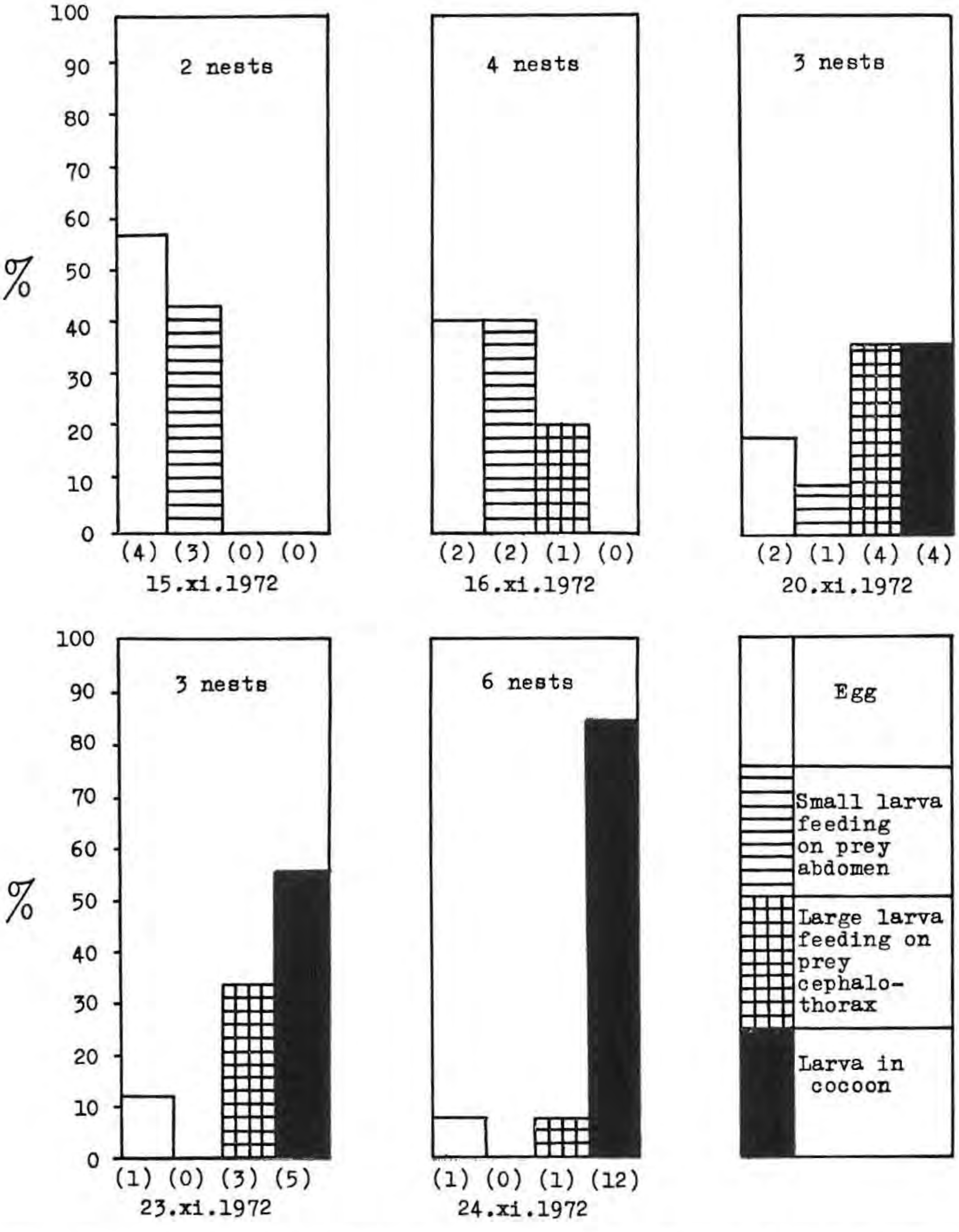


Fig. 1. Composition (expressed as a %) of wasp young (egg, small larva, large larva and larva in cocoon) collected at Hilton during the period 15—24.xi.1972. The actual number of each stage is indicated within brackets.

illustrates not only the synchrony of nesting within any one nesting bout but also the rapidity of development from egg to mature larva.

No evidence was found that might suggest that there was more than one generation of wasps per year. Indeed, in all the nests examined the most advanced young were fully-grown larvae within silken cocoons; no pupae were found. It seems likely that these larvae do not immediately pupate but rather enter a state of diapause in which the rest of the nesting season, the autumn and the dry winter months, are spent and that the stimulus for the breaking of the diapause is at least in part provided by the rains of the following spring and early summer. Presumably, development thereafter is rapid as is the previous development from egg to mature larva.

The behaviour associated with burrow excavation and turret construction consists of a cycle of events which is repeated many times over. Each cycle may be considered to consist of three major activities as indicated below.

(1) *Water carrying*

Flying from the nest under construction to the nearby water source, filling the crop with water and returning to the nest.

(2) *Shaft excavation (sinking) and turret building*

Regurgitation of some of the water onto the earth at the working face of the vertical shaft being sunk, the excavation with the aid of the mandibles of the resultant mud and the moulding thereof into a pellet (building block), the transport of this pellet up the shaft and its addition to the free edge of the turret rising up above the mouth of the shaft. This major activity is repeated a number of times within each cycle.

(3) *Grooming*

Grooming of the head in general and the antennae in particular before setting out to fetch the next crop-full of water—that is, before initiating the next cycle.

It will be seen that the excavation of the subterranean portion of the nest is intimately linked with the building of the turret above ground and that the size of the turret (provided it has not been damaged) provides a clear indication of the extent of the underground workings.

A wasp occupied in nest building in the Grahamstown garden on 16.xii.1972 was observed for a period of 60 minutes. During this time 13 of the above defined cycles were completed. About 12 minutes were devoted to water carrying and about 48 minutes were spent on activities at the nest (shaft excavation and turret building as well as grooming). Within the 60 minutes, 68 mud pellets were formed from excavated materials (derived from the excavation of the vertical shaft) and placed in position on the free edge of the turret.

Similarly, a wasp, observed at Hilton on 1.iii.1973, completed 11 of the above defined cycles in a period of 39 minutes, of which 6 minutes were devoted to water carrying and 33 minutes to activities at the nest. Within the 39 minutes, 52 mud pellets were formed and positioned, resulting in an increase of turret length of between two and three centimetres.

The nests of both these wasps were situated close to the water source being utilised—the former about 7 metres distant, the latter 2,3 metres (Plate 2). When fetching water *D. pulchricoma* alights near the water's edge, walks the last few centimetres and drinks from the edge of the puddle. Similarly, when returning to the nest, she commonly alights 15 to 30 centimetres away from the turret and walks the rest of the way but occasionally alights much closer to the turret or even lands upon the latter. Flights to and from the water is generally direct and rapid.

On returning to the turret the wasp enters it head first. Shortly thereafter her head reappears at the free edge of the turret holding between her mandibles a glistening pellet of very wet mud. This is placed in position on the free edge of the turret by the wasp which builds from within the latter, only her head and prothorax emerging. Having positioned the pellet, the head disappears again only to reappear a short while later with the next pellet. The number of pellets formed by the removal of material from the shaft face and positioned on the turret edge varies from 2 to 8 (with an average of 5) per single water load. Though it could not be observed, it is believed that the very wet mud pellet, in addition to being held by the mandibles, is supported from below by the stiff mental bristles which would act in the manner of a pitchfork.

The last pellet of a batch having been formed and positioned, the wasp grooms thoroughly before departing for more water. This grooming, in which particular attention is given to the antennae, may take place in the turret entrance or on the ground next to it.

Nest construction appears to take place during the hottest period of the day—the building activities described were observed between about 10.40 a.m. and 1.30 p.m. although already begun before and continued after these times. Building is carried out only in strong sunshine; when the sun is obscured by clouds work ceases.

During the period of nest construction, when the females are frequent visitors to the puddles and pools where they obtain their water, their presence or absence at such water sources is a reliable guide as to whether nesting is taking place in any given locality. Males, which in the present study were never observed at the actual nesting sites, are found near these watering places. At Hilton, males, if not on the wing, could frequently be flushed from tussocks of coarse grass and sedges fringing pools visited by the females (Plate 2 and 4). These circumstances suggest that mating may take place at the pools, when the females come to these for water.

DESCRIPTION OF THE NEST TURRET

The turret built above the entrance to the subterranean part of the nest is more or less circular in cross section, is of variable diameter along its length and is curved in at least the vertical plane. For any given nest the extreme base or foundation of the turret wall is at a fixed distance from the nearest edge of the vertical shaft opening and is obviously a function of the size of the wasp builder. Therefore, any deviation from the circular in the shape of the shaft opening is mirrored in the shape of the turret foundation and large wasps build turrets of greater bore than do small ones. Generally the internal diameter of the turret at its base is about three times that of the vertical shaft, with the consequence that there is incorporated within the structure of the nest a platform-like disc of the ground surface, bounded at its circumference by the turret walls and pierced at its centre by the entrance to the vertical shaft. As the turret rises the bore generally increases slightly, then decreases again to form basally a weakly developed bulb-shaped bulge beyond which the bore continues to decrease gradually towards the distal turret opening. For 42 turrets measured, the outside diameter at the foundation varied from 14 mm to 26 mm, the most common diameter was 19 mm and the average 20,5 mm; the outside diameter at the distal end of 24 of these turrets (those which were considered complete or near-complete) varied from 10 mm to 18 mm, the most common diameter was 13 mm and the average 13,5 mm.

Turrets generally start off subvertically but almost immediately begin to curve over to one side to form an arch over the ground and to bring the turret entrance down close to the latter. If the turret is lengthened by the addition of further excavated material, it then levels out horizontally and runs parallel to the ground to which it may or may not be attached. This section of the turret may curve laterally or become sinuous. Only one of a total of 64 turrets studied did not initially rise up above the ground—instead, for its entire length it ran along the ground which latter formed the floor of the domed runway.

The height above the ground attained by the top of the turret arch was found to vary considerably in the 25 turrets suitable for measuring—from 13 mm to 65 mm; 50% of these turrets fell in the 24—27 mm range and the average height of all 25 turrets was 28 mm.

The length (measured along the outside of the curve) of 15 intact turrets belonging to nests containing at least one cell varied from 42 mm to 140 mm; 50% of these turrets fell in the 60—80 mm range and the average length of all 15 turrets was 77 mm.

The pellets used as building bricks in turret construction are roughly elongate-oval in shape with a slight constriction at the middle of the long axis and approximate best to the form of a two-seeded peanut pod. Each pellet is laid with its long axis orientated across the long axis of the turret. The pellets vary somewhat in size between different turrets and sometimes also within different sections of any one turret. This variation is probably due not only to differing wasp sizes but also to varying physical conditions of the soil. The pellets forming the walls of the basal bulge are generally closely packed and leave but few interstices of small size between them. Beyond the bulge the pellets tend to be more loosely laid and leave between them large spaces giving this section of the turret a lacy appearance. No smoothing or plastering of the bore of the turret is practised by the wasp and the individual pellets are as distinct on the inside surface of the turret walls as on the outside.

A well-built turret of typical form surmounting underground workings consisting of a single, sealed cell situated at the end of a 118 mm long vertical shaft (Fig. 2) was photographed in the field at Hilton (23.xi.1972) and is shown in Plate 6. Its dimensions are: outside diameters at base and at end 18 and 12 mm respectively; height of top of arch above ground 29 mm; total length 70 mm.

The turrets have little resistance to wetting and even a very light shower of rain will cause the pellets to melt and the turret to collapse. A total of 22 rain-damaged turrets were found at various times during the season, 20 of which had been subject to subsequent building activity. A new turret is frequently built out from what remains intact of the original one but is often inferior in construction and size to the latter and usually consists of little more than a crudely-added, narrow, lacy tunnel akin to the narrow distal portion of a normal extended turret. In one instance, where the original turret had only reached half the height of the basal bulge before being damaged by rain, the replacement of very inferior construction was built within the walls of the old structure.

Thus it is believed that the additions built subsequent to rain damage are not repairs but rather a continuation of normal building activity which would have taken place in any case at the free distal end of the turret but which activity has been shifted back in position to a new distal end—the point beyond which the original structure was destroyed. The inferior quality of the additions is thereby explained: what is more difficult to explain, however, is an instance in which a turret replacing a large collapsed one was of normal form though rather smaller than average.

The function of the turret is unclear. It seems unlikely that it would prove much of a deterrent to a determined parasite or even a casual one—it certainly did not prevent five separate instances of nest parasitism by leaf-cutting Megachilidae, though it must be stated that, perhaps significantly, in all five cases the turrets were not very extensive and consisted only of that portion up to the top of the arch. As already stated, the turret is destroyed by even a light shower but it is possible that its collapse may be of advantage to the wasp in that the debris plugs the entrance to the vertical shaft preventing flooding of the underground portion of the nest. Finally it may be of some advantage to the wasp that on coming up the vertical shaft it does not immediately emerge into the open but rather does so only after passing through the turret through the walls of which it is able to see the surroundings.

DESCRIPTION OF THE SUBTERRANEAN BURROW AND AN ACCOUNT OF THE SEQUENCE OF CELL CONSTRUCTION AND PROVISIONING

A total of sixty nests in various stages of construction was excavated during the present study. In Table I, the underground workings of these nests are grouped into nine categories according to the number of cells associated with each nest.

The subterranean portion of the nest consists of a vertical or near-vertical shaft near the lower end of which are situated a variable number of cells. The vertical shafts of the 42 nests included in categories B—I of Table I (i.e. those shafts which were complete as indicated by the presence near their ends of at least one cell) penetrated into the ground to depths ranging from 55 mm to 180 mm, with an average penetration of 113 mm. Of the total of these 42 shafts, 76% were between 90 mm and 130 mm deep (long) and with this latter category of shafts was associated 71% of the total of 108 cells. The bore of the vertical shafts varied from 5 mm (a single abandoned shaft) to 11 mm (a single shaft) with 53 of the total of 60 shafts (i.e., 88%) having a bore of between 6,5 mm and 8,0 mm.

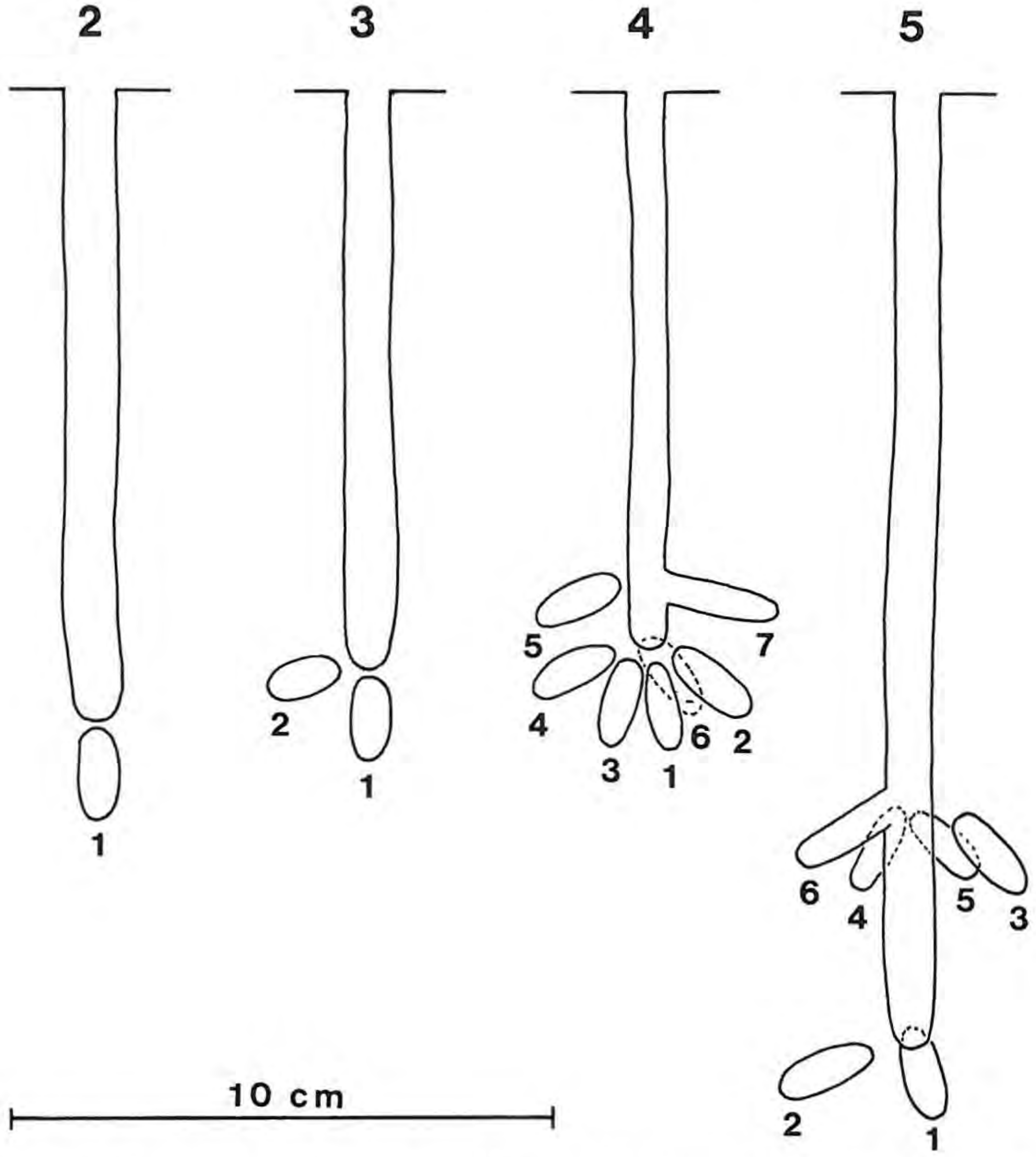
Table I. Analysis of the form of the underground workings of 60 nests of *Dichragenia pulchricoma* (Arnold) excavated near Grahamstown (26.x.1972–14.ii.1973).

Category	Description of underground workings	Number of nests
A	Shaft with no cells	18
B	Shaft with 1 cell (unprovisioned)	12
C	Shaft with 1 cell (provisioned)	6
D	Shaft with 2 cells (at least 1 provisioned)	6+(2)
E	Shaft with 3 cells (at least 2 provisioned)	5
F	Shaft with 4 cells (at least 3 provisioned)	3
G	Shaft with 5 cells (at least 4 provisioned)	2
H	Shaft with 6 cells (at least 5 provisioned)	4+(1)
I	Shaft with 7 cells (at least 6 provisioned)	1
	TOTAL:	60

NOTE: Figures in brackets ( ) pertain to three nests in which for some unknown reason more than 1 cell was unprovisioned—in the former instance two nests each containing 2 cells, neither provisioned, in the latter instance one nest of 6 cells, only four of which were provisioned.

The cells which vary in length from 14 to 19 mm are formed by the sealing off by means of earthen plugs of the distal portion of short (15—25 mm), usually downwardly-inclined sideshafts which branch off from the vertical shaft at or near its terminal (bottom) end. These side shafts (and therefore also the cells) are excavated at roughly a common depth and are arranged around the end of the vertical shaft in a more or less radiating pattern (like the spokes of a horizontally orientated cart wheel). A cell may, however, lie directly beneath the end of the vertical shaft and may represent the sealed off original terminal portion thereof. (Figs. 2—4.)

In one nest with an exceptionally long vertical shaft, cells were found to have been



Figs. 2—5. Plans of the underground workings of four nests of *Dichragenia pulchricoma* (Arnold) excavated at Hilton during November, 1972, showing various degrees of complexity and also the sequence of cell construction and provisioning. For details of the condition of the prey spider and of the developmental stage of the wasp young within each cell see Table II.

constructed at two distinct levels—two from the end of the vertical shaft 180 mm below the surface of the ground, and a group of four radiating out from the shaft at a point 130 mm below the surface. (Fig. 5.)

The earthen plug between cell and vertical shaft is flush with the wall of the latter and once in position leaves little indication of the proximal part of the side shaft.

One cell at a time is excavated and as a rule only a single open cell is found at any one time in any one nest. As soon as the cell has been provisioned and oviposition has occurred, it is sealed, after which work commences on a second cell. It was not established where the earth utilized for plugging the cell comes from, but as it does not differ in colour or other appearance from the earth through which the vertical shaft passes, it is believed that it is obtained from within the nest. Possibly the earth is quarried near the end of the vertical shaft at a point close to the cell being closed, and possibly this quarry may subsequently form a convenient starting point for the excavation of the next cell.

The sequence of cell construction and provisioning in multicellular nests may readily be established by virtue of the degree of development attained, at the time of examination, by the wasp young within each of several cells. Clearly, the most informative nest in this respect is one which is still being worked upon by the adult female and which shows a wide range of cell conditions—from a newly excavated, open, and as yet unprovisioned cell to one (but preferably not more than one) containing a mature larva within a silken cocoon.

Figs. 2, 3 and 4 show plans of the underground workings of three progressively more complex nests in which is indicated the sequence of cell construction, as inferred from the wasp young within them. Fig. 5, pertaining to an already mentioned nest, shows an unusual nest plan but the typical sequence of cell construction. Table II shows the condition of the provision (prey spider) and the developmental stage of the wasp young found within each of the cells of these four nests.

In those nests in which it was present, the cell situated immediately beneath the end of the vertical shaft was found to have been the first to be constructed and provisioned. No particular order of construction could be established for the cells radiating out around the end of the vertical shaft but, in those nests in which these cells were numerous, a tendency was noted for later cells to be constructed at a level slightly above initial ones without, however, altering the general clumped arrangement of the cells. In the underground workings shown in Fig. 5 the marked separation between the initial (lower) two cells and the later (upper) four is seen as the consequence solely of the excessively and abnormally long vertical shaft and the abandonment of the lower level after the construction of only two cells there in favour of the more normal depth for cell construction.

IDENTIFICATION, COMPOSITION AND PHYSICAL CONDITION OF THE PREY USED FOR PROVISIONING THE CELLS

From the 72 provisioned cells of *D. pulchricoma* excavated during the present study 38 identifiable prey spiders were obtained. These spiders ranged in condition from some individuals on which feeding by the wasp young had not yet commenced to others which had had the entire abdomen and much of the cephalothorax consumed. The prey spiders of the remaining 34 cells had been completely devoured with the exception of the cheliceral fangs which were always left uneaten by the wasp larvae. With the addition of one specimen taken from a wasp in the act of transporting it to its nest, a total of 39 prey spiders was available for examination. These were identified as follows:

Lycosidae
21 specimens (15 females, 5 males and one specimen of indeterminable sex) (One female, a subadult)

Pisauridae
Euphrosthenops sp. 12 specimens (9 females and 3 males) (One female, a subadult)

Sparassidae (formerly included in Clubionidae)
Olios sp. 3 specimens (2 females and 1 male)
Pseudomicrommata vittigerum (Simon) 2 specimens (both females)

Salticidae (= Attidae)
1 specimen (a female)

Immediately apparent from the above prey identifications is the preponderance of adult spiders over subadults, females over males, and members of the Lycosidae over those of other families.

While a nest of two or more provisioned cells may contain prey spiders of one family only, it more frequently contains representatives of more than one family. Thus individual nests were found that were provisioned with Lycosidae and Sparassidae, Lycosidae and Pisauridae, Pisauridae and Sparassidae, and Pisauridae and Salticidae.

The four spider families involved are all composed of strongly built, fast moving, wandering and predaceous ground-living forms which stalk and run down their prey on foot.

Of the total of 39 prey spiders examined, 32 had had all the legs amputated at the coxal-trochantal joint, three each had one leg remaining, and one had two legs remaining. The other three spiders were extensively eaten but between them possessed ten intact coxae from which the distal parts of the leg had been amputated. It is clear that *D. pulchricoma* habitually amputates the legs of its prey: that this amputation is carried out prior to the removal of the prey to the nest was demonstrated by the legless state of the spider, previously mentioned, which was taken from a wasp in the act of transporting it from the point of capture to the nest being provisioned. The pedipalps, by contrast, are not removed.

In size, the total length of the legless spider bodies varied from 8—13 mm, the most common length being 12 mm; the maximum width (measured across the cephalothorax and the leg stumps for all specimens except *Olios* sp. which was measured across the abdomen) varied from 4—6 mm, the most common width (58%) being 5 mm. The "dressed weight" of only one prey spider was established. This specimen, a freshly caught adult female lycosid of average size (total length 11 mm, maximum width 5 mm) and with all the legs amputated weighed 76 mg., somewhat less than double the weight of an average sized female wasp.

MODE OF TRANSPORT OF THE PREY AND THE POSITIONING OF THE LATTER IN THE CELL

Only once was *D. pulchricoma* observed transporting its prey. This was at Hilton (23.xi.1972) where a female wasp was seen carrying a legless female lycosid across open ground in an area in which were located several nest turrets. Progression, with the wasp facing the direction in which it was going, was by a series of short hopping flights, the wasp alighting every few centimetres and running a short distance before trying to take off again.

The spider, held beneath the wasp's body and straddled by the wasp's legs, appeared to be positioned dorsum up and head forward. Unfortunately, the point at which the spider was grasped by the wasp's mandibles was not noted but, on the basis of the otherwise identical mode of prey transport observed in a related wasp species, it is believed to have been the base of one of the chelicerae. The related wasp, "*Pseudagenia*" *spilocephala* Cameron (? another species of *Dichragenia*), whose transport of prey was closely observed on three separate occasions, carried its prey (legless female Lycosidae and *Olios* sp.) beneath it, dorsum up, head forward (as in *D. pulchricoma*), grasped by the base of a chelicera. The actual hunting

Table II. Condition of the provision (prey spider) and stage of development of *Dichragenia pulchricoma* (Arnold) young within each of the cells (listed in order of their construction) of four nests (see Figs 2—5) excavated at Hilton during November 1972.

Nest (Fig. No.)	Cell	Condition of cell	Condition of provision (prey spider)	Stage of development of wasp young
2	1	Sealed	Not fed upon	Egg
3	1	Sealed	Abdomen fed upon	Small larva
	2	Sealed	Not fed upon	Egg
4	1	Sealed	Completely devoured	Larva within silken cocoon
	2	Sealed	Completely devoured	Larva within silken cocoon
	3	Sealed	Completely devoured	Larva within ½-spun silken cocoon
	4	Sealed	Completely devoured	Very large larva
	5	Sealed	Abdomen fed upon	Small larva
	6	Sealed	Not fed upon	Egg
	7	Open	(None present)	(None present)
5	1	Sealed	Completely devoured	Larva within silken cocoon
	2	Sealed	Completely devoured	Very large larva (15 mm. long)
	3	Sealed	All of abdomen and part of cephalothorax eaten	Medium sized larva (11 mm. long)
	4	Sealed	Abdomen fed upon	Small larva (9 mm. long)
	5	Sealed	Not fed upon	Egg
	6	Open (Wasp builder found in this cell)	(None present)	(None present)

and stinging of the spider by the wasp and the process of leg amputation was not observed in either of the species.

The position in which the prey spider was placed in the cell by *D. pulchricoma* was without exception such that it rested with its ventral surface on the floor of the cell with its head towards that end of the cell nearer the vertical shaft.

OVIPOSITION AND IMMATURE STAGES

Oviposition upon the prey spider takes place only after the latter has been positioned within the cell. Great consistency with regard to orientation and site of attachment of the egg is shown—thus in the observed cases, the egg was without exception found to be securely attached in a somewhat oblique position to the side of the spider's abdomen, near the base of the latter. The morphological anterior end of the egg was uppermost (Figs. 6 and 7). There was no observable preference for either the right or the left side of the spider's abdomen, equal numbers of eggs (and also larvae) being found on both sides.

The young larva on hatching from the egg was found not to move away from the position in which the latter was laid but to commence feeding at the site thus determined for it. The point at which the spider's integument was punctured and where feeding began was on the dorsum of the abdomen to one side of the midline, in the region occupied by the spider's digestive gland (Plate 9). Young larvae engaged in feeding, during which the head was kept firmly applied to the puncture, were observed to engage in pulsating or pumping movements over the entire body. It was found that, when all the fluids had been thus imbibed and the larva had grown stronger, chewing of the harder portions of the abdomen began and the larva's fixed position upon the prey was relinquished. When the abdomen had been completely eaten, the cephalothorax was started upon, beginning at the posterior end and progressing forwards until the whole of the prey including the coxae and the pedipalps but excluding the cheliceral fangs was consumed.

When all the provision has been eaten, the mature larva spins its pale brownish-yellow, partly translucent, parchment-like cocoon which is attached to the cell's walls by fine silken threads. A small opening is left at that end of the cocoon that is situated at the distal end of the cell (i.e., that end away from the vertical shaft) and the head of the mature larva may be seen at this opening at the time cocoon spinning is completed. Thereafter the larva reverses its position within the cocoon thereby bringing the head toward that end through which the adult will emerge. Meconium is released at the cocoon's opening at which the hind end of the larva is now situated, to form a hard, dark-coloured plug sealing the cocoon and, by sticking onto the cell wall, further anchoring the former to the latter.

The uneaten cheliceral fangs of the prey are to be found adhering to the outside of the cocoon.

Measurements pertaining to the egg, to the larva at various stages of its existence (with reference to the site of its feeding upon the prey) and to the cocoon are given in Table III.

PARASITES AND OTHER ASSOCIATED ORGANISMS

In the sixty nests excavated during the present study remarkably few parasites and other associated organisms were present.

Two cocoons obtained from separate nests of *D. pulchricoma* at Hilton on 24.xi.1972, though similar to those of that species in general shape, appearance and size (12 mm × 6 mm), differed noticeably from them with respect to detail. Thus these two cocoons were harder, darker in colour and were constructed of a greater thickness of silk spinnings, the silk thread itself being coarser. Adhering to the outside of the cocoons were the spider's cheliceral fangs,

6

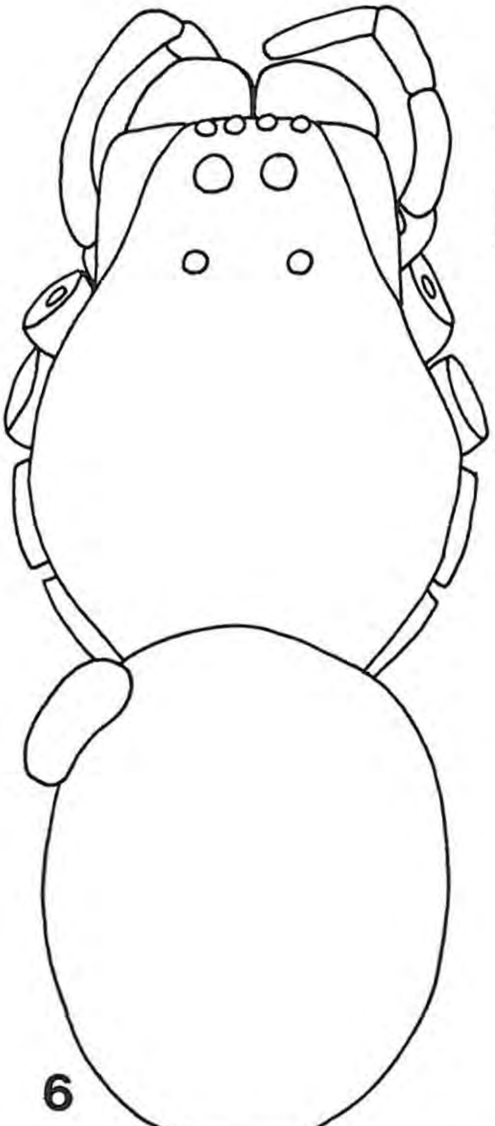


Fig. 6. Egg of *Dichragenia pulchricoma* (Arnold) in position on the abdomen of a lycosid spider (dorsal view).

7

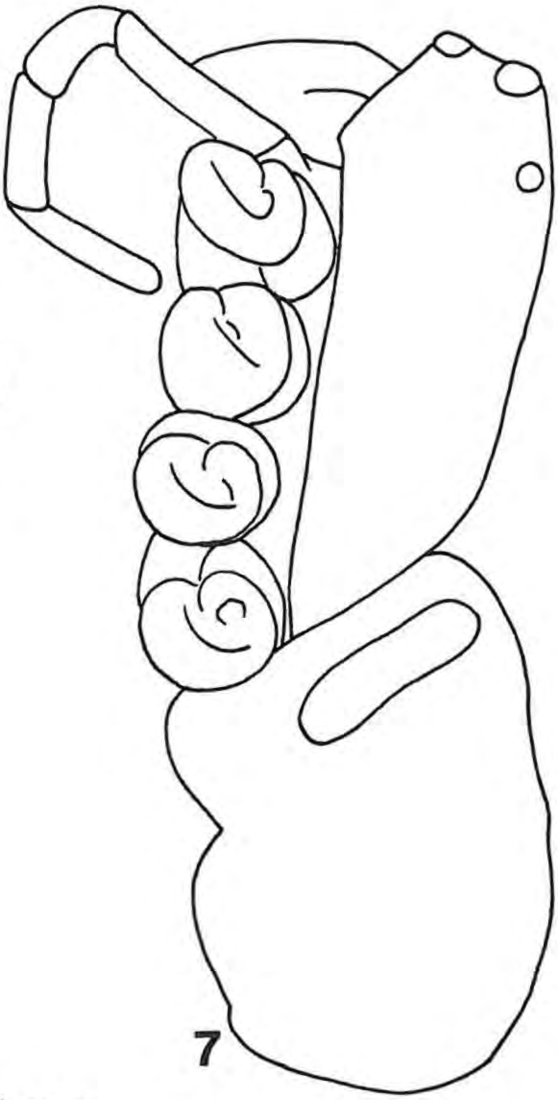


Fig. 7. The same (lateral view).

Table III. Measurements pertaining to the egg, to the larva at various stages of its existence (with reference to the site of its feeding upon the prey), to the cocoon and to the adult of *Dichragenia pulchricoma* (Arnold).

Stage	Size range (mm.)	Number measured
Egg	1,9 × 0,6—2,3 × 0,8 (average: 2,1 × 0,7)	6
Larva feeding on spider's abdomen	2—9	7
Larva feeding on spider's cephalothorax	9,5—15	4
Larva which has completed feeding but has not commenced cocoon-spinning	15—16	2
Cocoon	9,5 × 4—12,5 × 5,5 (average: 10,8 × 4,8)	20
Adult		
(*a*) female	10—16 (average: 13,1) (74% 12—14)	39
(*b*) male	8—11 (average: 9,6) (81% 9—10)	21

as is the case with *pulchricoma* cocoons. One of the two cocoons, damaged in the excavation, was opened (on the date of excavation) and within was found a developing pupa with legs, wing buds and head clearly distinguishable. The second cocoon was kept in a geletin capsule and 39 days later yielded a male *Ceropales punctulatus* Cam. (Pompilidae: Ceropalinae) which had emerged after cutting off one of the ends of the cocoon. *C. punctulatus* appears to be a common, widespread species and is represented in the Albany Museum by specimens from Mamathes (Lesotho), Kenton-on-Sea and various localities around Grahamstown. Dates of capture range from October to May. *Ceropales* species are known to be cleptoparasites on other Pompilidae but as far as can be ascertained no "host" wasp has hitherto been recorded for this species.

Five nests examined at Hilton during the period 16.xi.1972 to 1.xii.1972 were found to have been invaded for the purpose of nesting by leaf-cutting bees. In all cases the nest excavations were incomplete and consisted of a vertical shaft without any cells (Category A in Table I), surmounted by a turret that had barely attained the top of its arch. In Fig. 8 are shown, diagrammatically, the lengths of the leaf-nests constructed by these bees and their positions within the vertical shafts. A further *pulchricoma* nest, examined at Hilton during the same period, and consisting of 5 sealed cells and the beginning of a sixth cell, was found to have two disc-shaped pieces of bee-cut leaf in the vertical shaft. The bee responsible for the leaf-nest in one of the five former nests was captured, when emerging from the turret of the latter, and was identified as *Megachile* (*Eutricharaea*) *stellarum* Ckll. (Megachilidae: Apoidea). This species

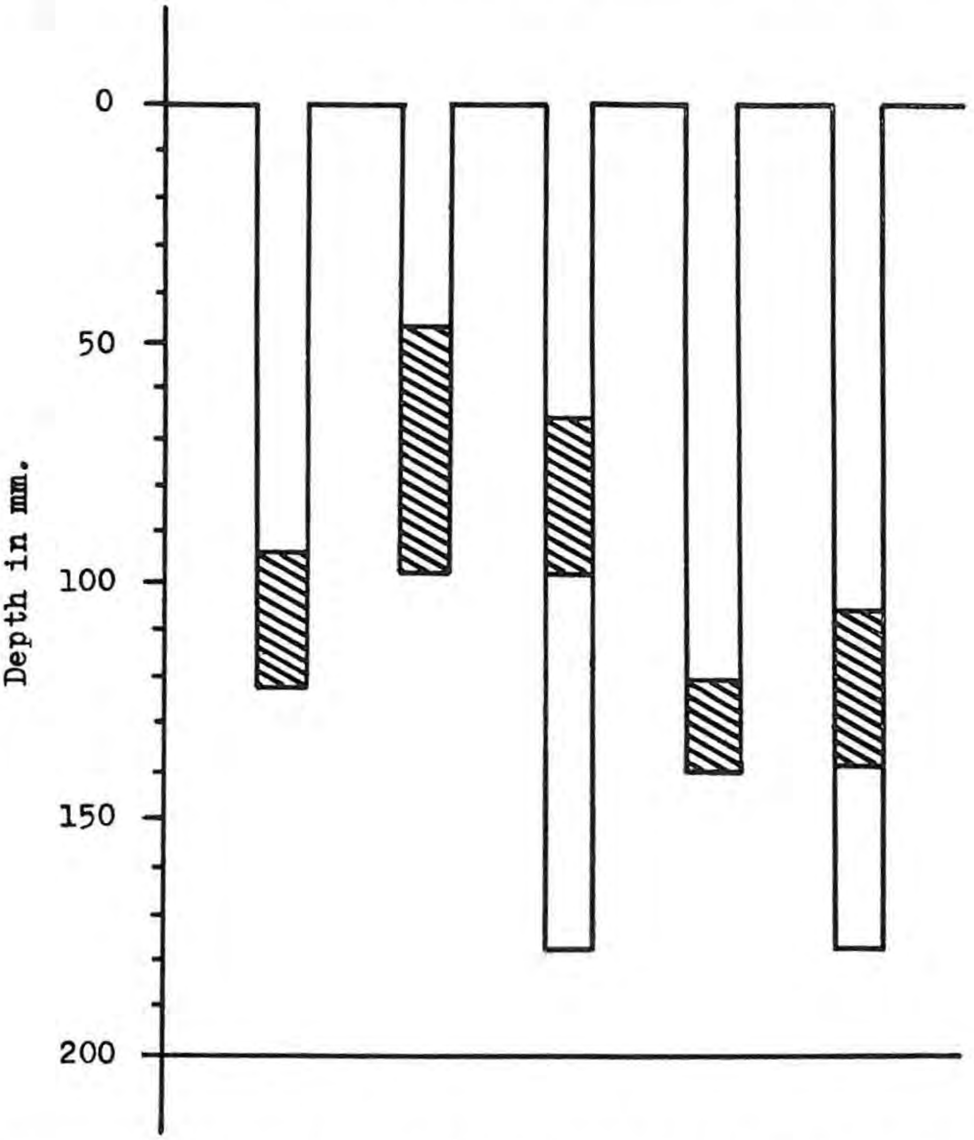


Fig. 8. Positions and lengths of megachilid leafnests within five vertical shafts of *Dichragenia pulchricoma* (Arnold).

has a wide distribution in East and South-East Africa (Pasteels, 1965:266) and is one of the most common megachilids around Grahamstown, where its flight period, as indicated by specimens in the Albany Museum collection, is from November to March. Little is known concerning its biology but it probably nests in any suitable cavity. While it is clear that in these cases *D. pulchricoma* was superseded by *M.* (*E.*) *stellarum* in its nests, it is not evident whether or not competition for the burrows arose—whether the bee ousted the rightful owner or whether it merely occupied the burrow left untenented following its abandonment by, or the death of, the pompilid builder.

Three multicellular nests excavated at Hilton during the period 1.xii.1972 to 6.xii.1972 each included one sealed cell whose contents was overrun by pale-coloured mites. Two of these cells contained prey spiders in a very poor state of preservation on which wasp eggs or larvae could not be found; the third cell contained the rotten remains of a mature larva in its cocoon. The remains of the mature larva and of one of the prey spiders were also covered with the hyphae and the small white fruiting-bodies of a fungus.

FLOWERS VISITED BY ADULT WASPS

Adult *D. pulchricoma* of both sexes have been observed visiting flowers for the purpose of imbibing nectar. The following associations of wasps and their forage flowers have been recorded: one female on *Foeniculum vulgare* Mill. (Umbelliferae) at Belmont Valley, Grahamstown on 24.i.1970 (C. F. Jacot-Guillarmod); three males on *Maytenus linearis* (L.f.) Marais (Celastraceae) at Hilton, Grahamstown on 6.xii.1972 (F. W. & S. K. Gess); and three females on *Zizyphus mucronata* Willd. (Rhamnaceae) at the Koonap River near Adelaide (C.P.) on 20–22.xii.1972 (C. F. Jacot-Guillarmod). The flowers of all three plant species are small and inconspicuous, pale yellow or greenish-yellow in colour, with nectar, secreted on a freely exposed disc, easily accessible to short-tongued wasps such as *pulchricoma*.

DISCUSSION

The ethology of *Dichragenia pulchricoma* (Arnold) exhibits two outstanding features which mark this species as unique, firstly within its tribe, secondly within its family. Both these features pertain to the nest—to the subterranean position of the cells and to the presence of a turret rising above the burrow entrance.

As already shown, *D. pulchricoma* is, judged on morphological grounds, a member of the tribe Macromerini (= Auplopodini) of the subfamily Pepsinae, and is closely related to species of the genera *Phanagenia*, *Auplopus* and *Ageniella*, with which it has in common certain aspects of behaviour with respect to prey selection, prey mutilation and prey transport.

The four spider families (Lycosidae, Pisauridae, Sparassidae and Salticidae), species of which are, in the present paper, recorded as being the prey of *D. pulchricoma* are amongst the eleven families recorded as prey of the genera *Phanagenia*, *Auplopus* and *Ageniella* by various authors: Evans and Yoshimoto (1955:17), Kurczewski (1961:23–4), Kurczewski and Kurczewski (1968a: 6–8, and 1968b: 369), Peckham and Peckham (1898:164), Richards and Hamm (1939:73), Townes (1957:143–219) and Wasbauer and Powell (1962:395).

Amputation of the legs of their prey spiders at the coxal-trochantal joint, prior to the removal of the prey to the nest is a characteristic behavioural feature of the Macromerini and is recorded in *Phanagenia*, *Auplopus* and *Ageniella* by the above listed authors.

The method of transporting the prey to the nest practised by *D. pulchricoma* is the same as that reported for *Phanagenia* by Kurczewski (1961: 23—4), a method apparently adopted also by *Ageniella* but not by *Auplopus* (Kurczewski, 1961: 24, and 1968a: 6—8). The latter, though also straddling the prey, transports it venter up, grasped by the spinnerets and not dorsum up, grasped by the base of a chelicera, as is the case in the other genera.

Although there is a strong similarity between *D. pulchricoma* and members of the other genera in various aspects pertaining to the prey, there is a remarkable dissimilarity in the form and situation of the nest.

The Macromerini are characterized by their construction using wholly foreign materials, primarily mud, of aerial nests consisting of separate but adjacent cells. In the nature of their construction these nests parallel those built by some Eumenidae and some Stenogastrinae (Vespidae).

Among the species whose nesting is better known is the widespread North American *Phanagenia bombycina* (Cresson). An early account, based upon examination of a nest found in New Hampshire was published by the Peckhams (1898: 164—5). The nest in question was built under a stone and consisted of sixteen small mud cells about 15 × 8 mm. Townes (1957: 143) lists various records and confirms that "its nest of mud cells is placed usually under stones".

Concerning the very large genus *Auplopus*, Townes (1957: 145) states that probably all species nest in mud cells. Two instances of the nest-building of the North American *Auplopus architectus* (Say) were reported by the Peckhams (1898: 165—6): one set of three cells (each 8 mm long by 5 mm wide) being constructed in the folds of an undisturbed furled flag upon a porch, another set of two cells being fastened to the inside of a boat house. Concerning the same species, Townes (1957: 165) states that the cells which are made of hard clay are always "under a stone in the open, in an irregular group of usually three to five, plastered to the stone and against one another, in a place the stone happened to be raised above the soil enough to give the female space". Other North American species of *Auplopus* are recorded by Townes as building their mud cells in a variety of locations such as under logs, under loose bark or in various holes and crevices including old mud nests of species of *Sceliphron* and *Trypoxylon*. Evans and Eberhard (1970: Fig. 67) published a drawing of the nest of a Philippine species.

Among the few species of the genera *Phanagenia* and *Auplopus* whose nesting has been noted, some degree of variation in the placement of the mud cells thus occurs but in all cases the nests have been aerial. No record of subterranean nesting by a member of the Macromerini has been found in the literature available to the authors for consultation, and *D. pulchricoma* which does construct its cells in the ground thus appears to be unique within its tribe.

The form of the subterranean portion of the nest of *D. pulchricoma* seems to approximate most to the nest of the North American *Priocnemis minorata* Banks which has been closely described and figured by Yoshimoto (1954). *Priocnemis minorata* belonging to the tribe Pepsini of the subfamily Pepsinae (which includes as its other tribe the Macromerini), constructs an open nest in heavy clay-loam soil, containing from one to seven cells arranged more or less spirally in ascending order around the common vertical shaft excavated by the wasp. Several other species of the tribe Pepsini, notably *Priocnemis exaltatus* (Fabr.) in Sweden and two species of *Priocnemioides* in Chile have likewise been observed by various authors (see Evans, 1953) to construct several lateral cells from a common burrow. However, the nest of *D. pulchricoma* differs from those of these behaviourally advanced Pepsini and indeed from the nests of all other Pompilidae (at least those species whose nesting has been studied and recorded) in having the entrance to the subterranean burrow surmounted by a mud turret.

The ethology of *D. pulchricoma* thus appears to be in some respects intermediate between that of the ethologically advanced species of the tribe Pepsini (such as *P. minorata*) which construct multicellular subterranean nests and that of those Macromerini (such as *Phanagenia* and *Auplopus* species) which construct aerial mud nests. However, rather than forming a connecting link between these two ethological groups, it seems likely that the ethology of *D. pulchricoma* represents a side branch arising at this point from the main stream of the ethological evolution of the Pompilidae.

As indicated by Evans (1953) in his account of the comparative ethology of the Pompilidae, the Macromerini which build aerial nests belong to a special group arising from ground nesting forms which like themselves belong to an advanced ethological type characterized by the fact that nest building precedes hunting, a sequence not widespread in the Pompilidae but shown by all species constructing multicellular nests. It is clear that ethologically *D. pulchricoma* shared the same origin with these other Macromerini with which, as shown, it has in common the behaviour with respect to prey selection, mutilation and transport, while at the same time retaining the more conservative nesting situation. Like them, *D. pulchricoma* is a worker in mud but, whereas *Phanagenia* and *Auplopus* species which freed themselves of the ground use this medium to build aerial cells, *D. pulchricoma* uses it to build a turret with which to surmount the burrow entrance. In this connection it is of interest that the use of the pygidium as a "trowel" for smoothing the surface of the mud structure as reported for *Auplopus* by Evans and Eberhard (1970: 100 and Fig. 67) is not seen in *D. pulchricoma* which as already stated does no smoothing of its turret walls.

Finally, it is interesting to note the similarity between the multicellular subterranean nests surmounted by mud entrance turrets as built by *Dichragenia pulchricoma* (Arnold) of the Pompilidae and those built by some Eumenidae and some Masaridae (*Ceramius* species) and that in all three families the ethological evolution with respect to the situation and form of the nest is from simple nests in the ground to free aerial mud nests, a trend paralleled also in the Sphecidae.

SUMMARY

The ethology of *Dichragenia pulchricoma* (Arnold) (Hymenoptera: Pompilidae: Macromerini) in the Eastern Cape Province of South Africa is described. Various facets of the nesting behaviour are dealt with but particular attention is given to the description of the form of the nest, which by possessing a mud entrance turret appears to represent a nest-type previously unknown within the Pompilidae. The nest situation and type as well as various aspects of behaviour relating to nest provisioning are compared with those exhibited by related genera and the position of the present species within the ethological evolution of the Pompilidae is suggested.

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Plate 1. Hilton, 15.xi.1972. Excavation of a nest situated on the side of a small erosion gulley.

Plate 2. Hilton, l.iii.1973. Situation of a nest (marked by arrow) on raised bank of earth. Note rain water pool, sedges and grasses.

Plate 3. Hilton, 9.ii.1973. Situation of a nest (marked by spray-can in lower left corner) at a step in the ground level of an eroded area. Note rain water pool.

Plate 4. Hilton, 12.xi.1972. Situations of nests (marked by figures) on bare earth path running parallel to water furrow.

Plate 5. Hilton, 23.xi.1972. Newly begun turret in bare sheet-eroded area. (Burrow opening at lower right is that of an eumenid.) (× 1)

Plate 6. Hilton, 23.xi.1972. Well-built turret of typical form surmounting the underground workings shown in Fig. 2. (× 1.2)

Plate 7. Hilton, 9.ii.1973. Turret of nest, the situation of which is shown in Plate 3. (x 1)

Plate 8. Hilton, 9.ii.1973. Turret of nest constructed next to base of dwarf-shrub. (x 0,7)

Plate 9. Young larva of *Dichragenia pulchricoma* (Arnold) in feeding position on abdomen of a lycosid spider. (× 6)

Ethological studies of Bembecinus cinguliger (Smith) and B. oxydorcus (Handl.) (Hymenoptera: Sphecidae), two southern African turret-building wasps.

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CONTENTS

INTRODUCTION

The ethology of some species of *Bembecinus* Costa, a genus distributed throughout the warmer regions of the world, has in recent years been reviewed by Evans (1955: 295—302 and 1966: 132—143). That author drew attention to the uniformity exhibited by the ethology of those species which had been investigated up to those dates. In a very recent publication by Evans and Matthews (1974: 131) it was again stated that "little diversity in behavior has been demonstrated within the genus". African species have received scant attention and, other than for a record of the prey of a single species (Bridwell, 1937, cited by Evans, 1966: 142), the published information concerning biology is limited to some general remarks by Brauns (1911: 92).

The present paper is concerned with some aspects of the ethology of two southern African species, *B. cinguliger* (Smith) and *B. oxydorcus* (Handl.), which, by lacking the tarsal comb or sand rake usually associated with the fore-legs of these wasps, differ from other African species and indeed, as far as can be ascertained, from all other species of the genus. Correlated with this difference in the structure of the fore-legs is a marked difference in the nature of the soil in which nesting takes place and in the manner in which the subterranean burrow is excavated by the wasps.

Techniques adopted by the authors for examining the subterranean burrow are not discussed here, being similar in most respects to those described previously (Gess and Gess, 1974: 118—119).

GEOGRAPHIC DISTRIBUTIONS

The distributions of both *B. cinguliger* and *B. oxydorcus* appear to be restricted to southern Africa. As far as can be judged from available records *B. cinguliger* is confined to the southern parts of the Cape Province, whereas *B. oxydorcus* which occurs together with *cinguliger* in at least part of the latter's range (the Eastern Cape Province) is far more widely spread, occurring also in the Cape Province north of the Orange River, in Lesotho (formerly Basutoland), the Orange Free State, the Transvaal and Rhodesia. Actual localities of specimens of the two species in the Albany Museum collection are listed below.

B. cinguliger (Smith)

Alice, Alicedale (New Year's Dam), Carlisle Bridge, Ceres, Fullarton, Grahamstown (Hilton, Hounslow, Strowan and Table Farm), near Klipfontein, near Lake Mentz, Tarkastad, Thorngrove (N of Cookhouse), Waterford and Willowmore (all Cape Province). The species probably occurs also at Bloutoring Station (between Touws River and Ladismith) for wasps observed nesting there by the senior author in December, 1962, are believed to have been this species.

B. oxydorcus (Handl.)

Fort Brown, Grahamstown (Hilton), Kimberley, Koonap River (17 miles from Adelaide on Grahamstown road), Queenstown, Willowmore (all Cape Province); Tlametlu River (Lesotho); Aldam, Kroonstad, Senekal (all Orange Free State); Pretoria (Transvaal); Bulawayo (Rhodesia). Other localities from which this species has been recorded include Dunbrody (Cape Province) (Cameron, 1905: 323, as *Stizus Johannis* Cam.) and Bothaville (Orange Free State) (Arnold, 1929: 292).

Flight periods as indicated by the above specimens are October to March for *B. cinguliger* and December to April for *B. oxydorcus*.

LOCALITY AND DESCRIPTION OF NESTING SITES

Field observations in the present study were conducted at Hilton, a farm situated 18 kilometres WNW of Grahamstown (33° 19′S, 26° 32′E) in the Albany Division of the Eastern Cape Province of South Africa. Lying within the region of overlap in the distribution of the two *Bembecinus* species this locality is well suited to an investigation of these wasps. An account of the climate and vegetation of Hilton has previously been given (Gess and Gess, 1974: 191—192). Most of the observations were made during the summer of 1973—74 but certain observations dating from previous nesting seasons and also from the summer of 1974—75 have been included.

B. cinguliger and *B. oxydorcus* at Hilton showed the same preferences with respect to nesting sites and indeed were in some instances found nesting together. Nesting sites were

Plate 1. Hilton, 6.xi.1973. A nesting site of *B. cinguliger* (Smith).
Plate 2. Hilton, 11.iii.1974. A nesting site of *B. oxydorcus* (Handl.).

without exception found to be localized patches of bare earth occurring in low-lying areas sparsely covered by small, low-growing shrubs, mostly *Pentzia incana* (Th.) O.Ktze (Compositae) (Plates 1 and 2). The soil, derived from the Dwyka Series, was of a reddish brown clayey nature and contained no stones. In all cases nesting sites were found to be situated close to temporary sources of water. This water, a result of rain, had collected in muddy pools, erosion gullies and shallow furrows.

Both species were found to nest in pseudo-colonies which might, particularly in the case of *B. cinguliger*, become very populous with nest entrances situated close together. Excavation in the soil of a nesting area was found to bring to light many decapped *Bembecinus* cocoons dating from past nesting seasons, indicating the repeated use of the same nesting areas by successive generations of these wasps, a phenomenon made possible by the very slow regeneration of the plant cover of a denuded area.

FLIGHT SEASONS, MATING DANCE, PERIOD OF ACTIVITY OF ADULT WASPS AT THE NESTING SITES AND ADULT SLEEPING HABITS

The pattern of the build-up and subsequent decline in the numbers of the adult population of one of the species, *B. cinguliger*, at Hilton during a previous summer, that of 1970—71, was established as a by-product of the use of three Malaise traps of the pattern designed by Townes (1972). In the graph (Fig. 1) the average numbers of specimens caught per day between successive clearings of the traps' collecting jars are plotted at points midway in time between the dates of clearing during the four-month period November to February. During this period a total of 1248 specimens (152 males and 1096 females) was captured. Though trapping was continued for a full twelve months, the only occurrence of *B. cinguliger* in the catch was during the above four-month period, clearly showing that the species is univoltine. That the species is proterandrous and that females are present in the field longer than are males, as is clearly indicated in the graph, was borne out by the 1973—74 field observations. Thus the first sighting of a male of that season was on 3.xi.1973 but the first sighting of a female was not until 14.xi. 1973. The dates of emergence appear to be remarkably consistent in successive years. Thus during the 1974—75 nesting season first sightings of males and of females were on 8.xi.1974 and on 15.xi.1974, respectively.

No specimens of *B. oxydorcus* were caught in the Malaise trap. Field observations at Hilton during 1973—74 indicate that the flight period of this species starts later in the summer than does that of *B. cinguliger* and that this species is also proterandrous. Thus the first sighting of the season for males was on 2.i.1974 and the first sighting of a female on 7.i.1974.

The end of the 1973—74 flight season of *B. cinguliger* was during mid-March, the last sign of activity being observed on 13.iii.1974; the flight season of *B. oxydorcus* had not yet ended when field work was discontinued on 18.iv.1974.

Although *B. cinguliger* is still flying when *B. oxydorcus* starts nesting and although *B. cinguliger* and *B. oxydorcus* in some cases use the same nesting areas there is little direct competition between them as when nesting in *B. oxydorcus* is reaching its height that of *B. cinguliger* is rapidly falling off. It will be seen from a graph (Fig. 1) that the decline in nesting activity of *B. cinguliger* corresponds with a decline in the number of individuals following a peak in mid-December.

During the early part of the flight season of *B. cinguliger*, from the time of male emergence and lasting through the period of female emergence until some time after the initiation of the season's first nests, the newly emerged wasps execute what the Raus (1918: 9—17), writing about *Bembix nubilipennis* Cresson, so elegantly termed a "sun-dance".

In *B. cinguliger* this activity takes place at the bare patches of earth utilized for nesting by this wasp during season after season. It consists essentially of the proterandrous males patrol-

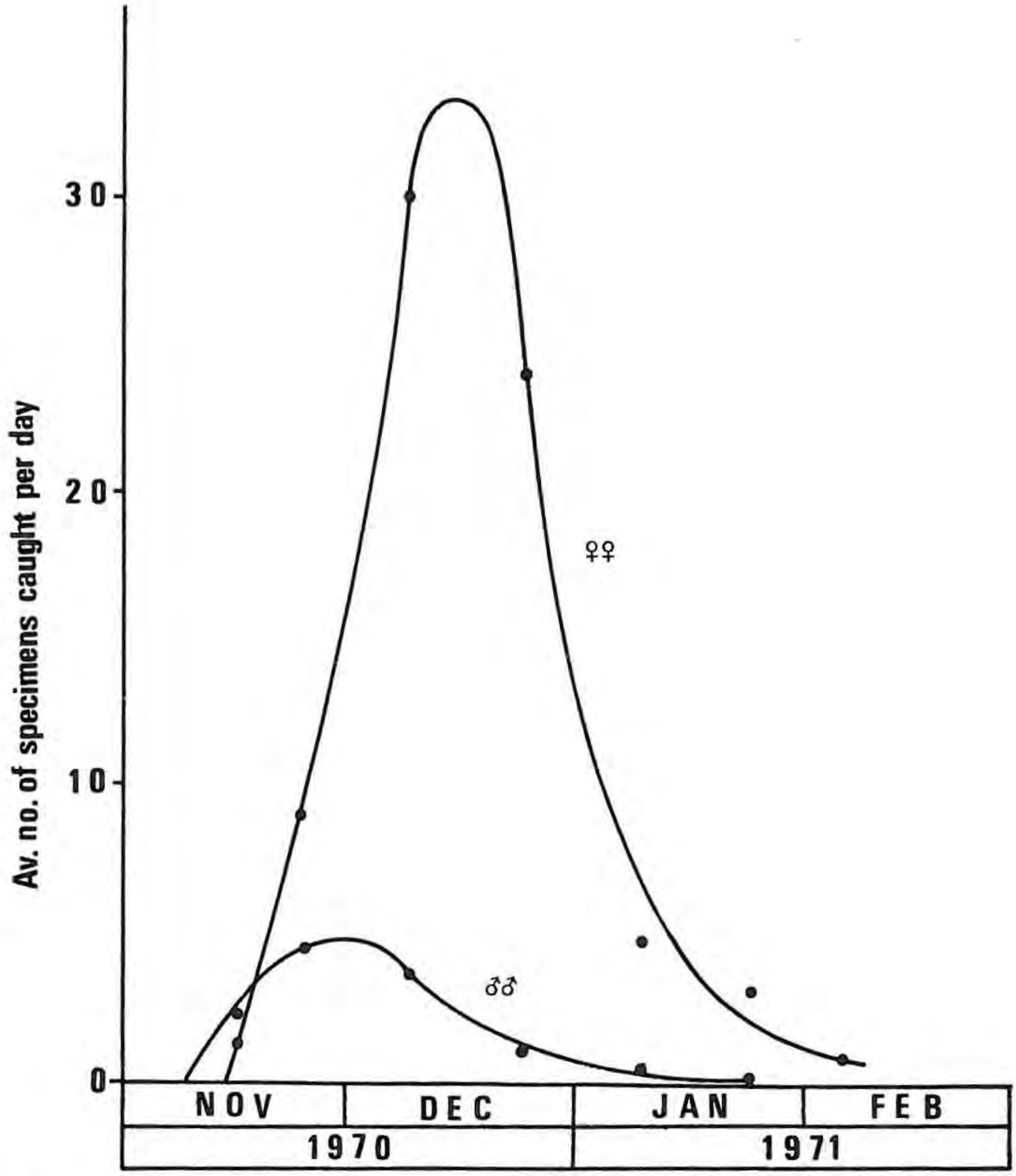


Fig. 1. Graph showing the average numbers of specimens of *Bembecinus cinguliger* (Smith) caught per day by three Malaise Traps at Hilton during the period Nov. 1970 to Feb. 1971.

ling these areas by flying on an irregular path within the confines of the bare patch at a height of 2—8 cm above the ground. When uninfluenced by other individuals, a male executes a slight up and down bobbing movement while flying along his path. However, whenever another individual is spotted the male flies rapidly towards it and the two individuals, possibly joined by further individuals, fly rapidly around each other, sometimes bumping into each other, before resuming their separate flightpaths. Each individual from time to time settles on the ground where it rests with wings folded over the back. An individual flying past causes the settled male to rise up immediately and to follow it, a reaction brought about also by the passage across the dancing area of wasps of other species and even by inanimate objects. Thus the authors found that small objects thrown across the bare area at a low height above the ground were immediately followed by several males, attracted to the objects from their patrolling flights or from their situations on the ground. A distinct humming sound is produced by the wasps flying about in numbers. It is clear that the activity of the males is directed towards locating and mating with the females as these emerge from the ground. Some days after the "dancing" has commenced and at a time when females have emerged, attempts at copulation may be witnessed between dancing wasps. Occasionally successfully copulating pairs may be seen to rise up together to a greater height above the ground and to fly off into the low bushes fringing the bare areas.

The above described "sun-dance" is a very noticeable feature of the beginning of the flight season of *B. cinguliger* at Hilton and has been noticed over a period of five or six years. However, no such activity has been noted for *B. oxydorcus*, probably due to the fact that this species occurs in so much smaller numbers. Clearly the existence of a "sun-dance" in certain species of wasps is dependent upon the formation by these wasps of pseudo-colonies situated in definite nesting areas. Similarly, the level of activity and therefore the degree to which it is noticed is dependent upon the number of individuals participating in the "dancing" which in turn is dependent upon the density of nests within a pseudo-colony.

Activity of the adult wasps at or near the nesting sites was found to be restricted to the hottest part of the day from late mid-morning until early afternoon.

Neither *B cinguliger* nor *B. oxydorcus* was found to spend the night in the nest, for nests inspected early or late in the day never contained adult wasps. Similarly, wasps were not found sheltering in the nests during the day if the weather was unsuitable for normal nesting activities. Indeed, adult wasps were absent from the nesting areas and not only from the nests themselves during these times.

As reported previously by Brauns (1911: 92) *B. cinguliger* (recorded by Brauns as *Stizus clavicornis* Handl.) is in the habit of forming sleeping clusters. Brauns at Willowmore (Cape Province) reported large assemblages of several thousand individuals, mostly females, forming clusters the size of a small child's head on bushes and low plants growing in sheltered localities.

Jacot-Guillarmod (pers. comm., 1973) reported seeing such a sleeping cluster at Hilton on the evening of 5.xii.1964. A sample taken at the time and now in the Albany Museum collection consists of 62 females and 36 males.

During the present study at Hilton, an extensive search by the authors of a wide area, including the type of situation in which Jacot-Guillarmod made his observation, led to the discovery on the morning of 11.i.1974 of a single sleeping cluster of *B. cinguliger*. Subsequent discussions with Jacot-Guillarmod led to the conclusion that the situation of the present sleeping cluster was virtually identical with that of 1964.

The present sleeping cluster was situated within a large tussock of the coarse grass, *Digitaria macroglossa* Henr., growing on the edge of the bank of a narrow, incised watercourse which at the time of discovery contained no water (Plates 3 and 4). The thousands of individuals clustered in the centre of the tussock exhibited no particular orientation except in

Plates 3 and 4. Hilton, 14.i.1974. Grass tussock (*Digitaria macroglossa* Henr.) utilized by *B. cinguliger* (Smith) for sleeping.

so far that those on the outer blades of grass were mostly facing inwards (that is, were orientated facing the basal end of the grass blades). At the time these observations were made (9.30 a.m.) the sky was heavily overcast and there was a cool breeze blowing. Very little movement of the clustered wasps took place when the grass blades were separated by hand in order to obtain a better view of the aggregation within the tussock. Neither on this nor on any of the subsequent occasions on which the sleeping cluster was examined was any aggression shown by the wasps. The few wasps which were disturbed rose up, flew about for a short time and then settled down on the tussock again.

A sample taken on this occasion (11.i.1974) consisted of 136 individuals all of which were females. From the samples taken in the first week of December and the second week of January, albeit in different years, it would appear that a sleeping cluster contains individuals of both sexes during the early stages of the wasps' flight season but only females during the later stages. This change in the composition of the members of a sleeping cluster is probably nothing more than a reflection of the fact that, whereas males are relatively common at the beginning of the flight season, their numbers fall off markedly in the later stages at a time when females are still common (see Fig. 1).

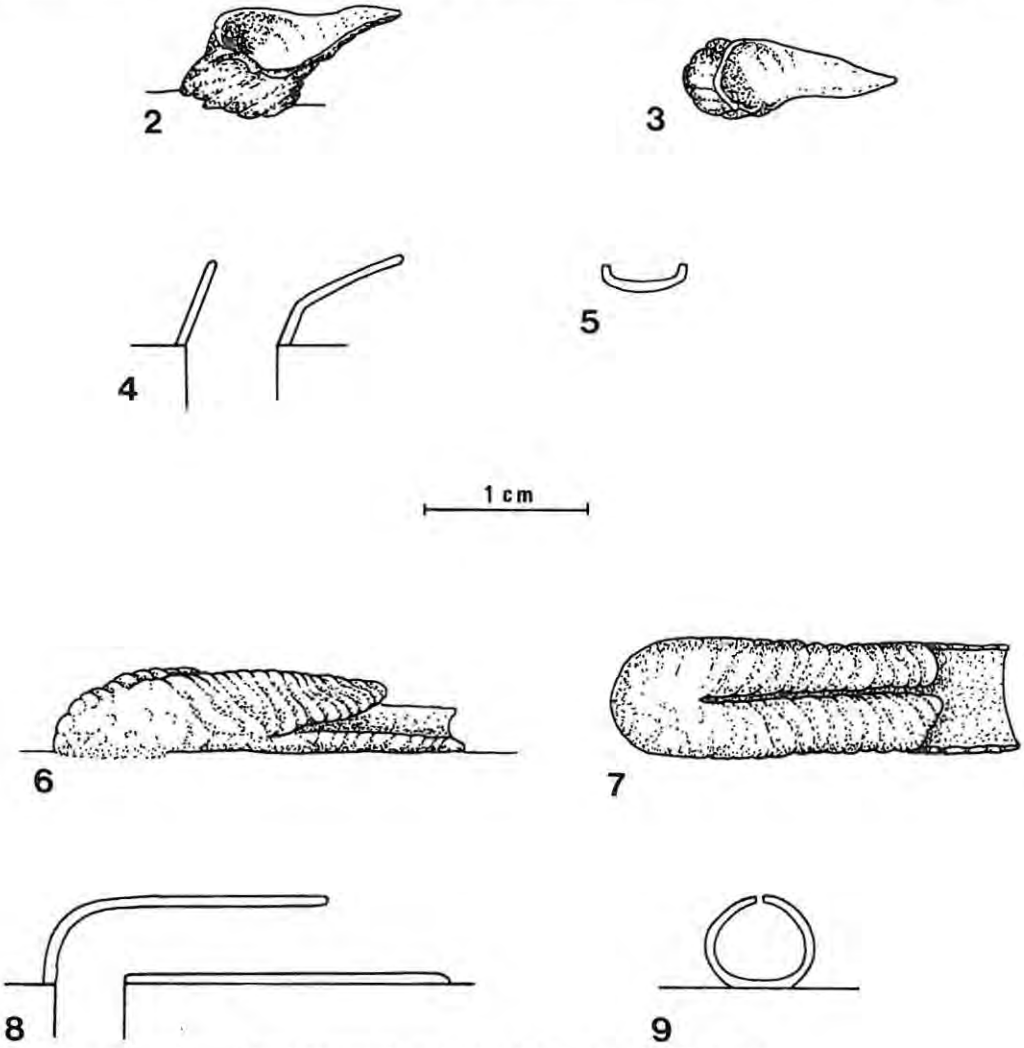
It is noteworthy that the situation of the sleeping place was at a considerable distance from the nearest nesting areas and that the soil near the watercourse was sandy and thus unsuitable for nesting. It appears that the members of the sleeping cluster were drawn from a wide area as the number present was far greater than that in any one nesting area.

The sleeping cluster was kept under observation for a period of forty-six days, from 11.i.1974 (the date of discovery) until 25.ii.1974. During this period use was made of the same tussock night after night to the exclusion of any other similar tussocks in the vicinity. The tussock utilized by the sleeping cluster was inspected a total of seventeen times in the forty-six days. Thirteen of these inspections were made in the morning, one in the afternoon and three in the evening. It was found that the behaviour of the wasps belonging to the sleeping cluster at the tussock was very strongly influenced by the weather. It was found that 9.25 a.m. on a hot, sunny, dry, windstill morning most of the wasps had already left the vicinity of the tussock, some were sunning themselves on the surrounding vegetation and a few were still in the centre of the tussock. At 10.55 a.m. on a similarly fine day no wasps at all were to be found either in the tussock itself or in the vicinity thereof, all having flown to the nesting areas. At similar times on mornings when the sky was overcast or a cool breeze was blowing most of the wasps of the sleeping cluster were found to have remained in the tussock and only a few individuals were sometimes visible on the outer grass blades. If conditions were slightly better with the sun periodically breaking through the cloud cover, many individuals were found sunning themselves on the outside of the tussock, on the surrounding vegetation and on the ground, particularly the sandy floor of the dry watercourse, and some were found flying about in the immediate vicinity of the tussock. If, as the morning progressed, the weather improved, wasps left to go to the nesting sites. However, if the weather deteriorated, wasps returned from the nesting sites and sheltered in the tussock. If weather conditions remained unfavourable throughout the day, the wasps did not leave the tussock or its immediate vicinity at all.

The time of return to the tussock in the afternoon on fine days was not established but at 6.00 p.m. on a warm sunny evening (13.i.1974) the wasps were found to be inside the tussock with none on the outer blades.

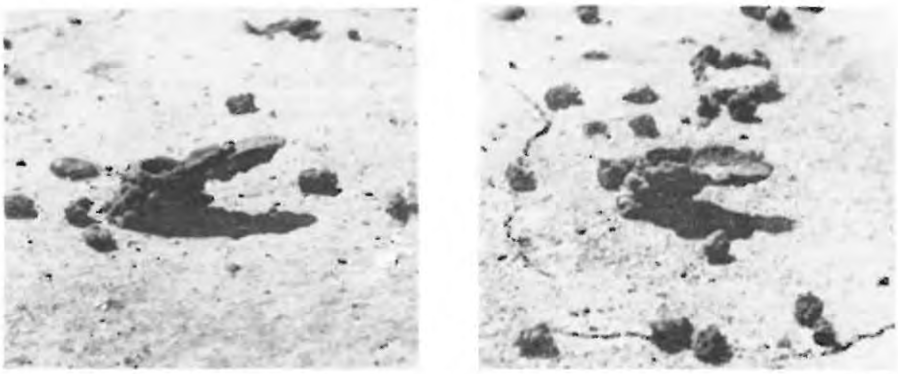
At all times the absence or presence of wasps at the tussock could be correllated with the reverse situation at the nesting sites.

Despite a careful search by the authors no sleeping cluster of *B. oxydorcus* was located though Brauns (1911: 92) reported that individuals of this species at Willowmore assembled in the evening in greater or lesser numbers on vegetation growing at the edge of pools, though never forming the dense clusters formed by *B. cinguliger*. In view of the similarity of behaviour of *B. oxydorcus* to that of *B. cinguliger* with respect to their absence or presence at the nesting site depending upon the time of day and upon weather conditions it is not surprising that *B. oxydorcus* also forms sleeping aggregations. Taking into account the fact that the numbers of *B. oxydorcus* at Hilton were always far fewer than those of *B. cinguliger*, the aggregations were probably similar in their nature and size to those reported for the former by Brauns. At Hilton



Figs. 2—5. *B. oxydorcus* (Handl.) turret; Figs. 6—9. *B. cinguliger* (Smith) turret.
Figs. 2 and 6. Side view.
Figs. 3 and 7. View from above.
Figs. 4 and 8. Diagrammatic vertical section through long axis.
Figs. 5 and 9. Diagrammatic vertical section across lip.

Plates 5 and 6. Hilton, 22.i.1975. Nest turret of *B. cinguliger* (Smith) from side and from above. (x3,2)



Plates 7 and 8. Hilton, 11.iii.1974. Nest turrets of *B. oxydorcus* (Handl.) from side. (x1,5)

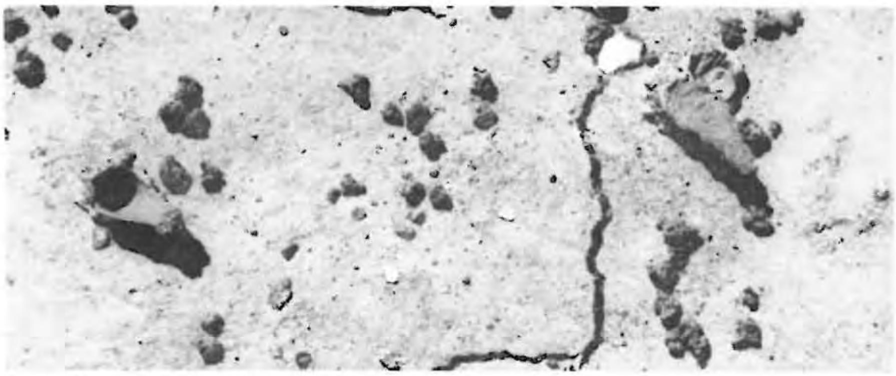


Plate 9. Hilton, 8 iii.1974. Nest turrets of *B. oxydorcus* (Handl.) from above. That on left open, that on right sealed. (x1,3)

Plate 10. Hilton, 11.iii.1974. *B. oxydorcus* (Handl.) female entering turret. (x3)

Plates 11, 12 and 13. Hilton, 22.iii.1974. Three stages in the sealing of a turret by *B. oxydorcus* (Handl.) (x4) a few individuals of *B. oxydorcus* were observed, on an overcast day, "sleeping" on vertical stems of low vegetation growing on the far side of an irrigation furrow bounding one side of a nesting area. However, these individuals being spaced out on the vegetation could not be described as forming an aggregation.

DESCRIPTION OF THE NEST TURRET

Bembecinus oxydorcus and *Bembecinus cinguliger* both construct an aerial mud turret above the subterranean portion of the nest. The turret for each species is distinct and constant in its design (Figs. 2—9 and Plates 5—13).

In both there is an extended lip to one side of the structure. In *B. oxydorcus* this lip is raised above the ground and extends from the edge of the shaft opening at an acute angle with the ground surface. However, in *B. cinguliger* the lip is most commonly in contact with the ground surface along its entire length.

Rising from the edges of the shaft opening and continuous with the base of the lip is a wall which in *B. oxydorcus* forms a short sloping cylinder and in *B. cinguliger* a hood covering the shaft opening. Thus the shaft opening in *B. oxydorcus* is visible from above whereas in *B. cinguliger* it is obscured by the hood.

In addition to this basic structure there is a rim extending along the sides of the lip. In *B. oxydorcus* this rim is barely 1 mm in height whereas in *B. cinguliger* it forms arched sides which almost meet above the lip to form a tunnel, open at its distal end and with in addition a slit opening dorsally along its entire length. For 31 completed *B. cinguliger* turrets measured the total length (measured to the distal end of the lip) averaged 34 mm (range 26—43 mm) and the length of the tunnel-like covered portion averaged 24 mm (range 19—33 mm).

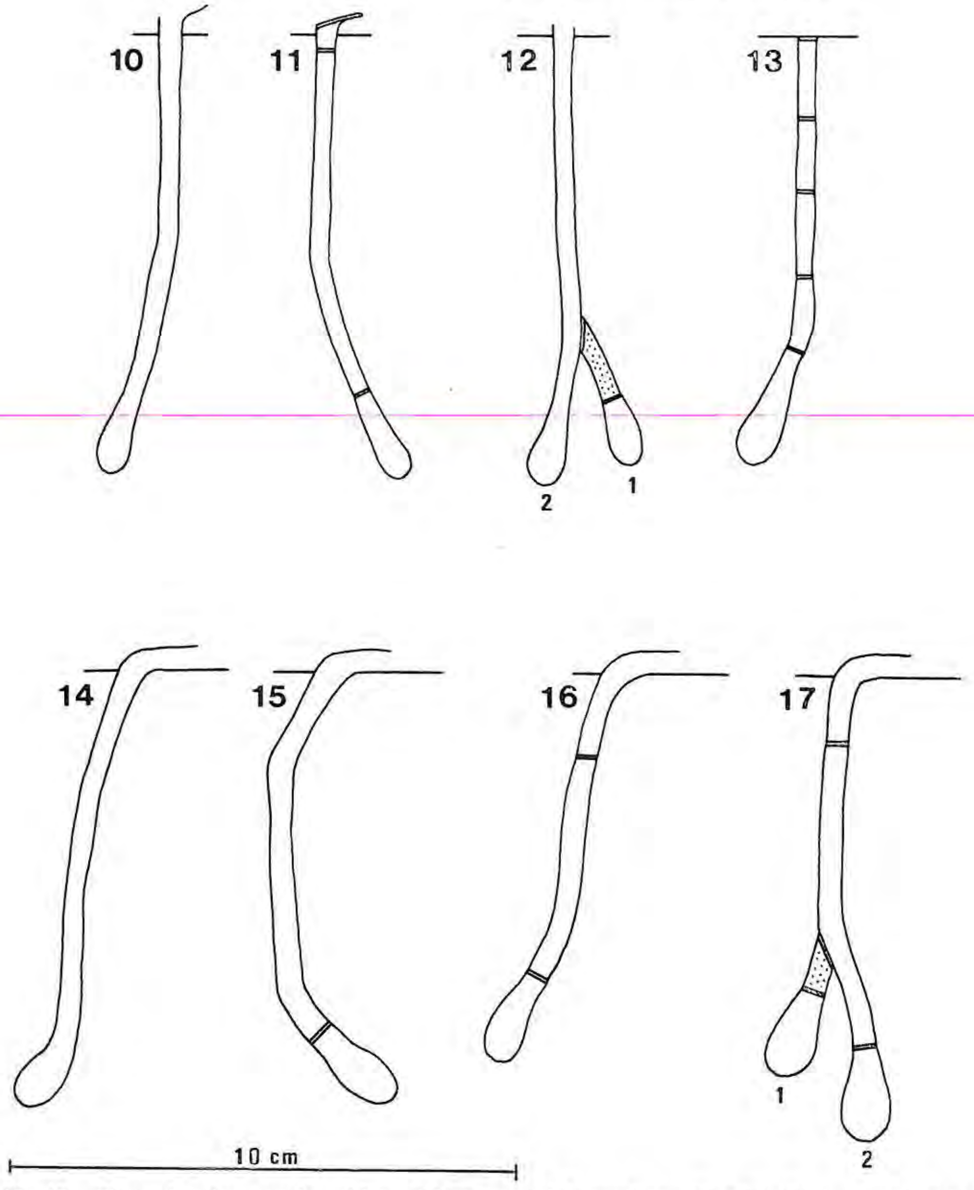
DESCRIPTION OF THE SUBTERRANEAN BURROW

A total of 54 nests in various stages of construction was excavated and investigated during the present study; 34 were those of *B. cinguliger* and 20 those of *B. oxydorcus*. In Table I the underground workings of these nests are grouped into three categories according to the number of cells associated with each nest.

TABLE 1. Analysis of the form of the underground workings of 54 nests of *Bembecinus* excavated near Grahamstown

Category	Description of underground workings	Number of nests	
		B. cinguliger	B. oxydorcus
A	Shaft with no cells	0	6
B	Shaft with one cell	29	12
C	Shaft with two cells	5	2
	Totals	34	20

The subterranean burrow consists of a shaft terminating in a single cell or branching dichotomously to terminate in two cells (Figs. 10—17). No nest was found with more than two cells.



Figs. 10—17. Plans of underground workings of four nests of *B. oxydorcus* (Handl.) (Figs. 10—13) and four nests of *B. cinguliger* (Smith) (Figs. 14—17).
Figs. 10 and 14. Nests each showing a single open cell.
Fig. 15. Nest showing one sealed cell.
Figs. 11 and 16. Nests showing temporary seals.
Figs. 12 and 17. Nests each showing two cells and the sequence of their construction.
Fig. 13. Nest with final seals.

The depth below the ground surface of the bottom of the single cell in nests of category B or of the first-constructed cell in nests of category C varied in *B. cinguliger* from 59 to 90 mm, with an average depth of 75 mm (88% between 65 and 85 mm). In *B. oxydorcus* the depth varied from 72 to 155 mm and averaged 97 mm; however, if two unusually deep nests (130 and 155 mm) are omitted as being atypical, then the depth varied from 72 to 102 mm and averaged 89 mm (75% between 79 and 99 mm).

In those nests having two cells, the second cell always terminated a side branch arising from the main shaft above the sealed first-constructed cell. In both species the depth below the ground surface of the second cell was always in excess of that of the first. In *B. cinguliger* the difference in depth varied from 3 to 10 mm with an average of 7 mm; in *B. oxydorcus*, for which only one measurement was obtained, the difference in depth was 6 mm.

In *B. cinguliger* the length of the cells varied from 12 to 19 mm (average 17 mm) and the width varied from 6 to 8 mm (average 7 mm); in *B. oxydorcus* the corresponding measurements were 15 to 20 mm (average 18 mm) and 6 to 7,5 mm (average 6 mm), respectively. The bore of the shaft was between 4 and 5 mm in *B. cinguliger* and between 3 and 4 mm in *B. oxydorcus*.

In summary, it may be seen that the subterranean burrows of the two species are very similar, the only differences being that the shafts and cells of *B. oxydorcus* are somewhat narrower but longer than are those of *B. cinguliger*.

AN ACCOUNT OF THE METHOD OF BURROW EXCAVATION, TURRET CONSTRUCTION AND NEST CLOSURE

Before the initiation of nest building *B. oxydorcus* females were seen to fly around the nesting area settling from time to time and scraping at the ground with their mandibles and fore-legs, flying up and returning to scrape in the same places.

Nest building in *B. cinguliger* and *B. oxydorcus* is initiated by the collection of a crop-full of water. In both species water is collected when standing on the mud at the water's edge and in *B. cinguliger* less commonly when standing on a floating object or alighting on the water surface itself.

The wasp then flies with this water to the nesting area where she regurgitates it onto the earth. The water and earth are then worked together to form very wet mud. The wasp then starts to excavate the shaft by removing the mud with the mandibles. *B. oxydorcus* places the mud around the opening of the shaft to form a collar of the same diameter as the shaft. To this she adds more pellets evenly but as she always alights and stands on the structure on the same side the portion which supports her gradually slopes away from the shaft opening at an acute angle with the ground and thus a lip develops. The portion furthest from the lip slopes to a lesser degree towards the opening resulting in an off-vertical cylinder bearing the lip on one side. In the structure of *B. cinguliger* this asymmetrical development is very much more marked than in that of *B. oxydorcus*. Most commonly the lip is in contact with the ground along its entire length. However, less commonly it is detached from the surface of the ground and runs parallel to this at a height of approximately 1 mm. Most commonly *B. cinguliger* initially remains standing on the ground and draws the first formed mud back with her mandibles and fore-legs so that the lip initial is in contact with the ground. She then adds mud to form a collar around the shaft opening and connected with the lip. She adds to this collar and to the lip in such a way that the latter is continued along the ground and the portion of the structure further from the lip slopes towards the shaft opening more markedly than in *B. oxydorcus* so that a hood over the opening develops.

When the cylinder of *B. oxydorcus* has almost reached its full height, the wasp starts adding more mud to the lip than to the rest of the structure so that it is extended more rapidly than the off-vertical walls. When adding pellets to the end of the lip the wasp backs out of the turret along it and steps off the end vibrating her wings rapidly to support herself in hovering flight. Similarly in the *B. cinguliger* construction, once the hood is almost complete considerably more mud is added to the lip than to the hood. In both species pellets are added along the sides of the lip to form a ridge. This ridge is added very evenly, the wasp placing pellets alternately on right and left sides. In *B. oxydorcus* the ridge is complete when about 1 mm high whereas in *B. cinguliger* the wasp continues to add to the ridge in such a manner that it forms sides to the lip which curve over and almost meet above it leaving only a narrow slit opening. Thus a tunnel-like structure is formed and this is extended further by continued additions of pellets to the floor and sides. The additions to the sides always alternate even when extensions to the floor intervene and when building is interrupted by water collection. In order to add mud to the highest parts of the hood and tunnel the wasp leaves the floor and stands upside down on the inside of the structure. This change in position is also noticed in *B. oxydorcus* which plasters the inside of its structure standing on the inner surface of the walls and with its head downwards.

In *B. cinguliger* nesting at a distance of 18 metres from its water source, it was found that the turret was completed within about 45 minutes and that it required about 15 loads of water.

When the turret is completed, the shaft is not yet of its full depth. The additional mud excavated is removed from the shaft in the form of pellets, which are carried out one at a time and dropped 30—40 cm from the nest. In performing this the wasp follows an elliptical flight path. After pellet dropping has started there are still occasional additions to the turret. In the case of *B. cinguliger* it was found that each water load was sufficient for the formation of 13—20 pellets.

B. cinguliger was at times heard to make a buzzing sound when excavating the shaft below the surface of the ground. It is believed that the loosening of the earth at the working face of the excavation was, on these occasions, facilitated by vibrations of the mandibles produced by manipulating the flight mechanisms as described by Spangler (1973) for other Hymenoptera.

As seen from the description of the subterranean burrow plan, a second branch shaft is in some cases constructed after the original shaft with its terminal cell has been completed and has been supplied with an egg and fully provisioned. The portion of the original burrow below the opening to the second shaft is found to be filled with earth pellets. As the wasps, at this stage, were not seen to carry pellets into the burrow it is thought that the pellets excavated from the second shaft are probably dropped into the first shaft and not carried out of the nest as was the case in the construction of the latter.

During nest construction there is no regular occurrence of grooming. However, when the regular pattern of water carriage and pellet formation is disturbed, both *B. cinguliger* and *B. oxydorcus* will alight on the ground and groom before continuing building.

B. cinguliger and *B. oxydorcus* were both found to seal their nests at the end of each working day and to open them at the beginning of each successive working day. The temporary seals each consist of a thin mud plate attached around its circumference to the sides of the shaft and positioned at right angles to them. Two such temporary seals are made: one immediately above the cell which is still being provisioned and a second at a depth varying from 3—19 mm below the ground surface. *B. oxydorcus* in addition seals the turret but no such turret sealing was found in *B. cinguliger*. The sealing of the turret in *B. oxydorcus* makes it possible to record the time taken from nest initiation to the completion of that day's temporary closure. It was found that this first day's activity which presumably included at least oviposition was completed in 75 minutes.

The turret seal in *B. oxydorcus* is made by the wasp from the rim of the cylindrical portion of the turret and the ridge on the sides of the lip. The wasp arrives at the nest with a crop-full of water and alights on the lip. She first moistens the rim at a point furthest from the lip and draws the resultant mud towards hersef. Gradually more of the rim is moistened and drawn across the opening. Mud is consistently taken alternately from right and left sides. When the water in her crop is exhausted, the wasp flies off and fetches a second load. Work is continued in the same way as before until the end of the lip is reached. The builder then steps off buzzing her wings to support herself whilst she completes the sealing at the tip and then flies off. Finally she returns with a third load of water with which she moistens and smooths off the seal. (Plates 11—13)

When opening the nest, the wasp alights on the lip and moves forward onto the lid. She moistens the surface of the lid at a point furthest from the lip, forms a pellet, flies off and drops it. She returns along the lip and repeats the process until the lid is removed. The upper inner seal is then removed in a similar way. Whilst she is engaged in this the tip of her abdomen is visible. Finally pellets are carried out from deeper down out of sight and these are presumably from the lower inner seal. The opening of all three seals is completed in five minutes. As the turret lid is thrown away in the form of pellets the turret must become shorter with each successive day.

In both *B. oxydorcus* and *B. cinguliger*, in nests with two cells, the shaft bearing the original cell is sealed off from the new branch shaft which bears the second cell. The seal separating the two shafts is not at right angles to the shaft wall but is in the same plane as the secondary branch wall so that there is no unevenness in the wall of the shaft terminated by the second cell (Figs. 12 and 17).

After the cell or cells are finally completely sealed the wasp makes two or three further seals at intervals in the shaft (Fig. 13). The spaces between these seals are not filled with earth.

IDENTIFICATION AND COMPOSITION OF THE PREY

Prey that was in a physical condition which allowed identification with respect to family (or superfamily), stage of development and sex was obtained from 31 of the 39 *B. cinguliger* cells excavated and totalled 223 individuals (Table II).

TABLE 2. Analysis of the prey found in 31 cells of *B. cinguliger*

Prey Taxon	Sex and developmental stage				Totals
	Adult Females	Adult Males	Nymph Females	Nymph Males	
HOMOPTERA: AUCHENORRHYNCHA Cicadoidea: Cicadellidae (about 10 species)	91 (4)	57 (3)	22 (1)	9	179
HOMOPTERA: AUCHENORRHYNCHA Fulgoroidea: Family? (2 species)	14	16	0	0	30
DIPTERA Tephritidae (2 species)	Sex not determined		—	—	14
					223

Note: Figures within brackets refer to stylopized individuals.

The prey most commonly utilized for provisioning were species of Cicadellidae and 30 of the 31 cells contained individuals of this family, 18 cells being provisioned solely with cicadellids and the remaining 12 being provisioned with other prey in addition. Ten cells contained Fulgoroidea and other prey and six cells contained Tephritidae and other prey. Seven cells were provisioned with a mixture of Cicadellidae and Fulgoroidea, three with a mixture of Cicadellidae and Tephritidae and one with a mixture of Fulgoroidae and Tephritidae. Two cells were provisioned with a mixture of all three prey taxa. It was found that any one cell might contain more than one species of any one or more of the three prey taxa and in the case of the Cicadellidae might contain both adults and nymphs. In length (measured from the front of the head to the end of the abdomen) the Cicadellidae ranged from 1,8—5,4 mm and the Fulgoroidea from 3,9—4,1 mm. The Tephritidae were 2,9 mm long.

With respect to *B. oxydorcus* the number of prey available for examination, obtained from only nine cells, was much smaller but indicated similar prey preferences to those exhibited by its congener. Thus the most commonly utilized prey were species of Cicadellidae of which both sexes and both adults and nymphs were represented. There were no Fulgoroidea in the sample but several Tephritidae were present.

Though no conclusive observations were made on hunting by *Bembecinus* and thus on the source of the prey brought to the nests, circumstantial evidence is very strong that the prey is obtained on the low-growing *Pentzia* bushes which, as noted above, surround the nesting sites. Both *B. cinguliger* and *B. oxydorcus* have been noted flying about among these plants which when swept with an insect net are found to yield many Cicadellidae. It is more than likely that the Tephritidae found in the *Bembecinus* nests are also obtained on the *Pentzia* bushes, where they probably develop in the flowers. Their occurrence in the same niche as the Homopterous prey and their similar size are undoubtedly contributory factors in the atypical acceptance by the wasps of this Dipterous prey.

OVIPOSITION AND PROVISIONING, IMMATURE STAGES

Eggs were found in three nests of *B. cinguliger* and in two nests of *B. oxydorcus*. In the former species two eggs were found in first cells and the third in a second cell; in the latter species both eggs were found in first cells. The eggs of both species were found to be pearly-white and almost straight; those of *B. cinguliger* were about 3,2 mm long and 0,8 mm in diameter; no measurements were recorded for *B. oxydorcus* eggs.

In both species the egg was found on the floor of the cell, in *B. oxydorcus* on loose earth and in *B. cinguliger* at the top of a small cone of earth. In all five cases the cells also contained a single cicadellid prey placed close to the egg. Thus in no case was an egg found in an otherwise empty cell. The only other cells containing but a single prey were two cells (one of each *Bembecinus* species) each containing a very small, newly-hatched larva. All other cells each contained a larva and two or more prey or, in the case of cells with large larvae or larvae in cocoons, the dismembered and fragmentary remains of many prey. The fragmentary nature of the prey remains made it difficult to establish the total number of prey provided for and consumed by each larva but the number appeared to be large. However, an estimate was obtained from a closed cell of *B. cinguliger* in which the larva had not developed (there was a small fly puparium present in the cell) and which contained a total of 41 prey: 19 females, 16 males and 5 female nymphs of the family Cicadellidae, and one male fulgoroid. In both species it was found that the Homopterous prey was without exception so positioned within the cell that the head was directed inwards and the ventral side was up.

Provisioning in both species was found to be progressive, the first prey being brought into the cell shortly after the egg had been laid and the second prey being brought in only after the larva had hatched. Provisioning thereafter appeared to be rapid, prey being brought in at a rate faster than it was consumed. Thus various cells occupied by small *Bembecinus* larvae and still being provisioned were found to contain as many as from seventeen to thirty identifiable prey in addition to fragments of other, already consumed prey.

In *B. cinguliger* in the field eggs were found to hatch in under 24 hours. Thus four nests of which construction from the beginning was watched during the late morning of 12.xii.1973, and of which the positions were marked, were excavated and examined at the same hour on the following day: one cell contained an egg on the point of hatching together with one prey and the other three cells contained small (2,5—3,0 mm long) larvae together with one, two and three prey respectively.

The cocoons of *B. cinguliger* were found to be narrowly ovoid, from 14,5—16,0 mm in length (average of 11 : 15,0 mm) and with a maximum width of from 5,0—6,1 mm (average of 21 : 5,4 mm). The anterior end was comparatively wider and more rounded than the narrower and more pointed posterior end. The wall of the cocoon was hard and smooth and coloured like the soil in which the cells had been excavated and it was clear that it was composed of clay. The inside of the clay cocoon wall was lined with a thin layer of fine silk spinnings. One (rarely), two (most commonly) or three minute pores were present in the clay wall of each cocoon, situated irregularly around the circumference of the cocoon just about at the middle of the long axis. These pores were fairly easy to spot, the area immediately around them being darker than the cocoon walls generally. Surrounding the hard portion of the cocoon was a loose outer envelope of fairly sparse strands of silk to which adhered the dismembered uneaten remains—hemelytra, legs, head-capsules and other parts of the exo-skeletons of the Homopterous prey. This outer covering of characteristic prey remains renders *Bembecinus* cocoons immediately recognisable in the field. Cocoons dug out of the ground at Hilton on 26.ix.1974 still contained prepupae, indicating that pupation occurs in the spring at some time after this date.

Cocoons of *B. oxydorcus* were found to be very similar to those of *B. cinguliger* but were somewhat smaller—from 12,8—13,8 mm long and with a maximum width of from 4,5—5,0 mm. The three cocoons examined had four pores each. Cocoons dug out of the ground at Hilton on 8.x.1974 still contained prepupae.

PARASITES AND OTHER ASSOCIATED INSECTS

Evidence of only one case of parasitism was found in the 54 nests of both species dug out and examined during the nesting season and in numerous other nests investigated during the end of the winter diapause period. Thus on 31.xii.1973 a sealed cell of *B. cinguliger* was found which contained 41 small homopterous prey and one 2 mm-long dipterous puparium but no egg or larva of the rightful owner of the cell. Unfortunately the puparium was damaged in handling and a more precise identification was thus precluded.

Numerous female Mutillidae of several species were found walking about the nesting site of *B. oxydorcus* during March and April, 1974, and on two separate occasions a female of one of these species was seen entering an open nest during the temporary absence, probably while hunting, of the *B. oxydorcus* female. On the second occasion the *B. oxydorcus* female returned to the nest two minutes after the mutillid had entered it. Twice the sphecid went down into her nest and backed up and out again, then she turned around and went down the burrow backwards. On coming up and out again she was followed by the mutillid which ran out and then stopped a little way off. The sphecid then continued with her normal work.

Foreign Hymenoptera were in several instances observed entering or leaving *Bembecinus* nests and it appears that in some cases at least the nests had been invaded by the former for the purpose of nesting. Thus *B. oxydorcus* nests were found that had been taken over by the bee *Megachile* (*Eutricharaea*) *meadewaldoi* Brauns (Megachilidae), by *Pison* ?*montanum* Cameron (Sphecidae) and by an unidentified species probably of the family Eumenidae, all species habitually nesting in pre-existing cavities.

The *Megachile* was seen on 8.iii.1974 going down an *oxydorcus* turret carrying something colourful. The bee was captured when it emerged and the burrow when excavated was found to contain four pieces of pink petal introduced by the bee as nesting material. From their colour it was immediately apparent that the pink discs had been cut from the flowers of *Oxalis sp.* (near *stellata* E. & Z.) which grew in numbers in the vicinity of the *B. oxydorcus* nesting site. Examination of the flowers of these plants showed that several petals had holes corresponding in size and shape to the discs.

The *Pison* was seen in association with *B. oxydorcus* nests on three dates during March and April. Several females, two of which were subsequently captured, were observed entering and leaving the turreted nests on 8.iii.1974. On 11.iii.1974 a female carrying an immature spider (Salticidae) held beneath her was observed flying about low over the *B. oxydorcus* nesting area probably trying to locate the nest it had usurped but unable to do so due to the authors sitting on or near it. A further female was observed on 10.iv.1974 regularly visiting an old *B. oxydorcus* nest. Possibly it was preparing the burrow for use for the latter was found on examination to be half filled with loose earth but to contain no prey. Nothing is known concerning the usual nesting habits of *Pison* ?*montanum* Cam. but during the 1973/74 summer the species was found nesting at Hilton in wooden trapnests (4,8 mm and 6,4 mm bore) which the authors had suspended in bushes.

The supposed eumenid which had taken over a *B. oxydorcus* nest was not seen and was known only by its small, lacy, horizontally orientated eumenid-type mud entrance turret with which it had surmounted the opening at the top of the *B. oxydorcus* turret. First observed on 11.iii.1974, the nest furnished with this double turret was excavated two days later but was found to have no cell, egg or provisions.

A female bee, *Tetralonia minuta* Fr. (Anthophoridae) was captured on 12.xii.1973 on emerging from a *B. cinguliger* burrow after it had been observed entering it via the horizontal turret. It is not known what the purpose of this visit to the sphecid nest was, for according to Rozen (1969) this bee itself excavates its burrow. However, another female of this species was captured (11.xii.1973) at Hilton coming out of the emergence hole of a large ground-nesting species of Eumenidae, *Parachilus insignis* (Saussure), whose nesting area abutted that of *B. cinguliger*.

FLOWERS AND NEW PLANT GROWTH VISITED BY ADULT WASPS

During the present study at Hilton *B. cinguliger* (Smith) was observed during the late afternoon of 2.i.1974 foraging in numbers upon the white flowers of *Selago corymbosa* L. (Selaginaceae) and upon the yellow flowers of *Helichrysum ericaefolium* Less. (Compositae). Thirteen females and three males were caught on the former, three females on the latter. Similarly at noon on 15.ii.1974 several females were observed and caught while foraging on the very small yellow flowers of *Pituranthos aphyllus* (Cham. & Schlechtdl) Benth. & Hook. f. ex Schinz (Umbelliferae). All three forage plants were at a distance from the nesting areas but close to the sleeping tussock and it is certain that the purpose of the wasps' presence at the flowers was for imbibing nectar and not for catching prey.

At Hilton in previous years *B. cinguliger* was obtained on three occasions on the small, pale-yellow flowers of *Maytenus linearis* (L.f.) Marais (Celastraceae). The records are: 9.xii.1969 (F. W. Gess) 7 males, 11.xii.1969 (F. W. Gess) 6 males and 4 females, 11.xii.1969 (D. W. Gess) 2 females, and 6.xii.1972 (F. W. Gess) 4 males.

In addition to being attracted to the above flowers for the purpose of obtaining nectar, both sexes of *B. cinguliger* were found to be attracted to the glandular exudates associated with the new growth of *Acacia karroo* Hayne (Leguminosae). Thus, a male, the first individual of this species to be spotted during the 1973—74 flight period, was observed and caught on 3.xi.1973 on this new growth of an as yet flower-less *Acacia* bush. On 27.xi.1973 a female was observed and caught visiting the glands but not the flowers of this plant and on 12.xii.1973 an individual of undetermined sex was observed similarly employed.

B. oxydorcus was during the present study likewise found to visit flowers for the purpose of imbibing nectar. Thus on 2.i.1974 a male was captured on *Selago corymbosa* L. (Selaginaceae) where it was foraging in company of both sexes of *B. cinguliger*; on 9.i.1974 a female was captured on the yellow flowers of *Pentzia incana* (Th.) O. Ktze. (Compositae) and on 28.i.1974 five individuals, at least one a male, were observed on the flowers of this latter plant.

The above forage-flower records for the two species have been dealt with in some detail as they are of interest in the light of the statement by Evans (1955: 288) that he knew of no records of any species of *Bembecinus* coming to flowers and that "apparently the adults obtain their nourishment from some other source".

Lest it be construed, however, that *B. cinguliger* and *B. oxydorcus* at Hilton are unusual in this respect, attention is drawn to other flower-visiting records concerning these and other southern African species of *Bembecinus*. These records are listed below under the name of the forage plant.

Zizyphus mucronata Willd. (Rhamnaceae)

Bembecinus braunsi (Handl.)	1 male
Bembecinus cinguliger (Smith)	5 females and 2 males
Bembecinus haemorrhoidalis (Handl.)	1 male
Bembecinus oxydorcus (Handl.)	1 male

at Koonap River, 17 miles from Adelaide on Grahamstown road, 20—22.xii.1972 (C. F. Jacot-Guillarmod).

Foeniculum vulgare Mill. (Umbelliferae)

Bembecinus haemorrhoidalis (Handl.)	1 female (F. W. Gess)
Bembecinus sp. (undescribed)	5 females (F. W. Gess) and 4 females (J. G. H. Londt)

at Belmont Valley, Grahamstown, 17.i.—5.ii.1970.

Bembecinus polychromus (Handl.)	2 females and 1 male

at Johannesburg (Transvaal), 27.xii.1970 (J. G. H. Londt).

In addition to these records derived from material in the Albany Museum collection, Jacot-Guillarmod has stated (pers. comm., 1973) that he has collected the following species visiting flowers: *B. polychromus* (Handl.), *B. herbsti* (Brauns), *B. haemorrhoidalis* (Handl.) and *B. boer* (Handl.).

Of interest in connection with the attractiveness to *B. cinguliger* of the glandular exudates of *Acacia karroo* Hayne at Hilton are specimens, now in the Albany Museum collection, of three *Bembecinus* species collected by C. F. Jacot-Guillarmod on *Calpurnia intrusa* E. Mey. (Leguminosae) at Mamathes (Lesotho). The species concerned are *B. polychromus* (Handl.) (2 males), *B. herbsti* (Brauns) (3 males) and *B. braunsii* (Handl.) (2 males and 1 female).

Jacot-Guillarmod (1951: 235—236 and 1957: 10—13) has recorded the attractiveness of *Calpurnia intrusa* E. Mey. to Hymenoptera and has drawn attention to the fact that the plant "is most attractive in spring and early summer, when there are many young shoots, but no flowers" and that "when flowers appear it loses its attractiveness except for the flower-vistiting wasps . . .". The wasps "seemed to be attracted by the foliage and young shoots which apparently exude some substance that is attractive to them". *Bembecinus* species are not mentioned in these papers but according to Jacot-Guillarmod (pers. comm., 1973) those species recorded from *C. intrusa* were visiting the plant for the exudate and not for the nectar contained in the flowers. The reason for the attractiveness to *Bembecinus* species of the two leguminous plants, *Acacia karroo* Hayne at Hilton and *Calpurnia intrusa* E. Mey. at Mamathes, therefore appears to be the same.

A similar case of feeding on glandular exudates may have been recorded for the males of *B. tridens* (Fabr.) in Switzerland by Lüps (1973: 134). Those males were observed in numbers upon the needles of Scots Pines (*Pinus silvestris*) where they were thought possibly to be imbibing nutriment.

DISCUSSION

Concerning the genus *Bembecinus* Costa, Evans (1966: 132—133) has written that the available data on the more than fifteen species examined to that date "together present a remarkably consistent picture demonstrating that this genus is highly distinctive in its ethology, but suggesting that there are few notable specific differences in behavior within the genus".

The ethology of *Bembecinus cinguliger* (Smith) and of *B. oxydorcus* (Handl.), while conforming to the general pattern of behavior shown by those species of the genus that have hitherto been studied, exhibits some outstanding features which mark off these two species from their congeners and which indeed seem unusual within the Sphecidae.

The fundamental feature in which the present two species differ from other species of *Bembecinus* is that the former choose to construct their nests in soil of a different type from that usually chosen by the genus. Correlated with the difference in the chosen soil type is a well marked morphological difference with respect to the fore-legs of the wasps and the substitution of the usual method of nest excavation and closure practised by *Bembecinus* species by one more suited to the unusual nesting medium.

From the ethological study of the North American *B. neglectus* (Cresson) by Evans (1955: 287—295) and that author's reviews and discussions of the published observations on this and other species of the genus (1955: 295—302) and (1966: 132—143), it appears that, in those species at least, nesting occurs rather locally in restricted sandy areas. In the present authors' experience several southern African species (other than *cinguliger* and *oxydorcus*) similarly nest in sand. In *B. neglectus*, as in the reviewed species, burrow excavation in the sandy medium is essentially by digging, the earth being thrown back beneath the body by the fore-legs, the fore-tarsi being furnished for this purpose with a comb or sand rake. The existence of this tarsal sand rake appears to be typical of virtually all *Bembecinus* species and it may confidently be expected that the possessors of this structure all nest in sandy soil and excavate their burrows in the above indicated manner.

The nesting of *B. cinguliger* and *B. oxydorcus* in a hard clay soil, a nesting medium quite unsuitable for sand-raking (and thus for the great majority of *Bembecinus* species), is clearly correlated in the female wasp with the absence, possibly by secondary loss, of the usual long spines on the fore basi-tarsus which joint instead bears a dense row of short cilia.

Behaviourally the atypical nesting medium and the morphological modification of the fore-tarsi is correlated with the adoption of the use of water for softening the earth and with the habitual utilization of the mouthparts as digging tools and for forming mud pellets in which form the excavation spoils are removed from the burrow being sunk. While the use of water for the above purpose is entirely foreign to the behaviour of the hitherto observed *Bembecinus* species, if not also to other genera of Sphecidae, the use of the mandibles for removing small pellets of earth from an excavation has been observed by Evans (1955: 290) in *B. neglectus*. That wasp, when the soil it encountered was unusually firm or moist, was seen to carry out pellets which were deposited from one to four centimeters from the nest entrance. Similarly in *B. hungaricus japonicus* (Sonan) the use of the mandibles has been reported by Tsuneki (1969: 8) for assisting the fore-legs in excavating in damp sand and for carrying out of the nest small pebbles encountered during shaft sinking in pebbly ground.

A remarkable feature of the behaviour of *B. cinguliger* and of *B. oxydorcus*, however, is that at least some of the mud pellets derived from the excavation of the burrow are utilized for the construction of a turret surmounting the nest entrance. In this respect these two species are unique not only within the genus *Bembecinus* but also within the Nyssoninae for according to Evans (1966: 422) no member of this subfamily has been recorded to utilize mud in nesting. Indeed, where mud is utilized in nesting by Sphecidae, it is either for the purpose of forming cell partitions and plugs as in some species of *Trypoxylon* or for forming aerial mud nests as in other species of *Trypoxylon* and in *Sceliphron*. As far as can be ascertained by the authors no occurrence of a ground-nesting sphecid surmounting its burrow with a mud entrance turret has yet been recorded.

In the present two species the nature of the soil and the presence of the nest turrets precludes the method of closing the nest with sand as is usually practised by *Bembecinus* species and, in this activity also, mud is prepared and used for constructing seals and plugs.

Clearly the adoption of the use of water for burrow excavation, the utilization of the resulting mud pellets in the construction of a mud entrance turret surmounting the subterranean nest, and the use of mud in sealing the nest is intimately linked with the habit of nesting in clay soil. Similar burrow-excavating, turret-building and nest-sealing techniques in species nesting in clay soils have long been known in the Eumenidae and Masaridae (*Ceramius* species) and have recently (Gess and Gess, 1974) been described for a species belonging to the Pompilidae.

Considering the existence of the above notable points of difference pertaining to certain aspects of the nesting behaviour of sand- and clay-nesting *Bembecinus* species, it is remarkable how similar the two groups are in all other aspects of their behaviour, these not being influenced to any marked degree by the nature of the soil. Thus, in *B. cinguliger* and *B. oxydorcus* large numbers of individuals nest in close proximity giving rise to pseudocolonies, as has also been reported for the American species *B. godmani* (Cameron), *neglectus* (Cresson), *mexicanus* (Handl.), *nanus* (Handl.) and *cingulatus* (Smith) and for the European *tridens* (Fabr.).

In both *B. cinguliger* and *B. oxydorcus* the architecture of that part of the nest that is below the ground is very similar indeed to that described for *neglectus* and other species (Evans, 1966: 138 and Fig. 76), both with respect to nests containing one cell and those containing two. It seems of particular interest that this close similarity in nest plans should exist taking into account the very different soils and excavating techniques. However, these factors may be responsible for the burrows of the present species being subvertical rather than oblique as in the other species.

Like *B. neglectus*, neither *B. cinguliger* nor *B. oxydorcus* spends any time inside the nest when not actually excavating, opening, provisioning, inspecting or closing it and the greater part of the time including the night is spent away from the nest and the nesting area. *B. cinguliger* at least and probably also *B. oxydorcus* share with the South African *B. rhopalocerus* (Handl.) and *rhopaloceroides* (Brauns), the Argentinian *consobrinus* (Handl.) and the North American *godmani* and probably also *neglectus* the habit of spending the night in a sleeping cluster on or in vegetation.

In common with all other species of *Bembecinus* for which prey has been recorded (5 American and 6 Old World), the present two species provision their cells with small Homoptera. Similarly, as in other species, *B. cinguliger* and *B. oxydorcus* practise progressive provisioning. The egg is laid in an empty cell where, in *B. cinguliger* at least, it is glued to the top of a small mound of earth. The first prey is brought in before the egg hatches and is placed in a definite position relative to the mound bearing the egg.

It therefore appears that *B. cinguliger* and *B. oxydorcus* in most respects uphold the uniformity and uniqueness of behaviour exhibited by the genus; that the points of difference are adaptations to meet the challenge of nesting in a soil type otherwise unsuitable for and unexploited by the genus; and that the innovations in nest-building techniques, although apparently unique in the Sphecidae but paralleled in other families of Aculeata, in no way invalidate the inclusion of the two species in *Bembecinus*.

If the number of individuals in a population is any measure of the success of a species, then *B. cinguliger*, easily the most numerous wasp nesting in the clay soil of Hilton, must be considered extremely successful. *B. oxydorcus*, judged by the same criterion, is somewhat less successful at Hilton but may well come into its own at some other locality; its wide distribution in southern Africa certainly indicates success.

It has been shown that the behavioural and morphological departures from the norm manifested by the present two species have allowed them to invade a nesting substrate unsuitable for other species of *Bembecinus*. While this has undoubtedly been of great advantage to the present species, in that competition with their congeners for nesting sites has been eliminated, it must be asked whether the adoption of the clay nesting-substrate has not at the same time imposed any disadvantages or special conditions upon these wasps. Immediately apparent is their utter dependence upon a supply of water without which they are unable to manipulate the clay and the presence of which is thus a prime pre-condition for successful nesting. At Hilton, with its low mean annual rainfall and its generally dry summer months (see Gess and Gess, 1974: 191), the wasps are largely dependent upon ephemeral water, a result of irregular and unpredictable rain, collected in muddy pools, erosion gullies and shallow furrows. To make the best use of such unreliable water supplies it is thus of advantage if nest-building and provisioning can be accomplished rapidly and this indeed is a notable feature in the nesting behaviour of *B. cinguliger* and *B. oxydorcus*. It is fitting that this rapidity is in part made possible by the physical nature of the clay soil which, provided water is available, lends itself to quick manipulation.

As has been noted above, the time taken by *B. oxydorcus* to excavate a new nest, to oviposit in the cell, probably to bring in the first prey, and to seal the nest has been recorded as 75 minutes. Judging from the rapidity with which *B. cinguliger* constructs its nest (45 minutes to turret completion) the time taken by this species is probably similarly short. In contrast the time taken for these activities by the sand-nesting *B. neglectus* is considerably longer. Evans (1955: 290—291) has recorded the time taken by this wasp to dig a nest as averaging two hours and the time taken to seal it and to conceal the entrance as taking at least an hour.

In *B. cinguliger* at least and probably also in *B. oxydorcus* the egg develops very rapidly, the larva hatching in under 24 hours. Provisioning of the nest, apparently begun with a single prey on the day of oviposition, is pursued with rapidity the following day and under favourable weather conditions is probably completed within two days after oviposition. Provisioning is not only rapid but is notable for its economy of effort due to the fact that the nest is kept open from the start to the finish of a working day. In contrast, the nest of *B. neglectus* is invariably closed when the wasp leaves it. Introduction of each prey into the nest by that species is thus preceeded by the digging of the earth from the entrance and succeeded by the careful reclosure of the nest from the outside.

In *B. neglectus* the maintenance of a closure at the nest entrance is a measure to keep out parasites. It is thus notable that, despite the fact that the nest of *B. cinguliger* and of *B. oxydorcus* is left open for long periods, the incidence of parasitism appears to be very low. It therefore seems likely that the nest entrance turret serves as a protection against parasites.

Whereas the rapidity of nest-building and provisioning is thus geared to make the fullest use of the short time between the fall of rain and the drying up of the resultant pools, the extended flight period of the females (four months in *B. cinguliger* and over three months in *B. oxydorcus* at Hilton during 1973—74) enables nesting to take place over a considerable period of time whenever water is available. The survival of the species in any one locality in bad years of low rainfall is thus ensured; conversely, in good years of copious rains and ever-available water the population may build up to high levels.

SUMMARY

Some aspects of the ethology of *Bembecinus cinguliger* (Smith) and of *B. oxydorcus* (Handl.) (Hymenoptera: Sphecidae: Nyssoninae) in the Eastern Cape Province of South Africa are described. Particular attention is given to the consequences of these two species choosing to nest in a clay soil and not in sand as is more usual in the genus. Described in detail is the use of water in the construction of the nest which by possessing a mud entrance turret appears to represent a nest-type previously unknown in the Sphecidae. A comparison of *B. cinguliger* and *B. oxydorcus* with their congeners with respect to various aspects of behaviour including the formation of pseudo-colonies, the architecture of the subterranean part of the nest, oviposition, provisioning and adult sleeping habits indicates that despite some notable innovations the present species' inclusion in the genus *Bembecinus* must be upheld.

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An ethological study of Parachilus insignis (Saussure) (Hymenoptera: Eumenidae) in the Eastern Cape Province of South Africa

by

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and

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CONTENTS

INTRODUCTION

The genus *Parachilus* Giordani Soika (1960) is restricted in its distribution to the Ethiopian Region and includes eight species, six of which occur in southern Africa and two in East Africa. The southern African *Parachilus insignis* (Saussure), the subject of this paper, is the largest species and is a wasp of very striking appearance.

None of the species of *Parachilus* is well known and the authors' belief that nothing has been recorded concerning the nesting of any of the species belonging to the genus has been confirmed by Giordani Soika (pers. comm., letter dated 30.x.1974).

The present paper is the third of a series of publications dealing with the ethology of certain solitary wasps occurring at Hilton, a farm situated 18 kilometres WNW. of Grahamstown (33° 19'S., 26° 32'E.) in the Albany Division of the Eastern Cape Province of South Africa. In the two previous papers (Gess and Gess, 1974 and 1975) which like the present one dealt with ground-nesting species, an account was given of the climate and vegetation of Hilton as well as of the soil in which the previously studied species excavated their nests. As these descriptions hold good for *P. insignis* also, they will not be repeated here. It should be noted that all the species dealt with to date (that is including *P. insignis*) belong to the community of wasps nesting in clay soil, that all have similar requirements with respect to the availability of water and that as a result all might during the course of the summer be encountered using the same areas for the purpose of nesting.

The greater part of the present study was undertaken during the summer of 1973–4 but certain general observations dating from previous seasons and also from the summer of 1974–5 have been included.

TAXONOMIC HISTORY

Parachilus insignis with five other of the eight species now included in the genus *Parachilus* Giordani Soika was described as a species of the widespread genus *Pterocheilus* Klug. The remaining two species of *Parachilus* were also previously included in *Pterocheilus* to which genus they had been transferred from *Odynerus* Latreille. On account of the absence of long hairs on the labial palps in females of those of the above eight species then known to him, Bohart (1940) excluded these species from *Pterocheilus* and transferred them to the Ethiopian genus *Pseudochilus* Saussure which he characterized as being intermediate between *Odynerus* and *Pterocheilus*. While accepting the exclusion of *P. insignis* and related species from *Pterocheilus*, Giordani Soika (1960) on the grounds of differences in the length of the tongue, in the number of segments composing the maxillary palps, in the proportions of the labial palps, and in the site of the insertion of the basal vein on the subcosta, removed them from *Pseudochilus* and included them in his new genus *Parachilus* with *P. capensis* (Saussure) as the type species.

GEOGRAPHIC DISTRIBUTION

Considering the large size (length up to 23 mm) and the exceptional beauty of *Parachilus insignis* it is remarkable how little is known about its distribution. Described by de Saussure in 1856 from "le Cap de Bonne-Espérance", it was subsequently recorded from Pretoria (Transvaal) by Distant (1892: 210). More recently Giordani Soika (1960: 402) recorded specimens from the following localities: Mamathes (Lesotho); Chicago in the Lindley District and Thaba Nchu (both Orange Free State); Pretoria (Transvaal). In the Albany Museum collection the species is represented from only two localities, separated from each other by a mere 23 kilometres: New Year's Dam, Alicedale (1 female collected by J. G. H. Londt on 22.xi.1970 and 1 female collected by A. S. Greathead on 16.xii.1971) and Hilton, Grahamstown (numerous specimens of both sexes collected by the authors).

DESCRIPTION OF NESTING SITES

Three distinct and well-separated nesting sites of *Parachilus insignis* were located at Hilton over the period of several years that this species was observed. One site was situated on a bare

Plate 1. Hilton. A nesting site of *P. insignis* (Sauss.) on a bare earthen farm road.

Plate 2. Hilton. A nesting site of *P. insignis* (Sauss.) on a bare area below a water furrow.

earthen farm road (Plate 1), a second on a bare area below a water furrow (Plate 2) and a third on a slightly sloping area denuded of vegetation and topsoil by sheet erosion. All three nesting sites were localized patches of bare clayey earth occurring in low-lying areas sparsely covered by small, low-growing shrubs, largely *Pentzia incana* (Th.) O. Ktze (Compositae) and situated close to temporary sources of water. This water, a result of rain, had collected in muddy pools, erosion gullies and shallow furrows. Its distance from the nesting areas was measured for two of the sites and was from 6–14 metres.

Although the level of activity and thus the number of nests of *P. insignis* in any one of the three nesting areas varied from one nesting season to another it was found that, during the period of observation, the three sites were utilized by this species each year to the exclusion of any other similar bare patches which appeared potentially suitable for nesting. This situation had apparently existed for some considerable time, at least at two of these sites, both of which were subject to slow sheet erosion. There the gradual stripping away of the upper layers of the ground by water and wind action had exposed to the surface the remains of many nest cells excavated by *P. insignis* during the course of its nesting over past years.

The restriction of nesting to these three small nesting sites, the clustering of the nests within a nesting site, and the apparent lack of any appreciable emigration by emerging wasps from the site where they were reared to new nesting areas at a distance was seen to result in the formation and maintenance of well-marked pseudo-colonies at times containing a high density of active nests. Thus on 15.xi.1974 over 45 active nests, clustered in a roughly oval area 224 cm long and 168 cm wide, were counted in one of the nesting sites (that shown in Plate 2). Nest entrances were frequently clustered together as close as 4 cm and even less, the ground between them being littered with discarded pellets (Plates 3 and 4).

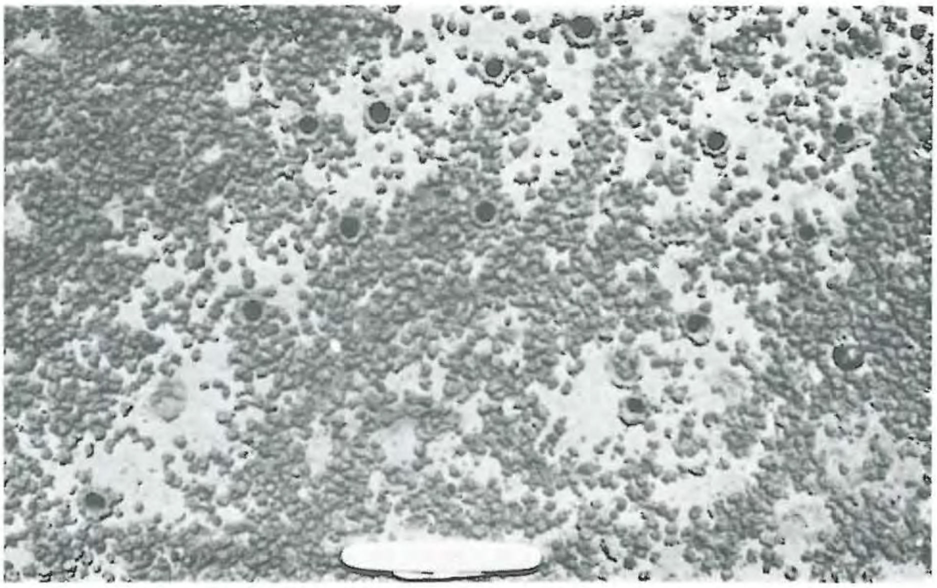
FLIGHT SEASON

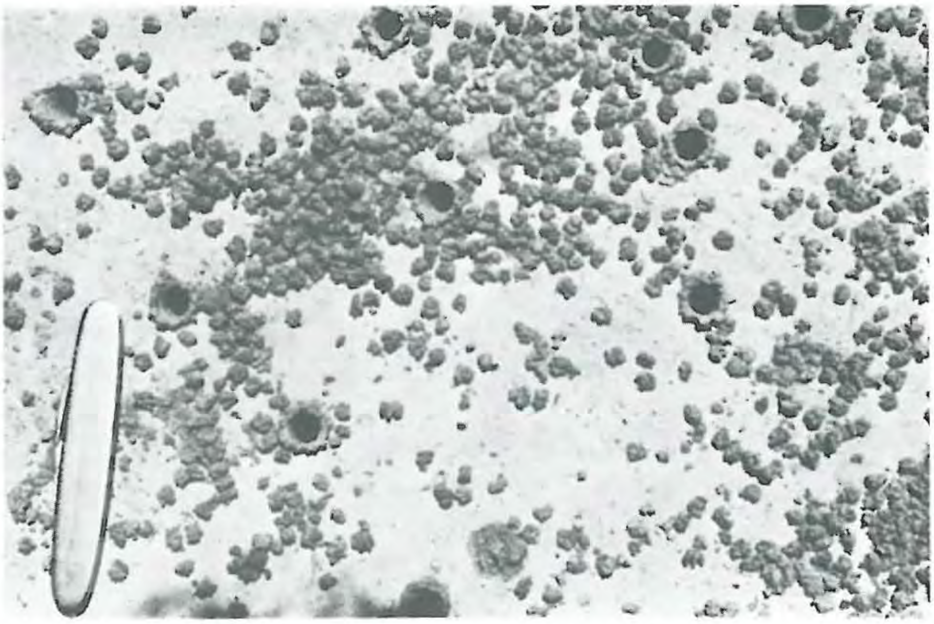
Parachilus insignis is univoltine, the flight season beginning at the very end of October and, depending upon weather conditions, continuing through to early January or even early February. Thus during the 1973–4 summer these wasps were first observed in small numbers on 29.x.1973 and last observed on 7.i.1974, being absent when next looked for on 14.i.1974. During the 1974–5 summer, they were very plentiful by 8.xi.1974 and were still nesting, though only in very small numbers, on 7.ii.1975. It was found that not all individuals emerged at the same time, for on 13.xi.1974, when adults were common and nesting was well under way, 29 sealed cells of the previous season were found on excavation by the authors to contain 15 prepupae and 14 pupae close to turning into adults. Emergence of adult wasps thus probably continues over some time.

BEHAVIOUR OF THE MALES

At the beginning of the flight season, when the nests were widely spaced, it was observed that there were as many males as females present in the nesting areas. The females which were observed building nests each had a male in attendance. Each male was stationed within a radius of about 60 cm from a nest and either rested upon the ground or perched upon a nail used by the authors to mark the position of the nest. He was observed to rise up, fly at and pursue any insect flying in the vicinity of the nest. The female was pursued whenever she emerged from her nest or returned to it but the male did not accompany her on her periodic flights out of the nesting area. Foreign males approaching the vicinity of the nest were pursued, jostled and sometimes engaged in battle on the ground. Other insects including would-be parasites such as bombyliids and chrysidids were similarly attacked and driven off.

As the nesting season advanced and the nests became crowded there was such seething activity that clear-cut male behaviour was no longer observable if it was still taking place.





Plates 3 and 4. Hilton, 13.xi.1974. Portion of a nesting area of *P. insignis* (Sauss.) showing open and sealed nest entrances and discarded pellets. Plate 3 (× 0,3), Plate 4 (× 0,5).

At no time was successful copulation observed. However, males were frequently observed grappling with females on the ground within the nesting areas.

TABLE I. Analysis of the provision found in closed egg and pantry compartments and in complete cells of *P. insignis*.

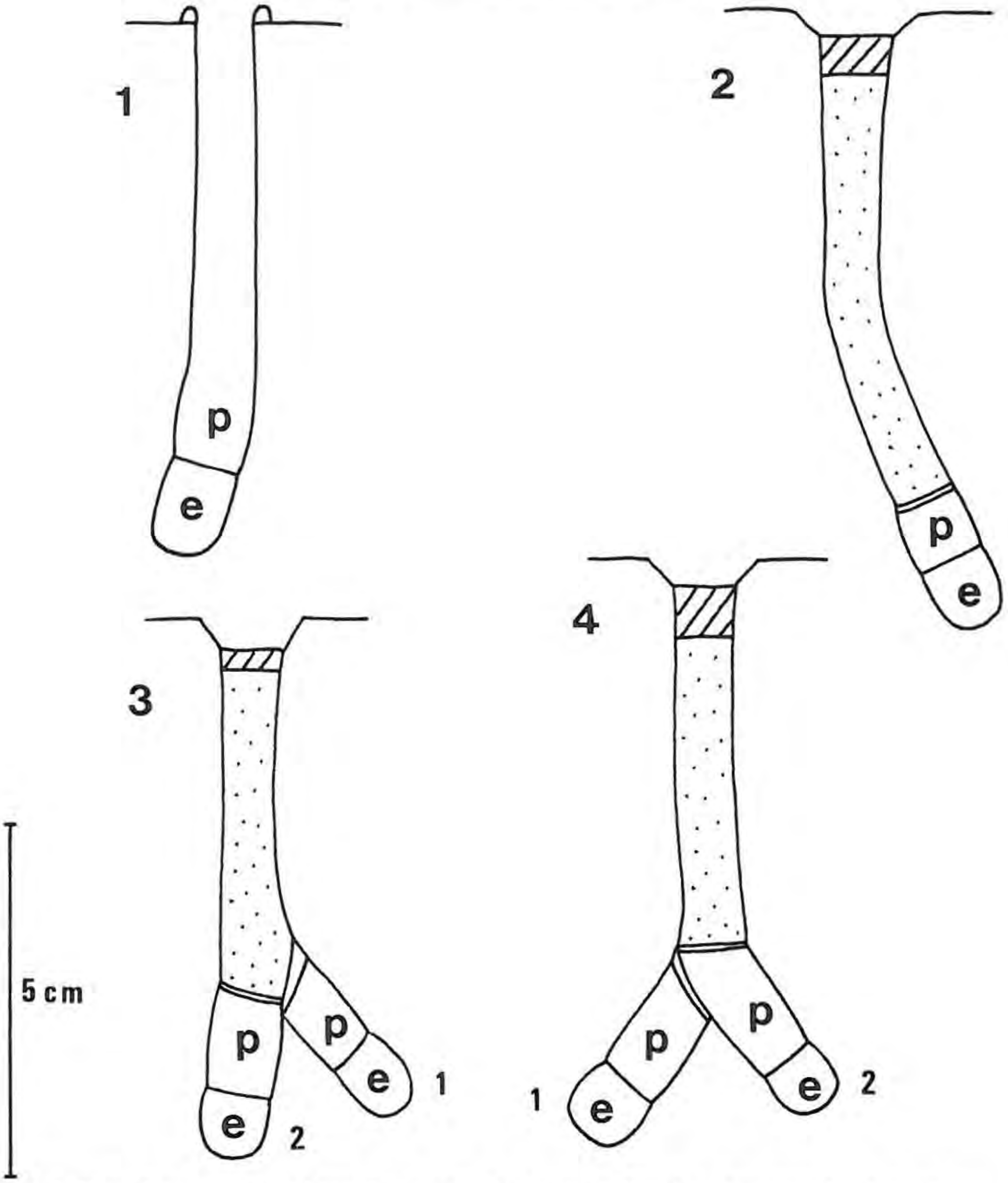
Part of nest	Size of sample	No. of prey constituting provision (range)	No. of prey constituting provision (average)	Mass of provision (range) mg	Mass of provision (average) mg
Closed egg compartment	21	2–4	2,7	125–322	220
Closed pantry compartment	13	5–13	8,0	473–913	703
Complete cells	11	8–17	10,7	832–1210	950

DESCRIPTION AND METHOD OF CONSTRUCTION OF THE NEST

The nest of *Parachilus insignis* consists of a subterranean burrow surmounted by a turret which is little more than a collar. This collar is made from mud pellets cemented together and smoothed on the inner surface only. The subterranean burrow consists of a shaft which is either simple terminating in a cell or in addition bears one lateral branch which leaves the main shaft just above the terminal cell and itself terminates in a cell which usually fills its entire length. Each cell is divided into two compartments, a lower (termed the egg compartment) containing the egg and a small number of prey caterpillars and an upper (termed the pantry compartment) containing a large number of prey caterpillars but no egg (Table I). These two compartments are separated by a thin mud plate. (Figs 1–4)

Water is required for nest-building and is collected by the female from a near-by puddle. She stands on the mud at the edge of the water to fill her crop. Several individuals were timed and took eleven seconds to perform this.

Nest excavation is initiated by the female regurgitating a cropfull of water onto the ground. Using her mandibles she works this water into the earth to form mud. This mud is formed into pellets which she lifts in her mandibles and arranges in a circle (inner diameter 5–7 mm) which is the foundation for the collar and also fixes the diameter of the shaft opening. While working the female stands outside the burrow, head down (Plates 5–7). The wasp adds pellets to the collar whilst rotating through 360° repeatedly so that pellets are added in spiral layering. The collar which is completed at an approximate height of 3 mm is thus built entirely from earth removed from the excavation of the burrow. Shaft excavation is continued but the pellets extracted are carried away from the nest and dropped except for an occasional pellet which is added to the collar. While working the wasp always enters the nest head first and emerges backwards. She leaves the nest in a constant direction, flies off, drops the pellet in a definite pellet-dropping area and before returning to the nest flies in a wide circle around it and finally alights on the collar and



Figs 1–4. Plans of underground workings of four nests of *P. insignis* (Sauss.). e—egg compartment; p—pantry compartment. Fig. 1. Open nest with sealed egg compartment and open pantry compartment. Fig. 2. Sealed nest with a single sealed cell. Figs 3 and 4. Sealed nests each with two sealed cells—sequence of construction of cells indicated.

Plate 5. Hilton, 13.xi.1974. Female *P. insignis* (Sauss.) at the entrance of the nest which she is constructing. (× *circa* 1,4). Plate 6. Hilton, 13.xi.1974. Two female *P. insignis* (Sauss.) disputing ownership of nest. (× *circa* 1,4).

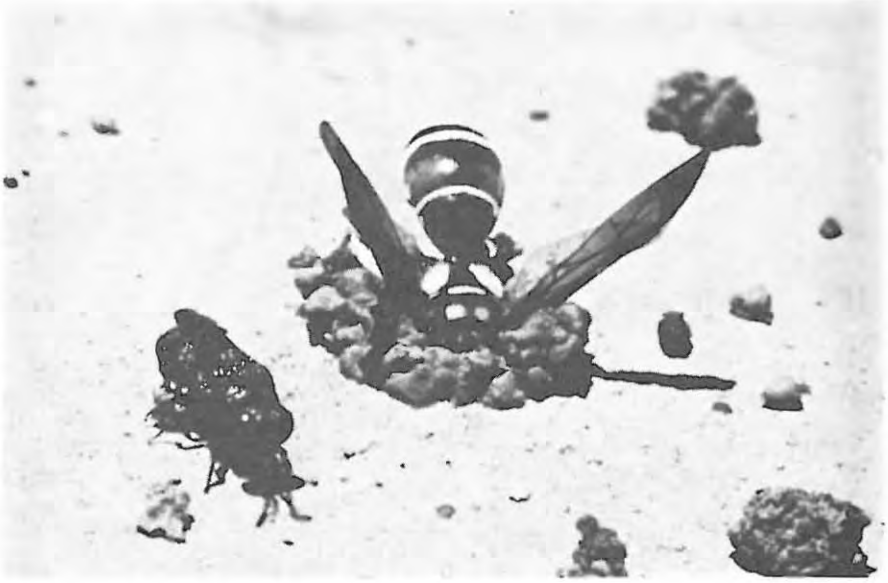


Plate 7. Hilton, 13.xi.1974. Female *P. insignis* (Sauss.) entering her nest and female *Octochrysis vansoni* (Brauns) on the ground close by. (× *circa* 2,5). Plate 8. Hilton, 13.xi.1974. Female *Octochrysis vansoni* (Brauns) inspecting nest entrance of *P. insignis* (Sauss.). (× *circa* 2,5)

enters the nest facing away from the pellet-dropping area (Fig. 5). All the individuals in a particular nesting site were seen to have their pellet-dropping areas in the same direction and to follow similar flight-paths. Six to eight pellets are excavated for each load of water and six to nine minutes elapse between successive water collections. A sample of 20 pellets was taken and their dry weight was found to be remarkably similar and to average 58 mg. When forming pellets the wasp is seen to rotate in the shaft and thus removes earth evenly ensuring that the shaft is circular in cross section. In one of the nests observed, it was found that the time taken from nest initiation through collar formation to completion of 25 mm of shaft was 36 minutes which indicates that the complete excavation of the nest could easily be accomplished in one working day. If the collar is destroyed by rain or in any other way there is no attempt to replace it. These observations were made early in the nesting season when individual nests, their builders and their pellet-dropping areas could easily be distinguished. Later in the season the nests were closely crowded and therefore pellet-dropping areas were no longer distinct. (Plates 3 and 4).

A total of 35 nests was excavated and drawn. Of this total 20 nests were still open and possessed single cells in various stages of provisioning, and were still being worked upon by adult female wasps. The other 15 nests had been completed and had been sealed. Ten of these sealed nests each possessed a single cell and five each possessed two cells.

All 28 nests (20 open and 8 sealed) excavated over the six-week period from the beginning of the nesting season up to 12.xii.1973 were found to be single-celled whereas five of the seven nests (all sealed) excavated two weeks later (on 27.xii.1973) were found to be two-celled. It therefore appears that single-celled nests are the rule in the first weeks of the nesting season but that two-celled nests may commonly be constructed during the second half of the nesting season at a time when nesting is very active. The fact that the state of development of the wasp young within each of the two-celled nests was in all cases very similar indicates that, at the time of construction of the two-celled nests, there was an abundant supply of prey and that the two cells were constructed and provisioned within a very short time of each other. A similar change during the course of a nesting season from the construction of nests containing one cell to that of nests containing more than one cell has been recorded for a population of *Bembix americana* (Sphecidae) by Alcock (1973) who has fully discussed the probable reasons for the phenomenon.

The depth below the ground of the bottom of the single cell or, in the case of nests with two cells, the bottom of the lower cell ranged from 60–105 mm (average 80 mm, 76 per cent in the 71–90 mm range). The bore of the main shaft at its mouth varied from 5–7 mm but was most commonly in the 6,5–7,0 mm range. As the shaft descended, its bore generally increased slightly and at about half its length (depth) varied from 7–9 mm (average 8 mm). The cells at the ends of the shafts varied in bore from 7–10 mm (average 9 mm). The lower portion of the cell, the egg compartment, varied in height (length) from 6–15 mm (average 10 mm) and the upper or pantry compartment varied from 10–18 mm (average 14 mm). The mud partition between the two cell compartments was very fragile and thin—1 mm or less in thickness, whereas the mud plug, the cell closure, between the upper compartment and the shaft was robust and thicker—about 2 mm.

COMPOSITION, PHYSICAL CONDITION AND TRANSPORT OF THE PREY; PROVISIONING AND OVIPOSITION

Parachilus insignis at Hilton was found to prey exclusively upon larval Psychidae (bagworms). Two species were taken and these could readily be distinguished in the field by the coloration of their heads. Thus in one species the head was uniformly rufous in colour, in the other species it was pale ochreous with brown spots. Whereas the arrival of provisioning wasps with their prey at the nesting sites was frequently observed, the hunting and the method utilized to de-bag the bagworms was unfortunately never witnessed. However, a careful search of the dwarf shrubs which surrounded the nesting sites to a considerable distance revealed that both

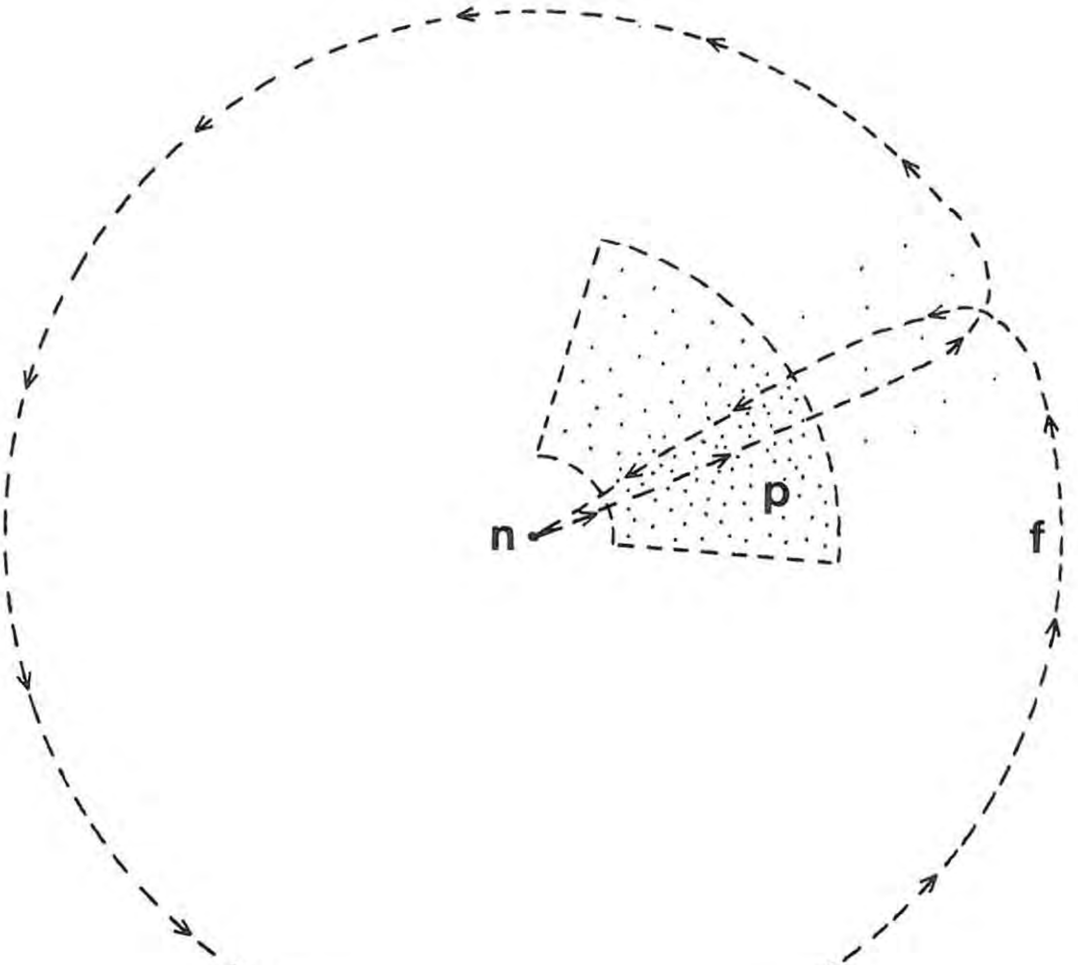


Fig. 5. Diagrammatic plan of pellet-dropping area and of flight-path taken during pellet-dropping phase of nest construction. f—flight path; n—nest entrance; p—pellet-dropping area.

species of prey were to be found occurring on these plants and that the bags constructed by the two species were distinct. The bag of the rufous-headed species was constructed of relatively longer, fine sticks of similar length, orientated parallel to the long axis of the bag. The only specimen found was feeding on a yellow daisy-flower (? *Gazania* sp.) (Compositae). The bag of the species with the pale-ochreous, brown-spotted head was constructed of relatively shorter, fine sticks of varying lengths, orientated tangentially at right-angles to the long axis of the bag. Thus whereas the proximal ends of the sticks were incorporated in the body of the bag the distal portions ($^{2}/_{3}$ to ¾ of the length in the case of longer sticks) stuck out to the sides. Seen end-on the bag thus appeared ornamented with whorls of protruding sticks. Five or six specimens were found, all feeding upon the dwarf-shrub *Pentzia incana* (Th.) O. Ktze (Compositae).

Both species were represented in the prey throughout the nesting season but one species was consistently more common than the other. Thus of a total of 318 prey caterpillars examined (258 from opened cells and 60 taken from ants raiding nests) 287 specimens were of the species with the pale-ochreous, brown-spotted head and only 31 specimens were of the rufous-headed species. The two species did not differ from each other in size and taken together prey of both species varied in length from 6–18 mm. Of 156 specimens, the length of which was measured, 73 per cent were in the 9–13 mm range. The average mass was 87 mg.

A total of 144 prey caterpillars was examined with respect to the location of sting sites which were visible as small dark lesions. It was found that each caterpillar was stung in three places on the underside of the thorax: on the prothorax, on the mesothorax and on the metathorax, in all cases in front of the legs. No sting sites were found on the abdominal segments nor anywhere else on the body. The prothorax invariably bore at least one sting. The mesothorax and metathorax in the great majority of cases likewise bore at least one sting though occasionally there were no stings in these two segments. Occasionally any one of the three segments bore more than one sting. The 144 prey examined together bore 158 stings on the prothorax, 180 on the mesothorax and 169 on the metathorax.

Paralysis of the prey was only partial, tactile stimulation resulting in squirming movements. Prey which was for some reason or other not eaten continued to defaecate for some time and remained alive for considerable periods but was generally inactive. Thus of 77 stung prey obtained from provisioned cells on 27.xii.1973 and kept in gelatin capsules, 46 individuals (60 per cent) were still alive on 7.ii.1974 (42 days later), 4 individuals (5,2 per cent) were still alive on 19.iii.1974 (82 days later) and one individual was still alive but very weak on 26.iv.1974 (120 days later). None of these specimens pupated. However, a 13 mm long rufous-headed larva with stings on all three thoracic segments, obtained from a nest cell opened on 27.xi.1973, pupated successfully and emerged as an adult male on 17.iii.1974.

P. insignis flies with its caterpillar prey from the site of capture to the nest. The prey, carried ventral side up and with the head facing the direction of travel, is held closely beneath the wasp's body by the latter's mandibles and legs. On arrival at the nest opening the wasp alights on the ground next to it, relinquishing her hold of the prey with her legs but not her mandibles. Raising the anterior part of her body the wasp then proceeds to work the prey forwards towards the nest opening and lets it drop down the nest shaft. The wasp then flies off to continue the hunt and it is only after several prey have been transported to the nest and dropped down the shaft that the wasp herself goes down the latter to arrange them in the cell. If, on the occasions when the wasp goes down the shaft herself, she is carrying a caterpillar, she does not enter the hole with the prey beneath her but lowers it in ahead of her.

The provision found in closed egg and pantry compartments and in complete cells was analysed and is presented in Table I. When considering the mass of the provision supplied for an egg, it is significant to note the mass of the adult wasp. The mass of females ranged from 135–222 mg and averaged 189 mg for a sample of 11 and the mass of males ranged from 172–275 mg and averaged 230 mg for a sample of 7.

As the wasp is unable to turn around in her cell she enters the nest backwards in order to oviposit. The egg is suspended from the upper surface of the egg compartment by a short filament of average length 4,5 mm. The eggs were all very similar in size. The average length was 3,26 mm and the average width was 0,9 mm. The weight of the only egg weighed was 2 mg.

A total of 39 egg compartments was examined of which 8 were open and 31 sealed. Each of the sealed egg compartments contained 2–4 prey and either an egg (in 23 compartments) or a small larva (in 8 compartments). Two of the 8 open egg compartments contained neither eggs nor prey having been examined before oviposition and provisioning had taken place. Of the remaining open cells one contained an egg and 2 prey and 5 contained prey (1, 1, 2, 7 and 11 individuals) but no egg. Whereas the number of prey in the two compartments containing 7 and 11 prey is so highly aberrant that the absence of an egg cannot be considered significant, the remaining 3 cells must be considered as having contained prey but no egg as it is remarkable that in all the closed cells excavated there is no case of an egg having been overlooked. The sample is however too small for any conclusions to be drawn.

NEST CLOSURE

After the cell or cells have been completed and sealed the shaft is filled with pellets and small crumbs of loose earth and the opening at the surface of the ground closed with a mud plug and smoothed off leaving a shallow depression 10–17 mm in diameter in the surface of the ground (Figs 2, 3 and 4). The earth and mud pellets used for nest closure are derived from the collar, a "quarry", scattered pellets and from loose earth where the ground has been disturbed. In the first case the wasp having filled her crop with water regurgitates it onto the collar and with her mandibles scrapes off and kneeds into a pellet a small quantity of the resultant mud. The pellet so fashioned is then dropped down the shaft. The antennae are held close to the mandibles seeming to monitor the progress being made with the pellet. Additional pellets are taken from a "quarry" a short distance from the nest (*circa* 30 cm). Pellets are formed as before and the wasp flies with each pellet and drops it down the shaft. As she returns to quarry further pellets in the same place a small crater develops. In addition previously discarded pellets and loose crumbs of earth lying near the nest may be collected and dropped down the shaft. When the shaft has been entirely filled, the wasp seals the opening by cementing together pellets to form a plug 4,5–9,0 mm in depth. Finally she moistens the surface of the ground on the sides of the depression and draws the resultant mud across the plug to give it a smooth finish. Sealed nests are difficult to distinguish from quarry sites.

PARASITES AND OTHER ASSOCIATED INSECTS

Several species of insects, belonging to different orders, were found in association with *Parachilus insignis*. They included parasites (Meloidae, Chrysididae and Bombyliidae), prey robbers (Formicidae) and users of old burrows (Apoidea).

A species of Meloidae, *Lytta enona* Péringuey was found to be a fairly common cleptoparasite in the nests of *P. insignis* where in its larval stage it feeds upon the stored caterpillars after first destroying the eumenid's egg. The seventeen individuals found in association with *P. insignis* nests are dealt with in an order determined by their developmental stage when found.

A triungulin larva, 1,0 mm in length with a darkly pigmented body and with well developed long legs and long slender cerci was found on 27.xi.1973 in a sealed egg compartment containing two prey and a collapsed *P. insignis* egg still hanging from its filament. In the hope of rearing this larva the contents of the egg compartment were transferred to a gelatin capsule but, unfortunately, the larva died two days afterwards. However, in view of other finds, the authors are satisfied that this larva was that of *L. enona*.

TABLE II. Developmental times for the later stages of the life history of *Lytta enona* Péringuey (Meloidae).

	Date of moult from 4th (scarabaeoid) to 5th (coarctate) instars	Date of moult from 5th (coarctate) to 6th (scolytoid) instars	Date of pupation	Date of full pigmentation and hardening of adult
1	10–20.i.74	24.xi.74	4.xii.74	17.xii.74
2	10–20.i.74	30.xi.74	—	—
3	10–20.i.74	10.xi.74	18.xi.74	7.xii.74
4	10–20.i.74	3.i.75	9.i.75	24.i.75
5	10–20.i.74	24.xi.74	5.xii.74	23.xii.74

On 27.xii.1973 five sealed egg compartments in as many nests were each found to contain a single foreign larva with small but functional thoracic legs. These larvae were feeding upon the provision laid in for the *P. insignis* larvae. In one case the remains of the *P. insignis* egg or newly hatched larva were found in the egg compartment. These foreign larvae were the 3rd (1st scarabaeoid) instar larvae of *L. enona*, the identification being established by the successful rearing through to the adult stage of four of their number. Dates of moulting from the 3rd to 4th instars were not recorded but developmental times for later stages of the life history are given in Table II. The lengths of the larvae when found varied from *c.* 10– *c.* 14 mm (average 12,6 mm). During the course of their development in the cell and later in the laboratory the larvae consumed from 6 to 8 caterpillars each between hatching and the end of the 4th (2nd scarabaeoid) instar, after which no further feeding took place. The non-feeding, diapausing 5th (coarctate) instar was characterized by the hardness of the brown-coloured integument and by the rudimentary nature of the legs and mouthparts. The non-feeding 6th (scolytoid) instar, with which development proceeded after the winter and spring months had passed, was softer and paler than the preceding instar but had functional legs. Larvae of this instar kept in Petri dishes moved about restlessly for a period of two to three days after which they lay motionless until they pupated. Pigmentation of the eyes and of the mandibles began six and eight days respectively after pupation.

A diapausing 5th (coarctate) instar larva was found associated with a nest of *P. insignis* excavated by the authors on 26.ix.1974 and six additional specimens were found associated with nests excavated on 13.xi.1973. The first-mentioned larva moulted to the 6th instar two days after collection, pupated on 20.x.1974 and was fully adult on 18.xi.1974.

Four adult beetles were obtained in the field. One of these was found on 13.xi.1974 inside a sealed nest of *P. insignis*, the others were found on different dates (7.xii.1973, 8.xi.1974 and 15.xi.1974) walking about on the ground within the nesting site of *P. insignis*.

Lytta enona Péringuey (1899: 319) was described from Uitenhage, about 120 kilometres from Grahamstown. Whereas the species was subsequently reclassified as belonging in the genera *Cantharis* and *Epicauta* by Péringuey (1909: 266) and by Borchmann (1917: 74) respectively, Kaszab (1953: 484) upheld its original inclusion in the genus *Lytta*. The species appears to be poorly represented in collections and nothing has hitherto been recorded regarding its life-history.

The biology of *L. enona* is unusual in so far that the larva feeds upon the paralysed insect prey with which a hunting wasp has provisioned its cell whereas meloid larvae generally feed either upon the buried egg packets of Orthoptera or upon the provisions laid in by pollen- and nectar-collecting Hymenoptera. When considered in terms of the discussion of the possible behavioural evolution of the Meloidae presented by Paoli (1938) it is clear that the food choice of *L. enona* would place this species in a category previously exemplified solely by the European *Cerocoma schaefferi* L. The larva of that species was found by Fabre (1943b: 268–80) to develop in the nests of a species of *Tachysphex* ("Tachyte manticide" of Fabre) (Sphecidae) where it fed upon small mantids with which the cells had been provisioned.

Two species of Chrysididae (Holonychinae) were found in association with the nests and nesting sites of *P. insignis* at Hilton. The more common of the two, *Octochrysis vansoni* (Brauns), a dark-green species with infuscated wings, was found over several seasons to be a constant attendant at each of the nesting sites and at times appeared to be as common there as *P. insignis* itself. Its appearance in early summer was found to coincide with that of the eumenid and its flight season appeared to be of similar length. The species was never observed anywhere other than at the nesting areas of *P. insignis*. Within the *Parachilus* nesting area *O. vansoni* is to be found resting upon the ground in close proximity to nests which are being worked upon (Plate 7). Every so often the chrysidids take to the wing to inspect open nests left unguarded while the eumenids have flown off to fetch water or to hunt. Having alighted upon the nest collars the chrysidids are seen to probe the nest entrances with rapidly quivering antennae (Plate 8) and occasionally to enter the nests. Remarkably little notice appears to be taken of the chrysidids by the female eumenids.

The very much less common of the two chrysidid species, *Pseudospinolia ardens* (Mocsary), a ruby coloured form with infuscated wings, does not differ in its behaviour from that described for *O. vansoni*.

It is remarkable that all the specimens (123 of *O. vansoni* and 5 of *P. ardens)* collected at the nesting sites over a period of several seasons appear to be females. These include specimens determined by Linsenmaier in 1972 which were used by the authors in naming subsequently collected material.

No conclusive proof was obtained that either species is a parasite or cleptoparasite of *P. insignis* but to the very suggestive circumstantial evidence may be added the fact that typical chrysidid cocoons of the correct size for either of the species were obtained from *P. insignis* cells excavated on 13.xi.1974. Unfortunately, the diapausing larvae within the cocoons, which were transferred to glass vials, did not develop further and died after several months.

Little is known about either species: *Octochrysis vansoni* was described by Brauns (1928: 388) from two males on a *Euphorbia* sp. at Vanrhynsdorp, Namaqualand (Cape Province, not Transvaal as incorrectly stated by Edney (1954: 637)); *Pseudospinolia ardens* was recorded by Edney (1947: 185) from the Cape Province. No hosts have been recorded for either species.

A single diapausing dipterous larva, identified as the 3rd instar of a species of Bombyliidae was obtained from a cell of *P. insignis* excavated on 13.xi.1974. Pale coloured, weakly curved and about 14 mm in length, the larva was amphipneustic with spiracles on the prothoracic and eighth abdominal segments and bore a pair of minute bristles ventro-laterally on each thoracic segment. Other than for the smaller degree of curvature of the body and the reduced length of the thoracic bristles the larva was very similar to that of a *Systoechus* sp., a locust-egg predator, described and figured by Greathead (1958: 6–10, Fig. 1 and Plate 1). At the time of writing (June 1975) the larva was still in a state of diapause and it was hoped that it might yet continue its development and that a specific identification might be possible.

During December 1973 the bombyliid *Exoprosopa leucothyrida* Hesse was very commonly found either resting on the ground or flying about within the nesting areas of *P. insignis*. Hesse (1956: 658) in his summary of the known biology of the genus *Exoprosopa* showed that the available evidence indicates that the species of this genus parasitize various species of Hymenoptera. It is thus not impossible that the above-described larva may be that of *E. leucothyrida*.

Some indication of the extent to which *P. insignis* is victim to the various parasites may be seen from an enumeration of the insects found in 38 cells excavated and opened by the authors on 13.xi.1974. Twenty-nine cells contained pupae or diapausing larvae of *P. insignis*, six cells contained coarctate larvae of *Lytta enona*, three cells contained cocoons of Chrysididae and one cell contained a diapausing larva of Bombyliidae.

An important prey robber to which the wasps of one of the nesting sites repeatedly fell victim during the 1973–4 nesting season was the camponotine ant *Plagiolepis steingroeveri* Forel. This pugnacious species which had nested in the ground at the edge of the *Parachilus* nesting area systematically raided the open nests of the wasps and carried off the caterpillars with which the cells were being provisioned. During a raid the provisioning wasps which were powerless to prevent the theft of their prey hovered above their nests and above the ants which appeared to take no notice of them but attacked the wasps when they alighted upon the ground.

It is significant that during the following (1974–5) season this particular nesting area contained but a fraction of the usual number of emergence holes and later showed a most striking reduction in the level of nesting activity when compared with that of previous years.

Several species of solitary bees, mostly Megachilidae, were found associated with open old burrows from which *Parachilus* had previously emerged.

The most regular use of these old burrows was made by *Creightoniella dorsata* (Smith), several females of which were observed to be nesting in them. The completed nest of one of these females, the only one excavated by the authors, was found to contain two 17 mm long cells constructed of leaf cuttings. The closure, also constructed of pieces of leaf was 32 mm in length and came to within 3 mm of the opening of the shaft at ground-level.

Other leaf- or petal-cutting species caught on emerging from old *Parachilus* burrows, which were however not excavated by the authors, were *Megachile (Eutricharaea) aliceae* Cockerell, *M. (E.) meadewaldoi* Brauns, *M. (E.) semiflava* Cockerell and *M. (E.) stellarum* Cockerell. At Hilton *M. (E.) meadewaldoi* has previously been recorded nesting in the burrow of *Bembecinus oxydorcus* (Handl.) (Gess and Gess, 1975: 40) and *M. (E.) stellarum* in the burrows of *Dichragenia pulchricoma* (Arnold) (Gess and Gess, 1974: 204).

An anthophorid bee, *Tetralonia minuta* Fr., a single female of which was captured on emerging from an old *Parachilus* burrow, has previously been recorded from a *Bembecinus cinguliger* (Smith) burrow at Hilton (Gess and Gess, 1975: 40). In neither case is the nature of the association clear.

SLEEPING AND SHELTERING BEHAVIOUR OF THE ADULT WASPS

Both sexes of *Parachilus insignis* spend the night and periods of unfavourable weather during the day sleeping or sheltering in their burrows. Thus on an overcast and cold morning at the very beginning of the flight season (on 30.x.1973), at a time when there were many open burrows from which wasps had emerged over the previous few days but before new burrows had been excavated by the wasps in any numbers, both males and females were found sheltering in the old (previous season's) burrows. When the sun appeared from behind the clouds at 11.30 a.m and the temperature rose these wasps left the burrows and flew off. It was clear that these wasps were not emerging for the first time but were leaving burrows to which they had returned the previous afternoon in order to spend the night in shelter. In sleeping or sheltering in the burrows the wasps, orientated facing the burrow openings, are situated in the upper part of the main shafts, their heads being about 15 mm below ground-level. A sheltering wasp's head and prothorax are clearly visible from outside and appear to block the shaft completely.

As nesting commences females no longer shelter in old burrows but in burrows which they are excavating or provisioning. Males, however, continue to shelter in the previous season's burrows.

During fine, warm, sunny weather the usual time of emergence by the wasps in the morning was not established but in the afternoon many females returned to their burrows as early as 3.30 p.m. During the day it was very noticeable that, whenever the sun was obscured by heavy clouds, the females backed into the burrows they were excavating or provisioning and sheltered there until the sun reappeared. During overcast, cold or rainy days the wasps remained in their burrows all day.

On 12.xi.1973 after three days of rain (during which time 26 mm fell) it was noted that nest collars and pellet-dumps had been washed away or had melted and that nests the existence of which was known could be located only by reference to marker-nails and by measurement, the nest openings having been filled with earth. As the morning passed some of these blocked-up nests were reopened from within by the sheltering wasps. One nest, opened from the outside by the authors was found to contain a live female sheltering between the filled-in portion and the provisioned and sealed egg compartment of the cell. The cell at a depth of 79 mm below the ground surface was quite dry despite the rain, the soil being damp to a depth of only about 50 mm. Undoubtedly, the presence of the sheltering female in the nest shaft helped in the formation of the earth plug sealing the nest and thus saved the cell from flooding.

DISCUSSION

Parachilus insignis shares with certain species belonging to several other odyneroid genera (such as *Euodynerus*, *Odynerus*, *Oplomerus*, *Paragymnomerus*, *Pterocheilus* and *Stenodynerus*) the habit of constructing original burrows in level ground.

With the exception of *Pterocheilus* all the genera listed above include species whose nest-building behaviour is similar to that of *P. insignis* in that they utilize water to soften the earth and carry away the excavation spoils in the form of mud pellets. Most but not all the species utilize some of the pellets to build mud turrets. Accounts of nesting behaviour relevant to the discussion include those of the following species: *Euodynerus annulatus annulatus* (Say) by Isely (1914: 277–81) (as *Odynerus annulatus* Say) and by Rau and Rau (1918: 300–12) (as *O. geminus* Cresson); *E. annulatus arvensis* (Saussure) by Isely (1914: 271–6) (as *O. arvensis* Saussure) and by Evans (1956: 267–8) (as *Rygchium annulatum arvense* (Saussure)); *E. dorsalis dorsalis* (Fabricius) by Isely (1914: 281–94) and by Rau and Rau (1918: 312–31) (both as *O. dorsalis* Fabr.); *Odynerus dilectus* Saussure by Linsley and Michener (1942: 27); *Oplomerus* species by Blüthgen (1961: 70–82), by Fabre (1943a: 81–103) (as *Odynerus*), by Grandi (1961: 55–62) (as *Hoplomerus*) and by Spradbery (1973: 48–50) (as *Odynerus*); *Paragymnomerus spiricornis* (Spinola) by Blüthgen (1961: 82); *Stenodynerus fundatiformis* (Robertson) by Evans (1956: 268).

When compared with the various accounts of nesting in the above-listed species, the nesting of *P. insignis* is seen not to deviate to any appreciable degree from the overall pattern but rather to be fairly typical of a ground-nesting, water-utilizing eumenid. Indeed, the similarity between the nesting behaviour of *P. insignis* and that of some of the other species, notably *E. dorsalis dorsalis* is most striking. With respect to the latter species one of the few differences lies in the arrangement of the cells which in contrast to the arrangement in *P. insignis* are built one above the other in the direct line of the burrow.

It is in its habit of dividing each cell into two compartments separated by a thin mud plate that *P. insignis* differs in its nesting behaviour from all the above species and indeed the authors have been unable to discover any instance of this behaviour in any other eumenid. As has already been shown, the cell's lower compartment (termed the egg compartment) contains the egg and a small number of prey caterpillars and the upper compartment (termed the pantry compartment) contains a large number of prey caterpillars but no egg. For the full development of the wasp larva the provision contained in both cell compartments is required. The young larva after having eaten the relatively small amount of provision present in the egg compartment breaks down the thin mud partition separating the compartments and then feeds upon the main supply of provision stored in the pantry compartment. The relative masses of the provision in the two compartments may be seen in Table I and the inadequacy for full larval development of the provision present in the egg compartment alone is apparent when compared with the mass of adult wasps. In this connection it is of interest that in *P. insignis* the males have a greater average mass and are thus generally of larger size than are the females. In connection with the apparent uniqueness of the physical separation of the cell into two compartments in *P. insignis* it should be noted that the statement by Malyshev (1968: 176) concerning Fabre's description of the cell of *Oplomerus reniformis* (Gmel.) (as *Odynerus*) can be misleading. A close study of Fabre's own account (1943a: 100) indicates that there was no actual separation of the cell into two parts by a wall as in *P. insignis* but that the cell merely had a wide and a narrow part.

In view of the one-time inclusion of *P. insignis* and its present congeners within the genus *Pterocheilus*, it is relevant to draw attention to the marked difference between *Parachilus* (as exemplified by *insignis*) and *Pterocheilus* with respect to the nature of the ground in which nesting takes place and to the method by which the nest is excavated. As has been shown *P. insignis* nests in clay soil which requires softening with water before it can be worked whereas those species of *Pterocheilus* for which nesting data could be found nest in sandy soil or at least in soil the nature of which is such that nest excavation (and nest sealing) can be accomplished without the use of water. Species of *Pterocheilus* whose nesting behaviour was considered in this connection comprise the European *chevrieranus* Saussure (Ferton, 1910 and Ahrens, 1924) and the North American *quinquefasciatus* Say (Isely, 1914: 294–6), *texanus* Cresson (Evans, 1956: 265–7) as well as four other species said to have similar life histories (Bohart, 1940: 164).

The above-indicated differences between the two genera with respect to choice of nesting substrate and method of nest excavation are correlated with morphological differences in the mouthparts of the female wasps which have been used as characters in separating *Parachilus* (and *Pseudochilus*) from *Pterocheilus*. Thus the long and pendulous, fringed labial palpi of *Pterocheilus* (see Bohart, 1940: Pl. 1, Fig. 17) are supposedly used in conjunction with the fringed mandibles to form a basket for carrying loose earth from the nest during its construction (see Evans and Eberhard, 1970: Fig. 55). In contrast, the labial palpi of *P. insignis* are furnished with sparse, short hairs (see Giordani Soika, 1960: Fig. 11) and the mandibles though furnished with a well-developed fringe of stiff hairs have these shorter than those of *Pterocheilus*. No psammophore as seen in *Pterocheilus* is thus present in *P. insignis* but the arrangement of hairs on the mouthparts is suited for holding pellets of mud.

SUMMARY

Some aspects of the ethology of *Parachilus insignis* (Saussure) (Hymenoptera: Eumenidae) in the Eastern Cape Province of South Africa are described. Nesting is dealt with in considerable detail as nothing concerning this activity has hitherto been recorded for any species of *Parachilus*. When compared with the published accounts of the nesting of representatives of several other odyneroid genera, the nesting of *P. insignis* is seen to be fairly typical of a ground-nesting, water-utilizing species. However, the division of each cell into two compartments separated by a thin mud plate marks off the behaviour of the present species from that of other Eumenidae. Whether this feature is unique to *P. insignis* or is common to all *Parachilus* species is unknown at present.

Lytta enona Périnquey (Meloidae) is recorded as a cleptoparasite in the cells of *P. insignis* where in its larval stage it feeds upon the paralysed caterpillars laid in as provision by the wasp.

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Ethological notes on Dichragenia neavei (Kohl) (Hymenoptera: Pompilidae), an African spider-hunting wasp building a turreted, subterranean nest

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INTRODUCTION

In a recent paper Gess and Gess (1974) described the ethology of *Dichragenia pulchricoma* (Arnold) (Pompilidae: Macromerini) in the Eastern Cape Province of South Africa. Of particular interest was the form of the nest which, by possessing a mud entrance turret surmounting the subterranean burrow and cells, was believed to represent a nest type previously unknown within the Pompilidae.

In the present paper an account of some aspects of the ethology of a closely related species, *Dichragenia neavei* (Kohl) **comb. nov.** (syn. *Pseudagenia neavei* Kohl, 1913 and *Pseudagenia mygnimioides* Bischoff, 1913) is presented. *D. neavei*, like *D. pulchricoma*, surmounts its subterranean nest with a mud turret. Mention of turret building by *D. neavei* (as *Pseudagenia mygnimioides* Bischoff) has previously been made by Chapman (1958) in a very brief account based upon the discovery of a single nest in the Rukwa Valley, Tanzania. This record of turret-building in the Pompilidae was overlooked by the present authors when writing their earlier (1974) paper on *Dichragenia* and was not noticed either by Evans and Eberhard (1970, see p. 76). In view of the fragmentary nature of Chapman's data it is considered warranted to publish the present more extensive observations particularly as an opportunity is thus afforded for comparing the nesting of *D. neavei* with that of *D. pulchricoma*.

THE NESTING OF DICHRAGENIA NEAVEI (KOHL)

Dichragenia neavei is similar in size and facies to *D. pulchricoma* and like it has fuscous wings and ferruginous legs. The two species may however readily be distinguished in the field by the coloration of the pronotum, ferruginous in *D. neavei* and black in *D. pulchricoma*.

During the six weeks from 26.x.1972 to 6.xii.1972 within which period the ethology of *D. pulchricoma* was being studied at Hilton and at Clifton, localities near Grahamstown (33° 19'S., 26° 32'E.) in the Eastern Cape Province of South Africa, *D. neavei* was commonly observed in company with the former species at puddles and temporary pools at both localities. It was clear

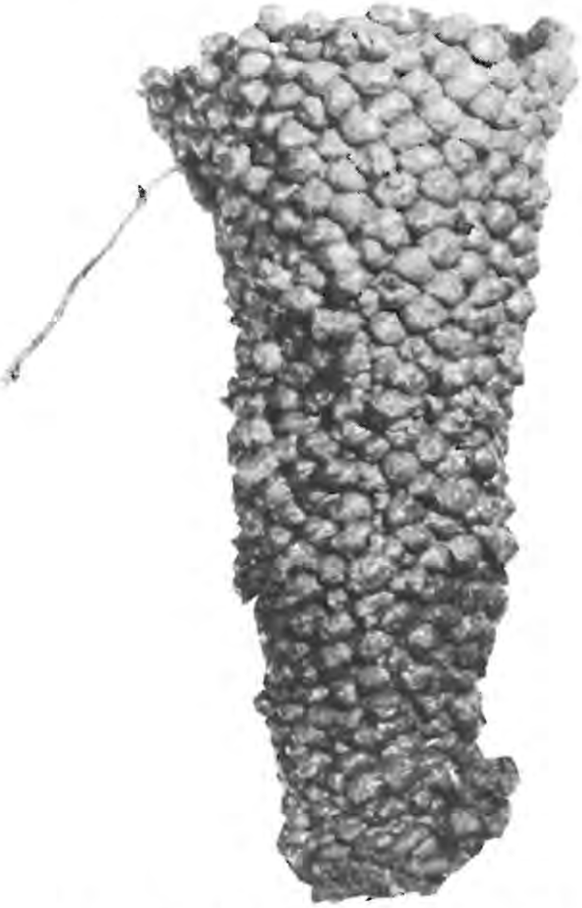


Plate 1. Hilton, 9.i.1974. Turret of *Dichragenia neavei* (Kohl). (× 2).

that the females of *D. neavei*, like those of *D. pulchricoma*, were collecting water and it was assumed, correctly as it later transpired, that it was for the same purpose–namely for nest construction. However, whereas large numbers of nests of *D. pulchricoma* were located and positively identified as being those of that species, no nests of *D. neavei* were found and it was not until the following summer that the first was discovered. Subsequently two further nests of *D. neavei* have been located.

The first nest (Fig. 1) of *D. neavei*, discovered on 9.i.1974, aroused the authors' interest due to its large, upright funnel-shaped turret (Plate 1). In height this turret rose 57 mm above the surface of the ground, in diameter it increased from 12 mm at its extreme base to 28 mm at its distal opening. Seen from above the turret was nearly radially symmetrical. The mud pellets used as building bricks in turret construction were spirally arranged and were closely packed. Small interstices were however left between them, especially distally. Whereas the individual pellets were very distinct on the outer surface of the turret walls, some smoothing of the pellets had been done on the inner surface. Believed at the time of discovery to be merely an aberrant turret of *D. pulchricoma*, it was nevertheless collected and the nest below it excavated. Two cells were found. The first-constructed, situated at a depth of about 75 mm below the ground surface, was sealed and contained a prey spider with its head orientated towards the shaft-end of the cell. No egg or wasp larva was found. The second cell, situated at a greater depth, was open and had not yet been provisioned. The female nest builder was not seen.

The second nest was spotted on 18.iv.1974. Due to lack of time the turret was not collected nor were the underground workings excavated. The turret was similar to that of the first nest.

The third nest (Fig. 2) was discovered on 10.i.1975 when a female *D. neavei*, seen walking about on the ground, was followed to it. The wasp which entered the turret and went down into the nest below was captured upon re-emerging. The capture of this female enabled the true builder of the funnel-shaped turrets to be identified and ended the long search for the nest of *D. neavei*. The turret was collected and the subterranean part of the nest was excavated. In height this turret rose only 19 mm above the surface of the ground, in diameter it increased from 11 mm at its extreme base to 26 mm at its distal opening. In all other respects it was very similar to the turret of the first nest and like it showed evidence of some smoothing of the inner surface of the walls. Three sealed cells were found near the end of the main nest shaft at a depth of between 130 and 140 mm. Each cell contained a prey spider but in only two cells was a wasp egg found.

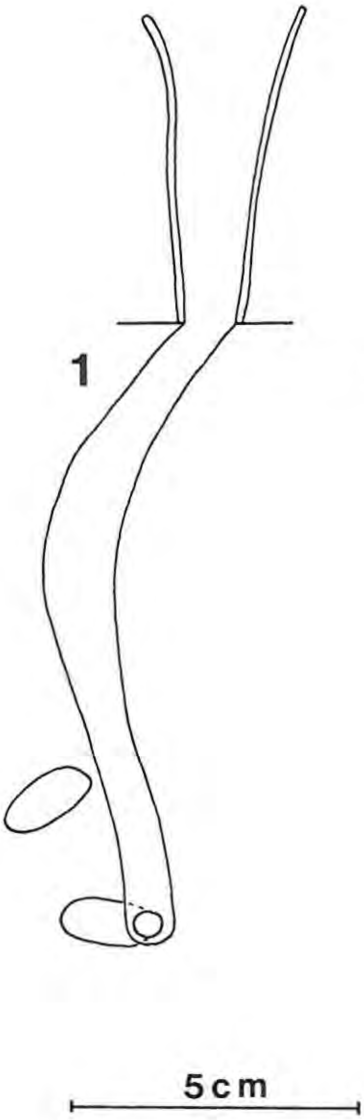
All three nests of *D. neavei* were, like those of *D. pulchricoma*, built in places where the ground had been disturbed and partially denuded of vegetation. Similarly, all three were close to temporary sources of rain-water. The first nest was situated on partially denuded ground flanking a water furrow, the second on the raised bank of earth running parallel to a water furrow and derived from the excavation there of (near site shown in Gess and Gess, 1974: Plate 2), and the third on slightly sloping ground intersected by small erosion gullies in places trapping shallow pools of water (near site shown in Gess and Gess, 1974: Plate 3).

Whereas the mud turrets of *D. pulchricoma* were most often found completely exposed in bare areas and were only occasionally in more protected situations as at the base of dwarf shrubs, all three turrets of *D. neavei* were found to be situated well under or within dwarf shrubs, those of the first and second nests actually having small branchlets passing through the turret walls. These branchlets thus incidently helped to support the large funnel-shaped structures in an upright position. Owing to their position the turrets of *D. neavei* are much more difficult to spot than are those of *D. pulchricoma*.

A female *D. neavei* was observed transporting its prey at noon on 28.i.1974. The wasp carried its prey across open ground, walking forwards, straddling the prey with its legs. The spider, an immature specimen of indeterminable sex of *Palystes* sp. (Sparassidae), had had all its legs amputated and was carried dorsal side up, head forwards, held by the wasp's mandibles at the base of the right chelicera. No attempt was made by the wasp to fly. Captured and weighed the "dressed weight" of the prey spider was found to be 137 mg whereas the weight of the wasp was a mere 48 mg.

The four prey spiders obtained from the provisioned cells of the first and third nests were all of the family Lycosidae. The first nest contained an adult male and the third an adult male and two immature specimens of indeterminable sex. Three of the spiders had had all the legs amputated at the coxal-trochantal joint and the fourth had one leg (the left front) remaining. In all cases the pedipalps were intact. Three of the spiders were 10 mm long and one was 9 mm long; the width across the carapace was 4 mm and across the carapace to the ends of the leg stumps 5 mm. All the prey spiders were alive and responded to tactile stimulation.

The eggs found on the spiders in two of the cells of the third nest were both attached to the side of the spider's abdomen near the base of the latter, in a position very similar to that shown for the egg of *D. pulchricoma* (see Gess and Gess, 1974: Figs 6, 7). The attachment of the egg



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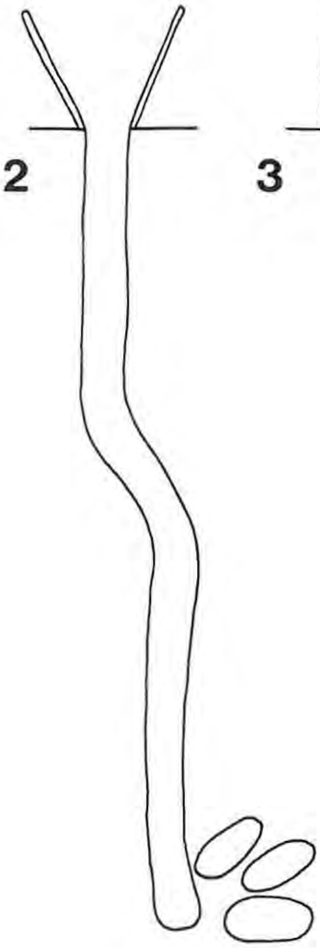

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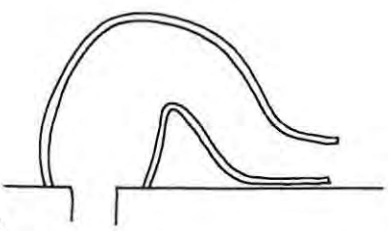

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Figs 1 and 2. Vertical plans of the turrets and underground workings of two nests of *Dichragenia neavei* (Kohl) studied at Hilton. Fig. 3. Vertical plan of the turret of a nest of *Dichragenia pulchricoma* (Arnold) studied at Hilton.

was over its entire length with the exception of the extreme anterior end which was sited uppermost. One egg was attached to the left side of the spider's abdomen and the other to the right side. Both eggs were 2,3 mm in length.

DISCUSSION

The ethology of *Dichragenia neavei* (Kohl), as far as can be ascertained from the small number of nests examined and from the few observations made during the present study, appears to be very similar indeed to that of *D. pulchricoma* (Arnold) described and discussed at length by Gess and Gess (1974).

D. neavei, like its congener and indeed like species of other genera of Macromerini (such as *Phanagenia*, *Auplopus* and *Ageniella*) selects for its prey certain errant spiders, the legs of which it amputates at the coxal-trochantal joint prior to removal to the nest. Like *D. pulchricoma* and species of *Phanagenia* and *Ageniella* (but not *Auplopus*) *D. neavei* straddles its prey and walking forwards transports it dorsum up, grasped at the base of a chelicera.

In common with *D. pulchricoma* and a few species such as *Priocnemis minorata* Banks (tribe Pepsini) but in marked contrast to the above three macromerine genera (which construct aerial nests), *D. neavei* constructs a multicellular subterranean nest in clay soil. In the adoption of the use of water to soften the hard soil, in the removal of the spoils of nest excavation in the form of mud pellets and in the use of these mud pellets in the construction of a turret surmounting the nest entrance, the behavior of *D. neavei* closely parallels that of *D. pulchricoma* but differs from that of all other hitherto studied Pompilidae. This similarity in the ethology exhibited by these two species leads to the conclusion that it is probably typical for the genus *Dichragenia* Haupt as a whole.

It is of interest that it is in the architecture of that physical artifact of behaviour, the nest turret, the possession of which by *Dichragenia* at present appears unique within the Pompilidae, that the most notable differences in nesting between the two species are apparent. Thus whereas the turret of *D. neavei* is funnel-shaped (Figs 1 and 2 and Plate 1) that of *D. pulchricoma* is retort-shaped (Fig. 3 and also Gess and Gess, 1974: 195–196, Plates 6–8). Furthermore, whereas the bore of the turret of *D. neavei* is the same at its base as is that of the nest shaft at its top, that of the turret of *D. pulchricoma* in the same position is about three times that of the shaft. A difference is also to be seen in the fact that whereas *D. neavei* turrets exhibit some smoothing of their inner surface no such smoothing is seen in *D. pulchricoma* turrets.

The account of the nesting of *D. neavei* given by Chapman (1958) brief as it is nevertheless raises some interesting questions. According to that author *D. neavei* in constructing its turret uses its jaws, forelegs and the tip of the abdomen to place each pellet. In the present study *D. neavei* was not observed in the act of turret construction but *D. pulchricoma* which was watched for considerable periods on two occasions was seen to use the mandibles only. The tip of the abdomen was never used. Use of the pygidium as a "trowel" for smoothing the surface of a mud structure, the nest, has however been reported for *Auplopus* by Evans and Eberhard (1970: 100 and Fig. 67). Chapman also reported *D. neavei* sealing the nest by filling the shaft with earth and by placing debris, small stones and twigs within the mud turret. The present authors have never observed such behaviour in either *D. neavei* or *D. pulchricoma* and, although in the case of the latter species a total of sixty nests was excavated, no evidence of nest sealing was found. In both species, however, each cell within a nest is individually sealed off from the common shaft by means of a mud plug, the existance of which is strangely not mentioned at all by Chapman. Further observation of *D. neavei* at work is obviously necessary in order to resolve these questions.

The study of the ethology of the present two species has on a generic level yielded taxonomic characters which have confirmed the validity of the genus *Dichragenia*, erected on the basis of what might be considered rather minor morphological features. At the same time it has clearly indicated relationships with certain other genera. Furthermore it has been shown that the architecture of the nest turrets is a useful character distinguishing the two species. It is clear that further ethological studies of Ethiopian Macromerini, of which there are more than 120 described species, would be very rewarding and might well be of great assistance at both the generic and the specific levels in any future revision of this, at present, very confused group.

SUMMARY

Some aspects of the ethology of *Dichragenia neavei* (Kohl) in the Eastern Cape Province of South Africa are described and are compared with the known ethology of *D. pulchricoma* (Arnold). Attention is drawn to some points of variance between the present observations and those made on *D. neavei* by Chapman (1958) in Tanzania.

ACKNOWLEDGEMENTS

The authors wish to thank Mr T. C. White of the farm Hilton for his much appreciated kindness over the years in allowing them free access to his land. Thanks are due also to Mr M. C. Day of the British Museum (Natural History) for confirming the senior author's identification of the wasp and for drawing attention to the synonymy. The senior author is grateful to the C.S.I.R. for a running expenses grant for field-work during the course of which the present observations were made.

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Ethological notes on Holotachysphex turneri (Arnold) (Hymenoptera: Sphecidae: Larrinae) in the Eastern Cape Province of South Africa

by

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INTRODUCTION

The genus *Holotachysphex* de Beaumont, 1940 (= *Phytosphex* Arnold, 1951 and *Haplognatha* Gussakovskij, 1952) consists of six species found in Africa, Madagascar, the eastern Mediterranean area, southwestern USSR, and the Oriental Region. Most of these species were originally included in the genus *Tachysphex* Kohl. According to Bohart and Menke (1976: 282) *Tachysphex* and *Holotachysphex* are similar in general facies but the presence of a number of basic differences warrants their separation.

The only hitherto published observations on the nesting of *Holotachysphex* are those by Brauns concerning *H. turneri* (Arnold) at Willowmore in the Cape Province of South Africa. According to Arnold (1923: 166), reporting upon Brauns' observations, this species "nests in hollow stems of *Aloe*, *Datura*, etc., lying on the ground; the partitions between the cells being formed of earth and little pebbles". The prey was not recorded. The statement that the stems were lying on the ground indicates that they were dried out. In the case of the *Aloe* the hollow stem is most likely that of an old inflorescence.

In view of the paucity of biological information on the genus it is considered justified to publish the present notes on the nesting of *H. turneri* (Arnold).

THE NESTING OF HOLOTACHYSPHEX TURNERI (ARNOLD)

Information on the nesting of *H. turneri* (Arnold) was obtained as a result of the utilization for nesting purposes by this wasp of five trap-nests of the types described by Krombein (1967 and 1970). All the trap-nests concerned were in the field at Hilton, a farm situated 18 kilometres WNW of Grahamstown (33° 19'S., 26° 32'E.) in the Albany Division of the Eastern Cape Province of South Africa. Hilton is about 270 kilometres E. of Willowmore, the site of Brauns' observations. An account of the climate and vegetation of Hilton has previously been given (Gess and Gess, 1974: 191–192).

All five trap-nests utilized by *H. turneri* were 165 mm long and had a bore of 6,4 mm. All were suspended horizontally from living branches of small trees, one from *Salix mucronata* at a height of 2 metres above the ground and the other four from *Acacia karroo* at a height of a little above 1 metre. Trap-nest A (that on *Salix*) was taken in from the field on 11.i.1974, trap-nests B, C, D and E on 9.xii.1975, 29.xii.1976, 3.i.1977 and 4.ii.1977 respectively, each trap-nest having been utilized by the wasp within the preceding three or four days.

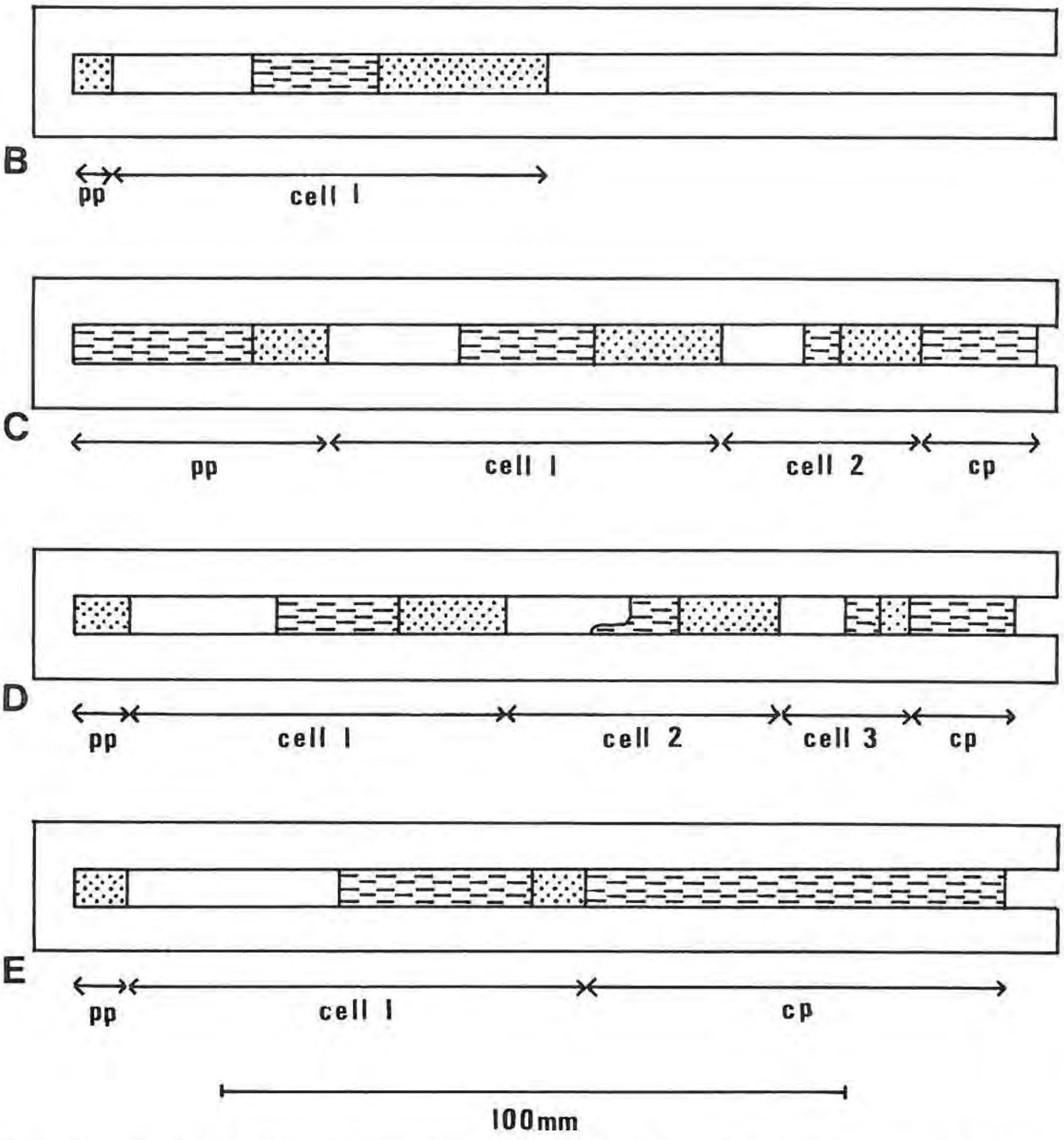

Fig. 1. *Holotachysphex turneri* (Arnold). Plans of nests B–E showing preliminary plugs (pp), cells, and closing plugs (cp) as well as nature of nesting materials: clods of clayey earth (stippled) and coarse detritus (dashed).

Due to the disarrangement of the nesting materials in nest A resulting from a mishap during the splitting open of the trap-nest no accurate measurements were possible and the account of nest architecture is consequently based mainly upon nests B–E (see Fig. 1) all in trap-nests with perspex windows and wooden lids.

H. turneri was found to have constructed a preliminary plug at the inner end of all five trap-nests, no empty space being left between this plug and the blind end of the boring. In nests B, D and E the plug consisted of small clods of clayey earth and was 6, 9 and 8 mm in thickness respectively. In nest C the preliminary plug was much more extensive and consisted of an initial 29 mm of coarse detritus (all derived from *Acacia* and consisting of small bits of bark, short lengths of twigs, seeds and leaflets), available to the wasp on the ground beneath the trap-nests, followed by 12 mm of the usual small clods of clayey earth. Four nests were completed of which nests A and E contained one cell each, nest C two cells and nest D three cells. Nest B was incomplete and contained a single cell. Each cell was capped by a partition consisting of two parts, an inner part composed of detritus and an outer part consisting of clods of earth, the whole plug thus being of the same composite nature as the preliminary plug of nest C. The seven capped cells were 21–75 mm long (mean 53 mm). The partitions closing these cells were 10–49 mm thick (mean 32 mm). The thicknesses of the detritus and of the earth in the partitions were 5–31 mm (mean 16 mm) and 5–29 mm (mean 16 mm) respectively. The closing plugs sealing the completed nests were composed of coarse detritus. The closing plugs of nests C, D and E were 19, 17 and 68 mm thick respectively.

The prey in all five nests consisted of nymphs of a single species of short-horned grasshopper belonging to the family Pyrgomorphidae (Acridoidea) and tentatively determined as *Pyrgomorphella* sp. by the author. A sample was submitted to Dr H. D. Brown who replied that the nymphs "are so small that they are almost impossible to determine with certainty, they could, for example, belong to *Pyrgomorphella*, as you suggest, or they could belong to *Pyrgomorpha* itself".

The number of prey stored in each cell was dependent upon size and varied from four individuals (9–10 mm long with a combined mass of 68 mg) in nest E and five individuals (11–12 mm long) in nest A to thirty-two individuals (3,2–6,7 mm long with a mean length of 4,5 mm) in nest B.

The prey were without exception stored facing the blind end of the trap-nest. Although paralysed, slight twitching movements indicated that the prey grasshoppers were alive. *H. turneri* eggs were found attached to prey in cells 2 and 3 of nest D and feeding larvae were found in cell 1 of that nest, in both cells of nest C and in the cells of nests A and B. No egg or larva was found on any of the prey in nest E. In all cases the anterior end of the egg or the mouth of feeding larva was sited just behind the base of the left prothoracic coxa. The length of the egg or later the body of the larva lay transversely across the thoracic sterna and extended beyond the prey on the right. In the five cells of nests C and D the grasshopper bearing the wasp egg or larva was positioned on its back; other prey in the cells by contrast were positioned on their venters or sides. In all five cells the egg- or larva-bearing prey was situated at the inner end of the cell and it appears that oviposition is probably on the first prey to be introduced into the cell.

Developmental data are limited. However, from the dates of the major events in the life-history given in Table I it appears that about three days elapse between oviposition and egg hatching and that the larva grows to maturity within about six to eight days. Available evidence indicates that the species is probably univoltine.

The cocoon is surrounded by fine silken threads attached to the walls of the cell and in places to the cocoon itself and forming a thin net-like envelope or shroud to which in places adhere fragments of prey exoskeleton, clods of earth and other debris from which the cocoon itself is thus kept isolated. The cocoon is oval about 10 mm long by about 4 mm wide, at its widest, and tapers slightly to the rounded ends, the anterior one being more bluntly rounded than the

TABLE I. Developmental dates for *Holotachysphex turneri* (Arnold) in trap-nests from Hilton.

Trap-nest	Cell	Date of oviposition	Date of egg hatch	Date of larval maturity	Date of cocoon spinning	Date of adult emergence and sex
A	1	?	pre 11.i.74	16.i.74	18.i.74	(died)
B	1	on or pre 9.xii.75	12.xii.75	(died)	—	—
C	1	?	on or pre 29.xii.76	4.i.77	5.i.77	7.ii.78 (♀)
	2	?	on or pre 29.xii.76	5.i.77	6.i.77	6.ii.78 (♀)
D	1	?	on or pre 3.i.77	11.i.77	11.i.77	6.ii.78 (♀)
	2	?	4.i.77	11.i.77	11.i.77	(died, cocoon empty)
	3	probably 2 or 3.i.77	5.i.77	11.i.77	12.i.77	(died, cocoon contained fully developed ♂)
E	1	(no egg or larva found in cell)				

posterior. The walls of the cocoon are composed of fine sand grains, silk and an oral secretion to form a hard shell with a granular but glazed surface.

The identification of the nests as those of *H. turneri* was made possible by the capture on 3.i.1977 of a nesting female which was observed carrying small clods of earth into a newly positioned trap-nest. The earth which was being collected on the ground beneath the branch from which the trap-nest was suspended was carried up to the nest in flight and was being used by the wasp in the construction of the preliminary plug. This female is believed to have been the builder of the nests in trap-nests C (taken in on 29.xii.1976) and D (taken in on 3.i.1977) as both these had in their turn occupied the identical position in the same trap-nest bundle as did the trap-nest being worked upon by the female when she was captured. On 3.i.1977 less than an hour had elapsed between the removal of trap-nest D and the initiation of the preliminary plug in its replacement.

DISCUSSION

The genus *Holotachysphex* was described by de Beaumont (1940: 179) as a subgenus of *Tachysphex* Kohl in which genus five of the six species now placed in *Holotachysphex* were of the nymphal Pyrgomorphidae. The author is grateful to the C.S.I.R. for a running expenses grant for field work during the course of which the present observations were made.

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Ethological notes on Kohliella alaris Brauns (Hymenoptera: Sphecidae: Larrinae) in the Eastern Cape Province of South Africa

by

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and

S. K. GESS

INTRODUCTION

The genus *Kohliella* Brauns, 1910 is endemic to southern Africa and includes two species poorly represented in collections.

Kohliella alaris Brauns, the type species, black and ranging in length from 6–11 mm, was described from Willowmore (Cape Province) (Brauns, 1910: 669) and was subsequently recorded from Hex River (Cape Province) and Bulawayo (Zimbabwe) (Arnold, 1924: 43) and from two localities on the Cape Peninsula (Beaumont, 1967: 510). In the Albany Museum collection it is represented by specimens collected by the authors at New Year's Dam, Alicedale and on Hilton, Grahamstown (both Cape Province). *K. stevensoni* Arnold, the second species, was described from Sawmills (Zimbabwe) (Arnold, 1924: 42).

It has been pointed out by Bohart and Menke (1976: 286) that, although *Kohliella* is similar to *Tachysphex* in general facies, only a few features such as the form of the collar, the male forefemoral notch, and the bare pygidial plate are common to both, and that *Kohliella* is probably best regarded as a specialized relic.

Nothing has hitherto been published regarding the biology of the genus.

The present paper is the sixth of a series of publications dealing with the ethology of certain solitary wasps occurring at Hilton, a farm situated 18 kilometres WNW. of Grahamstown (33° 19′S, 26° 32′E) in the Albany Division of the Eastern Cape Province of South Africa. An account of the climate and vegetation of Hilton has previously been given (Gess and Gess, 1974: 191–192).

THE NESTING OF KOHLIELLA ALARIS BRAUNS

Description of the nesting sites

At Hilton *Kohliella alaris* nests in sand on the floor of a sandpit and in close proximity to the sandpit in places where the vegetation has been removed leaving the sand bare or with very sparse plant cover (Figs 1 and 2). The sand, light coloured and fine grained, is derived from the weathering of Witteberg Quartzite and is of alluvial origin having been deposited upon its flood plain by a seasonal tributary of the New Year's River. *K. alaris* tends to nest in pseudo-colonies making use of only small areas within nesting sites which appear to offer suitable conditions for nesting throughout.

Fig. 1. Hilton, 12.i.1978. Portion of sand pit with figure marking a nesting site of *Kohliella alaris*.

Fig. 2. Hilton, 12.i.1978. Entrance to a nest of *Kohliella alaris* in nesting site shown in Fig. 1.

Flight period

Males and females of *K. alaris* have been collected at Hilton from early December to early March and nesting takes place throughout this period. During the summer of 1977–78, which was a particularly successful season for this species, nesting was at its height in mid-January.

Whereas most of the sphecids nesting in the sandpit commence their daily nesting activities before the hottest time of day and continue them into the early afternoon or on the hottest days cease activity before noon, *K. alaris* never appears before noon and rather commences its activities after noon, when the heat of the day is past its peak, and on the hottest days may delay its nesting activities until as late as 4.15 p.m., with the peak of nesting activity half an hour later.

Males are present in the nesting area and have been seen to attempt to mate with females in close proximity to the nests.

Plants visited by adult wasps

There are no records of *K. alaris* visiting plants. However, trees and shrubs must be visited by the females when hunting for it is in such situations that the prey occurs. It is probable that the wasps visit a belt of shrubs and small trees which occurs along the banks of the seasonal tributary near the sandpit. Although *K. alaris* was not observed in this situation, both males and females were caught in a Malaise trap erected between shrubs on the edge of this belt.

Identification of the prey

Twenty-six prey were recovered from *K. alaris* or its nests and without exception were nymphs of the Tree Cricket *Oecanthus capensis* Saussure (Gryllidae: Oecanthinae). Adult *O. capensis* in the Albany Museum were collected at Brak Kloof, a farm adjoining Hilton, during the months February to April.

Details of the prey and of their captors are given in Tables 1 and 2. It will be seen that the prey is mutilated by the wasp in that the antennae are cut off short (Fig. 3). Mutilation must take place immediately after prey capture as prey being transported to the nest are already in the "dressed" condition.

Fig. 3. Contents of the cell of nest 11 (see Table 1) consisting of three tree crickets, *Oecanthus capensis*, the third from the left bearing the egg of the nest builder shown on right. (x 2,8)

TABLE 1. Details pertaining to *Kohliella alaris* females, their prey and eggs associated in nests.

Date	Nest no.	Cell no.	Cell contents: prey in order of introduction into cell (where known), prey bearing *K. alaris* egg.	Prey weight (mg)	Prey length (mm)	Mutilations to prey	Wasp weight (mg)	Wasp length (mm)
13.i.78	1	1	(1) male nymph (with egg)	28	11,5	Both antennae shortened Left hind leg missing	—	—
			(2) female nymph	31	13,0	Both antennae shortened		
13.i.78	3	1	(1) male nymph (with egg)	36	12,0	Both antennae shortened Left hind leg missing	22	10,0
13.i.78	4	1	(1) female nymph	26	11,0	Both antennae shortened	—	—
13.i.78	6	1	(?) female nymph (with egg)	31	13,5	Both antennae shortened	22	10,0
			(?) male nymph	14	9,2	Both antennae shortened		
		2	(1) male nymph	44	14,0	Both antennae shortened		
17.i.78	7	1	(?) male nymph	5	6,2	Both antennae shortened	—	—
			(?) male nymph	4,5	6,0	Both antennae shortened		
			(?) male nymph	7,0	8,0	Both antennae shortened Right hind leg missing		
			(4) male nymph (with egg)	37	14,0	Both antennae shortened Right hind leg missing		
17.i.78	8	1	(1) male nymph	31	12,5	Both antennae shortened	25	10,0
18.i.78	10	1	(?) male nymph	20	11,8	Both antennae shortened	24	10,0
			(2) male nymph (with egg)	29	11,3	Both antennae shortened		
			(?) female nymph	50	15,8	Both antennae shortened Right hind leg missing		
9.ii.78	11	1	(?) female nymph	13	8,8	Both antennae shortened	—	—
			(2) female nymph (with egg)	29	11,3	Both antennae shortened		
			(?) male nymph	29	12,0	Both antennae shortened		
3.iii.78	14	1	(1) female nymph (with egg)	45	14,5	Both antennae shortened	—	—
			(2) female nymph	31	13,2	Both antennae shortened		

TABLE 2. Details pertaining to *Kohliella alaris* females and their prey associated during prey transport.

Date	Prey sex & developmental stage	Prey weight (mg)	Prey length (mm)	Mutilations to prey	Wasp weight (mg)	Wasp length (mm)
16.ii.76	female nymph	43	12,5	Both antennae shortened	18	9,3
16.ii.76	male nymph	21	8,3	Both antennae shortened	24	9,5
9.xii.77	male nymph	—	11,0	Both antennae shortened	—	—
20.xii.77	— nymph	—	6,3	Both antennae shortened	—	10,0
17.i.78	female nymph	46	14,5	Both antennae shortened	—	c. 10
17.i.78	male nymph	26	11,0	Both antennae shortened Right hind leg missing	25	10,0

Description of the nest (Figs 4a and b, 5a and b)

The nest of *K. alaris* consists of a short trench, approximately 10 mm long, leading to a subcircular entrance hole, slightly wider than high, average width 4,3 mm (sample of 12), from which a shallow entrance passage of similar diameter extends from 20–35 mm (sample of 9) and reaches an average depth of 13 mm (sample of 7) below the surface of the ground. From this shallow burrow one to several secondary branches of a steeper gradient lead off, some of which end in a more or less horizontal single cell at an average depth of 35 mm (range 16–70 mm, sample of 15). Some passages appear to remain unused and are free from sand whereas the passages which end in a cell are filled with loose sand. A secondary passage may be excavated in the same direction as the entrance passage or it may make a sharply acute to obtuse angle with it. Similarly, a cell may have its long axis following the same direction as the secondary passage or it may be at an angle to it. Such secondary passages which terminate in a cell are 15–60 mm long (sample of 11) and 4–5 mm in diameter and the cells have an average length of 16 mm (sample of 8) and an average diameter of 6,6 mm (sample of 9), therefore being of a slightly larger bore than that of the secondary passages.

Method of construction of the nest, provisioning and oviposition

K. alaris is a sand raker. After the wasp has selected a nesting site, nest construction is immediately initiated by her digging and raking away the soil. When the sand which is excavated in the construction of the nest begins to accumulate forming a pile, the wasp spreads it from side to side using a light dancing motion. Any particles which are too big to be extracted from the excavation by raking are carried out by the wasp in her mandibles. At the start of nest excavation the wasp is easily distracted by passing insects such as ants but makes no attempt to chase them. However, as nest construction becomes more advanced she becomes more determined and aggressive making attempts to drive away passing insects.

Hunting takes place after a cell has been excavated and the nest temporarily sealed with sand. The wasp having located, captured, stung and mutilated her prey she flies with it to the nest holding it beneath her with its head facing the direction of travel. She alights close to the

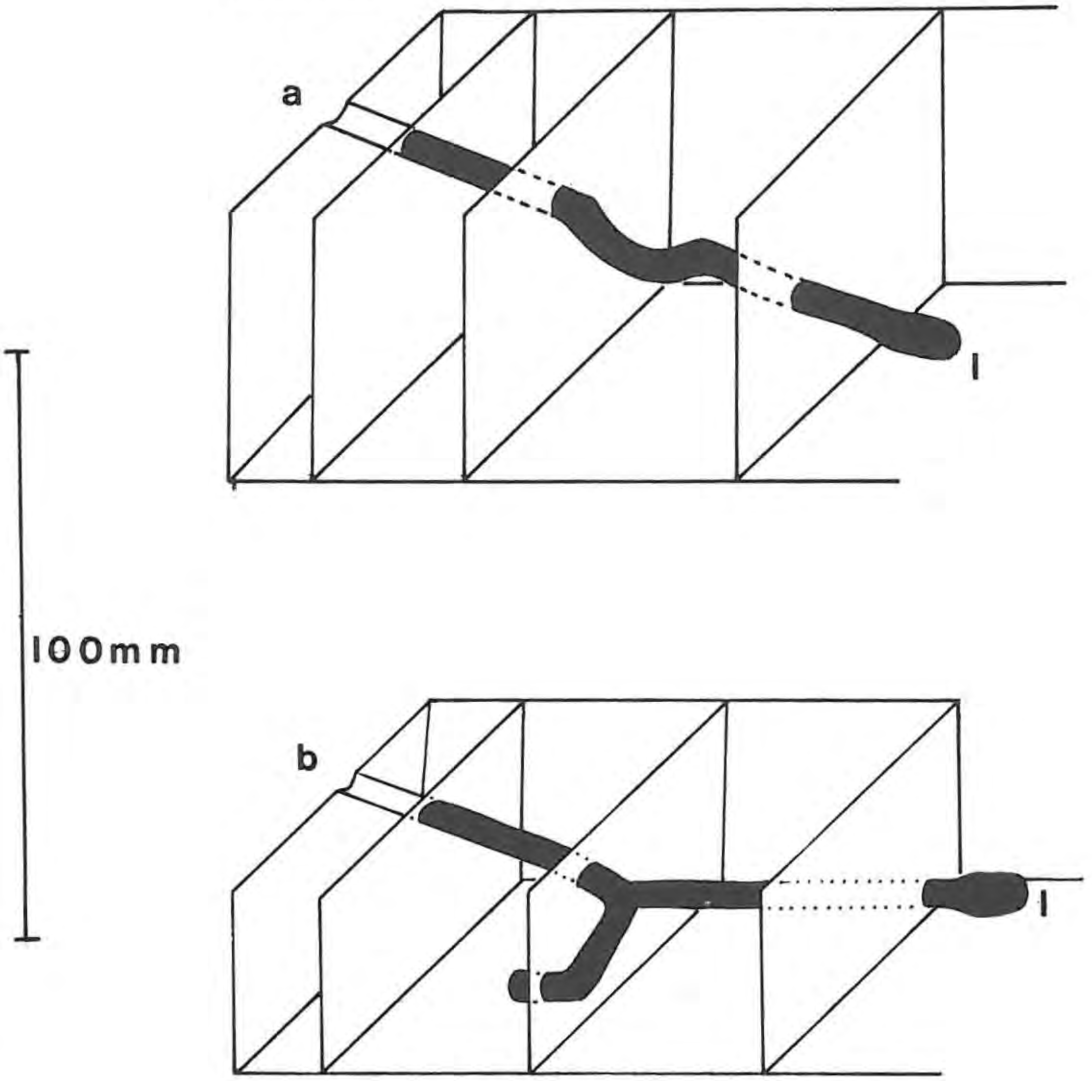

Fig. 4a and b. Plans of nests 8 and 3 of *Kohliella alaris*.

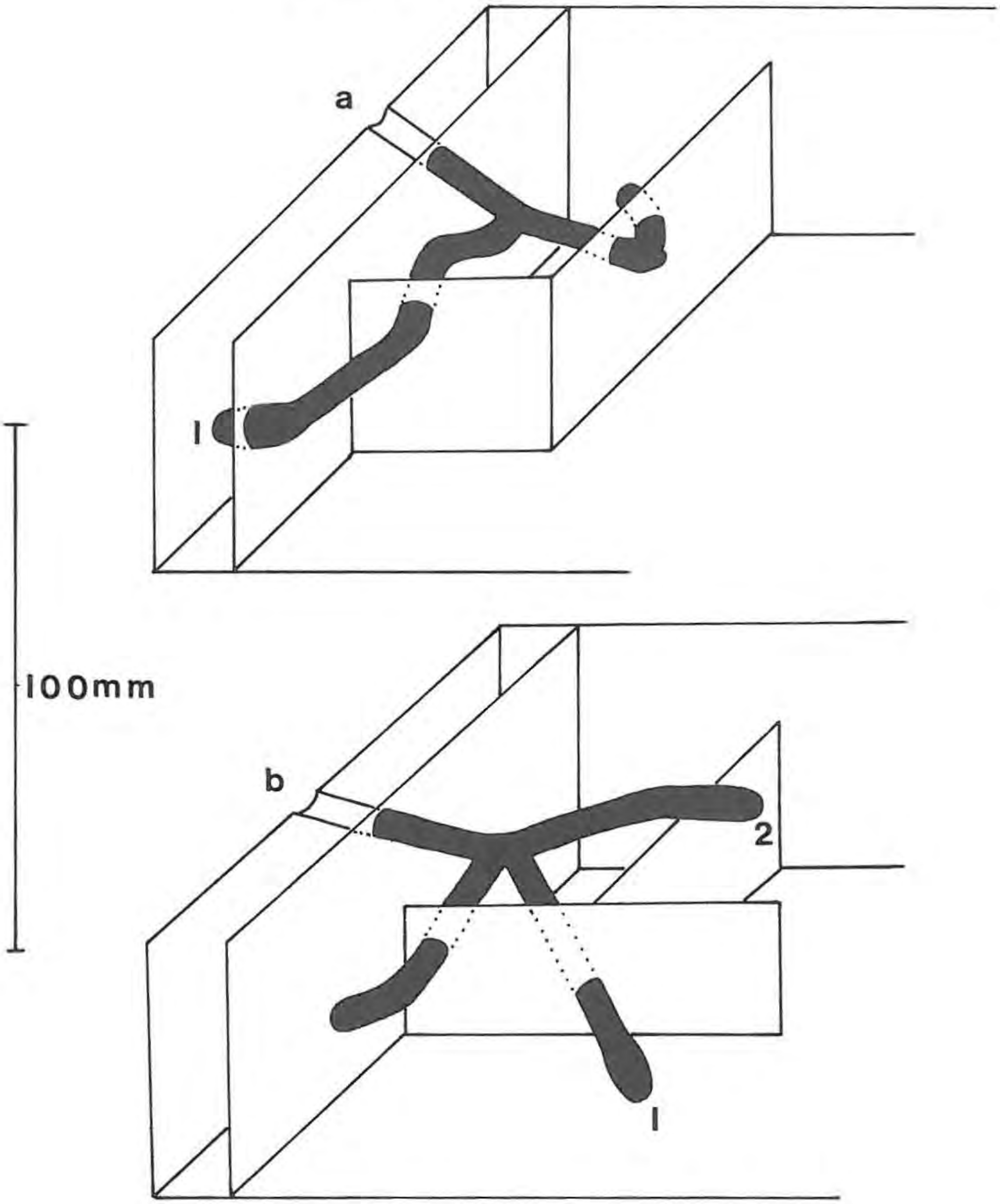

Fig. 5a and b. Plans of nests 1 and 7 of *Kohliella alaris*.

entrance to the nest, puts down the prey, rakes the sand out of the nest entrance, enters, turns around within, and draws the prey in head first.

Fourteen nests were excavated from which the contents of ten provisioned or partially provisioned cells were obtained (see Table 1) and were found to consist of twenty prey, seven of which bore wasp eggs. In a cell several prey are positioned venter up facing the inner end of the cell and parallel to each other but with every prey slightly in advance of that succeeding it. The prey are incompletely paralysed and exhibit occasional trembling movements of the palps and continuous pumping respiratory movements of the abdomen.

The egg of *K. alaris* is slightly curved, pearly white and 2,6 mm long (average of 5) and 0,5 mm wide at its mid length. It is attached by its anterior end to the underside of the prothorax of one of the prey, posterior to either the right or left prothoracic coxa, and extends transversely across the venter of the prey (Fig. 3). For six of the eggs it was possible to establish the order of introduction into the cell of the prey to which they were attached. Three eggs were on the first prey, two on the second prey and one was on the fourth prey. In the instance of the fourth prey being selected for oviposition it was the only one of any considerable size weighing 37 mg whereas the first three weighed only 5, 4,5 and 7,0 mg respectively. It is therefore likely that if the first prey to be captured are very small oviposition is postponed until one of a suitable size is obtained.

The secondary passage leading to a cell is usually filled with loose sand whereas the entrance passage is left clear. When leaving the nest the wasp closes the entrance. She stands inside the burrow and rakes sand in towards herself and through underneath to behind herself, gradually advancing out of the nest. When only a small depression is left she rakes sand over it from all directions until it is completely obscured. Three nests which had been seen to be closed in this way were excavated and were found to have as yet incompletely provisioned cells. It is therefore clear that the wasp closes her nest between visits.

Parasites

Five miltogrammine sarcophagids were reared from maggot infested prey recovered from a cell excavated on 18.i.1978. The flies emerged from their puparia on 6.ii.1978.

DISCUSSION

Kohliella with *Parapiagetia*, *Holotachysphex* and *Prosopigastra* may be grouped around *Tachysphex*, one of the dominant sphecid genera and one of the most highly evolved members of the tribe Larrini (Bohart and Menke, 1976: 269). As these five genera together form a distinct evolutionary branch within the subtribe Tachytina and as nothing has hitherto been published concerning the biology of *Kohliella* it is of interest to compare the five genera with respect to various aspects of nesting ethology.

A considerable number of papers on the biology of *Tachysphex* species have appeared, important ones being listed by Bohart and Menke (1976: 270). A useful summary of the known biology of the Palaearctic species has been provided by Pulawski (1971: 16–20). In contrast little has been published on the biology of *Prosopigastra* and almost nothing on that of *Parapiagetia*. For both genera the known biology has been reviewed by Bohart and Menke (1976: 285 and 281 respectively) and for *Prosopigastra* additional data have been presented by Pulawski (1979) who has also summarized the life history of the genus. An account of the nesting of a species of *Holotachysphex, H. turneri* (Arnold) in trap-nests has been published by Gess (1978: 209–215). In addition, since the publication of this account, natural nests of *H. turneri* have been found by the authors at Hilton in old abandoned galleries of the carpenter bee, *Xylocopa caffrariae* Enderlein in the hollow internodes of dry culms of *Phragmites australis*, a reed fringing permanent and semi-permanent water bodies.

The nests of *Kohliella* like those of *Tachysphex* and *Prosopigastra* are situated in the ground, in friable soil; however, *Holotachysphex* by contrast nests up off the ground in hollow plant stems. The nests of *Parapiagetia* have not as yet been located but the presence in the female of fore-tarsal sand rakes and of a pygidial plate indicates that this genus like *Kohliella* is ground nesting.

Kohliella like almost all species of *Tachysphex* excavates its nest itself whereas *Prosopigastra, Holotachysphex* and the exceptional species of *Tachysphex* modify pre-existing cavities, frequently the galleries of other aculeate Hymenoptera.

The nests of *Kohliella* that were investigated were all still under construction; eight contained a single provisioned or partially provisioned cell and one contained two cells. It is therefore not known whether the number of cells constructed ever exceeds two. *Tachysphex* nests may be one- or two-celled or multicellular, those of *Prosopigastra* are multicellular and *Holotachysphex turneri* nests have been found with one, two and three cells. Thus it appears that all four genera show a tendency to construct more than one cell per nest.

Kohliella unlike *Prosopigastra* and *Holotachysphex* which leave the nest entrance open during provisioning maintains a temporary closure during this period. *Tachysphex* displays variability in its behaviour in this respect. As *Kohliella* maintains a temporary closure it may be assumed that like *Tachysphex, Prosopigastra* and *Holotachysphex* it constructs a final closure.

Kohliella like *Holotachysphex, Parapiagetia* and some species of *Tachysphex* preys upon Orthoptera. Other species of *Tachysphex,* however, prey upon Dictyoptera and *Prosopigastra* preys upon Hemiptera. In all genera nymphs are generally taken. The report that an unknown *Parapiagetia* species was seen transporting a caterpillar should, it is considered, be treated with great caution.

Kohliella like *Tachysphex* transports its prey held beneath its body and facing the direction of travel. *Kohliella, Tachysphex* and *Prosopigastra* are known to carry their prey in flight and judging from the small size of its prey and the situation of its nest *Holotachysphex* probably also transports its prey in flight. When the prey is large and heavy relative to the wasp, *Tachysphex* is known to transport it along the ground in short hopping flights.

Kohliella like some species of *Tachysphex* deposits the prey on the ground at the nest entrance, opens and enters the nest, turns around within it and then draws in the prey unlike *Prosopigastra* and some other species of *Tachysphex* which enter the nest directly.

Kohliella like *Holotachysphex* and *Prosopigastra* provisions each cell with several prey, however, *Tachysphex* when large prey are taken may provision with a single prey. In all four genera paralysis of the prey is incomplete. *Kohliella* like *Holotachysphex* and those *Tachysphex* species which provision their nests with Acrididae positions its egg attached immediately posterior to one of the prothoracic coxae and extending transversely across the venter of the prey.

From the above comparison of various aspects of the nesting ethology of the five genera it is evident that the latter form a fairly close-knit group. *Tachysphex*, the species-rich dominant genus around which the other genera are grouped shows a considerable ethological latitude or plasticity whereas the ethology of the other genera appears more circumscribed. However, this is likely to be merely an expression of the fact that the other genera have far fewer species and that data concerning these are limited. Among those ethological aspects considered *Kohliella* does not manifest any character which is unique to itself and which is not found also in the genus *Tachysphex* seen as a whole (though of course if compared with individual species of *Tachysphex* various differences do become apparent). On the other hand the ethology of *Kohliella* differs in several aspects from that of both *Holotachysphex* and *Prosopigastra*. (Not enough is known of the ethology of *Parapiagetia* to allow comparison.) Ethologically *Kohliella* therefore has the greatest affinity with *Tachysphex*, the affinity being greater than that shown by either *Holotachysphex* or *Prosopigastra* with that genus.

SUMMARY

Some aspects of the ethology of *Kohliella alaris* Brauns (Hymenoptera: Sphecidae: Larrinae) in the Eastern Cape Province of South Africa are described. In the study which was based upon a series of nests excavated in sand attention is given to the description of the nesting sites, flight period, plants visited by adult wasps, identification of the prey, description of the nest and method of its construction, provisioning and oviposition. The nesting of *Kohliella* is compared with that of the genera *Parapiagetia, Holotachysphex, Prosopigastra* and *Tachysphex* and is found to be very similar to that of the last named.

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Ethological studies of Jugurtia confusa Richards, Ceramius capicola Brauns, C. linearis Klug and C. lichtensteinii (Klug) (Hymenoptera: Masaridae) in the Eastern Cape Province of South Africa

by

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CONTENTS

ABSTRACT

Some aspects of the ethology of *Jugurtia confusa* Richards, *Ceramius capicola* Brauns, *C. linearis* Klug and *C. lichtensteinii* (Klug) (Hymenoptera: Masaridae) in the Eastern Cape Province of South Africa are described. The account of the ethology of *J. confusa* is the first published for *Jugurtia*. Those of the three *Ceramius* species clarify some uncertainties and misconceptions in the literature and add to the overall picture of the ethology of the genus.

INTRODUCTION

The two Old World genera *Ceramius* Latreille and *Jugurtia* Saussure each encompass about twenty-five described species the greatest concentration of which is found in southern Africa, particularly in the Cape Province. The remaining species are scattered over Africa north of the Sahara, southern Europe, Turkey, Armenia, and in the case of *Jugurtia* North-West Africa (Northern Nigeria, Upper Volta, Gambia and Senegal), Yemen and Persia.

Nothing has hitherto been published concerning the ethology of any *Jugurtia* species. With respect to *Ceramius* species a general outline of the ethology may be assembled from the publications of Fonscolombe (1835), Giraud (1871), Ferton (1901), Brauns (1910) and Gess (1965, 1968 and 1973). However, despite the number of publications dealing with the nesting of *Ceramius* species certain aspects have never been described. On the other hand incorrect interpretation of observed facts has led to the presence in the literature of uncertainties or misconceptions, chiefly connected with the form of cell provisioning practised.

The present paper is based upon field work carried out over a period of years at Hilton, a farm situated 18 kilometres WNW. of Grahamstown (33° 19'S., 26° 32'E.) in the Albany Division of the Eastern Cape Province of South Africa and as such is the seventh of a series of publications dealing with the ethology of certain solitary wasps occurring at that locality. The account is augmented as indicated in the text by a few observations made at Clifton, a farm situated 7 kilometres NNE. of Hilton. An account of the climate and vegetation of Hilton and Clifton has previously been given (Gess and Gess, 1974: 191–192).

DESCRIPTION OF THE NESTING SITES

The sites chosen for nesting by *Jugurtia confusa* Richards, *Ceramius capicola* Brauns, *C. linearis* Klug and *C. lichtensteinii* (Klug) on Hilton lie within the area utilized by *Dichragenia pulchricoma* (Arnold), *Bembecinus cinguliger* (Smith) and *Parachilus insignis* (Saussure) and described for these species (Gess and Gess, 1974, 1975 and 1976) as localized patches of bare clay earth occurring in low-lying areas, sparsely covered by small low-growing shrubs, largely *Pentzia incana* (Compositae), and situated close to temporary sources of water. *Pentzia incana* only is mentioned as being the dominant plant. For the purpose of this study it must, however, also be mentioned that the second most dominant plant is *Chrysocoma tenuifolia* (Compositae) and that there is in addition a lesser scattering of low-growing Mesembryanthemaceae including *Drosanthemum parvifolium*, *Drosanthemum floribundum* and *Ruschia* species. The nesting of the four species of masarids appears to be very localized as, although an extensive search was made, they were found to make use of only a few of the available apparently similar bare areas and to utilize the same sites each year. The chosen sites lie on both sides of a water furrow mentioned in Gess and Gess (1974, 1975 and 1976) and on a flat area between the furrow and a small shallow earthen dam situated below the former. Water is provided in shallow rainwater pools in the furrow in which water only flows for short periods after rain.

J. confusa and *C. capicola* nest in pseudo-colonies on level bare patches caused by sheet erosion or by the presence of a road or path and it seems probable from the situation of the single nest of *C. linearis* discovered that this species selects similar areas. *J. confusa* and *C. capicola* have not been found nesting in close proximity either to each other or to any of the other ground-nesting wasps with the exception of *Bembecinus cinguliger* although this was more in the nature of a fringe overlap in time and space. A single nest of *J. confusa* was found also in a pocket of clayey soil on a horizontal ledge of a raised river bank at some distance from the main nesting area. A second species of *Jugurtia*, *J. braunsiella* (von Schulthess) has occasionally been collected at Hilton but its nests have not as yet been located. *C. lichtensteinii* differs from the other three species of masarids under consideration in that it favours raised bare ground for nesting purposes, the nests located having been either on raised earth around a shrublet in an eroded area or else on artificially constructed banks of a furrow and of small drainage channels. Similarly, on the farm Clifton, *C. lichtensteinii* nests on raised banks of bare clayey soil on the sides of a donga (erosion gulley). At Clifton where *C. lichtensteinii* is more common than at Hilton, it has been found to nest in populous pseudo-colonies, thirty nests having been counted within an area of about a square metre.

FLIGHT SEASONS, DAILY FLIGHT PERIOD, LOCATION OF MATING AND OF SHELTERING

The flight periods for the masarids under consideration, like those of all clay-nesting wasps, are variable according to the climatic conditions prevailing in a particular year. Certain generalisations may, however, be made. The species sighted earliest are *J. confusa* and *J. braunsiella* which have been collected at Hilton as early as late September. The most abundant nesting observed for *J. confusa* was in the summer of 1976–77 when the greatest activity was from early November to mid-December after which there was no activity till mid-February to early April when there was a second but insignificant flush. In other years when the rain has been late there has been a shift in activity to January-February but this was less successful than in the years when nesting was early in the summer.

C. capicola and *C. lichtensteinii* are normally reaching their peak after the high-point of activity of *J. confusa* is over. Again the intensity of activity and the extent in time is governed by the climatic conditions in any particular year, however, early December to early January seems to be the most favourable time for these two species.

A nesting date for *C. linearis* is only known from one nest found on 10.xii.1974, however, from collecting dates for this species in the area it seems to be flying most commonly in November-December and therefore its greatest activity is probably somewhere between that of *J. confusa* on the one hand and *C. capicola* and *C. lichtensteinii* on the other.

The males appear in numbers shortly before the females and are present for most of the flight period, becoming scarce as the season advances. The hottest part of the day shows the greatest activity and this is the time favoured for nesting activities. *J. confusa* males were observed to fly low, 5–8 cm above the ground, particularly skirting bushes at the periphery of the nesting site and also alighting on the ground within the nesting area where they sun themselves and rise up to chase the females and each other. They are seen to descend rapidly upon the females and although mating was not observed it seems likely that it takes place within the vicinity of the nesting area. The females were always seen alone at the water where they stand on the mud at the edge of the water to fill their crops. Two females of *J. braunsiella* were collected whilst similarly engaged. In the three species of *Ceramius* on the other hand both males and females were observed together at the water and the females filled their crops whilst standing on the surface of the water. In *C. capicola*, the only species present in large numbers at Hilton, both sexes were frequently observed flying up and down the length of a puddle. They flew over the water 5–8 cm above the surface. The females frequently alighted on the water surface, the legs being held wide-spread. While thus resting on the water surface and gently drifting, the males were seen to alight on top of the females, when both would take off and fly away together, the male above the female grasping her. This was presumably followed by mating. The behaviour of *C. linearis* and *C. lichtensteinii* at the water and preparatory to mating was observed at Hilton and more particularly at Clifton to be identical to that of *C. capicola* as described above.

When the sun was obscured by cloud or when a breeze got up females of *J. confusa*, *C. capicola* and *C. lichtensteinii* were found to be sheltering in their nests. Those of *J. confusa* were seen backing down their burrows into the sheltering position, head uppermost about 5 mm below the opening of the shaft.

PLANTS VISITED BY ADULT WASPS AND COMPOSITION OF PROVISION

Records of *Jugurtia* species visiting flowers are few in number: at Hilton *J. confusa* was found on *Drosanthemum parvifolium* (Mesembryanthemaceae) (1 male, 8.xii.1976) and on *Acacia karroo* (Leguminosae) (1 male, 10.ii.1977) and *J. braunsiella* was found on *Lasiospermum bipinnatum* (Compositae) (1 male, 12.x.1977); at Clifton *J. braunsiella* was found on *Pteronia paniculum* (Compositae) (1 female, 27.x.1972). A female *J. confusa* caught in flight was found to be carrying an abundance of pollen on the fore-tibiae and tarsi which are covered with dense hairs, on the swollen antennae, and on the labrum and front of the clypeus.

Flower-visiting records pertaining to *Ceramius* species at Hilton are likewise few in number: *C. linearis* on *Drosanthemum floribundum* (Mesembryanthemaceae) (1 male, 29.xi.1976) and *C. lichtensteinii* on a 'purple mesem' (Mesembryanthemaceae) (1 male, 26.x.1977) and on *Senecio pterophorus* (Compositae) (1 female and 2 males, 29.xi.1979; 1 female, 1.xii.1979; 2 males, 2. xii.1979). However, both males and females of *C. capicola*, *C.*

linearis and *C. lichtensteinii* have previously been recorded in the Grahamstown district on various species of Mesembryanthemaceae (Gess, 1973: 115–116).

The provision supplied by *J. confusa, C. capicola, C. linearis* and *C. lichtensteinii* for the nourishment of their young is pollen bound together with nectar to form a loaf which partially fills the cell. This pollen bread varies in consistancy from dry and firm in *C. linearis* and *C. lichtensteinii* to moist and sticky in *J. confusa* and *C. capicola.*

A sample of pollen loaves was examined microscopically for each species, the pollen of the provision being compared with that of flowers found in the vicinity of the nesting area, including species of Mesembryanthemaceae and Compositae. In all cases it was found that the pollen used was that of Mesembryanthemaceae. With respect to the species of Mesembryanthemaceae present in the vicinity of the nesting areas an attempt was made to match the pollen by size with that used in the formation of the pollen loaves. In the case of *J. confusa* five pollen loaves were examined and one pollen size was found to be common to all and was matched with that of *Drosanthemum parvifolium.* However, some loaves contained in addition one or two other pollen sizes but these were not successfully matched. *C. capicola* loaves contained only one size of pollen which was matched with that of *Drosanthemum floribundum.* The *C. linearis* loaf on the other hand contained pollen of three sizes one of which matched with that of *Drosanthemum floribundum. C. lichtensteinii* was found to be using pollen of the same size as that of several species of *Ruschia.*

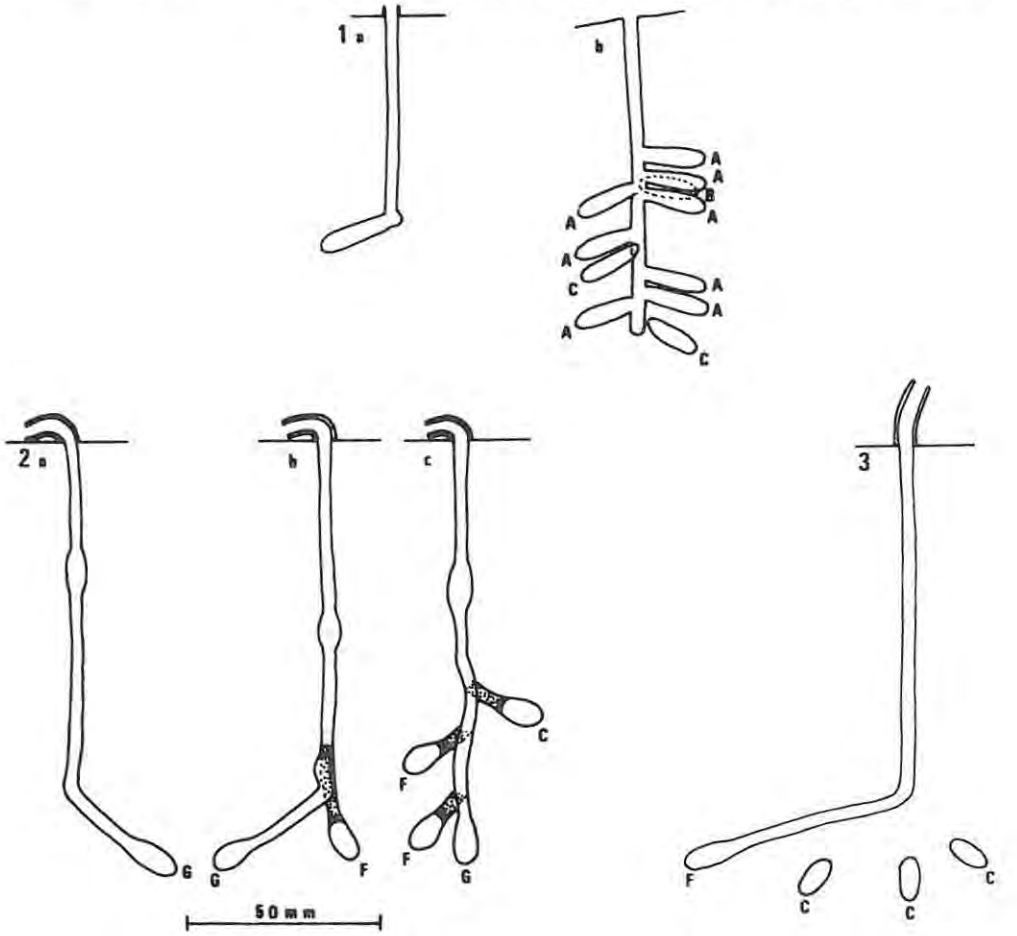
DESCRIPTION OF THE NEST

The nests of *J. confusa, C. capicola, C. linearis* and *C. lichtensteinii* all consist of a subterranean burrow surmounted by a cylindrical mud turret constructed from mud pellets cemented together; in *J. confusa* loosely so that in some cases the turret has a lacy appearance; in *C. capicola, C. linearis* and *C. lichtensteinii* closely and smoothed on the inside so that open interstices are extremely rare except near the free end in turrets of *C. lichtensteinii*. In all four species the turret is initially vertical to sub-vertical but, if of any considerable length, curves over becoming horizontal as in *C. lichtensteinii* or curves downwards and then, sometimes, continues in a horizontal plane close to the ground but always free from it as in *C. capicola*. In *J. confusa* more than a short vertical turret is extremely rare and may be considered aberrant.

The subterranean burrow of a newly-constructed nest consists of a vertical shaft which is either of constant diameter along its length as in *J. confusa* or has in the upper third a short bulbous portion as in *C. capicola* and *C. lichtensteinii* and from which at its lower end there branches a subhorizontal secondary shaft terminating in an excavated-cell within which is a constructed mud-cell in *J. confusa* and *C. lichtensteinii* but not in *C. capicola* and *C. linearis*.

In nests at a more advanced stage of construction further secondary shafts each terminating in a cell are present. In *J. confusa* and *C. lichtensteinii* a secondary shaft including its cell is barely longer than the cell itself whereas in *C. capicola* and *C. linearis* it is considerably longer than the cell. *C. linearis* differs from the other three species in that, in the single nest excavated, the cells all lay at a similar depth below the lower end of the main shaft whereas of those in the other three species only the deepest cell lies below the lower end of the main shaft, the other cells being at varying depths above it. In *C. lichtensteinii* the cells are arranged in loose whorls, one or two whorls being constructed in a single year. Additional whorls are constructed in succeeding years. These nests are therefore perennial in nature as probably are those of *J. confusa*.

All completed cells are sealed with a mud-plug which, in constructed mud-cells, takes the form of a stopper fitting into the neck of a cell like a cork into a bottle. The section of a secondary shaft between the sealed cell and the main shaft is filled with tightly packed earth and its opening to the main shaft sealed with a mud-plug.



Figs 1–3. Vertical plans of the turrets and underground workings of the nests of three species of Masaridae at Hilton. Lettering of cells as in key.

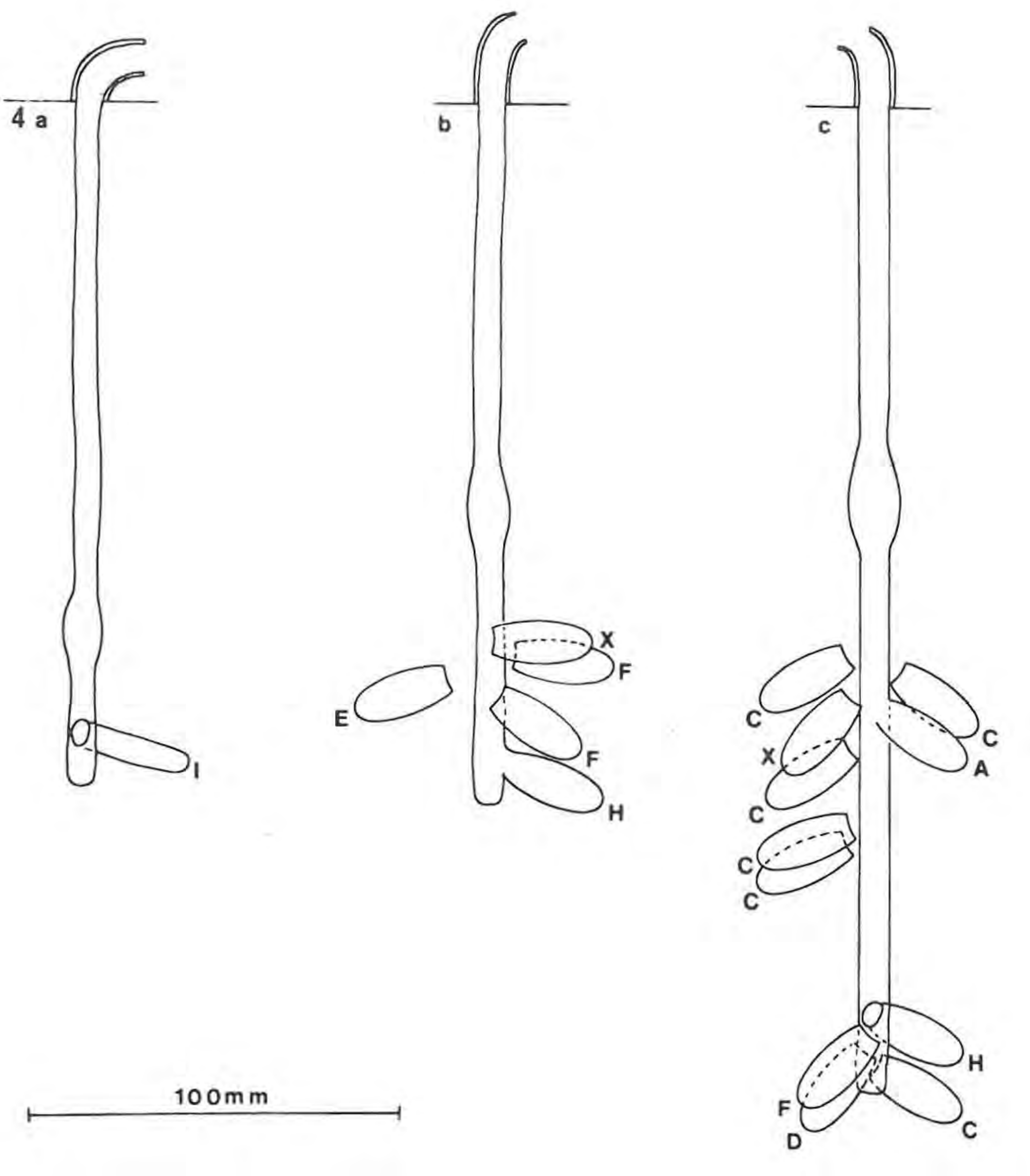
Figs 1a and b. Two nests of *Jugurtia confusa* Richards, investigated on 8.xi.1976 and 27.ix.1978 respectively.

Figs 2a, b and c. Three nests of *Ceramius capicola* Brauns, investigated on 7.xii.1976, 9.xii.1976 and 11.i.1977 respectively.

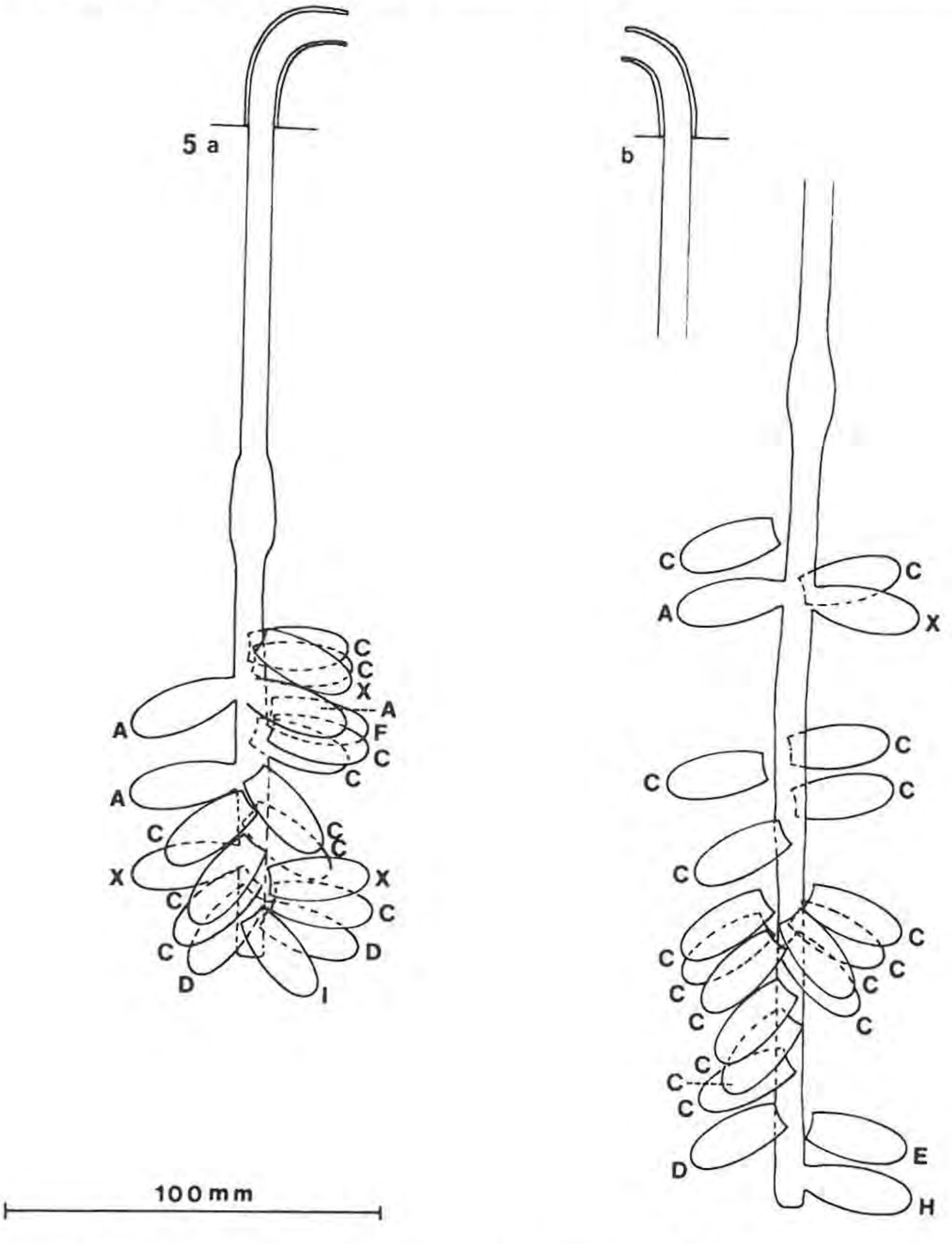
Fig. 3. Single nest of *Ceramius linearis* Klug, investigated on 10.xii.1974.

METHOD OF CONSTRUCTION OF THE NEST, OVIPOSITION AND PROVISIONING

The four species studied differ considerably in their size and as body size has a profound effect upon the dimensions of the nest built by each species, total body length and greatest body width (measured across the mesothorax) of average females of each species are given here. *J. confusa* is the smallest species, 10 mm long and 2,7 mm wide; the *Ceramius* species range from *C. capicola*, 12 mm long and 2,9 mm wide, through *C. linearis*, 15 mm long and 3,4 mm wide to *C. lichtensteinii*, 20 mm long and 5,6 mm wide. Males are generally slightly smaller than the females.



Figs 4a, b and c. Vertical plans of the turrets and underground workings of three nests of *Ceramius lichtensteinii* (Klug) at Hilton, investigated on 29.xii.1976, 31.xii.1973 and 3.i.1977 respectively. Lettering of cells as in key.



Figs 5a and b. Vertical plans of the turrets and underground workings of two nests of *Ceramius lichtensteinii* (Klug) at Hilton, both investigated on 3.i.1977. Lettering of cells as in key.

Water is required for nest construction and is collected by a female from a nearby puddle. Whilst filling her crop with water *J. confusa* stands on the mud at the edge of the water whereas the three species of *Ceramius* alight on the water surface.

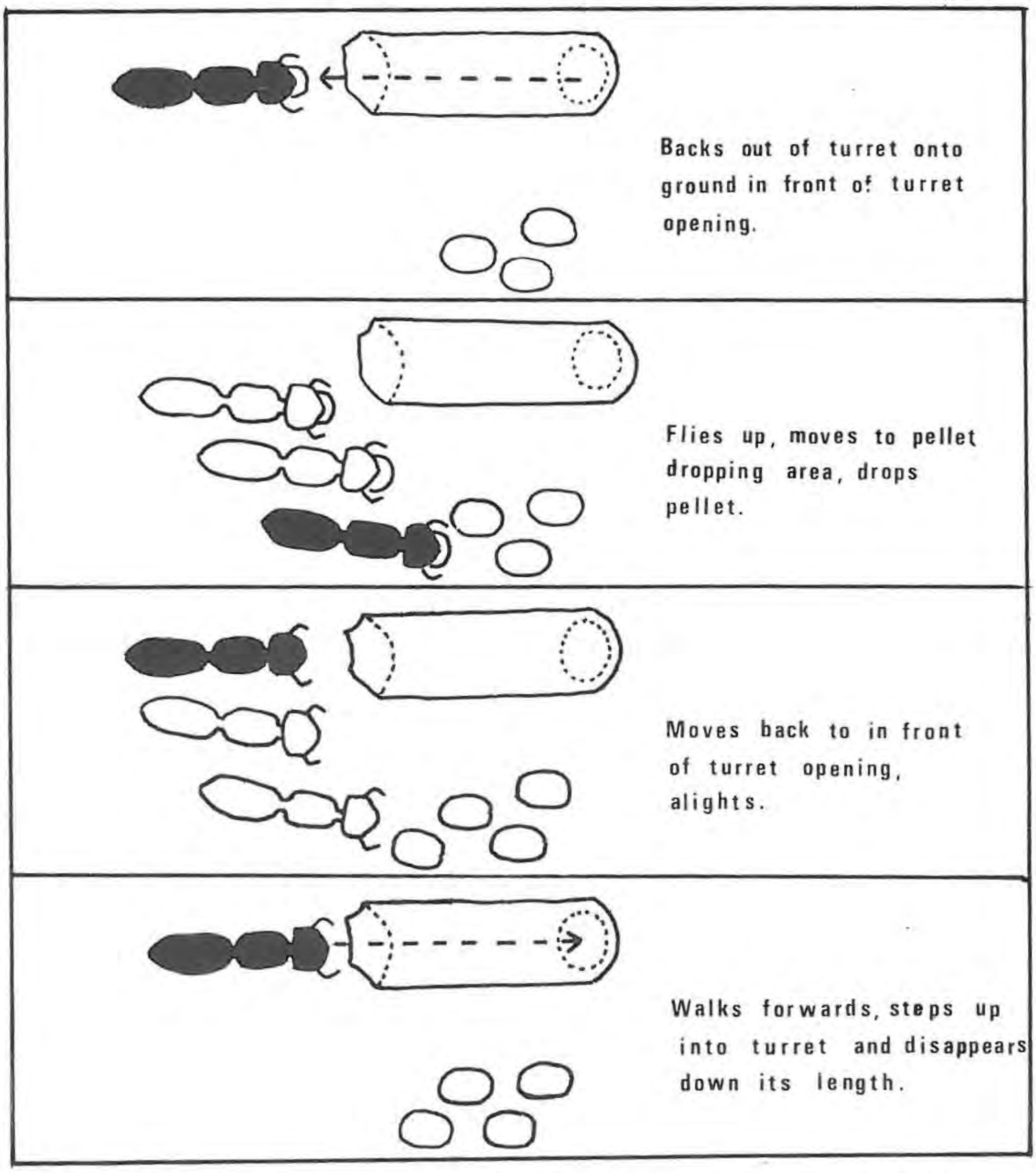
Nest excavation is initiated by the female's regurgitating water from her crop onto the ground. Using her mandibles she works this water into the earth to form mud from which she forms a pellet. A number of pellets are formed in this way from each crop-full of water. The first pellets excavated from the shaft-initial may be discarded. The shaft-initial is circular in cross section due to the female's rotating evenly, not altering the direction of rotation without first completing a circle. At the commencement of turret construction, the pellets, instead of being discarded, are laid down in a circle around the shaft-initial in such a way that the inner diameter of the turret will be the same as that of the shaft; in *J. confusa* 3 mm (average of sample of 13 measurements), in *C. capicola* 3,2 mm (average of sample of 10 measurements), in *C. linearis* 3,5 mm (one measurement) and in *C. lichtensteinii* 6,2 mm (average of sample of 7 measurements). In the construction of a vertical cylindrical turret pellets are added regularly whereas in a sloping or curved turret more pellets are added to what will be the upper side than to what will be the lower side. It is noticeable that in turrets of *C. capicola* the upper edge of the turret opening projects further than the lower edge.

The method of placement of pellets by *C. capicola* was observed most clearly. The wasp backs up the shaft with a pellet held in her mandibles and reaching the turret opening holds the sides of the turret with her legs whilst placing the pellet in position and smoothing it on the inner surface with her mouthparts and supporting it on the outer surface with the tip of the ventral surface of her abdomen which is curved around for this purpose (Fig. 8). As many as twelve pellets may be added to the turret per water load. If the turret is destroyed by rain or mechanical means, the wasp will build a new one of similar design and dimensions to the original one. In *C. lichtensteinii* and probably also in *J. confusa*, if a newly emerged female instead of initiating a new nest expands a maternal nest, a turret is still constructed at the commencement of nesting. In this case the mud required is obtained from the bottom of the main shaft.

Whilst turret construction is in progress the shaft increases in depth. The diameter of the shaft of *J. confusa* is maintained constant whereas the diameters of the shafts of *C. capicola* and *C. lichtensteinii* after the shafts have reached average depths of 35 mm (sample of 7) and 85 mm (sample of 5) respectively increase to 5,4 mm (average of 7 measurements) and 11,5 mm (average of 5 measurements) after which they decrease to their original measurements. The resultant bulbous portions of the shafts are 10 mm and 24–30 mm long. As the only nest of *C. linearis* excavated was in difficult ground it is not known whether or not this species constructs a 'bulb'.

After completion of the turret the wasp continues to excavate the shaft but the pellets then extracted are discarded. *J. confusa* has no clearly defined pellet-dropping area, however, the wasp does confine her arrivals and departures from the nest to a set quarter segment. Like *J. confusa*, *C. lichtensteinii* has no set pellet-dropping area but discards pellets in bushes at the edge of the clearing in which her nest is situated with the result that the distance from the nest is variable; 60–90 cm in one instance and about 300 cm in another. However, *C. capicola* has a clearly defined pellet-dropping area a few centimetres from and to one side of the turret. When discarding a pellet, a female *C. capicola* backs out from her nest until her head is free from her turret, flies sideways and slightly forwards just above the surface of the ground to the pellet-dropping area, drops the pellet and still orientated parallel to the turret flies in reverse sideways motion back to the nest entrance which she is then facing and enters (Fig. 6). In this way the pellet-dropping operation takes up the minimum of time and exertion and differs from that of most mud-excavating wasps including *J. confusa* and *C. lichtensteinii* which fly up in a wide circle when dropping pellets.

At this stage in nest construction *C. capicola* and *C. lichtensteinii* females when leaving the



Backs out of turret onto ground in front of turret opening.

Flies up, moves to pellet dropping area, drops pellet.

Moves back to in front of turret opening, alights.

Walks forwards, steps up into turret and disappears down its length.

Fig. 6. Sequence showing, in diagrammatic form, the method of pellet deposition after turret construction by *Ceramius capicola* Brauns.

nest to fetch water emerge from the turret head first whereas those of *J. confusa* still continue to emerge backwards. It is probable that the *C. capicola* and *C. lichtensteinii* females turn around in the newly constructed bulbous portion of the nest shaft.

Cycles of water carriage and pellet extraction were timed for *J. confusa*, *C. capicola* and *C. lichtensteinii* and were found to be performed rapidly and without interruption during active nest excavation. Water carriage took 1–2 minutes depending upon the distance from the nest to the water source and pellet extraction took 2–4 minutes depending on the dryness and hardness of the soil. Similarly, the number of pellets extracted per water load varied according to the dryness of the soil. Thus at the outset of nest excavation after rain when the surface layers of the soil only were damp wasps were observed to carry out a far larger number of pellets and more rapidly than they did once they had reached a lower level in the soil where the rain had not penetrated.

The shaft is sunk vertically to depths of 37–52 mm (average 43 mm, sample of 18) in *J. confusa*, 75–100 mm (average 89 mm, sample of 10) in *C. capicola*, 135–170 mm (average 150 mm, sample of 7) in *C. lichtensteinii* and 90 mm in *C. linearis* (single nest). From the bottom of the shaft a secondary shaft of the same diameter as the main shaft is constructed in a subhorizontal plane so that the distal end lies deeper than the bottom of the main shaft and is enlarged to form a cell. The average lengths of secondary shafts and of cells of the four species are: *J. confusa* 17 mm (sample of 7) and 15,6 mm (sample of 5); *C. capicola* 24 mm (sample of 10, range 10–45 mm) and 11 mm (sample of 10, range 10–12 mm); *C. lichtensteinii* 33 mm and 29 mm (sample of 10) and *C. linearis* 30 mm and approximately 12 mm (sample of one). The average diameters of cells are: *J. confusa* 5 mm (sample of 5); *C. capicola* 6 mm (sample of 10); *C. lichtensteinii* 11 mm (sample of 7); and *C. linearis* approximately 6 mm.

After cell excavation has been completed the cells of *C. capicola* and *C. linearis* are ready for oviposition whereas in *J. confusa* and *C. lichtensteinii* a mud-cell is first constructed within each excavated-cell. Mud for the construction of these cells must be quarried within the nest as these wasps do not fetch mud from elsewhere. In nests of *J. confusa* in which a mud-cell has been constructed there is an enlarged 'heel' at the bottom of the shaft. It is thought probable that at least part of the mud used in constructing the mud-cell is excavated from this source and that the mud used by *C. lichtensteinii* is similarly obtained by a deepening of the lower end of the main shaft. The mud-cells are easily separable from the walls of the excavated-cells. They have a rough outer surface on which the separate applications of mud are discernable. The inner surface, however, is carefully smoothed. The average thickness of the walls is 0,7 mm in *J. confusa* and 0,9 mm in *C. lichtensteinii*.

Oviposition takes place before the commencement of provisioning. The eggs are strongly curved, white in *J. confusa* and *C. capicola*, whitish-yellow to pale yellow in *C. lichtensteinii*, and are of average dimensions 2,51 mm by 0,76 mm (sample of one), 3,55 mm by 0,89 mm (sample of 8) and 6,24 mm by 1,42 mm (sample of 7) respectively.

The cell is then rapidly provisioned and sealed before the egg hatches. Exceptionally, open cells of *C. lichtensteinii* were found containing a young larva and little or no pollen bread. Thus, at Hilton during the period 12–31.xii.1973, of nine open cells in which oviposition had taken place seven contained eggs only and no provision, one contained a newly hatched larva (5 mm in length) and no provision, and one contained a small larva (6 mm in length) and a small amount of provision. However, of ten newly sealed cells, one contained an as yet unhatched egg and a complete pollen loaf and nine contained larvae of various sizes ranging from newly hatched (5,5 and 6 mm in length) to large with varying amounts of as yet unconsumed provision in inverse proportion to larval size. It therefore appears that under favourable conditions the cell is fully provisioned and sealed before the egg hatches but that, exceptionally, under unfavourable conditions such as bad weather, when 'mesem' flowers stay closed and wasps do not readily fly, or such as a scarcity of forage flowers the beginning of provisioning may be preceded by the hatching of the egg.

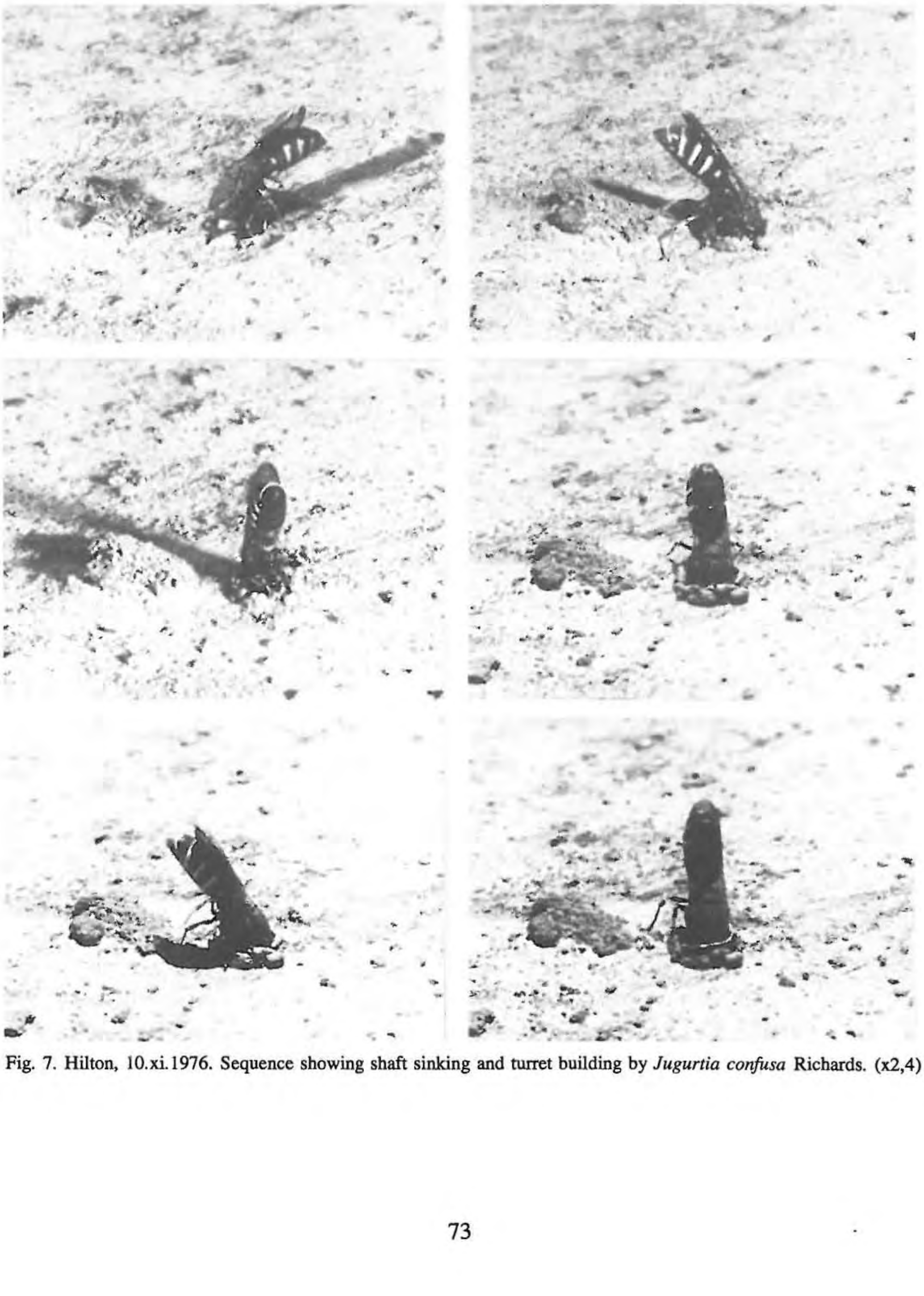


Fig. 7. Hilton, 10.xi.1976. Sequence showing shaft sinking and turret building by *Jugurtia confusa* Richards. (x2,4)

After a cell has been sealed the remaining section of the secondary shaft is filled with earth and sealed off from the vertical shaft with mud which is smoothed so that the entrance to a secondary shaft, once it is sealed, is no longer visible on the surface of the main shaft. *C. capicola* and *C. linearis* do not introduce earth into the nest from elsewhere and so the earth for filling a secondary shaft must be obtained within the nest and can only come from the excavation of another secondary shaft. Succeeding cells are constructed in the same manner, the number probably being dependent on the availability of water for nest construction and pollen and nectar for cell provisioning.

Twenty newly-constructed nests of *J. confusa* were excavated in the summer of 1976–77 and of these eleven contained one cell each (Fig. 1a) and nine were still at the stage of shaft excavation. Due to the drying out of the water supply nesting in the pseudo-colony to which these nests pertained ceased at this stage. However, the single nest found on the river bank and excavated in September, 1978, a year after it had first been noted contained eleven cells (Fig. 1b). This nest had a shaft 81 mm in depth with the cells radiating out from the shaft at depths of from 35–79 mm. Eight cells were open, empty and parchment-lined and were therefore cells from which the occupants had already emerged. Three cells were sealed, one containing an adult female ready to emerge and the other two each a prepupa. In addition one adult female was coming into and out of the nest and one male was sunning itself on the ground next to the nest. It seems highly probable that this nest may have been a perennial one.

Sixteen nests of *C. capicola* were excavated in the summer of 1976–77 and of these seven were one-celled (Fig. 2a), three two-celled (Fig. 2b), one four-celled (Fig. 2c) and the remaining five nests had not reached the stage of cell excavation.

The single nest of *C. linearis* excavated in the summer of 1974 contained four cells (Fig. 3).

Nineteen nests of *C. lichtensteinii* were excavated in the summer of 1973–74 and of these six were newly constructed (Fig. 4b) and thirteen had been initiated one or two years previously. A further five nests were excavated in the summer of 1976–77. Of these one nest was newly constructed (Fig. 4a) and the remaining four nests had been initiated one or two years previously. These four nests contained eleven (Fig. 4c), fifteen, twenty (Fig. 5a) and twenty-one (Fig. 5b) cells arranged in whorls of three to seven or more cells. As there seems to have been a low percentage of emergence of *C. lichtensteinii* at Hilton during the years when observations were made the infrequency of occurrence of newly constructed nests is not surprising.

LIFE HISTORY

Little information was gathered concerning the immature stages of the four masarid species. Hatching of the larva of *C. lichtensteinii* appears to take place about three days after oviposition for of four eggs obtained from unprovisioned open cells excavated on 31.xii.1973, one hatched on 2.i.1974 and three hatched on 3.i.1974.

After consuming the stored provision the then mature larva spins its cocoon which in *C. lichtensteinii* is parchment-like, brittle, brown in colour and in intimate contact with the inner end and the walls of the mud-cell from which its detachment is difficult. The posterior end of the cocoon—that is the end towards the inner end of the cell is rounded, whereas the anterior end of the cocoon—that is the end towards the mud-plug closing the mud-cell is truncate and is in the form of a flat circular plate separated from the mud-plug by an empty space. Cocoons of *C. lichtensteinii* measured from 19,0–21,5 mm in length, from 7,3–9,0 mm in width at their middle (where widest) and from 6,3–7,0 mm in width at their truncate end. The empty space between the truncate end of the cocoon and the inner surface of the mud-plug was from 4–8 mm long.

Having spun the parchment cocoon the larva changes into a prepupa characterised by its hunch-backed and flaccid appearance. Diapause takes place in the prepupal stage and may last until the following spring or may be extended over longer periods. Development after pupation in the spring appears to be rapid.

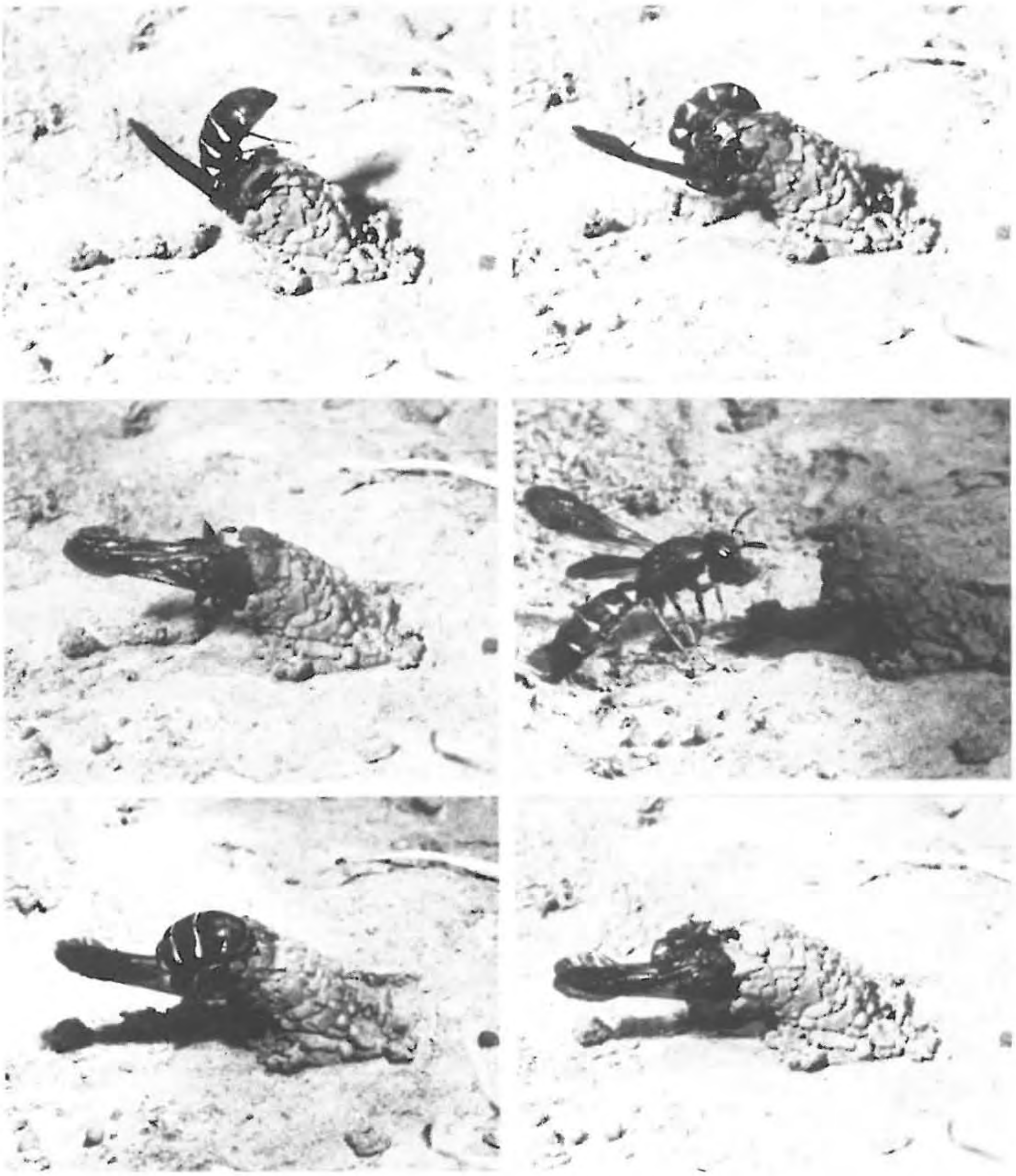


Fig. 8. Hilton, 6.xii.1976. Sequence showing turret building by *Ceramius capicola* Brauns. (x2,5)

PARASITES AND OTHER ASSOCIATED INSECTS

Parasites of Masaridae recorded at Hilton consist of species of Chrysididae, Mutillidae and Meloidae.

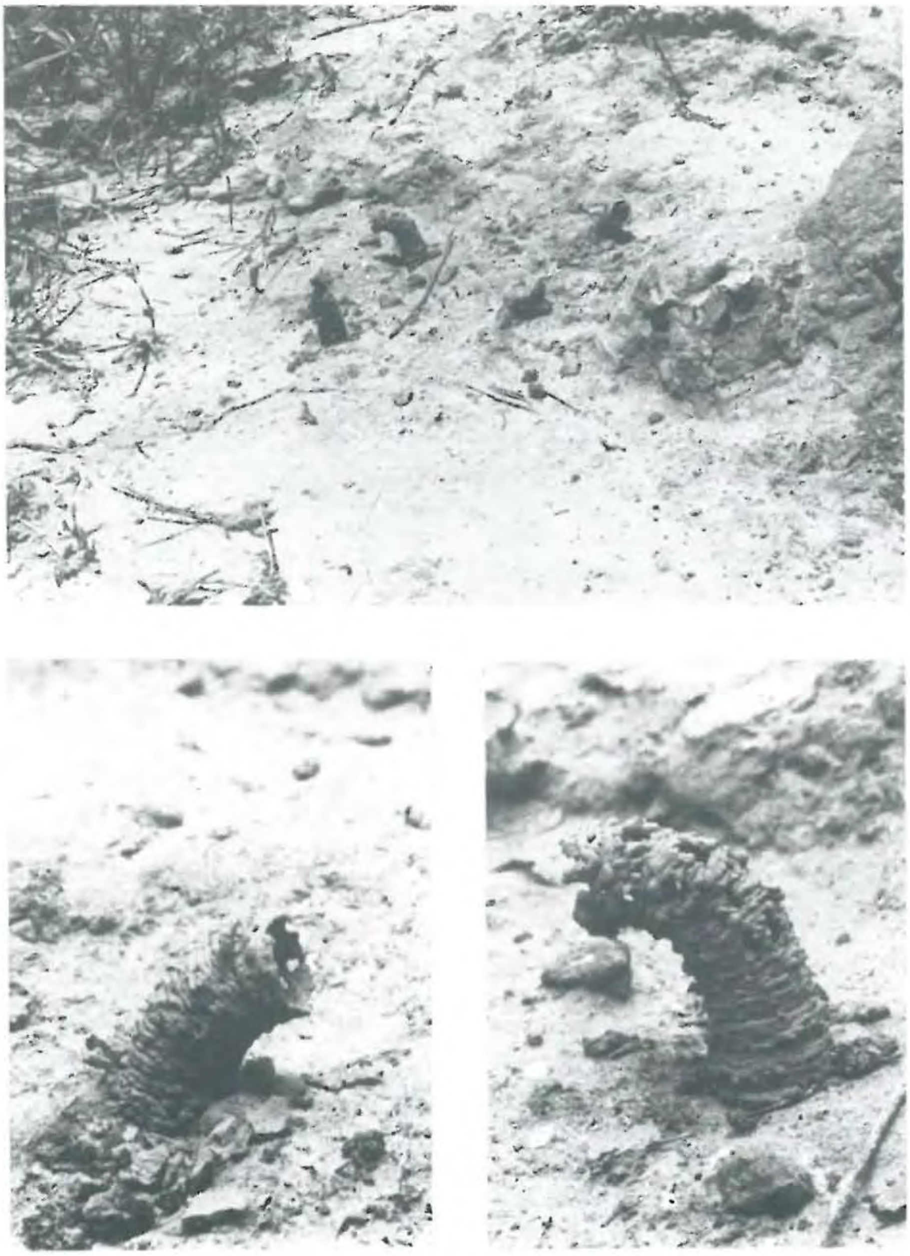
The genus *Allocoelia* (Chrysididae), the species of which as far as is known are all parasitic in the cells of Masaridae, was found to be represented at Hilton by *A. bidens* Edney. During the period 8–19.xi.1976 seven females of this small species were caught resting on the ground in the nesting area of *J. confusa* which without doubt constitutes its host. The appearance of the chrysidid coincided with the beginning of the nesting period of its host.

Though not yet collected at Hilton there seems to be no reason why other species of *Allocoelia*, namely *A. latinota* Edney and *A. capensis* Smith should not also occur there as both species have been collected in nearby vicinities. Thus *A. latinota* has been found associated with nesting *C. capicola* at Strowan and at Grahamstown (Cradock Dam), with *Ceramius* species *(capicola, lichtensteinii* and *linearis)* at Alicedale and with *C. linearis* at Kenton-on-Sea (Gess, 1973: 118–119). *A. capensis* was found associated with an extensive pseudo-colony of *C. lichtensteinii* on the farm Clifton on 7.i.1979 (D. W. Gess) and was recorded by Brauns (1910; 446) as parasitic in the cells of this wasp at Willowmore. The relative smallness of the nesting aggregations of *Ceramius* species at Hilton compared with the large pseudo-colonies of *C. capicola* and *C. lichtensteinii* located at Strowan and at Clifton respectively is the probable reason why the *Allocoelia* species parasitic in the nests of these wasps have not yet been collected at the former locality.

Three *C. lichtensteinii* cells that showed clear evidence of parasitism by Mutillidae were found in a nest excavated on 25.i.1973. In each instance there was an emergence hole sited in or near the mud-plug sealing the mud-cell and another in the truncate, disc-like anterior end of the parchment-like *C. lichtensteinii* cocoon within. The mutillid emergence hole in the truncate cocoon end was situated in the centre of the disc and left the edges of the latter attached to the sides of the cocoon. By contrast, *C. lichtensteinii* itself when emerging from its cocoon removes the disc entirely. Within each of the three *C. lichtensteinii* cocoons was found the smaller, very tough and leathery cocoon of the parasite, the space between the two cocoons being almost completely filled with very extensive, tough, brown silken spinnings. Also found in the space between the two cocoons was in one case the dry shrivelled remains of the mature larva or prepupa of the host and in the other two cases the remains of the host pupae. The mutillid cocoon, orientated the same way as the host's cocoon, had at its hind end an extensive deposit of meconium. In the same nest was found a live female *Dasylabroides* caffra (Kohl). The fine state of the vestiture and the completely unworn mandibles indicated that this individual had just emerged, doubtless from one of the three parasitized cells.

Subsequently six adults of *D. caffra* were reared from *C. lichtensteinii* cells excavated at Hilton and kept in Petri dishes in the laboratory. Three cells excavated on 5.xii.1973 yielded a male (on 17.i.1974) and two females (on 28.ii.1974 and 31.i.1975) and three cells excavated on 27.xii.1973 yielded three females (on 17.iii.1974, during January, 1975, and on 31.i.1975 respectively). Examination of the mud-cells and cocoons vacated by the parasites confirmed the earlier findings. It is probable, however, that *D. caffra* is not species-specific as regards its host and that *C. lichtensteinii* is therefore only one of a range of species parasitized.

Two adult specimens of a species of Meloidae, *Ceroctis groendali* (Billb.) were found in the nests of *C. lichtensteinii*. In addition, six meloid larvae in various stages of development were found associated with the cells of this wasp. Though none of these larvae was reared through to the adult stage and proof of the larvae's identity is thus not available, it is nevertheless believed that they were conspecific with the adults. On this assumption it may be stated that *C. groendali* is a fairly common cleptoparasite or predator in the nests of *C. lichtensteinii* where in its larval stage it feeds either upon the stored pollen loaf after first destroying the egg or newly hatched larva of the wasp or upon the fully grown larva itself. The eight individuals of the meloid found



Figs 9a, b and c. Hilton, 3.i.1977. Nest turrets of *Ceramius lichtensteinii* (Klug).
Fig. 9a (x0,4); Figs 9b and c (x1, 85)

in association with *C. lichtensteinii* nests are dealt with in an order determined by their developmental stage when found.

A triungulin larva with darkly pigmented body and with well developed long legs and long slender cerci was found in a sealed cell on 12.xii.1973, situated on the pollen loaf next to the *C. lichtensteinii* egg the hatching of which appeared to be imminent. Kept in a gelatin capsule this triungulin larva moulted to give rise to the second (caraboid) instar before dying.

A small larva, probably early third (first scarabaeoid) instar was found on 31.xii.1973 in a sealed cell containing a pollen loaf and a small, dead *C. lichtensteinii* larva. On the same date another sealed cell was found to contain a somewhat larger larva and a pollen loaf considerably reduced in size. This larva, kept in a gelatin capsule, continued to feed for some time on the pollen loaf but died as a large fourth (second scarabaeoid) instar larva.

A small larva, probably early third (first scarabaeoid) instar was found on 3.i.1977 in a sealed cell containing a large pre-spinning *C. lichtensteinii* larva and no pollen. The two larvae were transferred to a gelatin capsule and when next examined on 6.i.1977 the beetle larva was found to have grown considerably and to have eaten a hole into the wasp larva which it had thereby killed. The beetle larva moulted on 7.i.1977 and again between this date and 12.i.1977 when it was fully grown, having eaten all of the *C. lichtensteinii* larva except its skin. Transferred onto damp sand in a Petri-dish it moulted to the coarctate resting larval stage on the surface of the sand after a period of restless tunnelling through the sand. At the time of writing (March, 1980) the larva was still in a state of diapause.

A fully developed fourth (second scarabaeoid) instar larva (circa 10 mm long) was found associated with a *C. lichtensteinii* cell on 27.xii.1973 as was a coarctate resting larva (8 mm long).

The two adult beetles found in the *C. lichtensteinii* nests were both dead. The first was found on 25.i.1973, the second on 5.xii.1973.

C. groendali appears to be widespread in its distribution, Péringuey (1909: 218) recording it from "Cape Colony (Port Elizabeth, Grahamstown, East London), the whole of Orange River Colony, Natal, and the Transvaal". As this distribution is far more extensive than that of *C. lichtensteinii* (see Richards, 1962: 102; Gess, 1965: 224, 1968: 10 and 1973: 113) it is clear that *C. groendali* cannot be restricted to this wasp but must have other hosts as well, possibly ground-nesting solitary bees.

It is of interest that Brauns (1910: 446) recorded finding the coarctate larvae or the pupae ("Puppen") of a meloid in the cells of *C. lichtensteinii* at Willowmore. Specific identification was impossible as he was unable to rear them through to the adult stage. It seems possible, however, that the same species, *C. groendali*, was involved.

It is probable that nests of *C. lichtensteinii* may on occasion be utilized for nesting by *Megachile (Eutricharaea) stellarum* Cockerell. A female of this species was on 3.i.1977 seen entering and afterwards leaving a turreted nest of the wasp and on at least one occasion the remains of an old megachilid leaf nest were found in a turreted nest. Nesting of *M. stellarum* has previously been recorded in abandoned and incomplete burrows of *Dichragenia pulchricoma* (Arnold) (Gess and Gess, 1974: 204–206) and the females of this bee have also been observed leaving old burrows of *Parachilus insignis* (Saussure) (Gess and Gess, 1976: 98). As *M. stellarum* nests in pre-existing cavities in the ground it is likely that it will make use of any burrows of suitable size regardless of the identity of their excavators.

DISCUSSION

The earliest published accounts of the nesting of *Ceramius* species concerned two Palaearctic species observed in southern France: *C. fonscolombei* Latreille at Aix (Fonscolombe, 1835: 426–427) and *C. tuberculifer* Saussure (cited as *C. lusitanicus* Klug—see Richards, 1962: 29

and 112–115) in the area of Hautes-Alpes and in the valley of the Vallouise near Briançon (Giraud, 1871: 375–379) and at Montlouis and Cerdagne (Ferton, 1901: 137–139).

More recent published accounts bearing upon the nesting of *Ceramius* have all been concerned with southern African species observed in the Cape Province: *C. beyeri* Brauns, *C. bicolor* (Thunberg) (cited as *C. karrooensis* Brauns), *C. capicola* Brauns, *C. cerceriformis* Saussure (cited as *C. schulthessi* Brauns), *C. linearis* Klug (cited as *C. fumipennis* Brauns) and *C. lichtensteinii* (Klug) near Willowmore (Brauns, 1910; 387, 445–446), *C. bicolor* (Thunberg) on the banks of the Olifants River between Klawer and Clanwilliam (Gess, 1968: 13), and *C. capicola* Brauns and *C. lichtensteinii* (Klug) on Strowan near Grahamstown (Gess, 1973: 117–119).

Some details at least have therefore been published concerning the nesting of a total of eight *Ceramius* species, three of which, *C. capicola* Brauns, *C. lichtensteinii* (Klug) and *C. linearis* Klug, are the subjects also of the present studies. In order to obtain an overall picture of the ethology of *Ceramius* it is the intention in the present discussion to draw together and compare the various published accounts augmented by the present studies which latter furthermore enable some uncertainties and misconceptions present in the literature to be examined and corrected. At the same time the nesting of *J. confusa* Richards, the first *Jugurtia* species to be examined with respect to its ethology, is compared with that of species of *Ceramius*.

All the species of *Ceramius* enumerated above as also *J. confusa* have been recorded as nesting in the ground, the nests being surmounted by variously shaped mud turrets. The nature of the ground, when recorded, has been given as clayey and hard, bare or at most covered by sparse vegetation (Giraud, 1871; Ferton, 1901; Gess, 1968 and 1973; present paper). Nesting on slightly raised banks has been recorded for *C. fonscolombei* (Fonscolombe, 1835) and for *C. lichtensteinii* (present paper) whereas nesting on level ground has been recorded for *C. capicola*, *C. linearis* and *J. confusa* (present paper).

The formation of pseudo-colonies appears to be common and has been recorded for *C. tuberculifer* (Giraud, 1871; Ferton, 1901), *C. bicolor* (Brauns, 1910), *C. lichtensteinii* (Brauns, 1910; present paper), *C. capicola* (Gess, 1973; present paper) as well as for *J. confusa* (present paper).

The nearness of nesting sites to water is either stated or is implied by all authors and all the species are recorded as visiting this water. In the present paper it has been shown that with respect to the four species studied the purpose of visiting pools is to fill the crop with water which when regurgitated upon the clayey nesting substrate makes the latter more easily worked and thus makes nest construction possible. For *C. capicola*, *C. linearis*, *C. lichtensteinii* and *J. confusa* no evidence was ever obtained by the present authors either during the course of the present study itself or on any of the many occasions on which the species were collected at pools that the wasps were collecting anything but water. Similarly, Ferton (1901) with respect to the pool-visiting of *C. tuberculifer* made it abundantly clear that what the wasp collects is water, not mud, and stated that when captured on her way from a pool a female disgorged into his net her stored liquid ("son liquide").

However, other authors have claimed that some species at least collect not water but mud. Fonscolombe (1835) stated that *C. fonscolombei* went to ponds to collect sodden earth ("terre délayée") but later in his account appears to have been uncertain for he stated that the turret was constructed of pellets derived from the excavation of the nest (which would indicate the collection of water, not mud) or of pellets carried to the nest from without (which would support his earlier contention).

Similarly, Brauns (1910) stated that whereas *C. beyeri*, *C. lichtensteinii* and *C. linearis* settle on the water surface at the middle of the pool and collect water, *C. cerceriformis*, *C. bicolor* and *C. capicola* alight at the edge of the pool and collect mud in little pellets which he maintained are used by them for the construction of their cells and turrets.

With respect to *C. capicola* at least, the present study has shown Brauns to have been mistaken. *C. capicola* differs from *C. lichtensteinii* and *C. linearis* neither with respect to the part of the pool alighted upon nor with respect to what is collected at the pool: water. It seems hightly likely that Brauns was mistaken also with respect to the other two alleged mud-collectors, *C. cerceriformis* and *C. bicolor*.

It is of significance to note that alighting at the edge of the pool does not prove that mud, not water, is being collected there. As noted in the present study, *J. confusa* stands on the mud at the edge of the water but fills her crop with water like the three species of *Ceramius* which alight on the actual water surface.

The construction of a mud-cell within the excavated-cell has been reported for *C. tuberculifer* (Giraud, 1871; Ferton, 1901) and for *C. lichtensteinii* (Brauns, 1910). In the present study the construction of such a mud-cell by *C. lichtensteinii* has been confirmed and has been established also for *J. confusa*. However, no mud-cells could be demonstrated for either *C. capicola* or *C. linearis* and these species therefore differ from *C. tuberculifer* and *C. lichtensteinii* in what appears to be an important behavioural character. In the tentative grouping of the species of *Ceramius* given by Richards (1962: 83) *C. capicola* and *C. linearis* are placed in the same species-group together with *C. bicolor* and *C. socius* Turner which may therefore be expected also to omit the construction of a mud-cell.

The mud-cell constructed by *C. lichtensteinii* within the excavated-cell bears a close resemblance to the aerial cell constructed by *Pseudomasaris edwardsii* (Cresson) as described and illustrated by Torchio (1970). It is possible therefore to regard the construction of a mud-cell within an excavated-cell as in *C. tuberculifer, C. lichtensteinii* and *J. confusa* as being behaviourally intermediate between the excavation only of a cell as in *C. capicola* and *C. linearis* and the presumably more advanced construction of an aerial mud cell as in the genera *Gayella, Masaris, Pseudomasaris* and *Celonites*.

With respect to the four species of the present study it is interesting that a correlation exists between the type of cell and the length of the secondary shaft. Thus in *C. capicola* and *C. linearis* the simple excavated-cells terminate long secondary shafts whereas in *C. lichtensteinii* and *J. confusa* the excavated-cells containing the constructed-cells terminate very short secondary shafts.

Oviposition into the empty cell follows the pattern common to all Vespoidea and has been recorded for *C. tuberculifer* (Giraud, 1871; Ferton, 1901), *C. lichtensteinii* (Brauns, 1910; present paper), *C. capicola* and *J. confusa* (present paper). However, with respect to the latter three species no evidence was found during the present study that the egg was in any way attached to the cell wall being always found lying loose on the floor of the cell at its inner end. This is in contrast to the suspension of the egg by a filament from the top or side of the cell as in many Eumenidae or the glueing of the egg to a cell wall as in the Vespidae. The egg of *Pseudomasaris edwardsii* (Cresson) (Masaridae) is reported to be normally anchored by its narrowed posterior tip to the cell wall near its base (Torchio, 1970: 7) but it is not stated how this attachment is effected.

According to Ferton (1901) the egg of *C. tuberculifer* is deposited only provisionally at the bottom of the cell and after the cell has been provisioned with a firm pollen loaf of characteristic retort-like shape (see Ferton, 1901: Plate 1, Fig. 10) the mother moves the egg onto the neck of the "retort", in which position the little larva is alleged to begin feeding. Much as been made of Ferton's assertions by Malyshev (1968: 263) who, in his chapter on the genesis of bees, has based his "Secondary Bee Phase of Vespoid Type" upon them.

The present authors cannot accept Ferton's assertions concerning the transfer of the egg by the female wasp from a provisional site of deposition to a pollen loaf specially shaped for its reception. In the cells of *C. lichtensteinii* of which a large number were examined over the years, the egg was left where first deposited and the larva upon hatching found its own way onto the nearby pollen loaf. There is no reason to suppose *C. tuberculifer* to be different in this respect. Moreover, it is difficult to visualise how it would be physically possible for the female wasp to reposition her egg onto the pollen loaf as the latter would be situated between her and the egg. It is believed that the retort-shape of the pollen loaf described by Ferton was not the result of any moulding by the female wasp but was simply an artifact of the larva's feeding, that Ferton drew the wrong conclusions, and that Malyshev's hypothesis is therefore based upon false premises.

Some confusion exists in the literature as to whether *Ceramius* species practise mass provisioning or progressive provisioning.

Giraud (1871) recorded open *C. tuberculifer* cells each with a larva that either had no provision at all, had varying amounts of provision, or were almost full. The impression gained from the above is that mass provisioning is probably practised. However, somewhat later in his paper Giraud made a statement which may easily be taken ambiguously, namely that it appeared to him evident that the female wasp continues to carry in nourishment after the hatching of the larva, as was demonstrated by the insufficiency of the provision deposited in the cell of the young larva and by the presence of the female in the galleries leading to the cells.

Ferton (1901) with respect to the same species, and as already discussed above, described and figured a pollen loaf which by its completeness clearly indicates mass provisioning rather than progressive provisioning.

Brauns (1910; 445) with respect to *C. lichtensteinii* claimed that he had never found stored pollen and nectar masses in the cells with the larvae, even when the latter were still small and stated that it was certain that the wasp feeds its larvae until such time that they are full-grown, the provision being nectar ("Sicher ist, dass die Wespe ihre Larven solange füttert, bis dieselben erwachsen sind, und zwar mit Blumenhonig.").

Brauns' contention that *C. lichtensteinii* practises progressive provisioning has been mentioned by Richards (1962: 29) who did not comment other than to state that this was not recorded for the European species studied. Torchio (1970: 31), presumably on the strength of Brauns' assertion, has listed the genus *Ceramius* as practising progressive provisioning in contrast to the genera *Euparagia, Gayella, Paragia, Pseudomasaris* and *Celonites* which he lists as not provisioning progressively.

Malyshev (1968: 259) not only accepted Brauns' statement but elaborated upon it, writing that: "This method of progressive feeding of the larvae on honey (*sic*!), provided when it is needed and only given directly into the larva's mouth, is bound to reflect the moment . . . when the instincts of the wasp were transformed into those of the bee". Malyshev's hypothesis once again is based on false premises for in *C. lichtensteinii* provisioning is not progressive.

As was established in the present study and as has been dealt with in some detail earlier in the present publication *C. lichtensteinii* (as also *C. capicola, C. linearis* and *J. confusa*) practises mass provisioning, and, under optimal conditions of favourable weather and an abundance of forage flowers, provisioning and sealing of the cell is completed by the female before the egg hatches. Under less favourable conditions the rate of provisioning is slowed down leading to the finding of unsealed cells containing larvae and varying amounts of provision as recorded by Giraud, and under really unfavourable conditions the situation as reported by Brauns results. There is certainly no shred of evidence that *Ceramius* differs in any way in its method of provisioning from the other genera for which this facit of behaviour is known.

Brauns (1910: 445) stated with respect to *C. lichtensteinii* that several females appeared to work in a single nest as he frequently saw several females disappearing one after the other down the same turret. The present authors found no evidence that more than a single female nests in a nest at any one time either with respect to *C. lichtensteinii* or with respect to *C. capicola, C. linearis* and *J. confusa*. However, as already stated earlier in the present publication, *C. lichtensteinii* (as also *J. confusa*) has perennial nests resulting from the reuse of the nest in successive nesting seasons by females produced in the nest. The present authors believe Brauns' misconception may readily be explained by what appears to be the likely sequence of events in a perennial nest at the beginning of the flight season. Thus, at that time it seems probable that the several wasps, both males and females that have emerged from their cells in the nest should initially remain associated with the nest for shelter, returning to it at night or when the weather is unfavourable. It seems likely also that this co-existence in the nest should persist until such time when one of the females, possibly the first-emerged and therefore the most advanced, has reached the stage of maturity when her nesting urges begin, when she takes over the nest and drives out from it the males and the other females which latter have to emigrate and initiate new nests. That both sexes of species of *Ceramius* do for the greater part retire to the nests for the night is recorded by Brauns (1910: 446). Similarly, in the present study, females of *C. lichtensteinii*, *C. capicola* and *J. confusa* were found to shelter in their nests during periods of unfavourable weather. It is therefore believed that Brauns' observation of several females entering a single nest was made during the post-emergence—pre-nesting period at the beginning of the flight season and that the females concerned were sheltering rather than nesting. Brauns' further observation that sometimes both sexes may be found at night perched upon plants (1910: 446) most probably pertains to individuals which have been evicted from the nest in which they developed, the females amongst them not yet having initiated new nests.

Summing up, the picture of the ethology of *Ceramius* and *Jugurtia* which emerges from the studies to date is as follows:

1. Nesting is in the ground.
2. There is a tendency towards the formation of pseudo-colonies.
3. Water is required for the excavation of the nest and is collected from a pool by the female, in *Ceramius* standing on the surface of the water and in *Jugurtia* at the edge of the water.
4. The nest consists of a main shaft and secondary shafts each terminating in an excavated-cell and is surmounted by a turret constructed of mud pellets.
5. *C. lichtensteinii*, *C. tuberculifer* and *J. confusa* in addition construct a mud-cell within each excavated-cell but such constructed mud-cells are absent in nests of *C. capicola* and *C. linearis*.
6. The mud for constructing turrets and mud-cells is obtained entirely from within nest excavations.
7. The egg is laid free within the empty cell.
8. Mass provisioning is practised and the provision is in the form of a pollen loaf.
9. Each nest is worked upon by a single female in any one season.
10. In *C. lichtensteinii* and *J. confusa* there is reuse of nests in successive years.
11. *Ceramius* and *Jugurtia* are in their ethology very similar.

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KEY TO LETTERING OF CELLS IN FIGS 1–5.

A. Cell open, containing old cocoon from which adult wasp has emerged.
B. Cell closed, containing pupa in cocoon.
C. Cell closed, containing prepupa in cocoon.
D. Cell closed, containing mature larva spinning cocoon.
E. Cell closed, containing mature larva prior to cocoon spinning.
F. Cell either open or closed, containing still feeding immature larva.
G. Cell either open or closed, containing egg with provision.
H. Cell open, containing egg without provision.
I. Cell open, empty.
X. Cell either open or closed, development of young aborted.

Prey and nesting sites of some sympatric species of Cerceris (Hymenoptera: Sphecidae) with a review and discussion of the prey diversity of the genus

by

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CONTENTS

ABSTRACT

Nineteen sympatric *Cerceris* species are examined in relation to frequency of occurrence, nature of nesting sites and of prey. Their nesting sites and prey are discussed in relation to their ecological displacement. There follows a review and discussion of the prey diversity of the genus *Cerceris* which puts forward the hypothesis that *Cerceris* is an Old World genus and that its original prey was hymenopterous. Prey records of a total of twenty Afrotropical species are included of which twelve are new associations and three confirm previously published records.

INTRODUCTION

The genus *Cerceris* Latreille is cosmopolitan in its distribution and with over 850 known species is the largest genus of the Sphecidae. All species are ground-nesting and provision their young with insect prey.

The present paper is based upon observations of sympatric *Cerceris* species made over a period of seven years at Hilton, a farm situated 18 kilometres WNW. of Grahamstown (33°19'S., 26°32'E.) in the Albany Division of the Eastern Cape Province of South Africa.

In view of the large overall number of species and the frequency with which considerable numbers of species often occur together, both spatially and temporally, the ecological displacement of the species—that is the different ways in which the species exploit their habitat—is of great interest. Clearly of importance in such ecological displacement is specificity in such basic ethological factors as the choice of nesting site, and more particularly the choice of prey. It is these aspects of the ethology of the *Cerceris* species at Hilton which are set forth in the present account.

This is the eighth of a series of publications covering some aspects of the ethology of solitary wasps occurring at Hilton, the climate and vegetation of which have been previously described (Gess and Gess, 1974: 191–192).

Prey records, both published and unpublished, from localities other than Hilton have been included in the account in an attempt to draw together information on the chosen prey of as many Afrotropical *Cerceris* species as possible, little having hitherto been published on the subject.

THE CERCERIS SPECIES PRESENT AT HILTON AND THE RELATIVE FREQUENCY OF THEIR OCCURRENCE

Nineteen species of *Cerceris* have been recorded from Hilton. Arranged in alphabetical order these are: *C. amakosa* Brauns, *C. armaticeps caffrariae* Empey, *C. diodonta diodonta* Schletterer, *C. discrepans discrepans* Brauns, *C. dominicana* Brauns, *C. erythrosoma* Schletterer, *C. holconota holconota* Cameron, *C. hypocritica* Brauns, *C. languida languida* Cameron, *C. latifrons latifrons* Bingham, *C. lunigera* Dahlbom, *C. nasidens obscura* Schletterer, *C. nigrifrons nigrifrons* Smith, *C. oraniensis* Brauns, *C. pearstonensis pearstonensis* Cameron, *C. pictifacies* Brauns, *C. ruficauda ruficauda* Cameron, *C. rufocincta polychroma* Gribodo and *C. spinicaudata spinicaudata* Cameron.

The species varied greatly in the frequency of occurrence, as reflected by catches and sightings. The most commonly met with species, in decreasing order, were *C. latifrons*, *C. languida* and *C. rufocincta polychroma*, *C. holconota*, *C. spinicaudata* and *C. pearstonensis*. Less commonly met with species were *C. nigrifrons* and *C. ruficauda*, *C. lunigera*, *C. nasidens obscura* and *C. oraniensis*. Rare were *C. hypocritica*, *C. amakosa*, *C. diodonta* and *C. pictifacies*, *C. dominicana* and *C. erythrosoma*, *C. discrepans* and *C. armaticeps*.

The flight periods of all the *Cerceris* species at Hilton fall between mid-October and mid-April.

IDENTIFICATION OF THE NESTING SITES

Nests belonging to ten species were located at Hilton. All were constructed in level or nearly level bare ground which was sufficiently friable to allow the females to excavate their burrows using their mandibles and legs but no water. The ground was firm though in sandy situations the firm underlying sand was sometimes overlain by a layer of loose material.

Six species were found to nest in sandy soil, two sites being particularly favoured: a sandpit (see Gess and Gess, 1980: Fig. 1) and the area adjacent to it, and a very gently sloping bank margining a car track where the latter crosses the bed of a seasonal tributary of the New Year's River. The sand, light coloured and fine grained, is derived from the weathering of Witteberg Quartzite and is of alluvial origin having been deposited upon its flood plain by the above seasonal water course.

The species found nesting in these sites were: *C. holconota* (seven nests; both in the sandpit and on the gently sloping bank where it nested in company with *Bembix albofasciata*); *C. languida* (many nests; in the sandpit in very fine sand where it nested in company with *Bembecinus braunsii* and *B. haemorrhoidalis*); *C. latifrons* (many nests; as for *C. holconota*); *C. oraniensis* (4 nests; on level ground immediately above and below the lip of the sandpit); *C. rufocincta* (several nests; in the sandpit where it sometimes nested in company with *Bembecinus braunsii* and *B. haemorrhoidalis*); and *C. spinicaudata* (three nests; as for *C. holconota*).

Four species were found to nest in disturbed clayey soil immediately adjacent to a water furrow (see Gess and Gess, 1976: Plate 2). The clayey soil, reddish-brown in colour, is derived from the weathering of Upper Witteberg Shales previously known as Lower Dwyka Shales and referred to as such by Gess and Gess (1974: 192 and 1975: 24). Though less compacted than undisturbed clayey soil the substrate nested in by the four species was nevertheless less friable than the soil in sandy areas. The species concerned were: *C. lunigera* (1 nest); *C. pearstonensis* (1 nest); *C. ruficauda* (1 nest) and *Cerceris* sp. A (1 nest). The last listed species is unidentified owing to the unfortunate escape during the opening up of the nest of the female nest builder. Whereas it is very probable that the species was one of the nineteen recorded from Hilton, it is clear, knowing its chosen nesting substrate and prey, that it was not one of the named species recorded above as having been found nesting.

IDENTIFICATION OF THE PREY

The identity of the prey of thirteen of the nineteen species of *Cerceris* recorded from Hilton is known. Prey identifications for nine of these species were made at Hilton, seven of the associations having been previously unknown and the other two confirming previously recorded associations. For four of the ten species for which prey identifications were not made at Hilton information as to the nature of the prey taken is available from other sources. The *Cerceris* species are dealt with individually below.

Cerceris sp. A.

In a nest excavated on 6.xii.1974 and containing forty-one uneaten prey this species was found to have provisioned its cells solely with a 3,5–4,0 mm long metallic-green species of PTEROMALIDAE (Hymenoptera: Chalcidoidea).

Cerceris erythrosoma Schletterer

This species was not associated with its prey at Hilton but is known to provision with beetles of the family CURCULIONIDAE. Brauns (1911: 239 and 1926: 278) recorded the prey as a species of *Tanymecus*. Similarly, prey associated with females collected by Jacot Guillarmod at Mamathes in Lesotho and now in the collections of the Albany Museum consist in one instance of a 10 mm long specimen of *Tanymecus makkaliensis* Fhs. (det. G. A. K. Marshall) and in five instances of 6,8–7,6 mm long specimens of *Protostrophus* sp. near *sceleratus* H. v. S. (det. R. T. Thompson).

Cerceris holconota holconota Cameron

Six females seen transporting prey were captured, four after they had revealed their nests which were subsequently excavated to recover the prey stored in the caches. The thirteen prey obtained were representative of six families of Hymenoptera as detailed below: BRACONIDAE, ?Genus & sp. (1 female, 13.i.1975); BETHYLIDAE, ?Genus & sp. (1 female, 20.xii.1974); TIPHIIDAE, *Anthobosca* sp. (1 male, 13.i.1975), *Braunsomeria* sp. (4 males, 13.i.1975 and 1 male, 16.xi.1977), *Mesa incisa* (Cameron) (2 females, 20.xii.1974); MUTILLIDAE, *Dasylabris eunyce* (Péringuey) (1 male, 13.i.1975); FORMICIDAE, ?*Camponotus* sp. (1 winged male, 11.xii.1975); HALICTIDAE, *Lasioglossum* sp. (1 female, 20.xii.1974).

Cerceris languida languida Cameron

A female transporting prey was captured on each of the following three dates: 24.xi.1977, 10.i.1978 and 23.ii.1978. The first female was allowed to enter her nest which was subsequently excavated and yielded 32 prey from the cache. All 34 prey obtained from the three females were beetles of the family PHALACRIDAE and represented a single, 1,7 mm long, black *Olibrus* sp.

Cerceris latifrons latifrons Bingham

Females transporting prey were captured on 19.xi.1973 (1), 20.xii.1974 (1), 10.i.1975 (1), 9.xii.1975 (4), 2.xii.1977 (3) and 2.i.1978 (1). All eleven prey obtained were beetles of the tribe Hopliini, SCARABAEIDAE: MELOLONTHINAE. Two 4,4–4,7 mm long species were represented. The prey taken at Hilton agrees with that recorded by Arnold (1940: 106) for the subspecies *C. latifrons sedula* Arnold from Rhodesia, namely "an unidentified species of beetle (Hoplinae)".

Cerceris lunigera Dahlbom

One female seen transporting prey on 6.xii.1974 was captured after revealing her nest. The two prey obtained from the cache in the excavated nest were bees of the family HALICTIDAE, namely *Halictus* sp. (female) and *Lasioglossum* sp. (female).

Cerceris nasidens obscura Schletterer

This species was not associated with its prey at Hilton but according to E. McC. Callan (*pers. comm.*) it has been found provisioning nests in Grahamstown with "small melolonthid beetles", SCARABAEIDAE: MELOLONTHINAE. The tribe to which the beetles belong is apparently not Hopliini.

Cerceris nigrifrons nigrifrons Smith

This species was not associated with its prey at Hilton. However, Brauns (1926: 320) reported the prey to be beetles of the family BUPRESTIDAE, for instance *Sphenoptera* sp. in Rhodesia.

Cerceris oraniensis Brauns

Four females, each carrying a single prey, were captured at or near their nest entrances on 16.ii.1978. A fifth prey was obtained from the cache of a nest excavated on the same day. All the prey were beetles of the family CURCULIONIDAE and represented a single, 7,0–7,4 mm long *Protostrophus* species.

Cerceris pearstonensis pearstonensis Cameron

This species was not associated with its prey at Hilton but was found at other localities to provision with beetles of the family CURCULIONIDAE. At Strowan, near Grahamstown, on 30.xi.1970, a female was caught when flying with a 4,6 mm long *Protostrophus* sp. Prey associated with two females collected by Jacot Guillarmod at Mamathes, Lesotho, and now in the collections of the Albany Museum are likewise small weevils. The larger of the two, 4,4 mm long, is a *Protostrophus* sp., the smaller, 4,2 mm long, belongs to some other genus.

Cerceris ruficauda ruficauda Cameron

A nest of this species excavated on 10.xii.1974 was found to contain twenty-six uneaten prey, beetles of the family CHRYSOMELIDAE: CRIOCERINAE. A single 3,4 mm long blackish-bronze species was represented.

Cerceris rufocincta polychroma Gribodo

Eight females seen transporting prey were captured, one after it had revealed its nest which was subsequently excavated to recover the prey stored in the cache. The ten prey obtained were representative of two families of Hymenoptera as detailed below: TIPHIIDAE, *Anthobosca rufithorax* (Cameron) (1 female, 2.i.1978), *Tiphia* sp. (1 male, 13.xii.1977 and 1 male, 2.i.1978); MUTILLIDAE, *Chrestomutilla* sp. (1 male, 24.i.1978), *Dasylabroides caffra* (Kohl) (1 female !!, 13.xii.1977; 1 male, 17.i.1978; 2 males, 24.i.1978), *Psammotherma flabellata* (F.) (1 male, 20.xii.1974; 1 male, 13.i.1975).

Cerceris spinicaudata spinicaudata Cameron

Three females seen transporting prey were captured after revealing their nests which were subsequently excavated to recover the prey stored in the caches. The nine prey obtained were all small bees of the family HALICTIDAE. Species of two genera were represented: *Lasioglossum* spp. (4 females representative of 3 species, 20.xii.1974; 1 female, 10.i.1975) and *Nomioides* sp. (probably *N. halictoides* Blüthgen) (4 females, 20.xii.1974).

Prey associated with two females collected by Jacot Guillarmod, one at Strowan, near Grahamstown (27.ii.1972) and the other at Mamathes, Lesotho, and now in the collections of the Albany Museum are likewise females of species of *Lasioglossum*. The present records confirm the association given by Brauns (1926: 337) who wrote: "I found it carrying *Halictus* sp. for larval food".

It should be noted that, though the genus *Halictus* occurs in southern Africa, most species at one time allocated to it are now included in the closely related genus *Lasioglossum*. Brauns' record may thus apply to either *Halictus* or *Lasioglossum*.

PROVENANCE OF THE PREY

For some species at least it was established where the prey taken by them was to be found, therefore allowing the situation to be identified in which the wasps hunt and respond to prey of certain size and behaviour. For other species it is possible to speculate concerning the identity of the situation by using circumstantial evidence.

Olibrus sp. (Phalacridae) the sole prey of *C. languida* was found to be very common in the flowers of *Lasiospermum bipinnatum* (Compositae), an annual herb growing in the sandpit and elsewhere. Recorded from this plant in October and November during the first weeks of the wasp's flight period, the beetle was undoubtedly present both then and later in the summer in the flowers of other herbaceous composites as well. The flowers of species of *Senecio*, a genus of common occurrence at Hilton, were found by H. Andreae (*pers. comm.*) to be frequented by three *Olibrus* species at the Cape. The beetle is associated throughout its life with its host plant, the egg being laid in the flower and the larva feeding in the capitulum until full-grown when it bores down the stem to pupate in the ground. In European species there may be six generations in the year (Imms, 1957: 801). From the above it is apparent that *C. languida* must hunt for its prey in the flowers of Compositae, probably all small annuals like *L. bipinnatum*. The commonness of such plants and the large number of generations of *Olibrus* probably developing upon them makes possible the extended flight and nesting period—continuously from the first half of October to the beginning of March—established at Hilton for *C. languida*.

The Hopliini (Scarabaeidae) which constitute the prey of *C. latifrons* are as a tribe characteristically found in the flowers of Compositae so that this wasp may be expected to hunt in a similar though not necessarily the same situation as that pertaining to *C. languida*.

The *Protostrophus* sp. (Curculionidae) found to be the prey of *C. oraniensis* was common on the foliage of the annual herbaceous weed *Conyza bonariensis* (Compositae) during the only period, mid-February, during which this wasp was observed nesting. The beetle infested plants, growing in the sandpit, were in close proximity to the nests.

Protostrophus, recently monographed by Van Schalkwyk (1968) is a very commonly met with genus, the majority of the 136 recognized species being found in South Africa. The species are inconspicuous, mostly dull coloured and are unable to fly. In body length they range from 3–9mm. The beetles are apparently not restricted to any particular plants, the eggs being dropped to the ground where ever the females are feeding. The larvae lead a subterranean life, probably feeding upon decaying vegetable matter. Mass emergences of thousands of adults have been recorded when great damage may be done by their feeding on the foliage of many different plants including seedling trees. From the observed presence at Hilton of *Protostrophus* sp. on the foliage of *Conyza* and the known biology of the weevil genus it would appear that *C. oraniensis* hunts for its prey amongst foliage at no great height above the ground. It is probable that the other two *Cerceris* species known to prey at least partly upon *Protostrophus* and occurring at Hilton, *C. erythrosoma* and *C. pearstonensis* hunt in similar situations.

The species of Criocerinae (Chrysomelidae), the sole recorded prey of *C. ruficauda* may be expected to occur on foliage as is characteristic for the subfamily and it is there that the wasp undoubtedly does its hunting.

For the species of *Cerceris* which hunt Hymenoptera two possible hunting situations immediately present themselves: at flowers and young growth visited by the prey for purposes of foraging for nectar or glandular exudates, or at the nests of the prey.

It was noted at the time when the nest of *C. lunigera* and those of *C. spinicaudata* were excavated that they were situated in close proximity to the nests of various small bees some of which at least were those of species represented amongst the prey of the wasps. This was particularly striking with respect to *C. spinicaudata* and *Nomioides* sp. (probably *N. halictoides*) which nested next to one another in the sand. It therefore seems possible that the hunting of these two *Cerceris* species may take place at or near the nest entrances of their prey and in close proximity to the entrances of their own nests. The fact that only female bees are recorded as prey would lend support to this hypothesis. The latter would be in accord with the findings of Marchal (1887) as reported by Hamm and Richards (1930: 106) on the behaviour of *C. rybyensis* (L.) (= *C. ornata* Fabr.) in France. That wasp nested in a garden path in close proximity to innumerable nests of *Andrena* and *Halictus* on which species it was preying. The *Cerceris* was reported to circle round the nests, every now and then dropping to the ground, or even entering a burrow. Only bees returning home laden with pollen were attacked, and these were knocked down and stung as they hovered over their nests before entering.

With respect to *C. holconota* and *C. rufocincta polychroma* on the other hand, the wide range of unrelated prey of both sexes and of very diverse habits and behaviour makes it likely that the only situation in which these *Cerceris* species in hunting would meet all the prey species would be at flowers and young growth to which the latter would go for foraging purposes. In the areas in which the two *Cerceris* species nested—in and near the sandpit—the flowering plants known to have been visited by a mixed company of Braconidae, Tiphiidae, Mutillidae and others were *Selago corymbosa* (Selaginaceae) and various low-growing Compositae including *Helichrysum* and *Lasiospermum*. It therefore appears that *C. holconota* and *C. rufocincta polychroma* hunt for their prey on and around flowers of low-growing herbaceous plants.

DISCUSSION OF THE NESTING SITES AND THE PREY IN RELATION TO ECOLOGICAL DISPLACEMENT.

The existence at Hilton of two basically very different soil types, one clayey and the other sandy, and the specificity shown by the wasps in their choice of nesting substrate has resulted in the *Cerceris* species of that locality being divided for the purposes of nesting into two distinct non-competitive groups, indicating that an area with more than one type of friable soil can support a larger number of *Cerceris* species than one with a uniform soil type.

Other factors, for example the depth of the friable soil, will be limiting. The species nesting in sand place their caches at depths ranging from 60 ± mm in *C. rufocincta* to 500 + mm in *C. latifrons*. Therefore, whereas *C. latifrons* can only nest in relatively deep sand *C. rufocincta* and other shallow-nesters are less restricted.

Hunting by *Cerceris* species at Hilton appears to take place at no great distance from the nest. This being so, competition for prey between species such as for example the clay-nesting *C. lunigera* on the one hand and the sand-nesting *C. spinicaudata* on the other is avoided as, although both hunt halictine bees, their hunting areas are distinct. This is especially true for these species which are believed to prey upon bees nesting in close proximity to their own nests.

All the species are highly prey specific with the exception of *C. rufocincta* and more particularly *C. holconota* which, with their recorded prey representing respectively two and six families of Hymenoptera, appear to be catholic in their choice. With the high prey specificity generally shown competition for prey is effectively avoided despite the fact that a number of species nesting in the same soil type may hunt in very similar situations. The most commonly taken prey recorded or known for *Cerceris* species occurring at Hilton are species of Halictidae and Curculionidae, notably *Protostrophus* species. With respect to the three species hunting *Protostrophus* weevils, differences in preferred size range of prey either alone or in conjunction with differences in substrate-determined nest situation are likely factors of importance in the avoidance of competition.

REVIEW AND DISCUSSION OF THE PREY DIVERSITY OF THE GENUS CERCERIS

The most interesting aspect of the behaviour of *Cerceris* concerns the diversity of insects taken as prey by the genus and the specificity shown by individual species.

Provisioning is with adult Coleoptera or Hymenoptera, depending upon the *Cerceris* species. From data presented by Bohart and Menke (1976: 576) and by Iwata (1976: 150–151) it appears that eleven families of Coleoptera have so far been recorded as prey: Anthribidae, Bruchidae, Buprestidae, Cerambycidae, Chrysomelidae, Coccinellidae, Curculionidae, Nitidulidae, Phalacridae, Scarabaeidae and Tenebrionidae. Published records of Hymenoptera taken as prey mostly concern Apoidea.

Coleoptera appear to be the more commonly taken order and have been recorded as prey of *Cerceris* from many parts of the world. North American species of *Cerceris* provision exclusively with Coleoptera and the few records pertaining to South America concern prey of the same order. The few prey records for Australian *Cerceris* similarly concern Coleoptera. In the Palaearctic, Oriental and Afrotropical Regions of the Old World, however, there are, in addition to species provisioning with Coleoptera, a minority of species that utilize Hymenoptera. Thus the Palaearctic *C. rybyensis* (L.), *C. hortivaga* Kohl and *C. sabulosa* (Panzer) and the Oriental *C. pictiventris* Dahlbom provision with Apoidea, especially Halictidae and some in addition with Colletidae and Andrenidae.

Though Apoidea appear to be the most commonly taken non-coleopterous prey, four records of the use of Hymenoptera other than bees have been published (see Bohart and Menke, 1976: 576). In the Palaearctic, *C. stratiotes* Schletterer is believed to prey only on the chalcid, *Stilbula cynipiformis* (Rossi), a *Cerceris* species provisioning with halictid and andrenid bees was found to have also in its brood cells a species of *Psen* (Sphecidae), and a female *C. pekingensis* Tsuneki was reported to have taken a species of *Pison* (Sphecidae) into her burrow. The fourth record concerns the Oriental *C. langkasukae* Pagden which was reported carrying a species of *Hingstoniola* (Sphecidae) although her regular prey were buprestids.

The prey of eight Afrotropical *Cerceris* species has been recorded in print. On the African mainland, Curculionidae are taken by *C. chirindensis* Arnold (Arnold, 1932: 13), *C. emeryana varilineata* Cameron (Brauns, 1926: 322, as *C. varilineata* Cam.) and *C. erythrosoma* Schletterer (Brauns, 1911: 239 and 1926: 278); Buprestidae are taken by *C. nigrifrons* Smith (Brauns, 1926: 320); and Scarabaeidae are taken by *C. latifrons sedula* Arnold (Arnold, 1940: 106, as *C. sedula* Arnold). On Malagasy, Curculionidae are taken by *C. clypearis* Saussure; Chrysomelidae and Buprestidae by *C. albotegula* Arnold; and nomiine bees (Halictidae) by *C. nenitra* Saussure (all Arnold, 1945: 23, 41 and 42 respectively).

Additional records (all C. F. Jacot Guillarmod's and unpublished) obtained from the Albany Museum collections concern *C. bothavillensis* Brauns and *C. emeryana multicolor* Arnold (both from Mamathes, Lesotho) and *C. multipicta fuscifacies* Empey (from the Transvaal Lowveld) all of which took Curculionidae, in the case of the first named species, *Leurops sublineata* Marshall.

With the addition of the records from Hilton, the prey of a total of 20 (i.e. 10,6%) of the 189

Afrotropical species of *Cerceris* recognized by Empey (1969) is known. The corresponding figures for America north of Mexico are 21 (i.e. 27%) of 78 species (see Scullen, 1965 and Evans, 1971: 509). Of the twenty Afrotropical species concerned, fourteen species prey upon Coleoptera and six upon Hymenoptera whereas, as previously noted, all North American prey recorded comprised Coleoptera. With respect to both regions the most commonly taken prey are species of Curculionidae, 40% and 48% of the species for which prey is known taking this family in the Afrotropical Region and in America north of Mexico respectively.

Cerceris is most unusual though not unique (see *Bembix*) in the Sphecidae in provisioning with prey belonging to more than one order, with, as has been shown, a majority of species utilizing Coleoptera and a minority utilizing Hymenoptera. It is therefore of interest to examine which of these two orders constitutes the original prey taken by the genus.

Suggested relationships within the subfamily Philanthinae based entirely upon consideration and evaluation of morphological characters of presumed phylogenetic value have been discussed by Bohart and Menke (1976: 557–558) and shown by them in a dendrogram (Fig. 183). On the basis of the number of advanced characters appearing in each genus, *Cerceris* is seen as a highly advanced genus, surpassed only by the North American *Eucerceris*.

If on Bohart and Menke's dendrogram are entered details of the prey for each of the included genera (unknown for *Eremiasphecium*, *Odontosphex* and *Philanthinus*) it is seen that the species of Philanthinae prey pre-eminently upon Hymenoptera and that only *Cerceris* (partly) and *Eucerceris* (wholly) prey upon Coleoptera.

It therefore appears that within the Philanthinae the use of Hymenoptera as prey is primitive or unspecialized and that the use of Coleoptera is advanced or derived. In this case *Cerceris* in its prey selection represents the transitional stage between the less advanced condition and that shown by *Eucerceris*. In this connection Pagden's record (see Bohart and Menke, 1976: 576) of *C. langkasukae* carrying a hymenopteran although her regular prey were Buprestidae may represent atavistic behaviour in time of shortage of the coleopterous prey.

The change from Hymenoptera to Coleoptera by *Cerceris* can be shown to have been advantageous for two reasons. Firstly, it enabled that fraction which made the change to avoid competition with related genera (e.g. *Philanthus*) and possibly others (e.g. *Palarus*) for hymenopterous prey, and secondly, it made available to *Cerceris* as potential prey vast numbers of species of many families belonging to an order which at least in its adult stage was not being exploited by any other wasps.

The vast possibilities opened up by the adoption of the new prey may be considered to have led to an outburst of speciation in the fraction of *Cerceris* concerned, leading to the predominance of Coleoptera-preying species over Hymenoptera-preying species and to the overall magnitude of the genus *Cerceris*, which with a total of over 850 known species (Bohart and Menke, 1976: 575) is the largest genus of the Sphecidae.

Within the range of Coleoptera preyed upon, the most commonly taken by *Cerceris* appear to be species of Curculionidae and species of this family constitute the sole prey of *Eucerceris*. The preference for weevils may be attributable to the overwhelmingly greater number of species in the Curculionidae than in other families.

With respect of those Philanthinae which utilize Hymenoptera as prey, some interesting trends relevant to the prey taken by the various genera are apparent. Thus the sole recorded prey for *Pseudoscolia* and the most characteristic prey of *Trachypus*, *Philanthus* and the Hymenoptera-preying species of *Cerceris* are species of Halictidae though species of all three latter genera may also utilize other families of bees as well as wasps of several aculeate and non-aculeate families. On the other hand prey taken by three of the four genera of the Aphilanthopsini (prey is not known for the fourth genus) consists in each case of a single genus of Formicidae.

It is clear that the genera of the Aphilanthopsini are greatly specialized in their choice of prey (as is indicated also by the presence in *Clypeadon* and *Listropygia* of an "ant clamp" formed of the pygidial plate and the hypopygium) whereas the other genera represent the more unspecialized or primitive condition. In those species which utilize a wide spectrum of prey, the prey taken at any locality or time is probably dependant upon its abundance in the area and upon its size relative to the provisioning wasp. The frequency with which Halictidae are taken by species of *Trachypus*, *Philanthus* and the Hymenoptera-preying *Cerceris* species is undoubtedly due to the commonness of species and individuals of this bee family. There does, however, appear to be a tendency towards restriction in the range of prey taken. This may be seen in those of the Hymenoptera-preying *Cerceris* occurring at Hilton for which a number of prey records is available. Thus, in contrast to *C. holconota* for which six families including Halictidae are recorded as prey, *C. spinicaudata* appears to be restricted to Halictidae and *C. rufocincta polychroma* appears to specialize in Tiphiidae and Mutillidae.

Finally, from the fact that both Hymenoptera- and Coleoptera-preying species of *Cerceris* occur in the Old World but only Coleoptera-preying forms occur in the New World it may be speculated that *Cerceris* was originally an Old World Genus.

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Some aspects of the ethology of Dasyproctus westermanni (Dahlbom) (Hymenoptera: Sphecidae: Crabroninae) in the Eastern Cape Province of South Africa

by

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CONTENTS

ABSTRACT

Some aspects of the ethology of *Dasyproctus westermanni* (Dahlbom) are described. Of particular note is the orientation of the pupae which appears to be governed by gravity rather than the position of the nest entrance. Foraging records are given for *D. bipunctatus* Lep. & Brullé, *D. dubiosus* (Arnold), *D. immitis* (Saussure), *D. ruficaudis* (Arnold) and *D. westermanni* (Dahlbom). The ethology of the genus *Dasyproctus* is reviewed and discussed.

INTRODUCTION

Sixty-seven species of the genus *Dasyproctus* Lepeletier and Brullé (Sphecidae: Crabroninae) are listed by Bohart and Menke (1976:419) of which just over half occur in the Afrotropical Region. The remainder are known from the Oriental and Australasian Regions. Published biological accounts varying from fragmentary to fairly extensive pertain to six species:

D. agilis (F. Smith) and *D. buddha* (Cameron) from the Oriental Region and *D. barkeri* (Arnold), *D. bipunctatus* Lep. & Brullé, *D. kibonotensis* Cameron and *D. stevensoni* (Arnold) from the Afrotropical Region.

The present paper is an account of some aspects of the ethology of a seventh species, *D. westermanni* (Dahlbom) and is the ninth in a series of publications dealing with the ethology of certain solitary wasps occurring at Hilton, a farm situated 18 kilometres WNW. of Grahamstown (33° 19'S., 26° 32'E.) in the Albany Division of the Eastern Cape Province of South Africa.

In all, five species of *Dasyproctus* have been recorded from Hilton. These are: *D. bipunctatus* Lep. & Brullé, *D. dubiosus* (Arnold), *D. immitis* (Saussure), *D. ruficaudis* (Arnold) and *D. westermanni* (Dahlbom). With respect to *D. bipunctatus* three colour forms are present which by some authors (e.g. Leclercq, 1958) are accorded subspecific rank: *D. b. bipunctatus* Lep. & Brullé, *D. b. lugubris* (Arnold) and *D. b. simillimus* (Smith). *D. b. simillimus* (Smith) is listed as a good species by Bohart and Menke (1976). Foraging records are given for all five species.

DESCRIPTION OF NESTING SITES

Of the five species only *D. westermanni* was observed engaged in nesting activities. Nests were situated up off the ground within galleries hollowed out by the wasp in green subvertical pithy inflorescence stems of *Urginea altissima* (Liliaceae) growing on rising clayey ground immediately to the east of the New Year's River in dwarf karroo scrub characterised by *Pentzia incana* (Compositae) (Fig. 1).

Evidence of nesting by *Dasyproctus* was also found in the inflorescence stems of two species of *Gasteria* (Liliaceae) and in the stems of *Berkheya decurrens* (Compositae), all growing on clayey soil in various situations within thorn scrub. As the nests examined in these plants were all old ones from which the wasps had emerged it was not possible to establish the identity of the builders. It is possible, however, that these were the nests of one or more of the other species of *Dasyproctus*.

FLIGHT PERIOD

The flight periods of all five species at Hilton and elsewhere in the vicinity of Grahamstown fall largely between the beginning of October and the end of March though isolated individuals have been found both earlier and later in the summer. *D. westermanni* is known from November to mid March and was found nesting in *Urginea* at Hilton during December and January.

FLOWERS AND YOUNG GROWTH VISITED BY ADULT WASPS

At Hilton two species of *Dasyproctus* were collected on the yellow flowers of *Acacia karroo* (Leguminosae): *D. b. bipunctatus* (6.i.1977, 1 female and 13.i.1977, 1 male) and *D. dubiosus* (29.xii.1976, 2 males and 6.i.1977, 1 male). The young foliage of *A. karroo* was visited by *D. westermanni* (6.xii.1976, 1 female).

At Strowan, a farm lying between Hilton and Grahamstown, the yellow flowers of *Berkheya heterophylla* (Compositae) were visited by *D. b. bipunctatus* (12.x.1972, 4 females, 16.x.1972, 4 females, and 25.x.1972, 7 females) and by *D. b. simillimus* (16.x.1972, 1 female); at Belmont Valley, lying 25 kilometres SE. of Hilton, the yellow flowers of *Foeniculum vulgare* (Umbelliferae) were visited by *D. b. bipunctatus* (26.i.1970, 1 female), by *D. b. simillimus* (26.i.1970, 1 female, 5.ii.1970, 1 female, 28.iv.1970, 1 female), by *D. dubiosus* (20.i.1970, 1 male), by *D. immitis* (25.i.1970, 1 female) and by *D. ruficaudis* (20.i.1970, 1 female); at the Koonap River

Fig. 1. Hilton, 4.i.1978. Inflorescences of *Urgenea altissima* (Liliaceae) in dwarf karroo scrub characterised by *Pentzia incana*.

near Adelaide, 70 kilometres N. of Hilton, the greenish-yellow flowers of *Zizyphus mucronata* (Rhamnaceae) were visited by *D. b. bipunctatus* (1 female) and by *D. immitis* (1 male) (both 20–22.xii.1972).

IDENTIFICATION OF THE PREY

Prey was obtained only from *D. westermanni* and as in all species of *Dasyproctus* consisted of small flies. It appears that *D. westermanni* is an opportunist with respect to the flies it utilizes as prey and may take any suitably sized fly which it finds in its hunting area. All cells in which prey flies were in a condition allowing identification were found to have been provisioned with several species of flies though in some the preponderance of one or other species indicated that the wasp may, upon finding a ready supply of that species, have concentrated upon it or upon its source.

Seven dipterous families were represented amongst the prey found in nests examined during January, 1978. Details are listed below.

Simuliidae		
Simulium sp.	2,0 mm long	13 females, 4 males
Stratiomyidae		
1 sp.	5,2 mm long	10 specimens
Bombyliidae		
Bombylius delicatus Wied.	4,0 mm long	1 female, 1 male
1 sp. of Cyrtosiinae	1,4 mm long	3 specimens
1 sp. other	3-4 mm long	1 female, 1 male
Empididae		
1 sp.	3,0 mm long	1 male
Syrphidae		
1 sp.	3,6 mm long	1 specimen
Otitidae		
species A	2,2 mm long	3 females, 10 males
species B	2,4 mm long	1 male
Chamaemyiidae		
1 sp.	3,4 mm long	3 specimens

The presence amongst the prey of flies such as the Simuliidae and Stratiomyidae and possibly also the Otitidae may indicate that the chief hunting area of *D. westermanni* was in fairly close proximity to the nests, namely in the riverine vegetation fringing the New Year's River. Other flies such as the less commonly taken Bombyliidae were probably captured in the tract of open dwarf scrub nearer the nests and between the latter and the riverine vegetation.

DESCRIPTION OF THE NEST

The completed nest of *D. westermanni* consists of a circular entrance hole of 4 mm diameter bitten through the side of the green inflorescence stem of *Urginea altissima* (Fig. 2) and giving access to an ascending and a descending gallery of 4–4,5 mm bore hollowed out of the pithy centre of the stem. Both galleries are divided serially into a number of cells (Figs 3a, b, c and d).

A total of twenty-two nests of *D. westermanni* within nineteen subvertical stems was examined. Seventeen of the utilized stems each contained a single nest, one stem contained two nests and another contained three nests. The entrance hole to the nest was situated from 500–1 070 mm (average 770 mm) above the ground and in all but one instance was sited below the level of the lowermost elements of the cylindrical raceme which occupies the terminal two-fifths of the inflorescence stem. Heights above the ground of the bottom and the top of the raceme ranged from 820–1 360 mm (average 1 040) and from 1 550–2 100 mm (average 1 800 mm) respectively.

Of the twenty-two nests, twenty had completed ascending galleries and of this latter number nine had in addition completed descending galleries. The ascending galleries ranged in length from 42–114 mm (average 86 mm) and the descending galleries ranged in length from 78–122 mm (average 91 mm).

In length the serially arranged cells including the pithy plug sealing each ranged from 8–14 mm (average of 71: 11,2 mm), the thickness of the plugs or cell partitions being 1,5–2,0 mm. The number of cells in fully utilized ascending galleries ranged from five to eight; the only fully utilized descending gallery found contained seven cells. The maximum number of cells found in any one nest (the only one which had both galleries fully utilized and intact) was fourteen.

Fig. 2. Hilton, 4.i.1978. Portion of inflorescence stem of *Urgenea altissima* (Liliaceae) showing entrance hole of nest of *Dasyproctus westermanni* (x circa 0,5).

Neither gallery is filled with cells right up to the level of the entrance hole, the plug of the outermost cell in each case being some distance removed from it. In the above fourteen-celled completely utilized nest a vestibular space, 16 mm in length, was left between the two outermost cells. The nest entrance opening into this vestibule was not sealed.

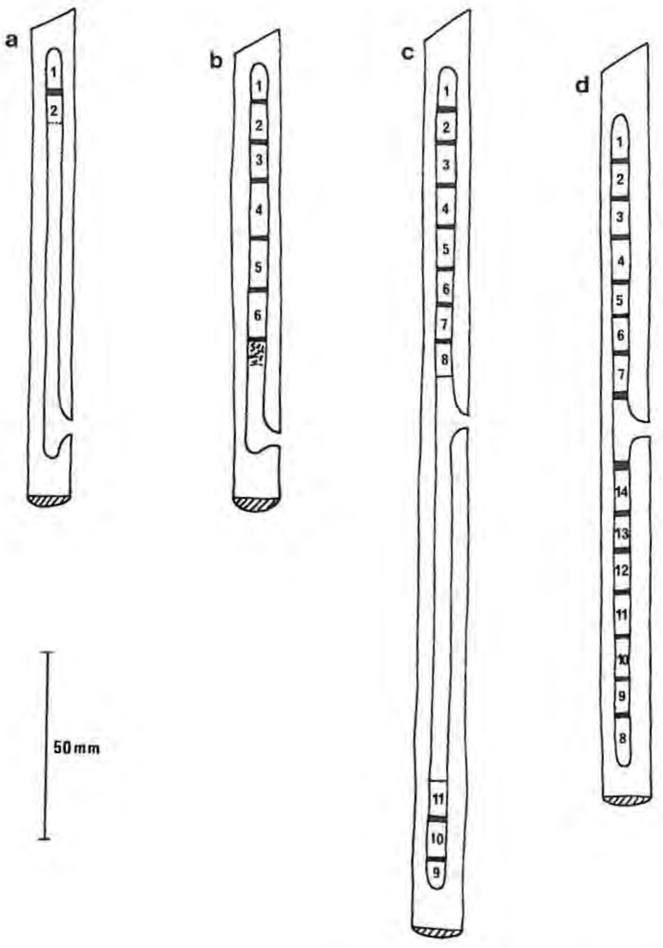
METHOD OF CONSTRUCTION OF THE NEST, OVIPOSITION AND PROVISIONING

A nest entrance hole having been bitten through the wall of the inflorescence stem and the pith centre having been reached, the wasp hollows out its galleries by biting off and removing the pith. Some at least of this pithy material appears, however, to be retained within the nest for the purpose of constructing the cell partitions.

The ascending gallery is invariably the first to be hollowed out and only after the full number of cells destined for this gallery has been constructed within it is a start made with the hollowing out of the descending gallery (Figs 3a, b, c and d).

Each cell is provisioned with a relatively large number of prey which are closely packed and are orientated to face the inner (i.e. blind) end of the cell. The prey is alive but partially paralysed. Two fully provisioned and sealed cells, the contents of which had neither been consumed nor had become mouldy, contained fourteen and twenty-six flies respectively.

It is not clear on which prey, in order of provisioning, oviposition takes place but it appears not to be on the first. A *D. westermanni* egg was found in each of the above two cells—in the first it was attached to a *Bombylius delicatus* Wied. (4 mm long male), one of the first three prey



Figs 3a, b, c, and d. Plans of nests of *Dasyproctus westermanni* in inflorescence stems of *Urginea altissima* in longitudinal section.

to be introduced into the cell; in the second it was attached to an Otitid (2,4 mm long male) situated about in the middle of the cell. Two partially provisioned and still open cells containing three and ten prey respectively were found in which no egg had yet been laid.

The egg of *D. westermanni* is white, very strongly curved and 1,9 mm in length. It is glued to the underside of the prothorax of the fly anterior to the legs—that is more or less in the neck region, the fly's head being pushed forwards to accommodate the anterior end of the egg in the space between the prothorax and the underside of the head. The egg extends laterally or postero-laterally across the ventral surface of the fly to either left or right. The newly hatched larva is orientated in the same way (Fig. 4).

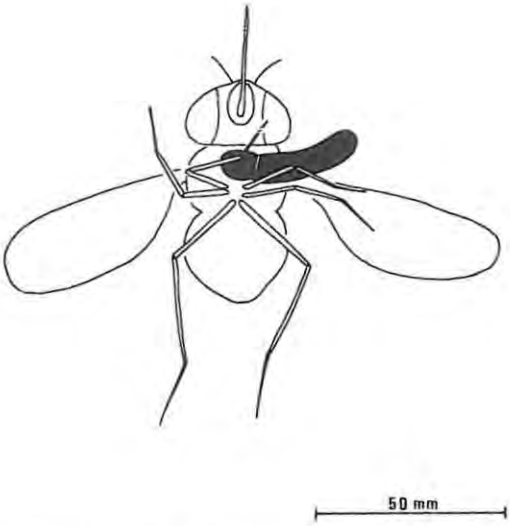


Fig. 4. Diagrammatic representation of bombyliid fly showing position of newly hatched feeding larva of *Dasyproctus westermanni*.

LIFE HISTORY

Due to the fact that in the nests examined all but two of the completed cells contained either provision and wasp young that had gone mouldy or cocoons containing spinning larvae or pupae, little information concerning the life history of the species could be obtained. The two eggs found on prey on 4.i.1978 and 10.i.1978 hatched on 5.i.1978 and 14.i.1978 respectively. Neither larva survived.

All twenty-six male and thirteen female wasps reared from the examined nests emerged during the period 10–27.i.1978. Development from egg to adult appears to be very rapid in the generation reared in *Urginea* stems, probably owing to the short time during which these stems are suitable for the nesting of *Dasyproctus*. It is probable that there is at least one other annual generation of the species but its nesting site has not been identified.

The silken cocoon of *D. westermanni* is brown and papery, 9 mm long and with a maximum width of 3,4 mm. Its anterior end is rounded whilst the posterior end has incorporated in it the dark brown meconium voided by the post-spinning larva. Adhering to the meconium at the hind end of the cocoon are the prey remains—wings, legs and other uneaten fragments which the mature larva on cleaning the cell prior to the start of cocoon spinning has concentrated behind it at one end of the cell.

The orientation of the cocoons and of the pupae within them is unusual and of interest in *D. westermanni* in that it appears to be governed by gravity rather than by the position of the nest opening as indicated to the spinning larva by the curvature of the cell partitions. Thus in all cells, whether constructed in ascending or descending galleries, the anterior end of each cocoon is orientated upwards, facing away from the ground. Thus in the first-constructed ascending gallery the anterior end of each cocoon is directed away from the nest entrance and the meconium and prey remains are between each wasp and the outer partition of its cell. In the later-constructed descending gallery, however, the orientation normally practised by wasps nesting serially in tubes is present—the anterior end of each cocoon is directed towards the nest entrance and the meconium and prey remains are between each wasp and the inner or blind end of its cell.

PARASITES AND OTHER ASSOCIATED INSECTS; MOULD

Three distinct categories of associated insects occur in *D. westermanni* nests: a parasitoid of *D. westermanni* itself, a species cleptoparasitic with respect to the stored provision, and at least one species possibly cleptoparasitic with respect to the nest galleries.

A 4,2 mm long dark metallic green and reddish bronze *Perilampus* sp. (Hymenoptera: Chalcidoidea: Perilampidae) was found to be a parasitoid in nine cells distributed over five nests studied during January, 1978. Previously, during the summer of 1974 two specimens of the parasite were reared from the same host. The *D. westermanni* larva is attacked after it has spun its cocoon in the normal manner but before it has changed into a pupa. Each parasitized *D. westermanni* cocoon yields a single perilampid. The emergence of the adult parasitoid from the host cocoon is timed to coincide within a few days with the emergence of adult *D. westermanni* from adjacent cells in the nest.

A 2,6 mm long yellowish-brown species of Phoridae (Diptera) was found to be a cleptoparasite in one nest. When opened on 18.i.1978 it was found that in both the ascending and descending galleries all the cell partitions, bar those sealing the two outermost cells (i.e. those closest to the nest entrance), had been broken down and that the provision stored in the breached cells had been almost completely devoured. In the ascending (older) gallery the cleptoparasites had already pupated, thirteen puparia being cemented in a group to the gallery wall at the end nearer the nest entrance. In the descending (newer) gallery were twenty-four as yet unpupated maggots. These were transferred to a glass vial where they pupated on 20.i.1978. Flies from both galleries emerged from their puparia towards the end of February.

A species of *Trypoxylon* (Sphecidae) which utilizes pre-existing cavities for its nesting was found in three instances to have taken over the galleries excavated by *D. westermanni*. Though it cannot with certainty be stated that actual competition for the excavated galleries took place between *Trypoxylon* sp. and *D. westermanni* it does appear that this may have been the case and that the galleries taken over by the former were ones being used by the builder, not abandoned ones. Thus all three *D. westermanni* galleries (which were ascending ones) were either in the process of being hollowed out or of being provisioned. One of the galleries had not yet reached its final length as evidenced by the fact that its blind end had not yet been rounded off as is the case with completed galleries; the second gallery had been completed but nesting by *D. westermanni* had not yet commenced; the third gallery had had three cells completed by *D. westermanni*, the point of succession being during the provisioning of the fourth cell.

Other insects found in *D. westermanni* galleries were females of *Heriades ?spiniscutis* (Cameron) (Megachilidae) (three instances) and a female of *Allodapula variegata* (Smith) (Anthophoridae) (one instance). The *D. westermanni* galleries used by these bees were clearly abandoned ones, no recently provisioned cells being present. It is possible that the bees were merely sheltering in the galleries but it cannot be ruled out that they might have commenced nesting had they been left undisturbed. If they had, they would clearly not have been competitors for the galleries as it appears that *Trypoxylon* sp. may have been.

The previously mentioned old nesting galleries of *Dasyproctus* sp. in *Gasteria* inflorescence stems were found to have been utilized for nesting by *Trypoxylon* sp., *Heriades ?spiniscutis* (Cameron) and *Allodapula variegata* (Smith) whereas the galleries in *Berkheya decurrens* stems had been utilized by *Heriades ?spiniscutis* (Cameron) and *Allodape* sp. (*rufogastra* Lep. & Serv. or *exoloma* Strand) (Anthophoridae).

Mould attacking the stored provision is of common occurrence in the cells of *D. westermanni* and effects a larger number of cells than do parasitoids and predators together. Details are given in Table 1 of the nesting success and mortality rate due to various causes in one hundred completed cells examined.

TABLE 1.

Nesting success and mortality rate due to various causes in one hundred completed cells of *D. westermanni* examined.

Total No. of completed cells*	No. of cells attacked by mould	No. of cells attacked by Perilampidae	No. of cells attacked by Phoridae	No. of cells attacked by other insects	No. of cells in which pupae died for unknown reasons	No. of cells from which *D. westermanni* adults emerged
100	30	9	13	1	8	39

*Excluding two cells containing newly hatched larvae which did not survive examination.

REVIEW AND DISCUSSION OF THE ETHOLOGY OF THE GENUS DASYPROCTUS

As already noted, published biological accounts varying from fragmentary to fairly extensive pertain to six species: *D. agilis* (F. Smith) and *D. buddha* (Cameron) from the Oriental Region and *D. barkeri* (Arnold), *D. bipunctatus* Lep. & Brullé, *D. kibonotensis* Cameron and *D. stevensoni* (Arnold) from the Afrotropical Region.

D. agilis and *D. buddha* were both recorded nesting in stems of Gramineae (sorghum and solid dead stems of *Coelorrachis* respectively) in which their cells were provisioned with Otitidae (mainly), Muscidae and Syrphidae and with Chloropidae and Otitidae respectively (see Bohart and Menke, 1976: 419).

Of the African species, *D. bipunctatus* Lep & Brullé (including its colour forms *simillimus* (Smith) and *lichtenburgensis* (Arnold)) is the best known. The species has been found by several observers to be restricted in its nesting to the inflorescence stems of the monocotyledonous families Amaryllidaceae, Iridaeceae and Liliaceae. The most comprehensive account of the nesting of this species (*D. bipunctatus sensu stricto*) is that by Bowden (1964: 425–437) who found it nesting near Kampala (Uganda) in the flowering stems of *Kniphofia* and *Aloe* spp. (Liliaceae), *Gladiolus* sp. (Iridaceae) and *Hippeastrum* (an American genus) (Amaryllidaceae). Six families of Diptera were represented amongst the prey, namely Chloropidae, Lonchaeidae, Muscidae, Simuliidae, Sphaeroceridae and Trypetidae. Most prey were *Atherigona* species (Muscidae: Coenosiinae). On the basis of the prey taken Bowden theorized that *D. bipunctatus* forages primarily over grass. *D. bipunctatus* was also found nesting in gladiolus stems near

Salisbury (Rhodesia, now Zimbabwe) by Cuthbertson (1937: 28–31). That author listed the prey as belonging to the Anthomyiidae, Sarcophagidae, Sapromyzidae, Syrphidae and Tachinidae.

D. bipunctatus simillimus, in the Western Cape Province at least, appears to nest by preference in the green flowering stems of *Watsonia* sp. (Iridaceae). The present author found it nesting commonly in such stems at Kirstenbosch (Cape Peninsula) on 22.xi.1964 and A. J. Hesse of the South African Museum (unpublished notes) recorded its prey found in *Watsonia* stems at an unnamed locality as Otitidae.

It seems that the "watsonia wasp" described by Skaife (1953: 338) is referrable to *D. bipunctatus simillimus* (Smith) and that the name, *Dasyproctus capensis* Skaife, given it in the above publication may be considered a hitherto overlooked and therefore new synonym of the former. In the new (1979) edition of Skaife's book the revisers have come to the same conclusion concerning the identity of the wasp in question and have substituted the name *Dasyproctus bipunctatus* for *Dasyproctus capensis*.

D. bipunctatus lichtenburgensis at Tanga on the East African coast was found to provision its cells in stems (unspecified) almost entirely with Otitidae (= Ortalidae) and to be subject to parasitization by a species of Mutillidae (Carpenter, 1942: 48).

In contrast with the above considered species with respect to the stems utilized for nesting are *D. barkeri*, *D. kibonotensis* and *D. stevensoni* all of which utilize dicotyledonous plants.

D. barkeri, described from Durban, Umgeni and Malvern in Natal, was recorded by Arnold (1927: 127) as "nesting in dry stems of the Kaffir-boom" (*Erythrina* sp.) (Leguminosae).

D. kibonotensis, studied as was *D. bipunctatus* at Kampala (Uganda), was found by Bowden (1964: 425–437) to be restricted to the stems of *Rubus sp.* (Rosaceae) for the excavation of its nests. The prey encompassed five families, namely Lonchaeidae, Muscidae, Platystomidae, Tachinidae and Trypetidae. Most prey were *Trirhithrum coffeae* Bezzi (Trypetidae), a dominant of the dipterous fauna of robusta coffee. On the basis of the prey taken Bowden theorized that this species forages in understory shrubs. Recorded parasites were Miltogramminae.

D. stevensoni in West Cameroon was found nesting in a stem of *Conyza bonariensis* (Compositae) in which the cells were provisioned with Milichiidae (Michener, 1971: 407).

As far as can be established from a consideration of so relatively few species, the nesting of *Dasyproctus* appears to present great uniformity in its basic features and the nesting of *D. westermanni* at Hilton here described appears, with the possible exception of pupa orientation to be dealt with below, to be very similar to the general pattern.

All the species nest up off the ground in galleries which they themselves excavate in the pith of usually live green plant stems. The serially arranged cells are separated by pith partitions and are provisioned with numerous small adult Diptera.

In *D. bipunctatus*, *D. kibonotensis* and *D. westermanni* the nest entrance is on the side of the stem and the nest galleries proceed in both directions through the stem, the gallery directed towards the stem apex (that is the ascending gallery) being completed first in all three species. Details of the nest plans of the two Oriental species and of *D. barkeri* are not available. With respect to *D. stevensoni* it is stated that the only nest examined was damaged in its collection but that apparently the entrance was at the broken end of the stem, rather than in the side of the stem. Confirmation of this apparently unusual nest form is required.

It is in the orientation, within the galleries, of the cocoons and of the pupae within them that *D. westermanni* differs from the other two species for which the orientation has been recorded. Thus Bowden (1964: 429 and 430) recorded both *D. bipunctatus* and *D. kibonotensis* larvae as pupating with their heads towards the entrance hole of the nest. In *D. westermanni*, as already described, all pupae are orientated with their heads away from the ground and towards the apex of the flower stalk, so that only those larvae in the descending gallery have their heads towards the nest entrance.

Using the trends shown by the reviewed species some speculation is possible concerning the identity of the builders of the old *Dasyproctus* nests found at Hilton in the inflorescence stems of *Gasteria* spp. (Liliaceae) and in the stems of *Berkheya decurrens* (Compositae). All the nests concerned had side entrances and both ascending and descending galleries. In the case of the nests in *Gasteria* it is not impossible that these were the work of *D. westermanni* but the fact that these plants were in a vegetation type different from that in which occurred the *Urginea* frequently utilized by *D. westermanni* may indicate the involvement of a different species. The nature of the inflorescence stalk utilized may indicate that *D. bipunctatus* might have been the species concerned. In the case of the nests in *Berkheya decurrens* it is probably correct to consider that they were the work of neither *D. westermanni* nor *D. bipunctatus* as all records indicate that these two species are restricted to monocotyledonous inflorescence stalks and that no species nests in both monocotyledonous and dicotyledonous plants. The nests in *Berkheya* are thus probably those of one of the other three *Dasyproctus* species recorded from Hilton, namely *D. dubiosus*, *D. immitis* and *D. ruficaudis*.

It is clearly of survival value to all species of *Dasyproctus* if the herbaceous plant stems in which they make their nests are protected in some manner or other from being eaten by large herbivores. With respect to those plants found to be utilized by *Dasyproctus* at Hilton it can be shown that all are so protected at least from the herbivores now common there, namely cattle, sheep and goats. Thus *Urginea altissima*, which grows freely exposed in the dwarf karroo scrub and which is very conspicuous when flowering on account of the long inflorescence stalks, is avoided by the above animals. This is undoubtedly due to the plant's toxicity to stock resulting from the presence in all parts of the plant of a glucoside having a digitalis action (see Watt & Breyer-Brandwijk, 1962: 717–718). It has furthermore been observed by the author that *Urginea altissima* is also left untouched under the more natural conditions of the Addo National Elephant Park where the herbivores in the portion of the park examined are buffalo, eland, hartebeest and a variety of smaller buck.

The *Gasteria* spp. at Hilton appear to be innocuous to herbivores, no indication to the contrary being found in Watt & Breyer-Brandwijk. However, these plants are found at Hilton only in the shelter of thorny shrubs such as *Acacia karroo* where they are thus physically protected from stock. *Berkheya decurrens* on the other hand grows in the open, often on disturbed ground, but is well protected from herbivores by the spinose projections of the leaves and involucral bracts.

Stems utilized elsewhere by *Dasyproctus* species may at least in some instances also be shown to be immune from destruction by herbivores. Thus the trailing stems of *Rubus* sp. (used by *D. kibonotensis*) are undoubtedly protected by the sharp prickles with which they are armed. With respect to *Watsonia* spp. (used by *D. bipunctatus*) it has been observed near Grahamstown that buck readily eat the actual flowers but not the inflorescence stalks (Jacot-Guillarmod, *pers. com.*).

It is apparent therefore that there is no consistency in the nature of the protection offered by the plants in which *Dasyproctus* nests as it may be due to their physiological or morphological nature or to their protected habitat.

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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

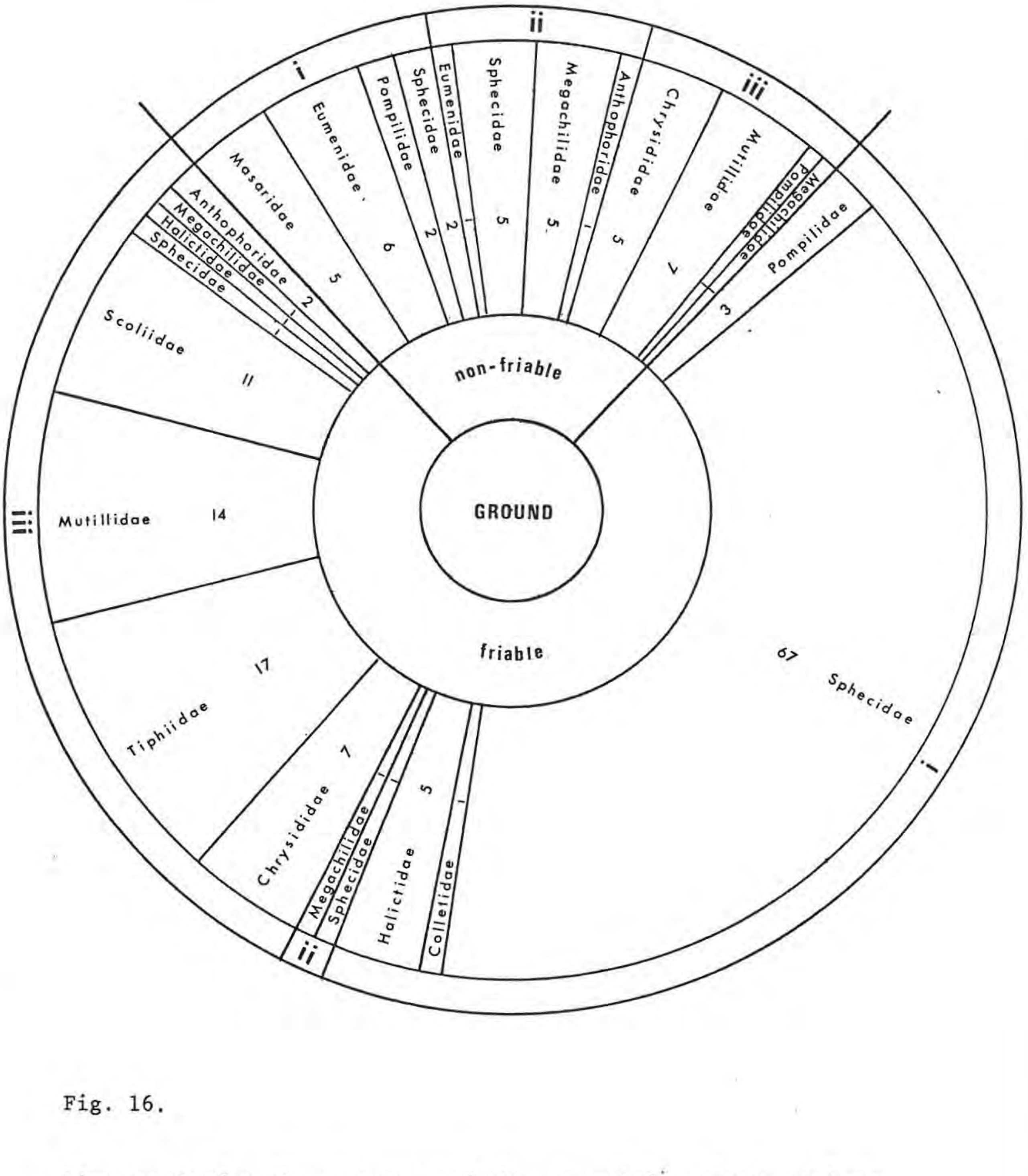


Fig. 16.

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 <u>not</u> modified by the nester.

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 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 practiced 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 1-1,5m 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 600mm, 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 effected 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 puddle in the vicinity of the chosen nesting site, is carried to the

Fig. 17.

Nest entrance of Cerceris oraniensis showing excavated soil in the form of "sand sausages". (x 1) 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 Jugurtia 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 & 19).

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 mentum (Figs 22 & 23 and Arnold, 1934: Figs 1,la). 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.

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 mandibles it follows that they may be considered soil carriers and it is not surprising that the nests excavated are without exception vertical or

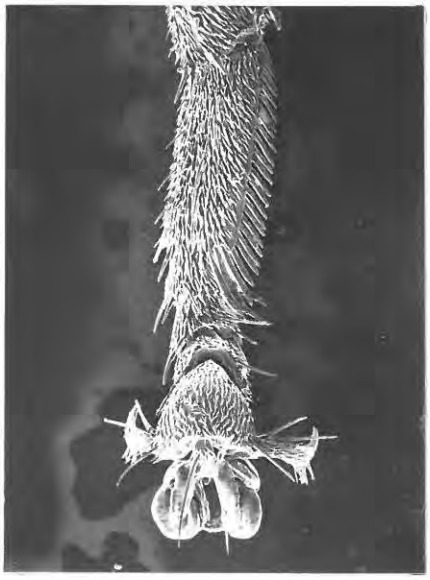


Fig. 18.

Left fore-tarsus of Bembecinus cinguliger showing dense row of short spines. (x 32)

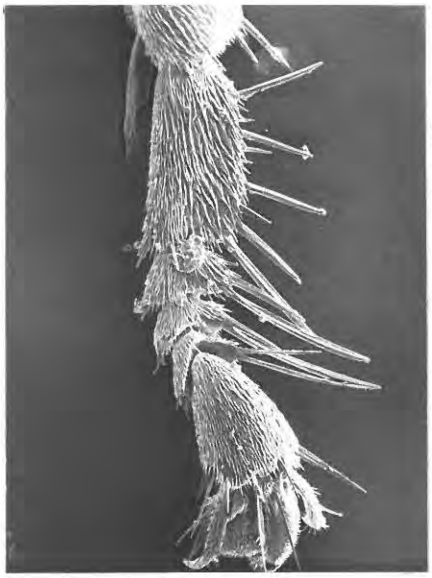


Fig. 19.

Left fore-tarsus of Bembecinus haemorrhoidalis showing long spines forming "sandrake" (x 32)

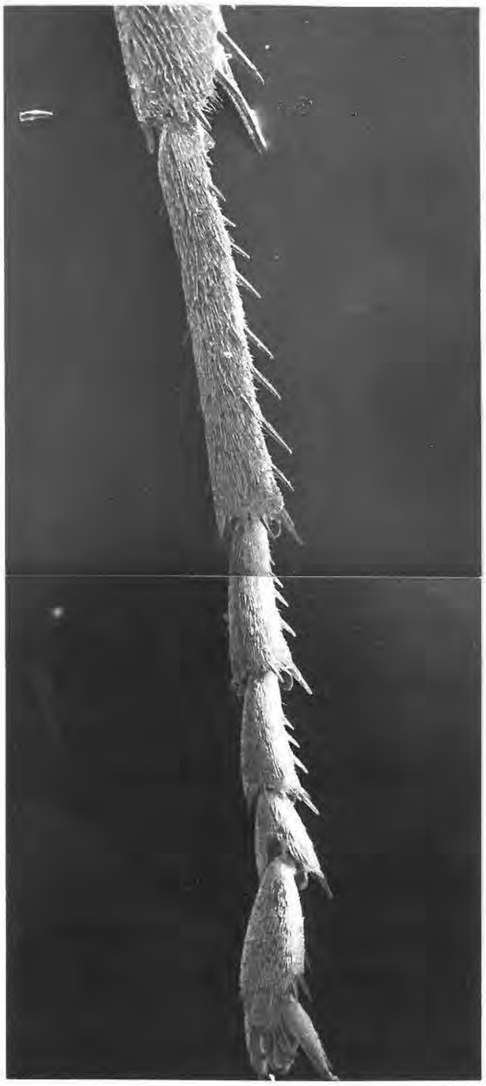


Fig. 20.

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

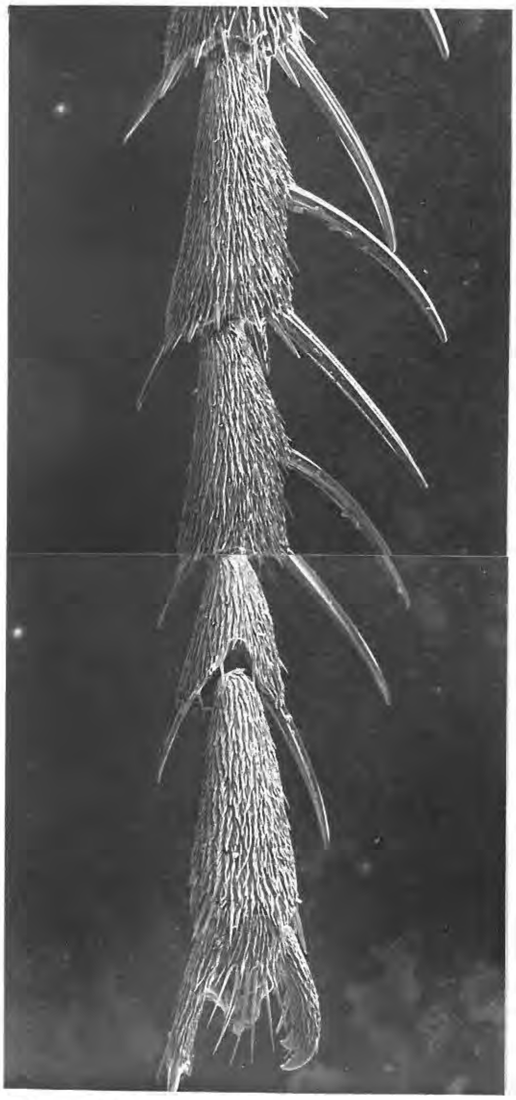


Fig. 21.

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

Fig. 22.

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

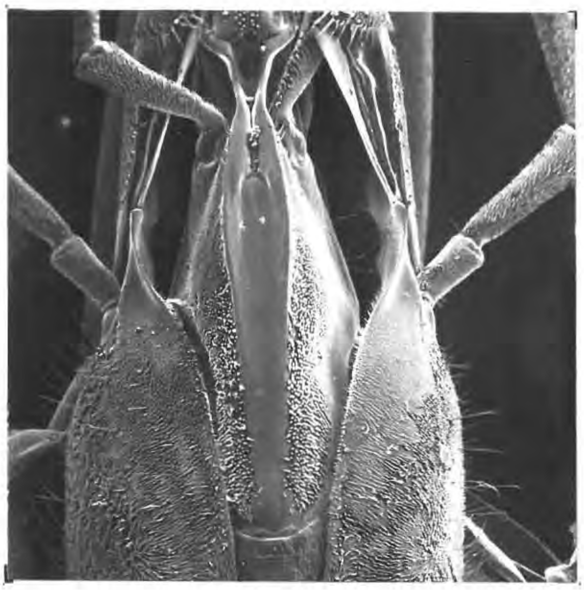


Fig. 23.

Underside of head of Batozonellus fuliginosus showing absence of forwardly directed bristles. (x 24) 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 sand-raking 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 pellet-carrying 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: 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 clepto-parasite.

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 preadaptive 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 multicelled 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' number of 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 preadaptive 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 labouriously over the ground. Frequently the wasp has difficulty in overcoming the obstacles on the way to the nest. By contrast, 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						
<u>Batozonellus fuliginosus</u>	2	1	1	2,25-7,61	4,93	4,93
<u>Tachypompilus ignitus</u>	16	1	1	1,00-8,52	4,2	4,2
SPHECIDAE						
<u>Chalybion tibiale</u>	3	15-21	17,4	4,65-6,52	5,87	0,37
<u>Pison montanum</u>	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 specialised 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 multicelled 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 pre-requisite 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 sand-rakes 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, notable Smicromyrme hecuba, are commonly found associated with all four species - the lack of a temporary closure during the working day of B. cingulige 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 by 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 bombyliid, 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 nest 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 Megachile 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.

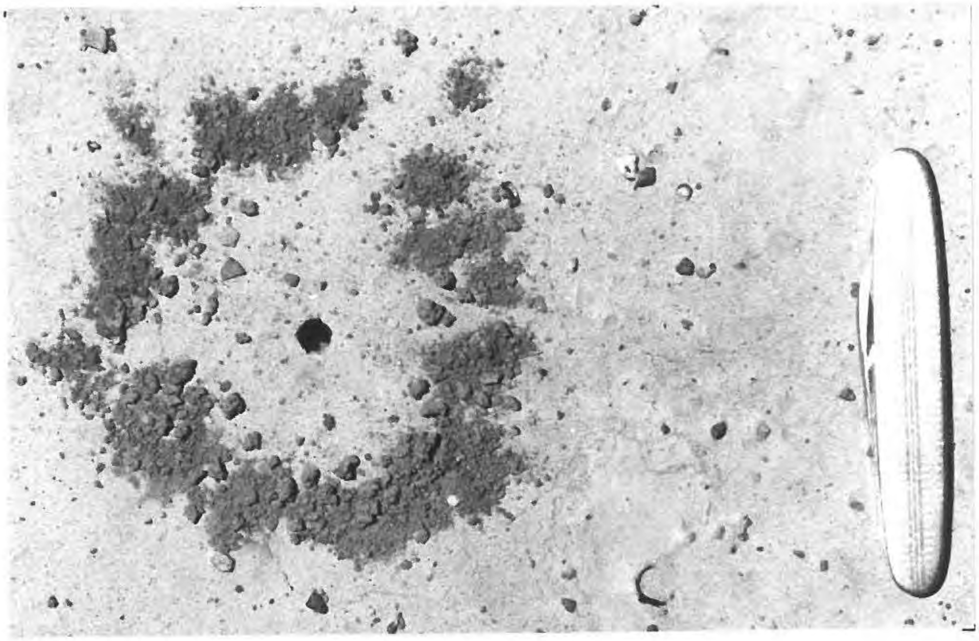
In common with other species of Ampulex, nesting would be commenced with hunting which would be followed by the introduction of the single prey into an unmodified pre-existing cavity which would then be closed with detritus. If the above interpretation of the nesting of A. mutilloides is correct, this 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 *Tachyshex* 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 initiated 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.



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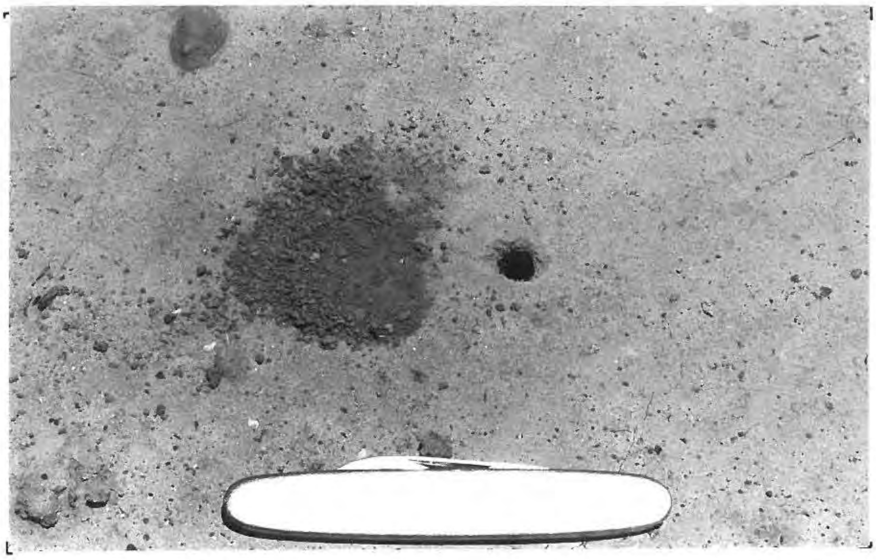

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Figs 24 and 25.

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. (x 0,7)

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-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 (Sphecodes sp.), Megachilidae (Coelioxys bruneipes and C. lativentroides) and Anthophoridae (Epeolus amabilis and Thyreus sp.).

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 clepto-

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 " " "
Sphecodes sp.	Halictidae	*Nomia* sp.	Halictidae
Coelioxys bruneipes	Megachilidae	*Megachile semiflava*	Megachilidae
Coelioxys lativentroides	Megachilidae	*Megachile* sp. OR *Creightoniella* sp.	Megachilidae "
Epeolus amabilis	Anthophoridae	*Colletes* sp.	Colletidae
Thyreus sp.	Anthophoridae	?	?

parasitic 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.

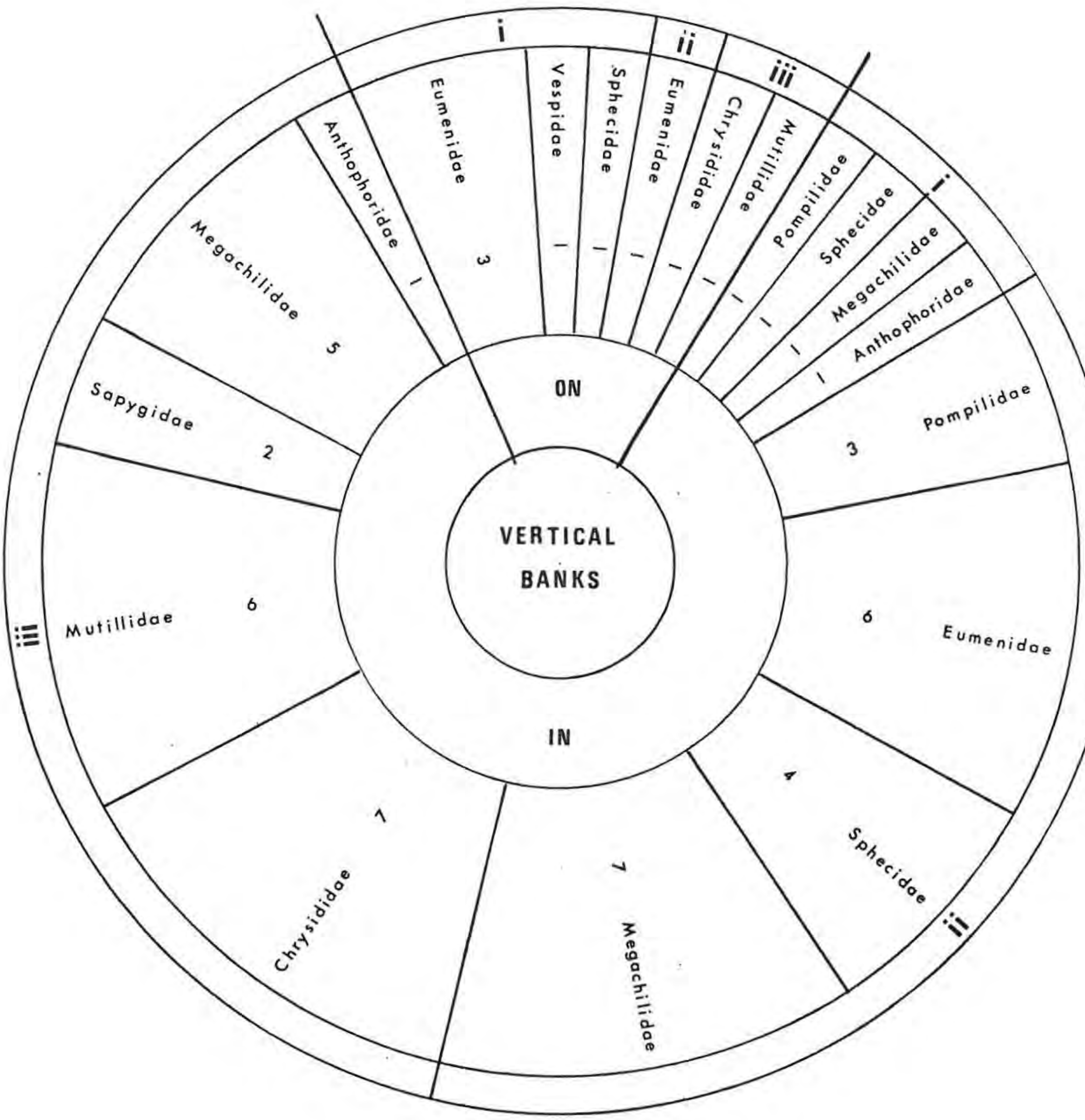

Fig. 26.

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 <u>not</u> 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-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 equalled 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 colonised 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. guerinii 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 simialrly 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).

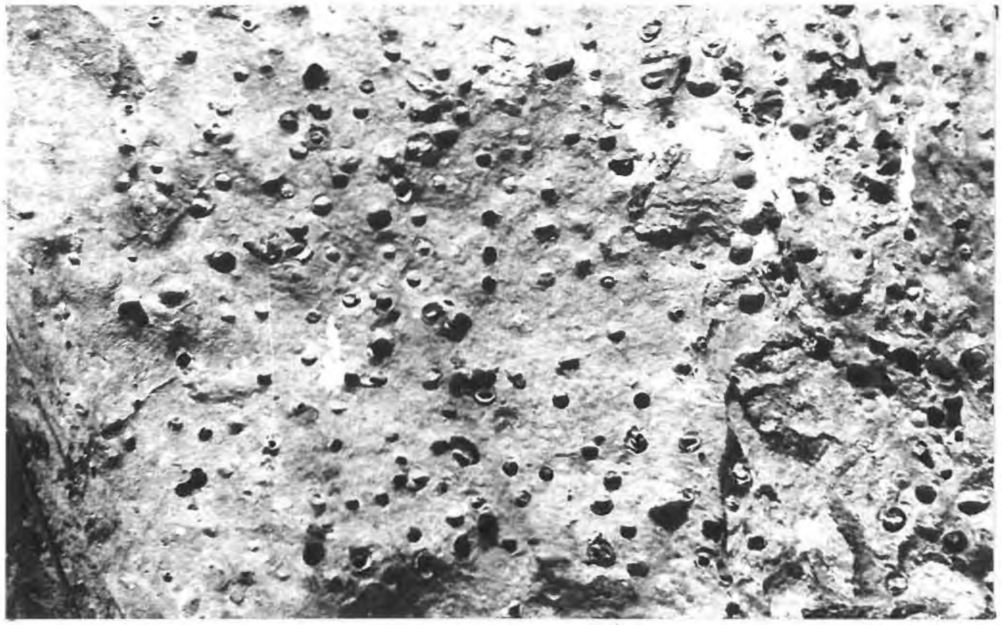

Fig. 27.

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

Fig. 28.

Section through "sandstone" bank showing pre-existing cavity modified for nesting and furnished with a downturned mud turret by Tricarinodynerus guerinii. (x 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).

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	-	-

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 <u>Ceratina</u> listed, approximately another ten species belonging to the genus are known to occur at Hilton.

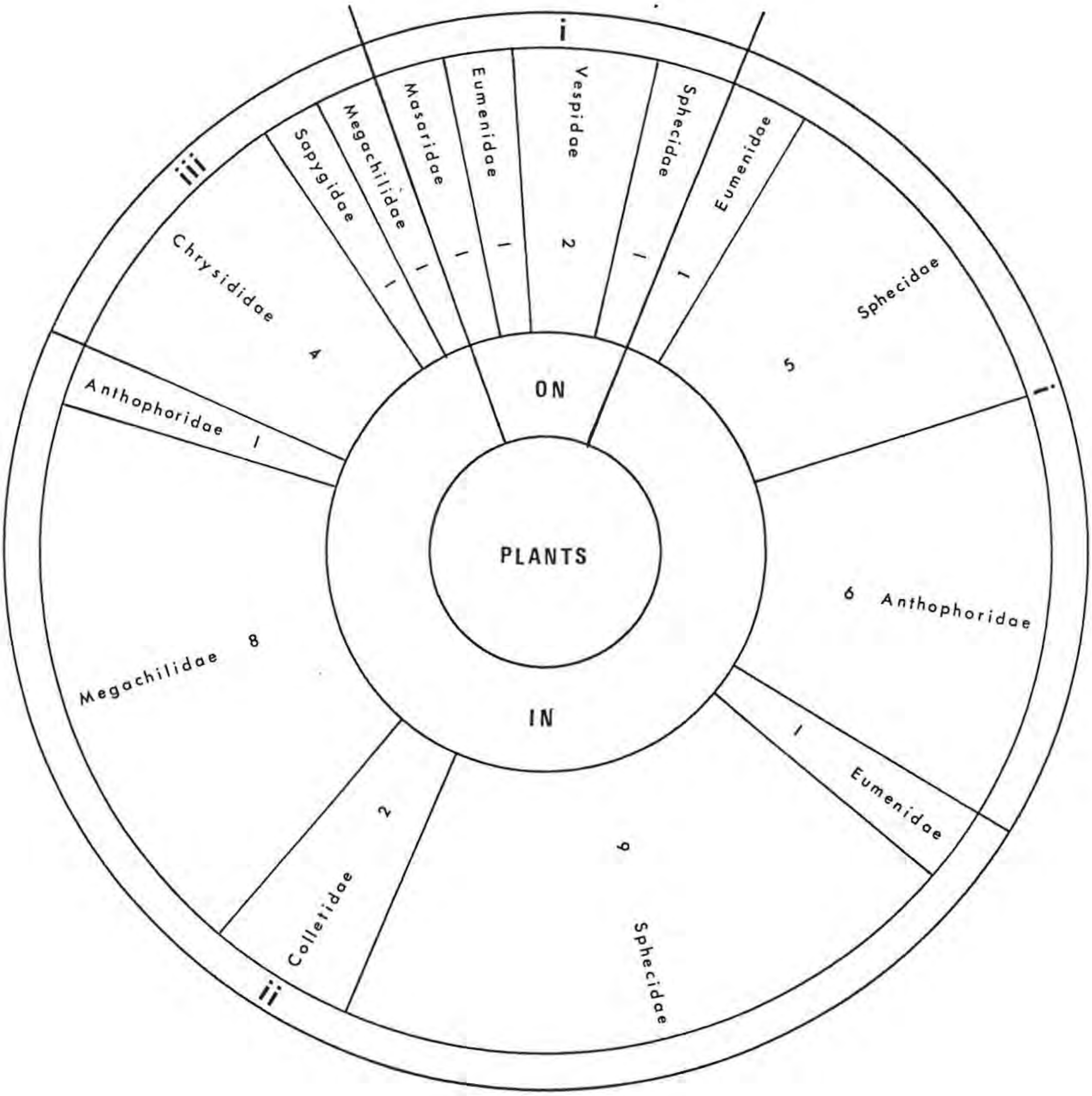

Fig. 29.

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 next constructed entirely by the nester.

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

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

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).

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 situations (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).

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 provisioned, 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

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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. (x 0,65)

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

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-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. túrneri. 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 evolved 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. This "buzzing" is the same as that already commented upon in connection with other Sphecidae, the ground-nesting Podalonia 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 additional 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 a 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-existance 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 8mm long M. gratiosa was found to be restricted to small bore (6,4mm) trap-nests whereas the 13mm long M. spinarum was found to use mostly larger bore (9,5 and 12,7mm) 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 clepto-parasites 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 of 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 appear 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 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.

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

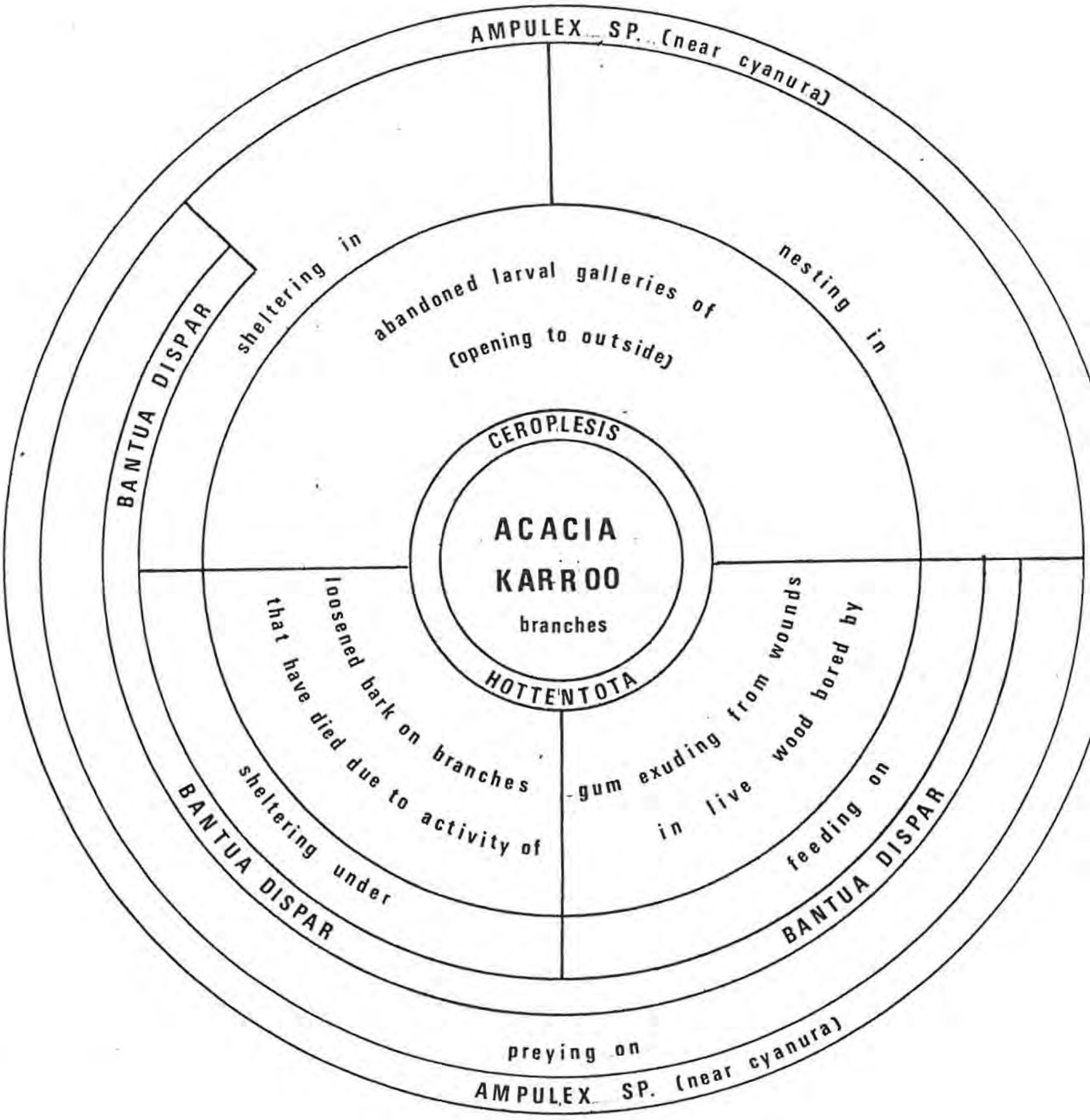

Fig. 34.

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).

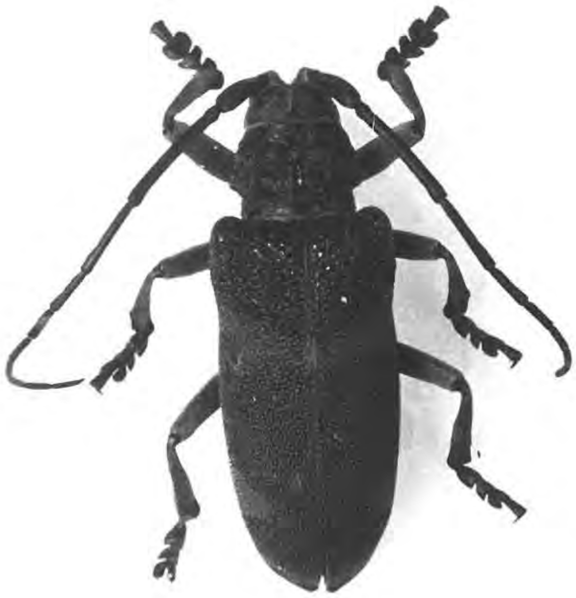

Fig. 35.

Ceroplesis hottentota, the larvae of which bore galleries in finger-thick branches of Acacia karroo. (x3)

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. (x3) 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 instals 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 coleopterus. 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

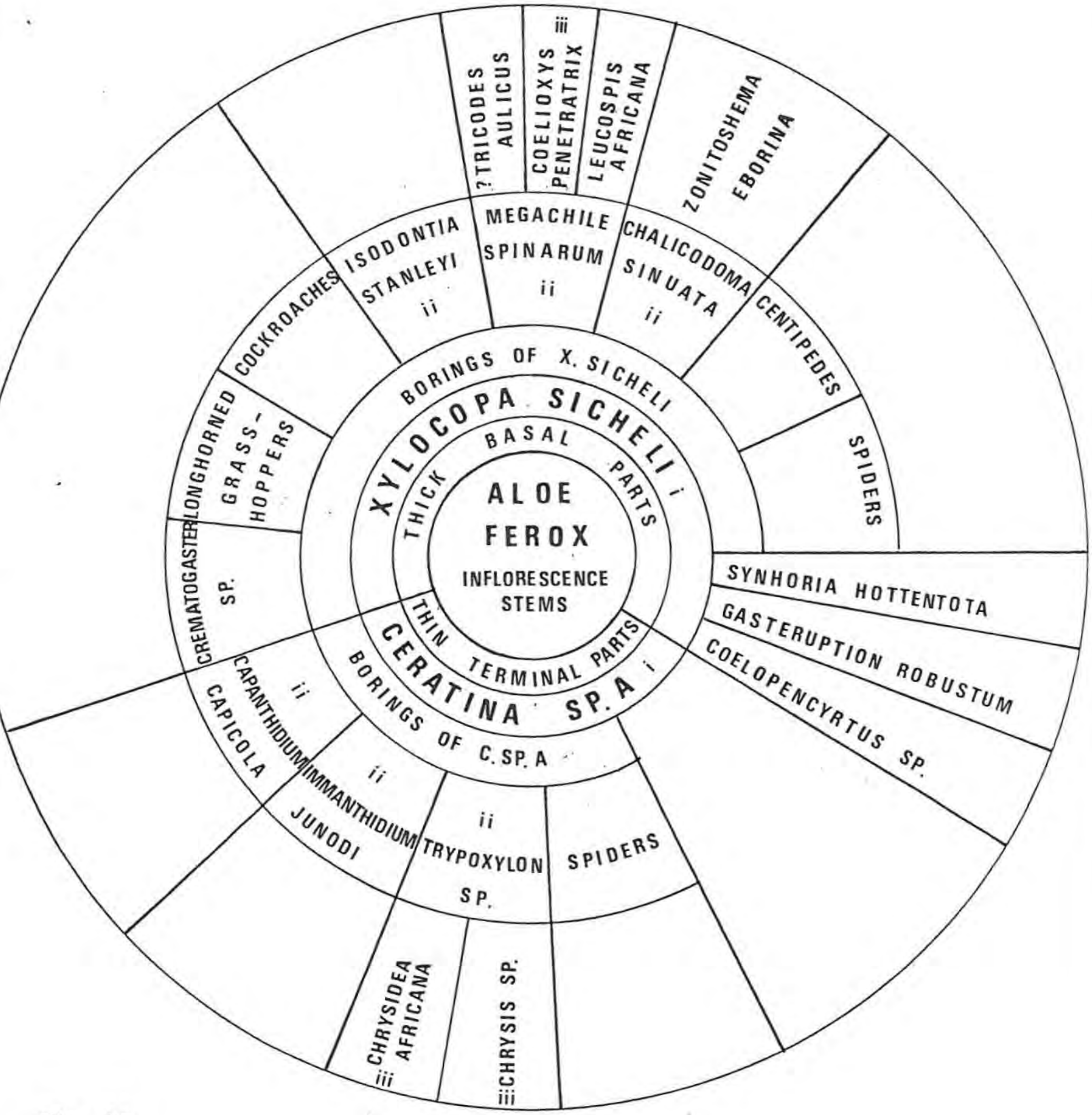

Fig. 37.

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.

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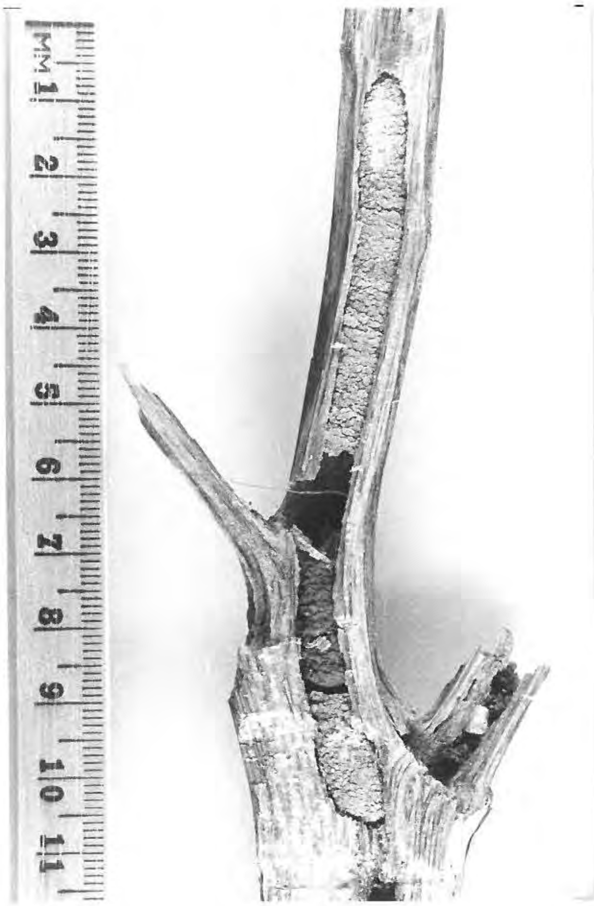

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Figs 38, 39 and 40.

Dry inflorescence stems of *Aloe ferox* cut longitudinally to show old galleries bored by *Xylocopa sicheli* and containing nests of

Isodontia stanleyi (Fig.38)
Megachile spinarum (Fig.39)
Chalicodoma sinuata (Fig.40)

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 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.

The study of the 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.

SUMMARY

A survey has been made 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.

The annotated list contains previously unrecorded information on the ethology of at least 85 species concerning which there was in most cases no previously recorded information at all. Expanded accounts of 34 species are included in the form of published papers. Eight species belong to the Pompilidae, a family represented in the Afro-tropical Region by 500-600 described species, on the biology of which little or nothing was previously published. Of these, two species of Dichragenia, D. pulchricoma and D. neavei 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 and B. oxydorcus 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. The two species of Parachilus are shown to sub-divide the cell into an egg compartment and one, in P. insignis, several, in P. capensis, pantry compartments in which way they differ in behaviour from the 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 is a mass provisioner and not as was previously believed a progressive provisioner. The accounts of the nesting of the two Parachilus species (Eumenidae), Jugurtia confusa (Masaridae) and Kohliella alaris (Sphecidae) are the first for the three genera to which these species belong. That of Holotachysphex turneri (Sphecidae) greatly augments what little was previously known of the ethology of its genus. Of particular interest with respect to Dasyproctus westermanni (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 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.

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.

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Appendix 1. Lists of plant species which characterize the vegetation communities of Hilton.

Pentzia incana Scrub

Principal species is:-

Pentzia incana (Th.) O.Ktze (Compositae) Ankerkarroo

Species of general occurrence is :-

Atriplex semibaccata R.Br. (Chenopodiaceae) Creeping Saltbush

Species of less general occurrence include:-

Lycium sp. (Solanaceae) Kareedoring
Aster filifolius Vent. (Compositae) Draaibossie
Helichrysum dregeanum Sond.& Harv. (Compositae) Bergankerkaroo
Chrysocoma tenuifolia Berg. (Compositae) Bitterkaroo
Pteronia incana DC. (Compositae) Asbossie
Melolobium candicans E. & Z. (Leguminosae) Heuningbossie
Hermannia spp. (Sterculiaceae) Pleisterbossie
Polygala leptophylla Burch. (Polygalaceae) Skarpertjie
Hibiscus sp. (Malvaceae) Hibiscus
Crassula sp. (Crassulaceae) Skilpadkos height < 2"
Pelargonium sp. (Geraniaceae)
Indigofera sp. (Leguminosae)

Widely scattered solitary species include:-

Urginea altissima Bak. (Liliaceae) Maerman
Aloe ferox Mill. (Liliaceae)
Asparagus sp. (Liliaceae)
Bulbine sp. (Liliaceae)
Albuca sp. (Liliaceae)
Cyanella lutea L.f.(Haemadoraceae) Five-fingers
Barleria pungens L.(Acanthaceae)

Grass species include:-

Themeda triandra Forsk. Rooigras
Cynodon dactylon Pers. Kweekgras

Pentzia incana -Chrysocoma tenuifolia Scrub.

Principal species are:-

Pentzia incana (Th.) O.Ktze (Compositae) Ankerkarroo
Chrysocoma tenuifolia Berg. (Compositae) Bitterkaroo

Species of general occurrence are:-

Drosanthemum floribundum (Haw.) Schwantes (Aizoaceae)
Drosanthemum parvifolium (Haw.) Schwantes (Aizoaceae)
Rushia spp. (Aizoaceae)
Atriplex semibaccata R.Br. (Chenopodiaceae) Creeping Saltbush
Helichrysum dregeanum Sond. & Harv. (Compositae) Bergankerkaroo

Species of less general occurrence include:-

Crassula sp. (Crassulaceae) Skilpadkos height <2"
Sutera microphylla (Benth.) Hein. (Scrophulariaceae)
Oxalis sp. (Oxalidaceae)
Emex australis Steinh. (Polygonaceae) Dubbeltjie
Hermania sp. (Sterculiaceae) Pleisterbossie

Widely scattered solitary species include:-

Bulbine sp. (Liliaceae)
Albuca sp. (Liliaceae)

Grass species include:-

Cynodon dactylon Pers.

Chrysocoma tenuifolia Scrub

Principal species is:-

Chrysocoma tenuifolia Berg. (Compositae) Bitterkaroo

Species of general occurrence are:-

Pentzia incana (Th.) O.Ktze (Compositae) Ankerkaroo
Drosanthemum sp. (Aizoaceae) 'Mesem'

Species of less general occurrence are:-

Lightfootia albens Speng. ex A.DC. (Campanulaceae) Witmuistepelkaroo
Helichrysum dregianum Sond. & Harv. (Compositae) Bergankerkaroo
Melolobium candicans (E.Mey.) E. & Z. (Leguminosae) Heuningbossie
Sutera campanulata (Benth.) O.Ktze (Scrophulariaceae)
Pharnaceum incanum L. (Aizoaceae)
Nemesia capensis (Th.) O.Ktze (Scrophulariaceae)
Selago corymbosa L. (Selaginaceae)

Widely scattered solitary or in solitary clumps are:-

Pituranthos aphylla (Ch. & Schl.) B. & Hf. (Umbelliferae) Wildeseldery
Eriocephalus africanus L. (Compositae) Kapokbossie
Elytropappus rhinocerotis (L.f.) Less. (Compositae) Renosterbos

Additional species occurring in sand pit include:-

Haplocarpha lyrata Harv. (Compositae) Bietou
Gazania oxyloba DC. (Compositae) Gousblom
Lasiospermum bipinnatum (Th.) Druce (Compositae)
Senecio sp. (Compositae)
Conyza bonariensis (L.) Cronquist (Compositae)
Phyllopodium cuneifolium Benth. (Scrophulariaceae)
Acrotoma inflata Benth. (Labiatae)
Hebensteitia integrifolia L. (Selaginaceae) Katstert
Walafrida geniculata (L.f.) Rolfe (Selaginaceae) Waterfinder Bush
Emex australis Stienh.(Polygonaceae) Dubbeltjie

Thorn Scrub and Riverine Bush

Shrub and tree species (Shrub 1-5m, trees >5m)

Principal species is:-

Acacia karroo Hayne (Leguminosae) Sweet Thorn   Shrub-small trees

Species of general occurrence are:-

Maytenus heterophylla (Ecklon & Zeyher) N.K.B.Robson
(=*Gymnosporia buxifolia* (L.)(Szyszyl))
(Celastraceae) Pendoring   Shrub
Maytenus linearis (L.f.) W. Marais
(Celastraceae) Pendoring   Shrub
Lycium spp.   (Solanaceae) Kareedoring   Shrub
Rhus sp.   (Anacardiaceae)   Shrub
Diospyros sp.   (Ebenaceae)   Shrub)

Species of less general occurrence include:-

Ehretia rigida (Th.) Druce
(Boraginaceae) Cape Lilac   Shrub
Maytenus polycantha (Sond.) W. Marais
(=*Gymnosporia polycantha* (Sond.) Szyszyl))
(Celastraceae) Pendoring   Shrub
Rhus lancea L.f.   (Anacardiaceae) Willow Rhus   Tree
Cadaba aphylla Willd.
(= *Cadaba juncea* Hook.f.)
(Capparidaceae)   Shrub

Herb and Dwarf Scrub species (<1m) include:-

Pentzia globosa Less. (Compositae) (In sandy areas only.)
Cotula heterocarpa DC. (Compositae) Stinkkruid.
Berkheya decurrens (Th.) Willd.
(Compositae) Disseldoring
Lasiospermum bipinnatum (Th.) Druce (Compositae)
Haplocarpha lyrata Harv.   (Compositae)
Senecio spp. incl. *Senecio leptophyllus* DC. (Compositae)
Oxalis sp. (pink fls.)(Oxalidaceae) Sorrel, Suring
Drosanthemum floribundum (Haw.) Schwantes
(Mesembryanthemaceae) "Mesem"
Asparagus striata (L.f.) Thunb. (Liliaceae)

Asparagus sp. (Liliaceae) Cat's Tail
Gasteria spp. (Liliaceae)
Haworthia sp. (Liliaceae)
Apicra sp. (Liliaceae)
Anagallis *arvensis* L. (Primulaceae) Pimpernel
Anchusa *capensis* Thunb. (Boraginaceae)

Notable parasitic species is:-

Loranthus *elegans* Cham. & Schl.
(Loranthaceae) Matches. On *Acacia* *karroo* Hayne

Grass species include:-

Danthonia *curva* Nees
Digitaria *macroglossa* Henr.
Diplachne *fusca* (L.) Beauv.
Eragrostis sp. (prob. *E.* *curvula* (Schräd) Nees)
Melica *racemosa* Thunb.
Sporobolus sp. (prob. *S.* *fimbriatus* Nees)

Appendix 2. Additional bound-in published papers referred to in the text.

a) Contribution to the knowledge of the South African species of the genus Ceramius Latreille (Hymenoptera:Masaridae).

b) Further contribution to the knowledge of the South African species of the genus Ceramius Latreille (Hymenoptera: Masaridae).

c) Third contribution to the knowledge of the South African species of the genus Ceramius Latreille (Hymenoptera: Masaridae).

F. W. GESS

CONTRIBUTION TO THE KNOWLEDGE OF THE SOUTH AFRICAN SPECIES OF THE GENUS *CERAMIUS* LATREILLE (HYMENOPTERA: MASARIDAE)

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By

F. W. Gess

South African Museum, Cape Town

(With 1 map)

Contents

Introduction

While arranging the Masaridae in the collection of the South African Museum according to the recent revision of the family by Richards (1962), it was found that this material, which was unfortunately not seen by Richards, supplemented his account in several instances, especially in the genus *Ceramius* Latreille.

In the present paper, dealing with the above genus, the hitherto unknown ♀ of *clypeatus* Richards and ♂ of *metanotalis* Richards are described; the ♂ assigned by Richards to *peringueyi* Brauns is removed from that species and together with a matching ♀ is described as a new species, *richardsi*, and lastly, *rex* de Saussure is resurrected. The locality records of all the specimens in the collection are given in the hope that these may aid in presenting a more complete picture of the distribution of the various South African species. Finally the distribution of the genus as a whole is discussed in the light of the biology of these wasps.

The sequence of species followed is nearly the same as that adopted by Richards, and this paper closely follows the presentation set by the latter in his revision. South African Museum is here abbreviated to S.A.M.

Descriptions of Species and Distribution Records

Ceramius cerceriformis de Saussure

Ceramius cerceriformis de Saussure, 1853: xxi, ♂; Richards, 1962: 97, ♂, ♀.
Ceramius (*Ceramioides*) *cerceriformis* de Saussure, 1854: pl. 4, fig. 1, ♂; 1855: 72, ♂.
Cerceris vespiformis de Saussure, 1855: 79, ♀.

Ann. S. Afr. Mus. **48** (11), 1965: 219–231, 1 map.

No specimens were found in the South African Museum collection that could be assigned to this species.

Ceramius schulthessi Brauns

Ceramius schulthessi Brauns, 1902: 182, ♀; Brauns, 1913: 196, pl. 2, fig. 6, ♂, ♀; Richards, 1962: 99.

Specimens examined: Cape Province: Willowmore, no date, 3♀♀ (one marked as co-type), 1. xii. 1904, ♀, xi. 1917, 2 ♀♀ (Dr. Brauns); Augusfontein, Calvinia, ix. 1947, 3 ♀♀ (S.A.M. Staff); Oudtshoorn, Zebra, x. 1951, 3 ♀♀ (S.A.M. Staff); Touws River—Hondewater (18 miles E. of Touws River), xii. 1962, ♀ (S.A.M. Staff); Bloutoring Station (30 miles E. of Touws River), xii. 1962, 4 ♀♀ (S.A.M. Staff).

Namaqualand: Between Kamieskroon and Springbok, x. 1939, 4 ♂♂ 4 ♀♀ (S.A.M. Staff); Wallekraal, x. 1950, ♀ (S.A.M. Staff).

Ceramius peringueyi Brauns

Ceramius peringueyi Brauns, 1913: 194, ♀; Richards, 1962: 100 [♀ only].
[*non*] *Ceramius peringueyi* Brauns, Richards, 1962: 100, ♂ [= *richardsi* sp. n.].

Specimens examined: Cape Province: Stellenbosch, x. 1888, holotype ♀ (L. Peringuey) (Transvaal Museum); Het Kruis, x. 1947, 3 ♀♀ (S.A.M. Staff); Paleisheuwel, xi. 1948, ♀ (S.A.M. Staff).

Ceramius clypeatus Richards

Ceramius clypeatus Richards, 1962: 99, ♂.

♀. Black; raised disk of clypeus to a variable degree, inner orbits at deepest portions of ocular sinus, spot of variable size on tempora, usually a small spot on prepectus, variably sized spot at apex of scutellum, rarely a minute spot on propodeal spine, occasionally a short basal streak along outer side of fore tibiae and rarely indicated basal spots on outer side of mid and hind tibiae, spots at sides of gastral tergites 1–4 and usually also on 5, sometimes produced inwards on 2–5 either forming narrow continuous or interrupted bands, *creamy-white to yellowish.*

Underside of antennal joints 4–12 though sometimes fewer, legs except coxae, trochanters and base of femora, *orange.* Wings light fuscous, veins brown. Length 14–16 mm., length of fore wing 10·5–11·5 mm., hamuli 18–24.

Altogether very similar indeed to the male, the peculiarly modified clypeus, for example, except in its greater width in the female, being virtually identical in the two sexes. The chief secondary sexual structural differences are the following: eyes somewhat smaller, further apart, interocular distance at level of sockets twice length of scape (without radicle); antennal scape less curved and less robust, segment 3 shorter, only half as long as scape (without radicle), 4–10 progressively wider, 10 about 1½ times as wide as long, 11–12 a little narrower; fore trochanter simple.

From the specimens examined it appears that in both sexes the longer spur of the hind tibia is not originally simple but may become so by the loss or wearing away of the fine spines situated near the tip of the spur. While the trifid condition is common, there is a specimen with a 4-spined spur and others with all graduations to the simple condition.

Specimens examined: Cape Province: Clanwilliam, Nardouw, ix. 1941, 11 ♂♂, 2 ♀♀ (S.A.M. Staff); Het Kruis, x. 1947, 7 ♂♂ (S.A.M. Staff); Citrusdal Dist., xi. 1948, 5 ♀♀ (S.A.M. Staff); 4 miles S. of Clanwilliam, ix. 1961, ♀ (S.A.M. Staff).

Ceramius richardsi sp. n.

Ceramius peringueyi (*non* Brauns) Richards, 1962: 100 [*partim*, ♂ only].

The ♂ of this new species, which has been adequately described by Richards, was unfortunately assigned by him to *peringueyi* Brauns to which species it most certainly does not belong. This misidentification was made obvious by the discovery in the collection of the South African Museum of a hitherto undescribed ♀ which closely matches Richards' ♂ in all important characters such as the unusual form of the clypeus. That this latter character is of value in associating the sexes is demonstrated by the discovery, also in the South African Museum collection, of the hitherto undescribed ♀ of *clypeatus* Richards, a closely related species, the ♂ of which was used by Richards as a comparison in describing what he thought was the ♂ of *peringueyi* Brauns. In *clypeatus* Richards the form of the clypeus is common to both sexes. I have pleasure in naming the ♂ under consideration and the here described matching ♀ after the author, Professor Richards. The true ♂ of *peringueyi* Brauns is thus still unknown.

♀. Black; spot on mandibles near base, large discal spot on clypeus, inner orbits to top of ocular sinus, streak at top of tempora, two widely separated streaks on hind margin of pronotum, dot at apex of scutellum, moderately large spot on prepectus, small anterior spots at base of fore tibiae and end of mid femora, narrow lateral spots on gastral tergites 1–5 (tergite 6 hidden) produced inwards and forming narrow incomplete bands on tergites 2–3 and centrally widened ones on 4–5, *creamy-white.*

Antennal segments 4–12 beneath, portions of mandibles, anterior vertical portion of clypeus beneath disk, whole of legs except coxae of all legs and trochanters and bases of femora on mid and hind legs, *reddish.*

Wings fuscous, venation dark brown.

Length 15 mm., length of fore wing 10 mm., hamuli 21.

Head, thorax and gaster with long, rather dense, whitish hairs. Mandibles strongly striate distally, ending in two large blunt teeth with a smaller more dorsal one. Clypeus elongate, strongly raised, anteriorly falling at right angles towards ventral margin; length of vertical part $\frac{3}{5}$ length of disk; from just below point of inflection two small curved teeth project upwards; ventral margin produced, somewhat lamellate, truncate and slightly emarginate; disk narrower at apex than at base; anterior-lateral margins raised and slightly lamellate. Antennal sockets separated by 3½ times their diameter; interocular distance at level of sockets twice the length of scape (without radicle); total length of scape 3½ times greatest width (at apex); segment 2 very short, 3 slightly shorter than 4+5+6, 4–12 all of about same length, 4–10 becoming gradually and progressively wider, 11 slightly narrower than 10, 12 narrower still, rounded at apex. Disk of clypeus and small, roughly triangular area above it and between antennal sockets almost smooth; frons punctured; posterior ocelli a little in front of hind margin of eyes; distance between eye and posterior ocellus: distance between posterior ocelli = 10 : 7; occiput behind eye somewhat wider than interocellar distance; occipital keel present.

Thorax with fairly coarse, separated punctures, the interstices shining, about as wide or wider than the punctures. Mesoscutum shining; prescutal furrows deep over their entire length, especially so behind. Raised disk of scutellum with rounded edges and without a central keel.

Metanotum with a central prominence, lateral depressions fairly deep but open. Tegula smooth and shining, only the base punctured. Propodeum with fairly long blunt spines; posterior surface almost flat; spiracle with anterior margin strongly produced backwards. Fore tibial spur regularly curved, tip somewhat recurved. Mid and hind tibiae with two spurs, longer spur of hind tibia simple. Inner keel of hind coxa present on proximal half only. Claws simple. Gaster shining; tergite 1 constricted posteriorly, more finely punctured than thorax; tergites 2–6 becoming progressively finer punctured, 2 somewhat contracted at base.

Specimens examined: Cape Province: Clanwilliam, ix. 1928 (Dr. Brauns), Holotype ♂ (Transvaal Museum, Pretoria); Paleisheuwel, xi. 1948 (S.A.M. Staff), Allotype ♀ (S.A.M.).

The female has ten mites present on the axillae and lateral depressions of the metanotum.

Ceramius nigripennis de Saussure

Ceramius (*Paraceramius*) *nigripennis* de Saussure, 1854: pl. 3, fig. 4, ♀; 1855: 69.
Ceramius nigripennis de Saussure, Richards, 1962: 100.
Ceramius hessei Turner, 1935: 296, ♂, ♀.
[*non*] *Ceramuis nigripennis* of other authors.

Specimens examined: Namaqualand: Kamieskroon, ix. 1930, ♂ holotype, ♀ allotype of *C. hessei* Turner, 24 ♀♀ (S.A.M. Staff); between Kamieskroon and Springbok, x. 1939, ♂, ♀ (S.A.M. Staff); Bowesdorp, xi. 1931, ♂, ix. 1941, 2 ♂♂ (S.A.M. Staff); Outiep, Garies, ix. 1953, ♂ (J. du Toit).

Ceramius toriger von Schulthess

Ceramius toriger von Schulthess, 1935: 383, ♀; Richards, 1962: 101.

Specimens examined: Cape Province: Augusfontein, Calvinia, ix. 1947, 19 ♀♀ (S.A.M. Staff); Tankwa Karoo, Waterval, xi. 1952, 10 ♀♀ (S.A.M. Staff); 5 miles N. of Nieuwoudtville, ix. 1961, 2 ♀♀ (S.A.M. Staff).

A single female from Namaqualand: Knersvlakte, x. 1950 (S.A.M. Staff), differs from the description of this species and from the above listed specimens in that the light coloured markings are more extensive and are yellow, not ivory. Structurally there are no differences. The distribution of the yellow markings is given below.

Black; large spots on basal half of mandibles, clypeus (except for oblique black streaks arising from bottom of antennal sockets, infuscation between ends of these streaks and lateral margins, and ferruginous lateral and apical margins), a large pentagonal spot enclosing a black triangle on frons above clypeus, inner orbits to centre of ocular sinus, spots behind eyes, uninterrupted pronotal band extending onto sides, large spots on mesopleura, sides of mesonotum next to tegulae, a small median spot in posterior region of mesoscutum, posterior quarter of scutellum and centre of metathorax, streaks on axillae, whole of propodeum behind level of spiracles, broad apical bands widened laterally on tergites 1–5, tergite 6 except for depressed area, whole of sternite 2, wide apical bands on sternites 3 and 4, portions of femora and tibiae, *yellow*.

In addition, the antennae are much lighter in colour, the scape being largely yellow.

Ceramius braunsi Turner

Ceramius braunsi Turner, 1935: 294, ♂, ♀; Richards, 1962: 101.

Specimens examined: Cape Province: Olifants River, between Citrusdal and Clanwilliam, x–xi. 1931, ♂ holotype, ♀ allotype, 3 ♂♂, 32 ♀♀ (S.A.M. Staff); Pakhuis Pass, Clanwilliam, ix. 1942, ♀ (S.A.M. Staff); 4 miles S. of Clanwilliam, ix. 1961, 2 ♂♂, 2 ♀♀ (S.A.M. Staff).

Ceramius jacoti Richards

Ceramius jacoti Richards, 1962: 101, ♂, ♀.
Ceramius nigripennis (*non* de Saussure) Brauns, 1913: 201, pl. 2, fig. 3, ♂.

Specimens examined: Cape Province: Hex River, i. 1884, ♀; Oudtshoorn, Zebra, x. 1951, 17 ♀♀ (S.A.M. Staff); Ouberg Pass, S.E. of Touws River, xii. 1962, ♀ (S.A.M. Staff); Verkeerde Vlei, Touws River–Hottentots Kloof, xii. 1962, 11 ♀♀ (S.A.M. Staff); Constable, xii. 1962, ♀ (S.A.M. Staff); Touws River–Ouberg Pass, xii. 1962, ♀ (S.A.M. Staff); 8 miles N.E. of Touws River, xii. 1962, ♀ (S.A.M. Staff); Bloutoring Station, 30 miles E. of Touws River, xii. 1962, 98 ♀♀ (S.A.M. Staff).

Ceramius beyeri Brauns

Ceramius beyeri Brauns, 1903: 69, ♂, ♀; Richards, 1962: 102, figs. 105–9.

Specimens examined: Cape Province: Willowmore, no date, ♀ cotype, 2 ♀♀ (Dr. Brauns); Somerset East, 25–30. xi. 1930, ♂, ♀ (R.E. Turner); Nieuveld

Escarpment, Rietvlei, i. 1949, ♀ (S.A.M. Staff); Tankwa Karroo, Renoster River, xi. 1952, 116 ♀♀ (S.A.M. Staff); Constable, xii. 1962, 3 ♀♀ (S.A.M. Staff); Matroosberg Station, xii. 1962, ♀ (S.A.M. Staff); Touws River–Hondewater (18 miles E. of Touws River), xii. 1962, 2 ♀♀ (S.A.M. Staff); Bloutoring Station, 30 miles E. of Touws River, xii. 1962, 2 ♀♀ (S.A.M. Staff).

Ceramius damarinus Turner

Ceramius damarinus Turner, 1935: 293, ♂, ♀; Richards, 1962: 102.

Specimens examined: S.W. Africa: Ongandjera, iii. 1923, type ♂, 2 ♂♂ cotypes, ♂, type ♀ (S.A.M. Staff); Kamanyab, iii. 1925, 2 ♂♂ (S.A.M. Staff).

Ceramius lichtensteinii (Klug)

Gnatho lichtensteinii Klug, 1810: 36, 38, pl. 1, fig. 3, e and f.
Ceramius lichtensteinii (Klug), Klug, 1824: 225; de Saussure, 1855: 73, ♀; Brauns, 1913: 193; Bequaert, 1928: 145; Richards, 1962: 102.
Ceramius macrocephalus de Saussure, 1854: pl. 3, fig. 2, ♀; Brauns, 1903: 65, 68, ♂, ♀.
Ceramius rufomaculatus Cameron, 1906: 325, ♀.
[*non*] ?*Ceramius rex* de Saussure, Richards, 1962: 102.

Specimens examined: Cape Province: Willowmore, 15. xii. 1899, ♂, 10. i. 1900, ♀ (Dr. H. Brauns); Dunbrody, 1900, ♂, ♀ (Rev. O'Neil), 1901, ♀ (J. A. O'Neil); Uitenhage, Dunbrody, no date, ♀ (Rev. O'Neil); Pearston, 1905, 2 ♀♀ (Dr. Broom); Aberdeen, xi. 1935, ♀ (S.A.M. Staff); Tankwa Karroo, Waterval, xi. 1952, 21 ♂♂, 9 ♀♀ (S.A.M. Staff); Bloutoring Station, 30 miles E. of Touws River, xii. 1962, 2 ♀♀ (S.A.M. Staff).

South West Africa: Damaraland, 1890, ♀ (R. Lightfoot). It is very doubtful whether this last record is correct.

Ceramius caffer de Saussure

Ceramius caffer de Saussure, 1855: 76, ♀; Richards, 1962: 104, figs. 110–113, 115, ♂, ♀.
Ceramius consobrinus de Saussure, 1855: 77, ♀; Brauns, 1913: 198, ♂, ♀.

Specimens examined: Cape Province: Stellenbosch, x. 1888, 3 ♂♂, 2 ♀♀, no date, ♀ (L. Peringuey), 1908, 26 ♀♀ (C. P. Lounsbury).

All the specimens carry mites in the acarinarium.

Ceramius metanotalis Richards

Ceramius metanotalis Richards, 1962: 106, fig. 114, ♀.

♂. Black; whole disk of mandibles, labrum, clypeus except very narrow margins, roughly rectangular area above and between antennal sockets (separated from clypeus by a narrow black line at suture and produced slightly upwards at inner margins of antennal sockets and with a small black tubercle at centre), narrow orbits up to centre of eye emargination, small occipital spots behind upper portion of eyes, underside of antennal scape, underside of 2nd segment and basal two thirds of 3rd segment, pronotal band (narrowly interrupted at centre and produced on to humerus and to tegula), a minute spot on postero-lateral corner of mesoscutum and inner corner of axilla, sometimes a small spot at tip of scutellum, sometimes a very narrow streak on lower part of axilla, a spot at angles of propodeum, a single dorsal spot on mesopleuron, legs (except dorsal portions of coxae and trochanters, hind surface of middle and hind femora and tips of tarsal segments 3, 4 and 5 of above legs), inner margin of tegula, distal part of humeral plate, large spot on each side of first gastral tergite (not or only narrowly joined at hind margin), bands on tergites 2–5 (strongly widened at sides and plano-convex medially at hind margins), posterior portion of tergite 6 and small spot at sides of tergite 7, almost all of sternites 2–5 and sides of sternites 6 and sometimes 7, *pale yellow*.

Antennal flagellum except some black dorsal suffusion on all segments bar the last, *ferruginous*. Wings faintly brownish, veins brown. Length 17, 18, 19 mm., length of fore wing 12, 13, 13 mm., hamuli (20, 21), 22 (20, 22).

The chief secondary sexual structural differences are the following: Sides of clypeus more converging ventrally; margin narrower and very slightly concave. Eyes larger, a lot closer together; interocular distance at level of sockets = 1·5 times length of scape (without radicle) (2·2 in ♀). Antennal scape strongly widened, curved as in ♀; segment 3 flattened in side view, narrow except at apex, a little shorter than scape (without radicle) and slightly longer than 4+5+6; 4–11 becoming progressively wider; 12 forming a powerful, long, flattened and fairly wide hook, curved at base and at apex; inner surface of hook with a low, off-central, longitudinal carina on distal half; 8–10 with a shining, slightly raised transverse swelling beneath; entire underside of 11 swollen and shining. Fore trochanter with a very large, crescentic lobe, curving outwards, outer edge transparent, somewhat sinuate. Segment 1 of mid tarsus longer, curved; 2–5 strikingly laterally compressed, wide in side view; 3 and 4 almost oval in outline. Gaster with tergite 7 elongate, apically with a wide, shallow, angular emargination; sternite 3 with disk transversely swollen, raised on each side into a mound ending in a blunt tubercle, without raised preapical lateral keels; sternite 4 unmodified in structure; disks of both sternites 3 and 4 covered with dense white pubescence; sternites 7 and 8 very similar to those of *caffer* de Saussure; prominence on 7 more pronounced.

Specimens examined: Cape Province: Bulhoek, Klaver–Clanwilliam, x. 1950, 3 ♂♂, 27 ♀♀ (S.A.M. Staff).

Six of the 27 females have mites in the acarinium. The three males are free of mites, however.

Ceramius rex de Saussure

Ceramius rex de Saussure, 1855: 75, ♀; Turner, 1935: 290.
Ceramius lichtensteinii (*non* Klug), Richards, 1962: 102.

A single female specimen from Namaqualand: Klipvlei, Garies, xi. 1931 (S.A.M. Staff), believed to be this species, bears the label '*Ceramius rex* Sauss. ♀, det. Turner'. Concerning this specimen, Turner (1935: 290–1) correctly stated that it corresponds to the description of *rex* de Saussure, but measures only 19 mm., not 24. His further statement that it is allied to *lichtensteinii* (Klug) is incorrect for the specimen is entirely different from the latter species, being allied to *caffer* de Saussure and *metanotalis* Richards, though distinct from both of these. Richards (1962: 102) treated *rex* de Saussure as a doubtful synonym of *lichtensteinii* (Klug) but did not see the specimen now under consideration which appears to be the true *rex* de Saussure. The following is a description of this specimen.

♀. Black; clypeus, a large, broad pentagonal spot between the antennae and above the clypeus (from which it is separated by a narrow black line at suture), a narrow streak on inner margins of eyes below, streak in ocular sinus, spot on mandibles near base, underside of scape, spots behind eyes (joined along occipital margin), pronotal band produced onto humerus and to tegula (leaving a triangular black area on side), spot at postero-lateral corner of mesoscutum, inner corner and streak on lower part of axilla, posterior part of scutellar disk and flap of posttegula, central area of metanotum and portion below acarinarium, whole of propodeum (except for black region anterior to spiracles on sides, black lateral streaks on posterior surface near junction with metanotum and two black marks just above oriface), a large spot on mesopleuron, spots on anterior surface of coxae 2 and 3, portions of trochanters, greater part of femora and tibiae of all legs, inner margin of tegula, wide posterior bands widening on sides on gastral tergites 1–5, almost whole disk of 6, two small streaks on posterior area of sternite 1, whole of sternites 2–5 except extreme base of 2, *pale yellow*.

Anterior margin of clypeus, distal half of mandibles, antennal flagellum (except some black dorsal suffusion), some suffusion on tibiae and entire tarsi, suffusion on gastral sternite 6, *ferruginous*. Wings faintly brownish, veins brown.

Length 19 mm., length of fore wing 13·8 mm., hamuli 23.

Head, thorax and base of first gastral segment with long whitish hairs, densest on head, dense on pleura, sides and angles of propodeum; rest of gaster with very fine tomentum-like pubescence.

Clypeus one third longer than wide at ventral margin, moderately coarsely punctured; ventral margin truncate, sharply angled, with a fairly wide, smooth border. Antennal sockets separated by 4·1 times their diameter; interocular distance at level of sockets twice the length of scape (without radicle); scape (without radicle) almost 3 times as long as greatest width; segment 2 very short, broader than long; 3 half as long as scape (without radicle), twice as long as greatest width, of same length as 4+5+6; 4–10 progressively wider; 10 about twice as wide as long; 11 and 12 a little narrower. Frons dull, finely punctured; POL : OOL = 1 : 1·7; posterior ocelli about half ocellar diameter in front of hind margin of eyes; occipital keel absent. Pronotum with spiracular lobe well defined by a furrow; lateral furrow partially obscured by legs, apparently rather weak; anterior margin apparently not markedly keel-like; dorsal surface finely and closely punctured. Mesoscutum dull, finely, confluently punctured; prescutal furrows well marked over their entire length, especially behind; parapsidal furrows fairly weak; median notal suture marked anteriorly by a smooth, shining, unpunctured line, posteriorly marked by a furrow. Suture between axilla and scutellum with a pit ventrally. Raised disk of scutellum convex, in profile smoothly arcuate to posterior margin, with a well marked, raised, median keel and moderate lateral keels posteriorly, dull, punctured like mesoscutum; lateral declivities more shining, feebly punctured. Metanotum with central prominence smooth; acarinaria present laterally; entrance to acarinarium large, larger than that of *caffer* de Saussure, about 4 times longer than wide, width nearly constant throughout, only very slightly wider laterally; part of metanotum in front of slit of about same width as latter. Mesopleuron dull, with very close microscopic punctures and sparse coarse ones. Metapleuron dull, with similar but less pronounced puncturation and with some microscopic transverse striae on dorsal half; as in *metanotalis* Richards with a marked bean-shaped depression dorsally in the posterior boundary. Propodeum with angles rounded; posterior surface shallowly concave; spiracle long and narrow with anterior margin produced backwards. Fore tibial spur regularly curved, slightly recurved at apex; mid tibia with two spurs; larger spur of hind tibia bifid. Claws with a small tooth. Gaster dull, with exceedingly minute and close punctures, smaller than those of *metanotalis* Richards, and with very fine tomentum; larger punctures completely absent from all tergites; tergite 1 very transverse, nearly 3½ times wider than long, a little constricted posteriorly, with a hyaline border; tergite 2 constricted anteriorly, maximum width 1¼ times greater than maximum width of tergite 1; tergite 3 of equal width anteriorly as tergite 2 posteriorly; tergites 3–6 becoming progressively narrower; sternites nearly flat, very closely and finely punctured.

Four mites are visible in the acarinaria.

Ceramius bicolor (Thunberg)

Philanthus bicolor Thunberg, 1815: 131, 289 [♂].
Ceramius karooensis Brauns, 1902: 282, ♀, 373, ♂.
Ceramius bicolor (Thunberg), Schulz, 1912: 68–69, 99; Bequaert, 1929: 79; Richards, 1962: 115, figs. 131, 132.

Specimens examined: Cape Province: Aberdeen, xi. 1935, 3 ♂♂, 8 ♀♀ (S.A.M. Staff); Murraysburg Dist., xi. 1935, 6 ♂♂, 2 ♀♀ (S.A.M. Staff); Augusfontein (Calvinia), ix. 1947, ♂, 2 ♀♀ (S.A.M. Staff); Oudtshoorn, Zebra, x. 1951, ♂ (S.A.M. Staff); Moordenaars Karoo, Lammerfontein, x. 1952, 3 ♀♀ (S.A.M. Staff); Willowmore–Vondeling, x. 1952, ♀ (S.A.M. Staff); Rooinek Pass, x. 1952, ♂ (S.A.M. Staff); Tankwa Karoo, Waterval, xi. 1952, 25 ♂♂, 85 ♀♀ (S.A.M. Staff); Touws River–Hondewater (18 miles E. of Touws River), xii. 1962, 5 ♂♂, 5 ♀♀ (S.A.M. Staff); Bloutoring Station (30 miles E. of Touws River), xii. 1962, 9 ♀♀ (S.A.M. Staff).

Ceramius linearis Klug

Ceramius linearis Klug, 1824: 227, ♂; Richards, 1962: 115, figs. 128–130, 113 (*b*).
Ceramius (*Paraceramius*) *linearis* de Saussure, 1855: 71, ♂.
Ceramius fumipennis Brauns, 1902: 275, ♂, ♀; Bradley, 1922: 397 (correction of Brauns).

Specimens examined: Cape Province: Algoa Bay, 25. xii. 1898, ♂, ♀ (Dr. H. Brauns); Dunbrody, 1900, ♀ (Rev. O'Neil); Aberdeen, xi. 1935, ♀ (S.A.M. Staff).

Ceramius capicola Brauns

Ceramius capicola Brauns, 1902: 278, ♂, ♀; Bradley, 1922: 397; Richards, 1962: 117.

Specimens examined: Cape Province: Willowmore, 1. x. 1899, ♀ (Dr. H. Brauns); Somerset East, 25–30. xi. 1930, 2 ♀♀, ♂ (R. E. Turner); Aberdeen, xi. 1935, 7 ♂♂, 3 ♀♀ (S.A.M. Staff); Murraysburg Dist., xi. 1935, 5 ♂♂, 11 ♀♀ (S.A.M. Staff); Teekloof, Fraserburg Dist., xi. 1935, 5 ♂♂, ♀ (S.A.M. Staff); Oukloof, Fraserburg Road, xi. 1936, 2 ♀♀ (S.A.M. Staff); Richmond Dist., xi. 1939, ♂ (S.A.M. Staff); Oudtshoorn, Zebra, x. 1951, 5 ♂♂, ♀ (S.A.M. Staff).

Ceramius socius Turner

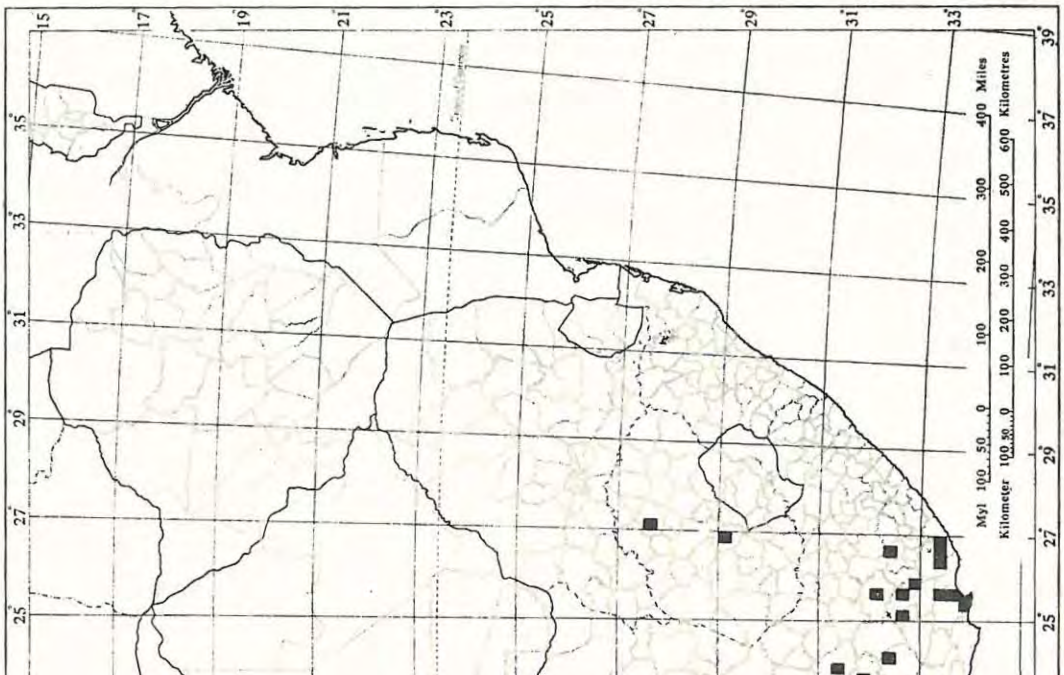
Ceramius socius Turner, 1935: 297, ♂, ♀; Richards, 1962: 117, figs. 113 (*a*), 134–136.

Specimens examined: Cape Province: Montagu, x–xi. 1919, ♀ (Collector's name not recorded); Worcester, ix. 1921, 2 ♂♂, 2 ♀♀ (R. E. Turner); Verkeerde Vlei (Touws River–Hottentots Kloof), xii. 1962, ♂, 13 ♀♀ (S.A.M. Staff); Constable, xii. 1962, 3 ♀♀ (S.A.M. Staff); Matroosberg Station, xii. 1962, ♂, ♀ (S.A.M. Staff); 8 miles N.E. of Touws River, xii. 1962, ♀ (S.A.M. Staff).

Discussion of the Distribution of the Genus *Ceramius*

The genus *Ceramius* occurs in two widely separated geographical regions in the Old World, one being the extreme south-west of the Ethiopian Region and the other that portion of the Palaearctic bordering on the Mediterranean Sea. Thus, in the Ethiopan Region, the genus is in the main restricted to the Cape Province where it is found in Little Namaqualand, the South Western Cape, the Little Karroo and the southern parts of the Great Karroo. It does not extend further east than the Great Fish River. Outside the Cape Province, one species (*damarinus* Turner) is endemic to South West Africa (Kaokoveld and Ovamboland), and one Eastern Cape species (*capicola* Brauns) has been recorded from two localities (Kroonstad and Thaba Nchu) in the Orange Free State. This distribution has been plotted by means of a $\frac{1}{4}$° square grid system on an outline plotting map (Map 1). In the Palaearctic, the genus occurs in Algeria, Morocco, Gibraltar, Portugal, Spain, the south of France, Greece, Turkey, Russian Armenia and probably Israel.

Climatically the above areas are characterised by a predominantly winter rainfall while the vegetation is generally low and semi-desert in nature.



MAP 1. Distribution of the genus *Ceramius* in the Ethiopian Region.

In South Africa, *Ceramius* favours those parts of the Karroid and False Karroid areas (as defined by Acocks, 1953) which lie within the winter rainfall region, though two of the nineteen species, *damarinus* Turner and *capicola* Brauns, have been recorded from summer rainfall regions.

A study of the records shows that in the southern hemisphere no species flies earlier than September or later than March, while in the northern hemisphere no species flies earlier than March or later than August. In other words, flight is restricted to the dry spring and summer months succeeding the winter rainy season.

Having ascertained where and when *Ceramius* occurs it seems of interest to examine the reasons. In this connection the biology of the genus has to be taken into account. As stated above, the adults fly during the dry months of the year succeeding the winter rainy season. During this time mating takes place and burrows lined with mud pellets are built in the ground and surmounted by mud chimneys. In these the eggs are deposited and, in the South African species at least, it is recorded by Brauns (1910, cited by Richards, 1962: 29) that the female continues to provision the young with pollen and nectar until these larvae are ready to pupate, when she seals the opening to the nest with a plug of mud. There is only one generation per year.

Two requirements for the successful run of the life-history are immediately apparent: there must be a copious supply of pollen and nectar at the time the young are being reared and there must be an extended dry period, not only to allow the adult to collect this pollen and nectar but also on account of the fact that the burrows in the ground remain unplugged during the larval stage. Despite some possible protection afforded by the chimneys, the larvae would have little chance of survival in case of heavy rain.

The combination of winter rainfall followed by an abundance of suitable flowers rich in pollen and nectar during an extended dry period is obviously the clue to the distribution of the genus *Ceramius*. The only areas fulfilling these requirements are those in which *Ceramius* occurs. In this connection it is likely that the flowers visited by *Ceramius* will prove to be low-growing Compositae and mesembryanthemums (Aizoaceae) which, following the winter rains, are such a striking feature of the semi-desert areas inhabited by *Ceramius* in South Africa.

SUMMARY

The account of the South African species of *Ceramius* included in the revision of the Masaridae by Richards (1962) is supplemented by the study of the material in the South African Museum collection.

One new species, *richardsi*, and the hitherto unknown ♀ of *clypeatus* Richards and ♂ of *metanotalis* Richards are described as is also a specimen thought to be *rex* de Saussure. The locality records of all the specimens in the collection are given and the distribution of the genus in South Africa is mapped. Lastly the distribution of the genus as a whole is discussed with reference to the biology of these wasps.

Acknowledgements

I wish to thank Dr. G. van Son of the Transvaal Museum, Pretoria for the loan of type material of *peringueyi* Brauns, *clypeatus* Richards and *metanotalis* Richards. The Trustees of the South African Museum are grateful to the Council for Scientific and Industrial Research for a grant to publish this paper.

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INSTRUCTIONS TO AUTHORS

MANUSCRIPTS

In duplicate (one set of illustrations), type-written, double spaced with good margins, including TABLE OF CONTENTS and SUMMARY. Position of text-figures and tables must be indicated.

ILLUSTRATIONS

So proportioned that when reduced they will occupy not more than 4¾ in. × 7 in. (7½ in. including the caption). A scale (metric) must appear with all photographs.

REFERENCES

Authors' names and dates of publication given in text; full references at end of paper in alphabetical order of authors' names (Harvard system). References at end of paper must be given in this order:

Name of author, in capitals, followed by initials; names of joint authors connected by &, not 'and'. Year of publication; several papers by the same author in one year designated by suffixes a, b, etc. Full title of paper; initial capital letters only for first word and for proper names (except in German). Title of journal, abbreviated according to *World list of scientific periodicals* and underlined (italics). Series number, if any, in parenthesis, e.g. (3), (n.s.), (B.). Volume number in arabic numerals (without prefix 'vol.'), with wavy underlining (bold type). Part number, only if separate parts of one volume are independently numbered. Page numbers) first and last, preceded by a colon (without prefix 'p'). Thus:

SMITH, A. B. 1956. New *Plonia* species from South Africa. *Ann. Mag. nat. Hist.* (12) **9**: 937–945.

When reference is made to a separate book, give in this order: Author's name; his initials; date of publication; title, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; place of publication; name of publisher. Thus:

BROWN, X. Y. 1953. *Marine faunas*. 2nd ed. **2**. London: Green.

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SMITH, C. D. 1954. South African Plonias. *In* Brown, X. Y. *Marine faunas*. 2nd ed. **3**: 63–95. London: Green.

SYNONYMY

Arranged according to chronology of names. Published scientific names by which a species has been previously designated (subsequent to 1758) are listed in chronological order, with abbreviated bibliographic references to descriptions or citations following in chronological order after each name. Full references must be given at the end of the paper. Articles and recommendations of the *International code of zoological nomenclature adopted by the XV International congress of zoology, London, July* 1958, are to be observed (particularly articles 22 and 51).

Examples: *Plonia capensis* Smith, 1954: 86, pl. 27, fig. 3. Green, 1955: 23, fig. 2.

When transferred to another genus:

Euplonia capensis (Smith) Brown, 1955: 259.

When misidentified as another species:

Plonia natalensis (*non* West), Jones, 1956: 18.

When another species has been called by the same name:

[*non*] *Plonia capensis*: Jones, 1957: 27 (= *natalensis* West).

NOVOS TAXA ENTOMOLÓGICOS

(Suplemento à *Revista de Entomologia de Moçambique*)

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Further contribution to the knowledge of the South African species of the genus *Ceramius* LATREILLE *(Hymenoptera: Masaridae)*

by

F. W. GESS

EDITOR

INSTITUTO DE INVESTIGAÇÃO CIENTÍFICA DE MOÇAMBIQUE

LOURENÇO MARQUES

FURTHER CONTRIBUTION TO THE KNOWLEDGE OF THE SOUTH AFRICAN SPECIES OF THE GENUS **CERAMIUS** LATREILLE (**HYMENOPTERA : MASARIDAE**)

by

F. W. Gess

(South African Museum, Cape Town)

INTRODUCTION

Since the revision of the *Masaridae* by RICHARDS (1962), and the recent account by GESS (1965) of *Ceramius* LATREILLE as represented in the collection of the South African Museum, some interesting additional material of this genus has come to hand.

In the present paper, a new species, *C. micheneri,* from the Olifants River Valley, Cape Province, is described as is the hitherto unknown ♂ of *C. toriger* VON SCHULTHESS. Some additional locality records of known species are listed, the first records of flowers visited by these wasps in South Africa are given and the nest superstructure of *C. bicolor* (THUNBERG) is described.

South African Museum is here abbreviated to S. A. M.

* * *

DESCRIPTIONS OF SPECIES AND DISTRIBUTION RECORDS

CERAMIUS MICHENERI SP. N.

(Text — figs. 1–6)

♂. Black; mandibles (except teeth), clypeus (except testaceous distal rim and spot at centre of disk and black lateral rims and «wings»), small elongate spot above each antennal socket, inner orbits (wide below, narrowing upwards) to top of eye, elongate lateral streak behind each eye, most of scape (except dorsal and ventral black streaks), entire posterior margin of pronotum to humeral angles, minute dot at postero-lateral corner of mesoscutum, spot on upper part of mesopleuron, inner corner and entire posterior margin of axilla, posterior quarter of scutellar disk, central area of metanotum, small spots at angles of propodeum, 4 elongate spots on prosternum (outer larger pair at postero-lateral angles opposite coxae, inner smaller pair between former on either side of midline), legs (except markings on posterior faces of coxae 1 and 2 and whole of posterior face of 3, mark on trochanter 3, streak on dorsal surface of femur 1 and streaks on posterior aspects of femora 2 and 3, posterior aspect of tibia 3, tarsi of 2 and 3 and claws of all legs), narrow posterior bands on tergites 1–6 (somewhat widened at centre and at sides), spot on sternite 1, large part of sternites 2 and 3 (including prominence on 3), disk of 4 to a more limited extent, lateral spots on sternites 5 and 6, posterior band on sternite 7 (curving forwards on sides, and, in centre including posterior face of prominence), *yellow*.

Antennal flagellum (except dorsal black suffusion), posterior aspects of mid and hind femora and of hind tibia, tarsal joints 1–4 of mid and hind legs, *ferruginous*. Last joint of mid and hind tarsi black.

Wings faintly brownish, veins brown.

Length about 13 mm, length of forewing about 8 mm, hamuli 22, 24.

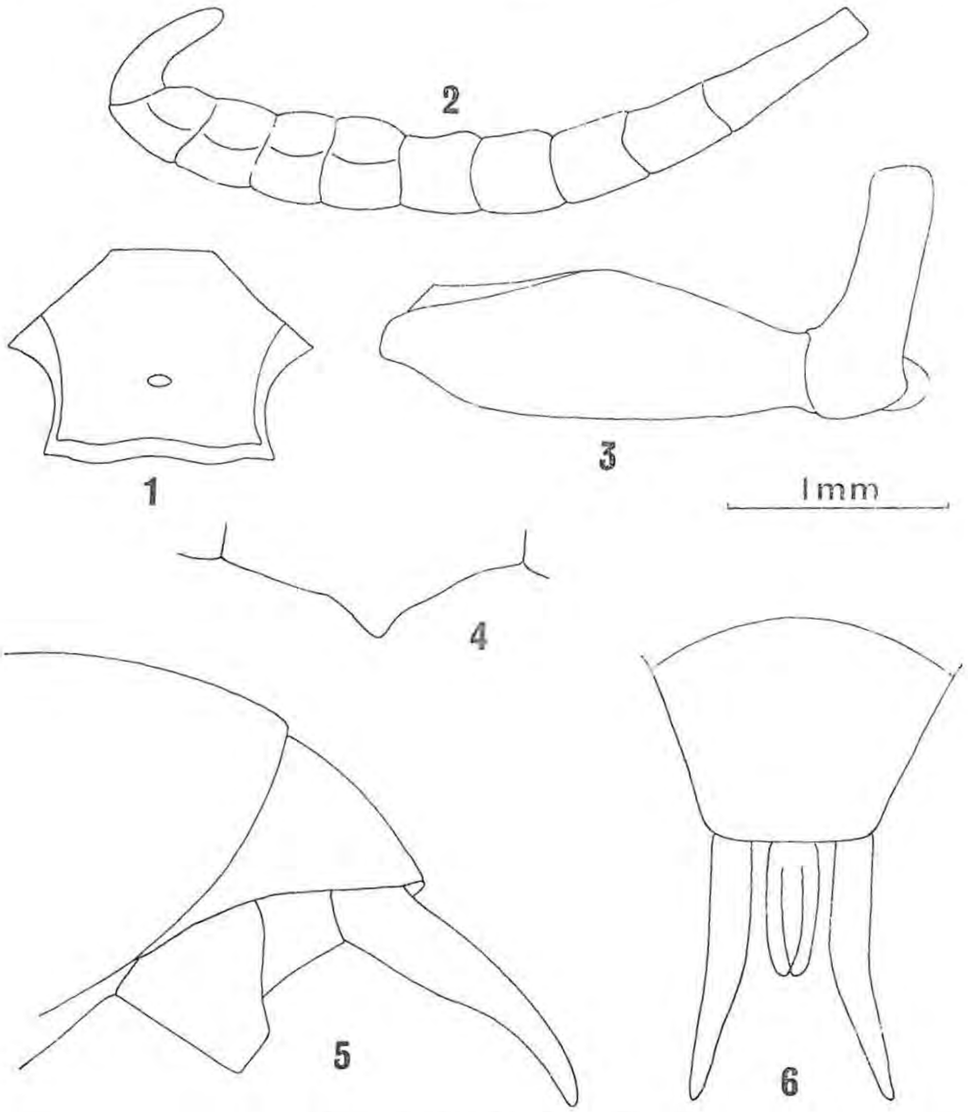
Clypeus (Fig. 1) excluding lateral wings roughly quadrate in shape, length equal to that of scape (without radicle), very slightly shorter at midline than wide at ventral margin; ventral margin truncate with a wide, extremely shallow emargination; angles well marked; surface of disk closely punctured except mid--distally, depressed centrally in distal half; margins smooth, ventral testaceous margin wide, very slightly upwardly bent.

Frons dull, very closely punctured with a small tubercle between the antennal sockets; vertex with larger, sparcer punctures and shining interstices.

Antennal sockets separated by $\frac{5}{8}$ length of scape (without radicle); interocular distance at level of sockets $1\frac{1}{2}$ times length of scape (without radicle); scape (without radicle) $2\frac{1}{5}$ times as long as greatest width (i. e. at distal end); segment 2 very short, almost concealed; 3 four fifths as long as scape, about 3 times as long as greatest width, of same length as $4+5$; 5 and 6, 7 and 8, and 9 and 10 of equal length respectively, each pair somewhat shorter than the preceeding pair; 11 of same length as 7 or 8; 12 somewhat curved, bent back towards the rest of the flagellum (to form a $\frac{1}{2}$ spiral) (Fig. 2) and reminiscent of that of *clypeatus* RICHARDS and *richardsi* GESS; segments 7–11 slightly swollen below and with a weak carina.

POL (distance between posterior ocelli) : OOL (distance between a posterior ocellus and compound eye) $= 1 : 1.3$; posterior ocelli about ocellar diameter in front of hind margins of eyes; occipital keel absent. Mandibles with 3 apical teeth, labial palps 4-segmented, maxillary palps 5-segmented.

Pronotum with spiracular lobe well defined by a furrow; lateral furrow strong, preceeded by a strong keel. Pronotum and mesoscutum closely and rather coarsely punctured, interstices shining; prescutal furrows strong posteriorly.



Ceramius micheneri sp. n. (♂)

Fig. 1 — Clypeus. Fig. 2 — Antennal flagellum. Fig. 3 — Fore femur and trochanter. Fig. 4 — Sternite 3 (profile, from left side). Fig. 5 — End of abdomen (lateral view). Fig. 6 — End of abdomen (dorsal view)

Scutellar disk wider than long, raised, convexly rounded, in profile smoothly arcuate to posterior margin, without median or lateral keels, punctured like mesoscutum.

Fore trochanter (Fig. 3) with a large, somewhat curved, flattened, parallel--sided lobe whose apex is rounded and not at all produced into a hook-like point; the lobe generally reminiscent of that of *schulthessi* BRAUNS but much longer. Mid tibia with 2 spurs; all claws simple.

Propodeum with angles rounded and posterior surface shallowly concave.

Gaster shining, closely punctured; punctures of tergite 1 finer than those of thorax but coarser than those of tergites 2–6, those of tergite 7 coarse. Tergite 1 strongly transverse, a little less than 4 times as broad as long, broadest just before posterior margin and then only very slightly narrowed; tergites 2–5 slightly constricted basally; tergite 2 1⅓ times width of tergite 1 and equal to width of tergite 3; remaining tergites becoming progressively narrower. Sternite 3 with a small raised transversely rounded prominence in centre (Fig. 4); sternite 7 with a strong, laterally compressed, bluntly pointed prominence sloping steeply up from anterior margin (Fig. 5); sternite 8 somewhat raised on each side and at base, depressed in centre. Parameres spiniform (Figs. 5, 6).

♀. Black; basal portion of mandibles, clypeus (except testaceous spot at centre of disk and black lateral rims, «wings» and distal margin — the latter black area sometimes extended proximally to testaceous spot and then biramously laterally produced), small elongate spot (sometimes reduced or absent) above each antennal socket, inner orbits to top of eye, elongate lateral streak (sometimes reduced or absent) behind each eye, a pair of larger spots on back of head capsule, entire posterior margin of pronotum to humeral angles (sometimes very narrowly interrupted anteriorly at midline), medial longitudinal streak (sometimes absent) on posterior half of mesoscutum between prescutal furrows, lateral margins of mesoscutum above tegulae, spot on upper part of mesopleuron, inner corner and entire posterior margin of axilla, posterior third of scutellar disk, central area of metanotum (to a variable degree), angles of propodeum, greater part of coxae, trochanters, femora and tibiae of all legs, narrow posterior bands on tergites 1–5 (widened at centre and strongly so at sides), a pair of spots of variable size on tergite 6, greater part of sternites 1–4 and sometimes also 5, *yellow*. While the light markings of the head, thorax and legs are a dark yellow, those of the gaster are lighter in colour.

Underside of antennal flagellum, apical portion of mandibles, markings on femora and tibiae and entire tarsi, *ferruginous*.

Wings faintly brownish, veins brown.

Length 12.5–14 mm, length of forewing 8.1–8.4 mm.

Apart from the secondary sexual differences the female is very similar to the male and shares with the latter the unique form of the clypeus, which character alone is sufficient to distinguish this species.

Antennal sockets separated by the length of the scape (without radicle); interocular distance at level of sockets 1.8 times length of scape (without radicle); POL : OOL = 1 : 1.2.

Specimens examined. — Cape Province: Citrusdal, 2–XI–1966 (Professor C. D. MICHENER), holotype ♂; Olifants River between Klawer and Clanwilliam, 14/15–X–1967 (F. W. & W. H. R. GESS), allotype ♀ and 13 paratypes ♀♀, collected at water of small stream. (All in S. A. M.).

I have pleasure in naming this species after Professor C. D. MICHENER of the University of Kansas, U. S. A., who collected the first specimen of this species and to whom I am much indebted for the gift of numerous *Masaridae* collected by him during his visit to this country.

The affinities of this new species are with the species of the *Ceramioides* group of species (i. e. *cerceriformis* DE SAUSSURE, *schulthessi* BRAUNS, *peringueyi* BRAUNS, *clypeatus* RICHARDS and *richardsi* GESS) and possibly with the group of 4 species comprising *nigripennis* DE SAUSSURE, *toriger* VON SCHULTHESS, *braunsi* TURNER and *jacoti* RICHARDS.

In common with these 9 species and in contrast to the remaining South African species of the genus, the present species has the combination of the following characters: a 2-spurred mid tibia, uncovered lateral depressions on the metanotum, a first gastral segment whose sternite is not truncate and whose tergite is not scale-like nor deeply separated from the following segment.

It is allied to the *Ceramioides* group by the possession of spiniform parameres and in the form of the male secondary sexual characters associated with the last antennal segment and the fore trochanter. Thus the antennae are narrowed towards the apex and bent in a half spiral (the last segment not being excavated beneath to form a strong hook as in the *nigripennis* group), while the process of the fore trochanter is wide, flattened and parallel-sided, reminiscent of that of *schulthessi* BRAUNS though not of *clypeatus* RICHARDS or *richardsi* GESS and very different from those of *braunsi* TURNER (racket-shaped) and of *nigripennis* DE SAUSSURE, *toriger* VON SCHULTHESS and *jacoti* RICHARDS (tip produced into a curved projection or recurved).

Characteres in which it differs from the *Ceramioides* group, however, and in which it is more akin to the *nigripennis* group are those of the propodeum and the base of the gaster. Thus the propodeum shows no sign of either spine-like processes or even blunt angular projections, while tergite 1 is not markedly convex nor is 2 much constricted at the base.

CERAMIUS TORIGER von Schulthess

(Text — fig. 7)

Ceramius toriger von Schulthess, 1935 : 383, ♀ ; Richards, 1962 : 101 ; Gess, 1965 : 222.

♂. Black ; most of mandibles, labrum, clypeus (except very narrow margins), area shaped like a three-pointed crown above and between antennal sockets (separated from clypeus by a narrow black line at suture and with a small dark tubercle at centre), narrow orbits up to centre of eye emargination, small occipital spots behind upper portion of eyes, greater part of antennal scape, transverse pronotal band (very narrowly interrupted at centre and not at all produced posteriorly on sides), legs (except fore coxae and dorsal portions of mid and hind coxae and trochanters, large areas on all femora, distal parts of last tarsal joint of mid and hind legs and claws of all legs), posterior bands on tergites 1–6 (narrowest at midline, expanded dorso-laterally and narrowed again at ends, band on tergite 1 interrupted at midline), pair of spots of very variable size on tergite 7, greater part of sternites 2 and 3, spots on postero-lateral corners of sternites 4–6, *yellow*.

Antennal flagellum except outer aspect of hook of last segment *ferruginous*.

Wings faintly brownish, veins brown.

Length about 14 mm, length of forewing 10.7 mm, hamuli 15–18.

The chief secondary sexual structural differences are the following: eyes larger, a lot closer together ; interocular distance at level of sockets 1.4 times length of scape (without radicle) (2.0 in ♀) ; antennal sockets separated by 0.7 times length of scape (without radicle) (1.3 in ♀) ; antennal segment 3 a little less than $\frac{3}{4}$ length of scape (without radicle), about same length as 4 + 5 + half of 6 ; segments 4–10 of about equal length but of progressively increasing width ; 11 somewhat longer, as wide as 10 ; 10 and 11 flattened beneath ; 12 about $1\frac{1}{2}$ times length of 11, proximally somewhat narrower than 11, narrowed from base to about middle, sides then parallel to near end, whole forming a strong, curved, flattened hook, similar to that of *jacoti* Richards and (to a lesser extent) *nigripennis* de Saussure.

POL (distance between posterior ocelli) : OOL (distance between a posterior ocellus and compound eye) = 1 : 1.5 (1 : 1.7 in ♀).

Fore trochanter with a long anterior process, flattened, parallel-sided and slightly and evenly curved in its proximal half or more, then strongly narrowed and with distal portion (of fairly constant width) recurved to form a strong hook, the whole somewhat reminiscent of that of *nigripennis* de Saussure.

Gaster with tergite 7 broad, apically truncate and with surface shallowly impressed ; median third of hind margin shallowly emarginate and postero-lateral corners well marked and angular.

Sternite 3 (Fig. 7, with for comparison Figs. 8–10) with posterior half raised medially into a strong prominence; the anterior surface of the prominence smoothly curved up from the front margin of the segment and ending apically in a truncate, tri-cusped transverse ridge; transverse ridge at each end flanked antero-laterally by a tubercle; posterior surface of prominence falling steeply from apex to a shelf extending posteriorly and then falling vertically to hind margin of segment.

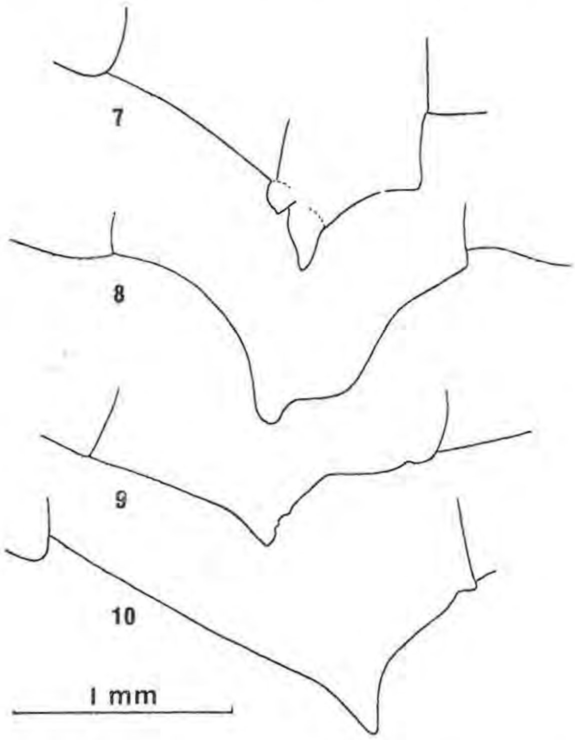


Fig. 7 — *Ceramius toriger* VON SCHULTHESS (♂), sternite 3 (profile, from left side). Fig. 8 — *C. braunsi* TURNER (♂), the same. Fig. 9 — *C. nigripennis* DE SAUSSURE (♂), the same. Fig. 10 — *C. jacoti* RICHARDS (♂), the same

Sternite 7 with a keeled, acute, posteriorly pubescent prominence.

Specimens examined. — Cape Province: Die Bos Road (30 miles East of Clanwilliam), 19–IX–1966 (Professor C. D. MICHENER), 3 ♂♂, collected «on blue-rayed *Compositae*». (In S. A. M.).

CERAMIUS SCHULTHESSI Brauns

Cape Province, Namaqualand: Swart Doringrivier (between Bitterfontein and Garies), 2/3–x–1966 (F. W. & W. H. R. Gess), 10 ♀♀, 4 ♂♂, collected at residual saline pools in river bed; 6 miles South of Garies, 7/8–x–1967 (F. W. & W. H. R. Gess), 20 ♀♀, 5 ♂♂, one ♀ caught on purple flowers of *Mesembryanthemum* sp. *(senso lato) (Aizoaceae)*, other specimens all collected at muddy pool.

Mites were clinging to all 10 ♀♀ and to ♂ from the former locality, and to 9 ♀♀ from the latter.

CERAMIUS RICHARDSI Gess

Cape Province: Citrusdal, 2–xi–1966 (Professor C. D. Michener), 5 ♀♀, 2 ♂♂. Three ♀♀ have mites clinging to them.

CERAMIUS NIGRIPENNIS de Saussure

Cape Province, Namaqualand: Swart Doringrivier (between Bitterfontein and Garies), 2/3–x–1966 (F. W. & W. H. R. Gess), 62 ♀♀, collected at residual saline pools in river bed; 8 miles East of Springbok on road to Pofadder, 7–x–1966 (F. W. & W. H. R. Gess), ♀, collected at muddy roadside rainwater pool; 6 miles South of Garies, 7/8–x–1967 (F. W. & W. H. R. Gess), ♀, collected at muddy pool.

Mites were clinging to 21 ♀♀ from the first locality.

CERAMIUS BRAUNSI Turner

Cape Province: 13 miles South of Clanwilliam, 2–xi–1966 (Professor C. D. Michener), 4 ♀♀.

CERAMIUS JACOTI Richards

Cape Province: 18 miles South-East of Touws River, 12–xi–1966 (Professor C. D. Michener), ♀.

CERAMIUS LICHTENSTEINII (Klug)

Orange Free State: Kroonstad, 10–i–1965 (D. J. Brothers), 2 ♀♀, 23–i–1965 (D. J. Brothers), 2 ♂♂.

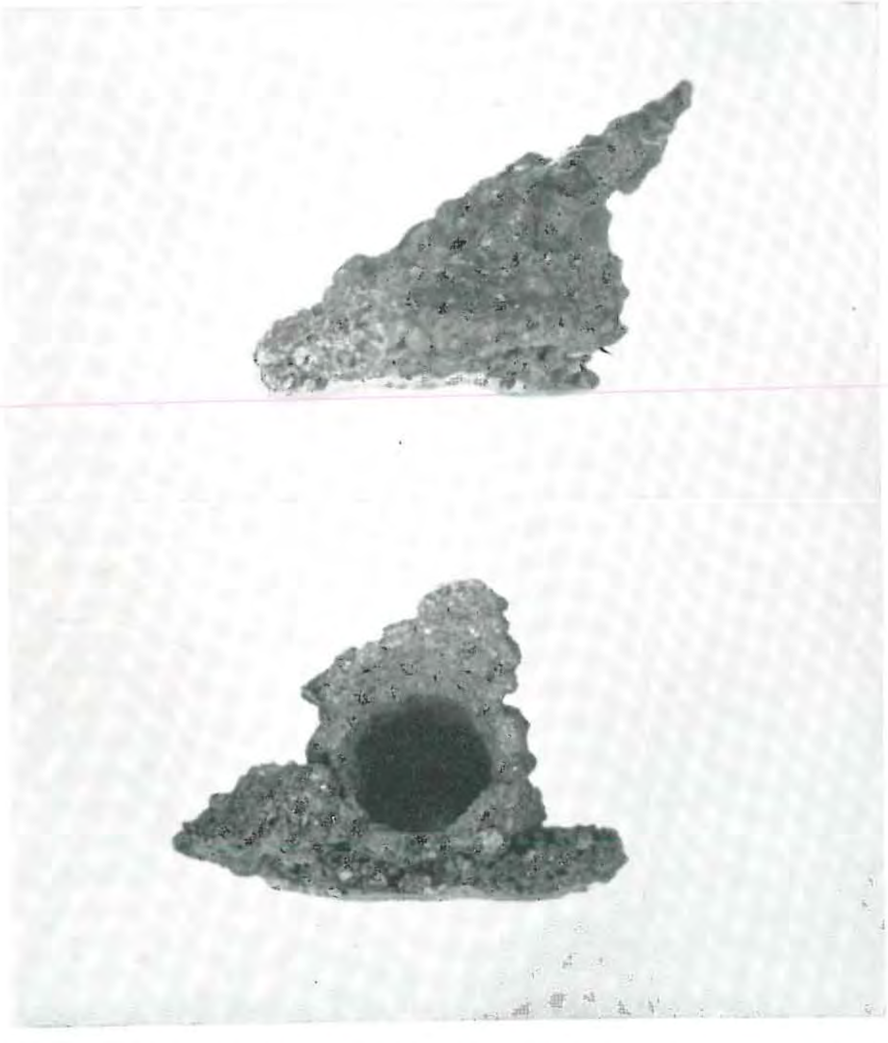


Plate 1 — *Ceramius bicolor* (Thunberg), burrow superstructure (×6), lateral view (above), front view (below)

Third contribution to the knowledge of the South African species of the genus *Ceramius* Latreille (Hymenoptera: Masaridae)

by

F. W. GESS

Albany Museum, Grahamstown

CONTENTS

INTRODUCTION

The South African species of the genus *Ceramius* Latreille are fairly well known, at least from a taxonomic aspect, having in recent years been studied by Richards (1962) and by Gess (1965 and 1968). Nevertheless, *Ceramius* material in the Albany Museum, in the private collection of Mr. H. N. Empey and in the collections made in South Africa by Dr. J. Rozen (1966 and 1968) and by Dr. and Mrs. H. Townes (1970), combined with continued collecting and field observations by the author and by Mr. J. G. H. Londt, has brought to light some interesting additional information.

In the present paper the hitherto unknown male of the very rare species *C. rex* de Saussure is described, *C. schulthessi* Brauns is sunk into synonymy with *C. cerceriformis* de Saussure, and additional locality records of several other species are listed. A table listing flowers visited by *Ceramius* species in South Africa shows a five-fold increase in the number of observed wasp-forage flower associations, the preferred flowers belonging to the Mesembryanthemaceae and Compositae. Also resulting from field observations are descriptions of the nesting sites and nest superstructures of *C. lichtensteinii* (Klug) and *C. capicola* Brauns, and the identification of a hitherto unrecorded parasite. A key restricted to the South African species of the genus but incorporating recent changes and additions is given.

DESCRIPTION, SYNONYMY AND DISTRIBUTION RECORDS

Ceramius rex de Saussure

Ceramius rex de Saussure, 1855:75, ♀; Turner, 1935:290; Gess, 1965:225, ♀.
Ceramius lichtensteinii (*non* Klug), Richards, 1962:102.

Described from the Cape Colony without precise locality, this species does not appear to have been collected again until over eighty years later when a single specimen believed to be conspecific was obtained in Namaqualand. This specimen, like the type a female, labelled "Klipvlei, Garies, xi. 1931 (S. A. M. Staff)" was stated by Turner (1935: 290—1) to correspond to the description of *rex* de Saussure, an opinion shared by Gess (1965: 225) who gave a detailed description of the specimen in question.

In an unsuccessful attempt to obtain further specimens, the author collected in the vicinity of Garies during early October, 1966 and again at the same time in 1967. Since then, however, a further specimen has come to hand—collected entirely by chance by Dr. and Mrs. H. Townes at Garies (25.ix.1970). This specimen, a male, clearly conspecific with the Garies female of 1931 and therefore believed to be the long unknown male of *rex*, is described below.

♂. Black; mandibles (except teeth at apex), clypeus, broad spot between antennal sockets and above clypeus (from which it is separated by a narrow black line at suture), a narrow streak on inner margin of eyes below extending as far as centre of ocular sinus, underside of scape and of second antennal segment as well as extreme base of third below, spots behind eyes (not joined along occipital margin), pronotal band produced onto humerus and to tegula (leaving a triangular black area on side), anterior corner of tegula, small streak margining postero-lateral corner of mesoscutum, small spot at apex of scutellum, flap of posttegula, small spots on posterior angles of propodeum, a large spot on mesopleuron, spots on mesosternum behind adjoining coxae, legs (except for black upper surface of coxae and trochanters and streak on femora, distal parts of third to fifth tarsomeres of middle legs, and to a less extent hind legs, and also pulvilli and claws of all legs), posterior bands widening markedly on sides on gastral tergites 1—6, baso-lateral spots on tergite 7, greater part of sternites 2,4 and 5 and lateral areas of 3,6 and 7, *yellow*.

Antennal flagellum except for black dorsal suffusion on all segments bar the last (which however has a little black basally), and extreme sides of tergite 7 *ferruginous*.

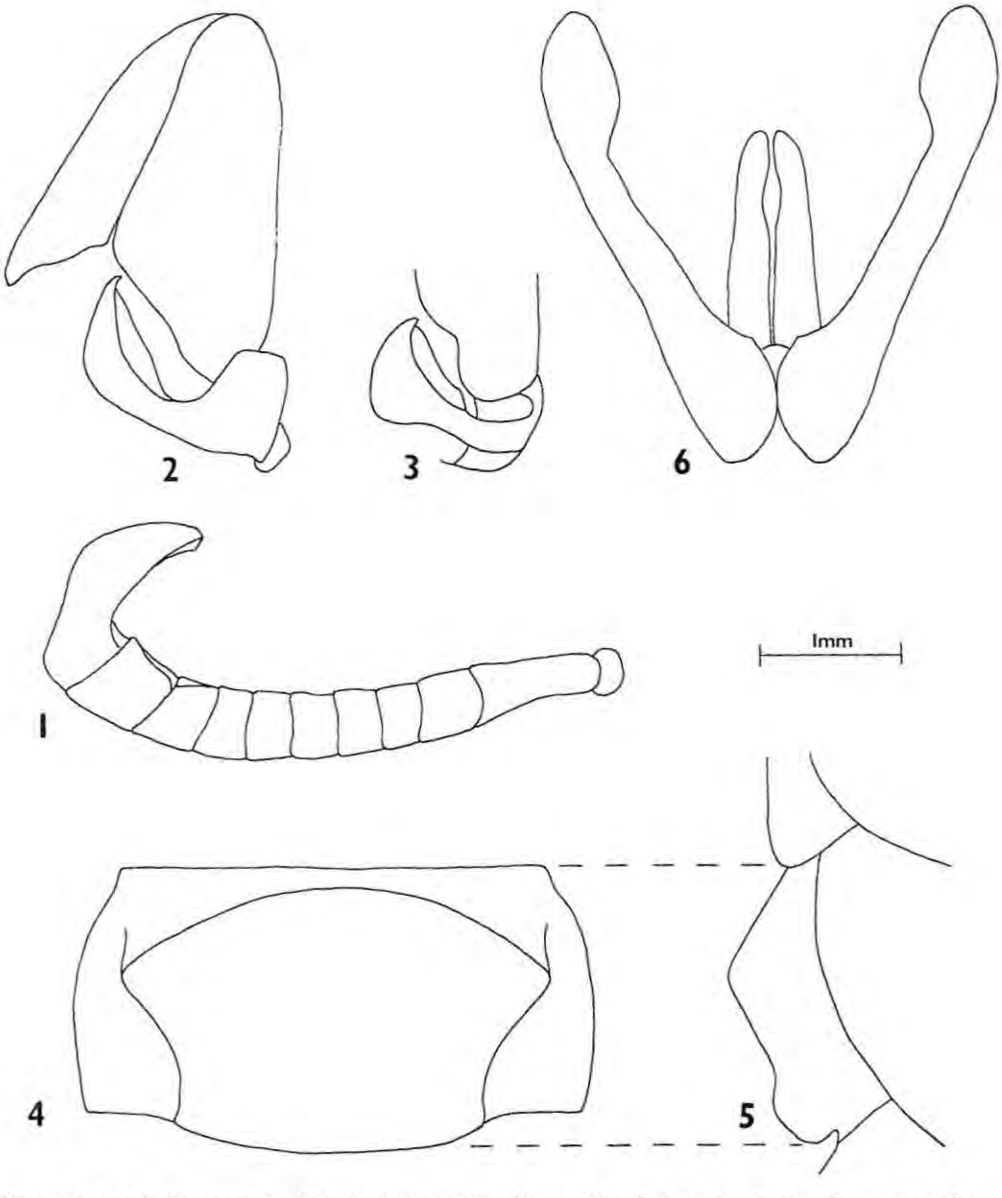
Wings faintly brownish, veins brown, subcosta and median vein almost *black*.

Length about 20 mm, length of fore wing 13 mm, hamuli 24.

Head, thorax, propodeum, first two gastral segments and seventh sternite with fairly sparse, long, whitish hairs; coxae, trochanters and femora posteriorly with similar but shorter hairs; concave portion of disc of sternite 3 with exceedingly dense, short, light ferruginous hairs; rest of gaster with very fine tomentum-like pubescence.

With the exception of the secondary sexual structural characters described below, very like the female in most respects including the structure and proportions of the clypeus, scutellum and acarinarium.

Antennal sockets separated by slightly less than twice their diameter (4,1 times in female); interocular distance at level of sockets one and a third times the length of scape (without radicle) (twice in female). Scape curved, strongly widened, twice as long (without radicle) as greatest width (almost 3 times in female); segment 2 very short, broader than long, largely concealed in end of scape; segment 3 flattened in side view, narrow except at apex, two thirds as long as scape (without radicle) and slightly longer than 4+5+6; 4—11 becoming progressively wider; 12 forming a powerful, long, flattened and fairly wide hook, inwardly curved at both base and apex; segments 8—11 modified beneath (Fig. 1). Fore trochanter (Fig. 2) with a very large, outwardly curved, crescentic lobe whose distal half is more or less



Ceramius rex de Saussure ♂. Fig. 1. Antennal flagellum. Fig. 2. Fore trochanter, femur and tibia. Fig. 4. Sternite 3 (ventral view). Fig. 5. Sternite 3 (profile, from left side). Fig. 6. Genitalia dorsal view). *Ceramius metanotalis* Richards ♂. Fig. 3. Fore trochanter and portion of femur.

evenly curved and of even width (in *metanotalis* (Fig. 3) abruptly curved and widened apically). Gaster with tergite 7 elongate, apically widely, very shallowly and angularly emarginate; sternite 3 (Figs. 4 and 5) with disc raised anteriorly and laterally and especially antero-laterally to form a carinate rim of a concave, wider than long, saucer-like depression; sternite 4 unmodified in structure; sternite 7 with a prominence. Genitalia (Fig. 6).

Specimen examined: Cape Province (Namaqualand): Garies, 25.ix.1970 (Dr. and Mrs. H. Townes) Metallotype ♂. (In the Albany Museum collection).

The acarinaria both contain mites, several of which are also present amongst the hairs on the propodeum.

The male of *rex* may readily be distinguished from the males of both *caffer* de Saussure and *metanotalis* Richards, which are the most closely related species, by the much more strikingly modified third sternite; from *caffer* by the absence of preapical lateral keels on sternite 4; and from *metanotalis* by the different shape of the lobe of the fore trochanter.

Ceramius cerceriformis de Saussure

Ceramius cerceriformis de Saussure, 1853: xxi, ♂; Richards, 1962:97, ♂, ♀.
Ceramius (*Ceramioides*) *cerceriformis* de Saussure, 1854: pl. 4, fig. 1, ♂; 1855:72, ♂.
Cerceris vespiformis de Saussure, 1855:79, ♀.
Ceramius schulthessi Brauns, 1902:182, ♀; Brauns, 1913:196, pl. 2, fig. 6, ♂, ♀; Richards, 1962:99; Gess, 1965:220; Gess, 1968: 10, syn.n.

Richards (1962) who examined the types of *cerceriformis*, *vespiformis* and *schulthessi* was "not altogether convinced" that *schulthessi*, which was "scarcely distinguishable" from *cerceriformis*, was distinct from the former, but the females which were compared "seemed to be distinct".

According to Richards' descriptions and his key the only differences between *cerceriformis* and *schulthessi* are in their puncturation and colouring. Thus both sexes of *cerceriformis* have the gaster impunctate while in *schulthessi* it is slightly shining and distinctly though finely punctured, at least on the first two tergites. In the female furthermore, the pronotum and mesonotum are dull with denser punctures in *cerceriformis*; more shiny with coarser, sparcer punctures in *schulthessi*. While sternite 2 is punctured throughout in the former, it is shining with a large almost unpunctured area on each side of the disc in the latter. Their colouration differs in that *cerceriformis* has very extensive, entirely yellow markings, while *schulthessi* is less extensively yellow-marked but has some red areas. The amount of red on gastral tergite 2 and yellow on 3—6 is however very variable.

Two pairs of wasps from Namaqualand (Swart Doringrivier and 6 miles South of Garies), representatives in the Albany Museum collection of longer series in the South African Museum, which were recorded as *C. schulthessi* Brauns (Gess, 1968), appear upon re-examination to fit the descriptions of *cerceriformis* reasonably well. Compared with these specimens, a series from Willowmore, fitting the description of *schulthessi* indicates some further minor differences: in the latter there seems to be a tendency for the disc of the scutellum to be somewhat more clearly margined, while the spine-like projections on the propodeum are generally more developed. However, the degree of development of these spines seems to vary also within a population.

While these small differences in the degree of puncturation, the degree of development of the propodeal spines, and the colouration do certainly exist, the similarity otherwise between *cerceriformis* de Saussure and *schulthessi* Brauns is such that it is impossible to separate the two using any other criteria.

Are these characters of any real value? As has been noted by both Brauns and Richards, the distribution and amount of red and of yellow in *schulthessi* is very variable. The degree of development of the propodeal spines is similarly variable, the variability in this case being present in both *cerceriformis* and *schulthessi*. It is believed that the remaining point of difference, namely that of the degree of puncturation, will with the examination of more material likewise be found to be variable and of questionable value.

On balance, the small differences in detail, of limited or questionable taxonomic validity, are far outweighed by the striking overall similarities, and there seems little if any justification in maintaining the specific integrity of the two forms on such slender evidence. *C. cerceriformis* de Saussure and *C. schulthessi* Brauns may best be considered as opposite extremes of a single widespread and very variable species; only much more extensive collecting can indicate whether they are sufficiently distinct to be accorded subspecific rank. *C. cerceriformis* de Saussure has priority and *C. schulthessi* Brauns must therefore sink into synonymy.

Ceramius cerceriformis de Saussure
Cape Province: Willowmore, 15.xi.1905 (Dr. Brauns) 4♂♂, 31.x.1967 (C. Jacot-Guillarmod) 9 ♀♀, ♂.

Ceramius richardsi Gess
Cape Province: Citrusdal, 2.xi.1966 (J. G. Rozen) 2 ♀♀.

Ceramius micheneri Gess
Cape Province: Citrusdal, 2.xi.1966 (J. G. Rozen) 2 ♀♀.

Ceramius nigripennis de Saussure
Cape Province: Garies, 23.ix.1970, ♂, 24.ix.1970, 3 ♀♀, ♂, 25.ix.1970, ♂, 27.ix.1970, 11 ♀♀, 8 ♂♂, 28.ix.1970, 4 ♀♀, ♂, 29.ix.1970, 4 ♀♀, ♂ (all Dr. and Mrs. H. Townes).

Ceramius braunsi Turner
Cape Province: Worcester, 16.ix.1972 (R. D. A. Bayliss) ♀.
This new locality is of interest as it to some extent links the previously known distributional areas—the region between Citrusdal and Vanrhynsdorp on the one hand and Willowmore on the other.

Ceramius jacoti Richards
Cape Province: Brandrivier road, 2 miles from junction with Ladismith—Riversdale road, 30.ix.1972 (C. F. Jacot-Guillarmod) 3 ♂♂.

Ceramius beyeri Brauns
Cape Province: Clanwilliam, 2—5.xi.1966 (J. G. Rozen) 2 ♀♀; Grahamstown, Bible Monument, 16.i.1969 (F. W. Gess) ♀; Willowmore, no date (Dr. Brauns) 3 ♀♀.

Ceramius lichtensteinii (Klug)
Cape Province: Alicedale, New Year's Dam, 2.xii.1970 (F. W. Gess) ♂, same date (J. G. H. Londt) 4 ♂♂; Dunbrody, no other data, ♀; Ecca Pass, 22.xi.1964 (D. J. Brothers) ♂; Fort Beaufort, 20.i.1960 (C. Jacot-Guillarmod) ♂; Fort Willshire near Alice, 21.i.1959 (C. Jacot-Guillarmod) ♀, ♂; Grahamstown, Bible Monument, 16.i.1969 (F. W. Gess) ♀; Grahamstown, Clifton, 7.xi.1972 (F. W. and S. K. Gess) 7 ♀♀, ♂, 9.xi.1972 (F. W. and S. K. Gess) 3 ♀♀; Grahamstown, Hilton, 1—4.xii.1970 (F. W. Gess—Malaise Trap) ♀; Grahamstown, Kranzdrif, 5.xi.1967 (C. Jacot-Guillarmod) ♀; Grahamstown, Plutos Vale, 8.xi.1964 (C. Jacot-Guillarmod) ♀; Grahamstown, Strowan, 9.xii.1968, 2 ♀♀, ♂, 11.xii.1968, ♀, 8.i.1969, ♀, 30.xi.1970, ♀, 2 ♂♂ (all F. W. Gess), 20.xii.1970 (C. Jacot-Guillarmod) ♂; 4 miles NE of

Steytlerville, 12.xi.1968 (J. G. Rozen and E. Martinez) ♀, ♂; Thorngrove, 29.i.1960 (L. Naerly) ♀; Victoria West, 10.i.1965 (H. N. Empey) 19 ♀♀, ♂; Waterford, 13.i.1965 (H. N. Empey) 8 ♀♀, ♂; 4 miles E of Waterford, 29.x.1967 (C. Jacot-Guillarmod) ♀; Willowmore, 12.i.1965 (H. N. Empey) ♂.
Orange Free State: Kroonstad, 10.i.1965, 3 ♀♀, 2 ♂♂, 16.i.1965, ♂, 23.i.1965, ♀, 27.i.1965, ♀, xii.1965, ♀, ♂, 31.xii.1965, ♂, 21.xii.1966, ♂ (all D. J. Brothers).

Ceramius bicolor (Thunberg)
Cape Province: Fullarton, Willowmore, 30.x.1967, 6 ♀♀, ♂; near Fullarton, Willowmore, 30.x.1967, ♂; Willowmore, 31.x.1967, ♀ (all C. Jacot-Guillarmod); 18 miles SE of Touwsrivier, 12.xi.1966 (J. G. Rozen) 2 ♀♀.

Ceramius linearis Klug
Cape Province: Alicedale, New Year's Dam, 22.xi.1970 (J. G. H. Londt) 10 ♂♂, 2.xii.1970 (J. G. H. Londt) 4 ♀♀, 4 ♂♂, same date (F. W. Gess) 3 ♀♀, 10 ♂♂, 16.xii.1971 (F. W. Gess) 2 ♀♀, 2 ♂♂; Carlisle Bridge, xii.1971 (R. Bayliss) ♀; Grahamstown, 13.vi.1959 (E. McC. Callan) ♀, 15.xii.1959 (E. McC. Callan) ♀, 12.xi.1960 (E. McC. Callan) ♀, 27.xii.1960 (E. McC. Callan) ♂, 8.xii.1964 (D. J. Brothers) 2 ♂♂, 18.xii.1969 (J. G. H. Londt) ♀; Grahamstown, Belmont Valley, 4.xii.1969 (J. G. H. Londt) ♀, 15.xii.1971 (J. G. H. Londt) ♀, ♂; Grahamstown, Boskey Dell, 24.ix.1967 (C. Jacot-Guillarmod) ♀; Grahamstown, Clifton, 17.x.1972 (F. W. and S. K. Gess) 11 ♀♀, 10 ♂♂, 26.x.1972 (F. W. and S. K. Gess) 24 ♀♀, 46 ♂♂, 27.x.1972 (F. W. and S. K. Gess) 2 ♂♂, 7.xi.1972 (F. W. and S. K. Gess) 8 ♀♀, 10 ♂♂, 9.xi.1972 (F. W. and S. K. Gess) 7 ♀♀, 13 ♂♂; Grahamstown, Hilton, 22.x.1967 (D. J. Brothers) 3 ♂♂, same date (C. Jacot-Guillarmod) ♀, 5.xi.1969 (C. Jacot-Guillarmod) ♂, 2—5.xi.1970, ♀, 5—9.xi.1970, ♀, 12—30.xi.1970, ♀, 3 ♂♂, 1—4.xii.1970, ♀, ♂ (all F. W. Gess—Malaise Trap); Grahamstown, Hounslow, 22.xii.1966 (C. Jacot-Guillarmod) ♀; Grahamstown, Plutos Vale, 8.xi.1964 (C. Jacot-Guillarmod) ♂; Grahamstown, Settlers' Dam, 30.xii.1971 (F. W. Gess) 4 ♀♀, 5 ♂♂; Grahamstown, Vaalvlei (Mosslands), xii.1971 (R. Bayliss) 2 ♂♂; Kenton-on-Sea, 15—30.xi.1970 (R. A. Jubb—Malaise Trap) ♂, 21.xi.1970 (J. G. H. Londt) 2 ♂♂, 1—8.xii.1970 (R. A. Jubb—Malaise Trap) ♀, xii.1971 (R. A. Jubb—Malaise Trap) ♀, i.1972 (R. A. Jubb—Malaise Trap) 2 ♀♀; Tharfield, 1906 (Mrs. G. White) ♂; Victoria West, 10.i.1965 (H. N. Empey) ♀; Willowmore, 12 i.1965 (H. N. Empey) ♂.

Ceramius capicola Brauns
Cape Province: Alicedale, New Year's Dam, 2.xii.1970 (F. W. Gess) ♀, 2 ♂♂, same date (J. G. H. Londt) ♀, ♂; Grahamstown, 18.xi.1958 (C. Jacot-Guillarmod) 4 ♂♂, 8.xii.1964 (D. J. Brothers) 4 ♂♂, 7.i.1967 (C. Jacot-Guillarmod) 5 ♀♀; Grahamstown, Belmont Valley, 5.xii.1969 (J. G. H. Londt) ♀, 14—20.xii.1971 (F. W. Gess—Malaise Trap) ♀, 15.xii.1971 (J. G. H. Londt) 2 ♂♂, 28.xii.1971—3.i.1972 (F. W. Gess—Malaise Trap) ♀; Grahamstown, Bible Monument, 6.ii.1969 (F. W. Gess) ♀; Grahamstown, Clifton, 26.x.1972 (F. W. and S. K. Gess) 2 ♂♂, 27.x.1972 (F. W. and S. K. Gess) ♀, 7.xi.1972 (F. W. and S. K. Gess) 3 ♂♂, 9.xi.1972 (F. W. and S. K. Gess) ♂; Grahamstown, Cradock Dam, 29.xi.1964 (C. Jacot-Guillarmod) 12 ♀♀, 13 ♂♂; Grahamstown, Hilton, 19.xi.1969 (F. W. Gess) 2 ♀♀, 4 ♂♂, 12—30.xi.1970, ♀, 4 ♂♂, 1—4.xii.1970, 2 ♂♂, 1—18.xii.1970, ♀, 3 ♂♂, 19—31.xii.1970, 2 ♂♂ (all F. W. Gess—Malaise Trap); Grahamstown, Strowan, 26.xii.1967 (C. Jacot-Guillarmod) 10 ♀♀, 3 ♂♂, 7.i.1968 (C. Jacot-Guillarmod) ♀, 27.xi.1968, 26 ♀♀, 37 ♂♂, 9.xii.1968, 3 ♀♀, ♂, 11.xii.1968, 11 ♀♀, 8 ♂♂, 8.i.1969, 13 ♀♀, ♂, 16.i.1969, 4 ♀♀, ♂, 22.i.1969, 2 ♀♀, 4 ♂♂, 6.ii.1969, 3 ♀♀, ♂, 18.ii.1969, 2 ♀♀, 12.xi.1969, 11 ♂♂, 22.xii.1969, ♀, ♂, 30.xi.1970, 3 ♀♀, 7 ♂♂ (all F. W. Gess), 20.xii.1970 (C. Jacot-Guillarmod) ♂, 19.xii.1971 (F. W. Gess) 6 ♀♀, 2 ♂♂.

Orange Free State: Kroonstad, 26.xii.1964, ♀, 5.i.1965, 2 ♀♀, ♂, 27.xi.1965, ♂ (all D. J. Brothers).

Ceramius socius Turner
Cape Province: 48 miles E of Barrydale, 13.xi.1966, ♀; 27 miles E of Montagu, 13.xi.1966, 3 ♀♀; 13 miles SW of Touwsrivier, 11.xi.1966, ♀; 18 miles SE of Touwsrivier, 12.xi.1966, 2 ♀♀; 5 miles NE of Worcester, 11.xi.1966, ♂ (all J. G. Rozen); 10 miles SW of Touwsrivier, 8.xi.1968 (J. G. Rozen and E. Martinez) 5 ♂♂.

TABLE LISTING FLOWERS VISITED BY *CERAMIUS* SPECIES IN SOUTH AFRICA

Wasp species	Plant species and family	Locality	Date	Authority and reference
beyeri Brauns	*Mesembryanthemum aitonis* Jacq. (white flowers) MESEMBRYANTHEMACEAE	Bible Monument, Grahamstown	16.i.1969	F. W. Gess
bicolor (Thunberg)	"Mesems" (whitish flowers) MESEMBRYANTHEMACEAE	Die Bos Rd. (30 m. E of Clanwilliam	19.ix.1966	C. D. Michener (Gess, 1968: 13)
	Psilocaulon acutisepalum (Berger) N.E. Br. (pink flowers) MESEMBRYANTHEMACEAE	Olifants River between Klawer and Clanwilliam	14—15.x. 1967	F. W. and W. H. R. Gess (Gess, 1968: 13)
capicola Brauns	*Aridaria plenifolia* (N.E. Br.) Stearn (cream flowers) MESEMBRYANTHEMACEAE	New Year's Dam, Alicedale	2.xii.1970	F. W. Gess and J. G. H. Londt
	Mesembryanthemum aitonis Jacq. (white flowers) MESEMBRYANTHEMACEAE	Bible Monument, Grahamstown	6.ii.1969	F. W. Gess
	Mestoklema tuberosum (L.) N.E. Br. (pinkish-purple flowers) MESEMBRYANTHEMACEAE	Strowan, Grahamstown	6.ii.1969	F. W. Gess
			18.ii.1969	F. W. Gess
	Ruschia sp. (white flowers) MESEMBRYANTHEMACEAE	Strowan, Grahamstown	27.xi.1968	F. W. Gess
			9.xii.1968	F. W. Gess
			11.xii.1968	F. W. Gess
			8.i.1969	F. W. Gess
			16.i.1969	F. W. Gess
			12.xi.1969	F. W. Gess
			22.xii.1969	F. W. Gess
			30.xi.1970	F. W. Gess
			19.xii.1971	F. W. Gess
		Belmont Valley, Grahamstown	4.xii.1969	J. G. H. Londt
	Ruschia sp. (purple flowers) MESEMBRYANTHEMACEAE	New Year's Dam, Alicedale	2.xii.1970	J. G. H. Londt
	Berkheya sp. (yellow flowers) COMPOSITAE	Thaba Nchu	1.xii.1952	C. Jacot-Guillarmod (Richards, 1962: 117)
cerceriformis de Saussure (= *schulthessi* Brauns)	*Mesembryanthemum* sp. (*senso lato*) (purple flowers) MESEMBRYANTHEMACEAE	6 miles S. of Garies	7—8.x.1967	F. W. and W. H. R. Gess (Gess, 1968: 10)

(*continued*)

TABLE LISTING FLOWERS VISITED BY *CERAMIUS* SPECIES IN SOUTH AFRICA

Wasp species	Plant species and family	Locality	Date	Authority and reference
	Mesembryanthemum crystallinum (L.) N.E. Br. (white flowers) MESEMBRYANTHEMACEAE	Willowmore	31.x.1967	C. Jacot-Guillarmod
jacoti Richards	*Pteronia incana* DC (yellow flowers) COMPOSITAE	Brandrivier road, 2 miles from junction with Ladismith—Riversdale road	30.ix.1972	C. Jacot-Guillarmod
lichtensteinii (Klug)	*Aridaria* sp. (cream flowers) MESEMBRYANTHEMACEAE	Clifton, Grahamstown	7.xi.1972	F. W. and S. K. Gess
	Mesembryanthemum aitonis Jacq. (white flowers) MESEMBRYANTHEMACEAE	Bible Monument, Grahamstown	16.i.1969	F. W. Gess
	Ruschia sp. (white flowers) MESEMBRYANTHEMACEAE	Strowan, Grahamstown	11.xii.1968 8.i.1969 30.xi.1970	F. W. Gess F. W. Gess F. W. Gess
	Ruschia sp. (purple flowers) MESEMBRYANTHEMACEAE	New Year's Dam, Alicedale	2.xii.1970	F. W. Gess and J. G. H. Londt
linearis Klug	*Aridaria* sp. (cream flowers) MESEMBRYANTHEMACEAE	Clifton, Grahamstown	17.x.1972 26.x.1972 27.x.1972 7.xi.1972 9.xi.1972	F. W. and S. K. Gess F. W. and S. K. Gess F. W. and S. K. Gess F. W. and S. K. Gess F. W. and S. K. Gess
	Aridaria dyeri L. Bol. (cream flowers) MESEMBRYANTHEMACEAE	New Year's Dam, Alicedale	2.xii.1970	F. W. Gess
	Aridaria plenifolia (N.E. Br.) Stearn (cream flowers) MESEMBRYANTHEMACEAE	New Year's Dam, Alicedale	2.xii.1970 16.xii.1971	F. W. Gess and J. G. H. Londt F. W. Gess
	Malephora sp. probably *M. mollis* (Ait.) N.E. Br. (cream flowers) MESEMBRYANTHEMACEAE	Clifton, Grahamstown	26.x.1972	F. W. and S. K. Gess
	Mesembryanthemum aitonis Jacq. (white flowers) MESEMBRYANTHEMACEAE	Settlers' Dam, Grahamstown	30.xii.1971	F. W. Gess
	Ruschia sp. (purple flowers) MESEMBRYANTHEMACEAE	New Year's Dam, Alicedale	2.xii.1970	J. G. H. Londt
	Ruschia sp. (white flowers) MESEMBRYANTHEMACEAE	Belmont Valley, Grahamstown	5.xii.1969	J. G. H. Londt
toriger von Schulthess	"Blue-rayed Compositae" COMPOSITAE	Die Bos Rd. (30 miles E. of Clanwilliam)	19.ix.1966	C. D. Michener (Gess, 1968: 9)

Note: In the above table the generic names of the plants belonging to the Mesembryanthemaceae are those used by Herre (1971). This author is followed also with respect to the family name—thus in the present paper the name Mesembryanthemaceae is substituted for the name Aizoaceae used in previous papers (Gess, 1965 and 1968).

NESTING SITES AND NEST SUPERSTRUCTURES

Nesting sites of both *C. lichtensteinii* (Klug) and *C. capicola* Brauns occur at Strowan, about two miles north-west of Grahamstown. The sites favoured for nesting are open, bare patches of hard clay soil situated in low scrub including various low-growing Mesembryanthemaceae such as species of *Ruschia* and *Mestoklema*. The nesting sites are thus located in close proximity to the plants whose flowers are visited by the wasps for the dual purpose of obtaining their own nourishment and collecting the pollen and nectar utilised by the females in provisioning their young. The same close proximity of nesting sites to forage plants was observed in the same two species at Alicedale and also in *C. bicolor* (Thunberg) at the Olifants River between Klawer and Clanwilliam. In all cases the nesting sites were found to be situated not far from water; at Alicedale only a few feet away from the edge of a large reservoir, at Olifants River less than one hundred yards from a small stream and at Strowan somewhat further than that from a farm dam. The need for water in nest construction has been indicated by Brauns (1910:446).

In *C. capicola*, which nests in populous colonies, nesting appears to take place at the same site year after year, providing the area has not been disturbed. In this species males appear in numbers shortly before the females and are present at the nesting site for most of the flight period of the latter, becoming scarcer as the season advances.

Some time after the females have commenced excavating their burrows in the soil, entrance tubes or chimneys are built surmounting the mouths of the latter. These chimneys appear to be fairly characteristic for each species. The inside diameter of the chimney is determined largely by the size of the wasp which builds it. The bore of the chimney built by *capicola* is thus much narrower (about 4 mm) than that built by *lichtensteinii* (about 7 mm). An aspect of the architecture which is not dictated by the build of the wasp, however, is the orientation of the chimney relative to the ground.

It has been noted for *bicolor* (Thunberg) by Brauns (1910:387) (under the name *karooensis* Brauns) and by Gess (1968:13 and Pl. 1) that the chimney does not project freely into the air but is applied to the ground and is thus incomplete as the underside is formed by the ground itself.

The chimney built by *capicola* at Strowan is always free of the ground and has a complete underside (Plate 1). While the base of the chimney may vary from almost vertical to strongly slanting, various degrees of curvature of the structure as a whole serve to bring the opening at its end close to the ground to one side of the mouth of the burrow. The more nearly vertical the chimney is initially, the stronger the curvature. The wasp when returning to the nest alights on the ground in front of the opening, steps up and walks into and down the length of the chimney. This description does not agree with that given by Brauns (l.c.) according to which the chimney of *capicola* is of the same pattern as that of *bicolor* described above. It is however possible that that pattern may be produced when a chimney begins at an extreme slant but this has not been seen at Strowan.

The chimney built by *lichtensteinii* at Strowan is, as previously described by Brauns (1910:445), complete and free of the ground, straight or only very slightly curved, and projects more or less vertically upwards (Plate 2). The opening at its end is thus more or less above the mouth of the burrow. Activity at a single nest may extend over several weeks and a chimney may be replaced if broken. At Strowan a burrow without a chimney located on 11.xii.1968 had by 8.i.1969 when next examined been fitted with one; this chimney was then removed but had been replaced by 16.i.1969 when again examined. The chimney of a second burrow removed on 8.i.1969 had been replaced by 22.i.1969 when re-examined. At Strowan *lichtensteinii* was found to nest singly rather than in colonies. One burrow and chimney of this species was found in the middle of a populous colony of *capicola*.

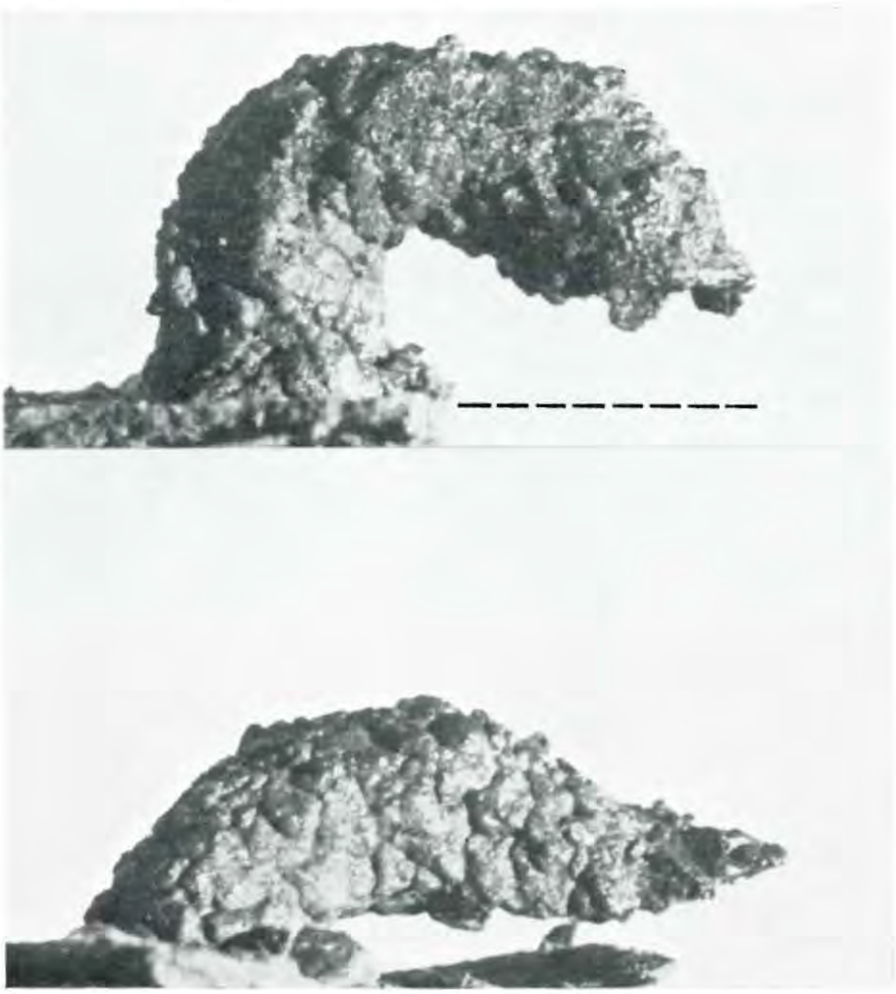


Plate 1. *Ceramius capicola* Brauns, nest superstructures (× 5,4) in lateral view. (The dashed line indicates the position of the surface of the ground.)

PARASITES

Allocoelia capensis Smith (Chrysididae) was recorded by Brauns (1910:446) as a parasite of *C. lichtensteinii* (Klug) in whose cells it develops. While this species has not been met with in the field, a related species, *Allocoelia latinota* Edney, has on several occasions been observed and caught at the nesting sites of *C. capicola* Brauns. Thus it was found associated with *capicola* Brauns by Jacot-Guillarmod at Grahamstown (Cradock Dam) on 29.xi.1964 and by the author at Grahamstown (Strowan) on 27.xi.1968, 9.xii.1968, 11.xii.1968 and 30.xi.1970. Londt while collecting *Ceramius* species (*lichtensteinii, linearis* and *capicola*) at Alicedale (New Year's Dam) on 2.xii.1970 obtained a specimen of the parasite while a further specimen

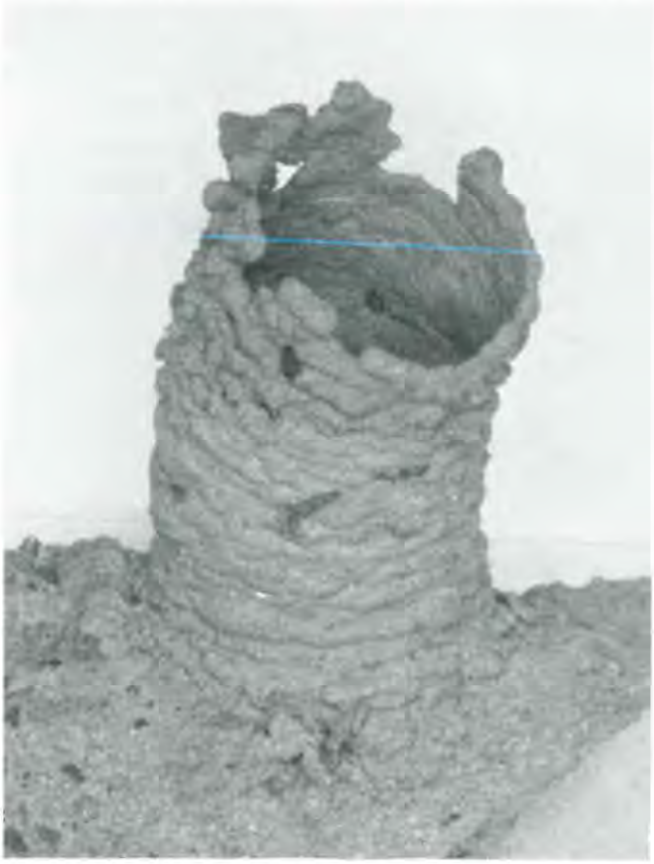


Plate 2. *Ceramius lichtensteinii* (Klug), nest superstructure (× 5).

was caught by Malaise Trap at Kenton-on-Sea in the period 1—8.xii.1970. As only *linearis* Klug has been recorded from the latter locality it would seem likely that this species is also host to *A. latinota* Edney.

In the description of *A. latinota*, Edney (1947:199) states that the pronotum is pale ferruginous. The present series of thirteen specimens shows that within a single population the pronotum of various individuals may vary from almost completely pale ferruginous, through various intermediate conditions, to totally black.

KEY TO THE SOUTH AFRICAN SPECIES OF *CERAMIUS* LATREILLE

Since the publication of Richards' account of the Masaridae (1962) papers by Gess (1965, 1968 and present paper) dealing with the South African species of the genus *Ceramius* have included the following changes and additions:

1. The sinking of *schulthessi* Brauns into synonymy with *cerceriformis* de Saussure. (present paper)

2. The raising out of possible synonymy with *lichtensteinii* (Klug) of *rex* de Saussure (1965) and the description of the previously unknown male. (present paper)
3. The removal from *peringueyi* Brauns of a male assigned to that species by Richards and the inclusion of this male together with a previously undescribed female in a new species, *richardsi* Gess (1965).
4. The description of both sexes of a new species, *micheneri* Gess (1968), of the previously unknown female of *clypeatus* Richards (1965), and the males of *metanotalis* Richards (1965) and *toriger* von Schulthess (1968).

At present nineteen South African species are recognised, of which only *peringueyi*, whose male has still to be collected, is not known in both sexes.

The following key to species based on that published by Richards is an attempt to provide a simplified version applying only to the South African (in fact Ethiopian) species but incorporating the above changes and additions.

1\. Mid tibia with one spur 2
— Mid tibia with two spurs 8
2\. Propodeum rounded. . . . . *bicolor* (Thunb.)
— Propodeum with dorsal angles produced into strong spines 3
3\. Males 4
— Females 6
4\. Fore trochanter with parallel-sided process, truncate at end . . . . . *linearis* Klug
— Fore trochanter with spatulate process 5
5\. Antennal segment 12 with apex narrowly black, somewhat thick, apex truncate *socius* Turner
— Antennal segment 12 entirely pale, thinner, narrowed to apex . . *capicola* Brauns
6\. Sparsely punctured part of frons spreading more upwards and sidewards, area between ocelli and eyes shining and clearly less closely punctured than adjacent parts *socius* Turner
— Sparsely punctured part of frons not spreading so much upwards and sideways, area between ocelli and eyes rarely with wide smooth interstices 7
7\. Larger; first gastral tergite longer, not so transverse (less than twice as wide as long). Propodeal spines larger . . . . *linearis* Klug
— Smaller; first gastral tergite shorter, strongly transverse (more than twice as wide as long). Propodeal spines smaller . . . . *capicola* Brauns
8\. Sides of metanotum with an acarinarium produced by the growth of the front margin over the usual lateral depression, leaving a small entrance on each side 9
— Lateral depressions of metanotum uncovered or at most partly filled in 11
9\. Entrance to acarinarium narrow throughout, slit-like, clearly narrower than part of metanotum in front of it . . . . *metanotalis* Richards
— Entrance to acarinarium wide at least laterally, of about same width as part of metanotum in front of it 10
10\. Entrance to acarinarium about twice longer than wide, widening laterally. Male with preapical lateral keels on sternite 4 . . . . *caffer* de Saussure
— Entrance to acarinarium about four times longer than wide, width nearly constant throughout, only slightly wider laterally. Male without preapical lateral keels on sternite 4 . . . . *rex* de Saussure
11\. Gastral sternite 1 ventrally truncate posteriorly, tergite 1 somewhat scale-like, very transverse, narrower dorsally than ventrally, deeply separated from 2. Propodeum always rounded 12

— Gastral sternite 1 almost flat, not truncate, tergite 1 not scale-like, not deeply separated from 2. Propodeum variable 14

12. Propodeal spiracle large and oval. Eyes strongly emarginate. Clypeus with strong lateral wings . . . . *lichtensteinii* (Klug)

— Propodeal spiracle narrow as usual. Eyes weakly emarginate. Clypeus without lateral wings 13

13. Claws toothed. Scutellum less margined, dorsal axillary sclerite more angular, almost spine-like. Prescutal furrow rather strong . . . . *beyeri* Brauns

— Claws untoothed. Scutellar disk clearly margined, dorsal axillary sclerite less angular. Prescutal furrows weak . . . . *damarinus* Turner

14. Propodeum with spine-like processes or at least with very blunt angular projections 15

— Propodeum rounded 19

15. Clypeus of both sexes unmodified. Male with strong processes on sternites 3, 7 and 8 16

— Clypeus of both sexes much modified, with apical teeth. Male with sternite 3 simple 18

16. Males (this sex not known in *peringueyi* Brauns) . . . . . . *cerceriformis* Sauss. OR *peringueyi* Brauns

— Females 17

17. Clypeus shorter, one and one-third times as long as scape, ventral margin straight, angles more marked. Depression in axilla deeper, defined outwardly by a strong keel *peringueyi* Brauns

— Clypeus longer, one and two-third times as long as scape, ventral margin a little rounded. Depression in axilla much shallower, not so closely defined outwardly by a keel . . . . *cerceriformis* Sauss.

18. Clypeus strongly raised, then bent at right angles, with two small curved diverging teeth just below the bend . . . . *richardsi* Gess

— Clypeus elongate, disc somewhat longitudinally impressed, apex with four small upturned teeth . . . . *clypeatus* Richards

19. Clypeus almost quadrate, very slightly shorter at midline than wide at ventral margin, its sides slightly divergent distally. Male antennae narrowed towards apex and bent in a half spiral; parameres straight and spiniform; process of fore-trochanter wide, flattened and parallel-sided . . . . *micheneri* Gess

— Clypeus considerably longer at midline than wide at ventral margin, its sides clearly convergent distally. Male antennae with last segment excavate beneath forming a sometimes strong hook; parameres stout, hardly spiniform; process of fore-trochanter either racket-shaped or with tip produced into a curved projection, or recurved . . 20

20. Males 21

— Females 24

21 Antennae with segment 12 much shorter and narrower than 11, barely hook-like. Fore trochanter with process racket-shaped . . . . *braunsi* Turner

— Antennae with segment 12 proximally as wide as 11 but almost at once strongly narrower, forming a strong, curved, flattened hook longer than 11. Fore trochanter with process parallel sided, tip narrower and curved or recurved and hook-like . . 22

22. Gaster with sternite 3 with a low bituberculate prominence. Tergite 7 with sides converging, apex rounded laterally and narrowly emarginate in middle and thus appearing bilobed . . . . *nigripennis* Sauss.

— Gaster with sternite 3 with differently formed prominence. Tergite 7 flattened, with sides subparallel or even slightly divergent distally, apically truncate or subtruncate with distinct lateral angles 23

23. Prominence of gastral sternite 3 wide, transverse, lamellate distally, backwardly directed . . . . *jacoti* Richards

— Prominence of gastral sternite 3 narrow, transverse, flanked anterior-laterally at each end by a tubercle and posteriorly by a raised platform . . . . *toriger* Schulthess
24. Gaster dull, not perceptibly punctured . . . . *nigripennis* Sauss.
— Gaster shining, finely punctured 25
25. Tergite 6 subtruncate, with a marked transverse impression . . . *toriger* Schulthess
— Tergite 6 rounded, not transversely impressed 26
26. Sternite 6 flat, with a distinct angular emargination at apex. Scutellum not margined (disc and sides therefore meeting in a curve), with a weak longitudinal prominence *braunsi* Turner
— Sternite 6 raised at apex, without a distinct angular emargination. Scutellum crenulately margined (disc and sides therefore meeting at an angle), with a well marked longitudinal prominence on posterior half . . . . *jacoti* Richards

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