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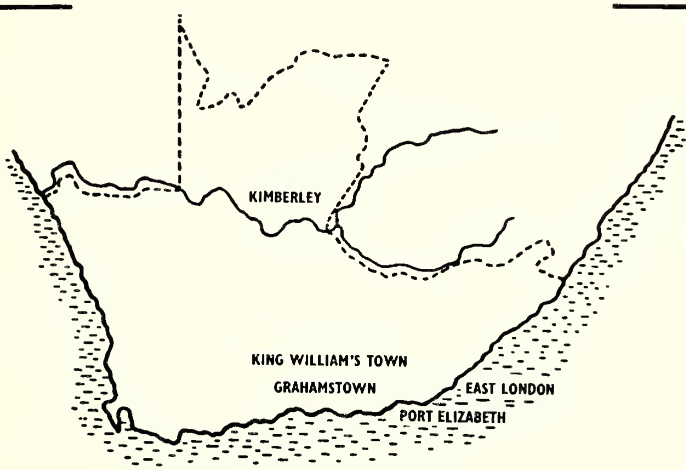

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Ethological studies of Bembecinus cinguliger (Smith) and B. oxydorcus (Handl.) (Hymenoptera: Sphecidae), two southern African turret-building wasps.

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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-

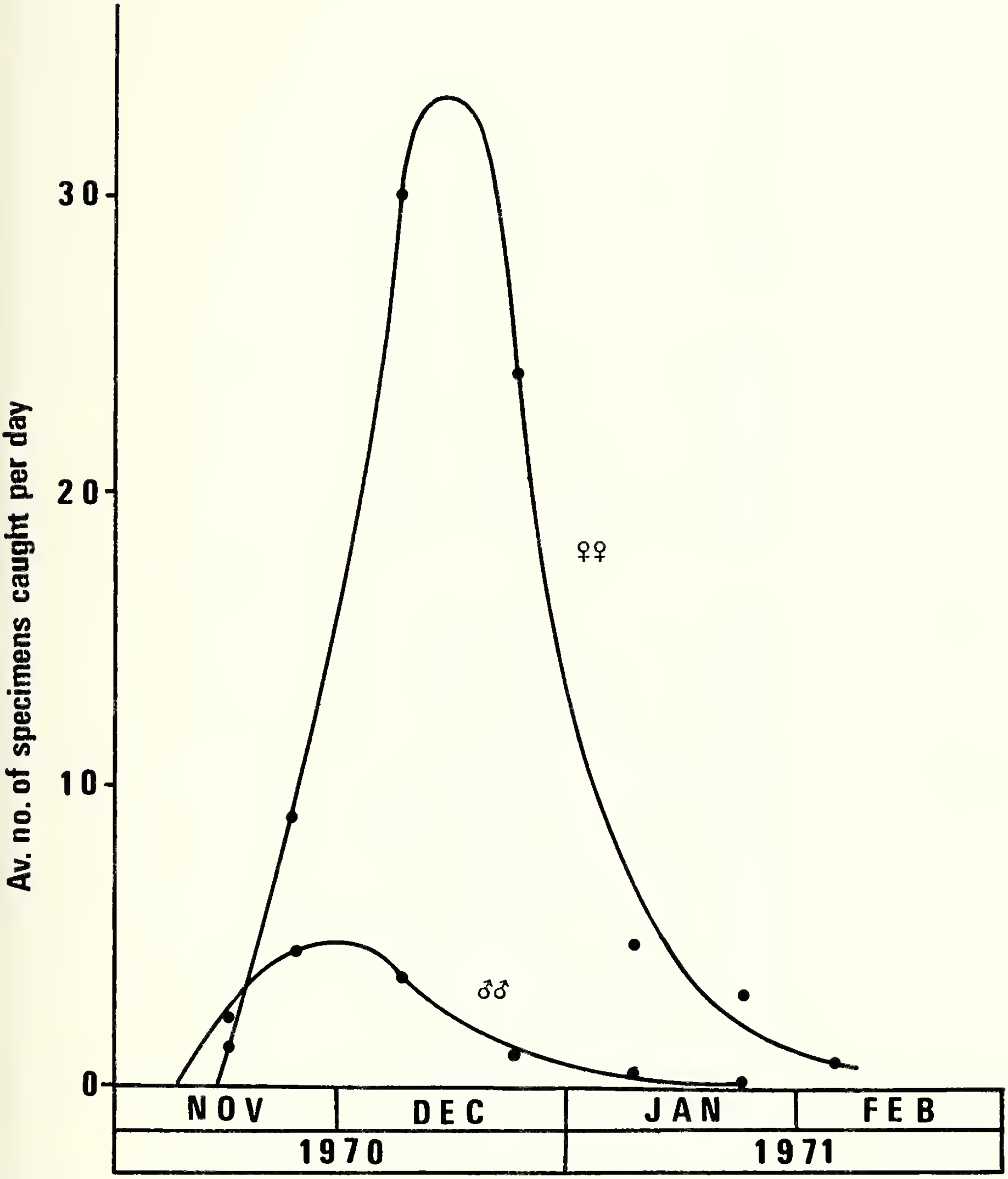


Fig. 1. Graph showing the average numbers of specimens of *Bembecinus cinguliger* (Smith) caught per day by three Malaise Traps at Hilton during the period Nov. 1970 to Feb. 1971.

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).

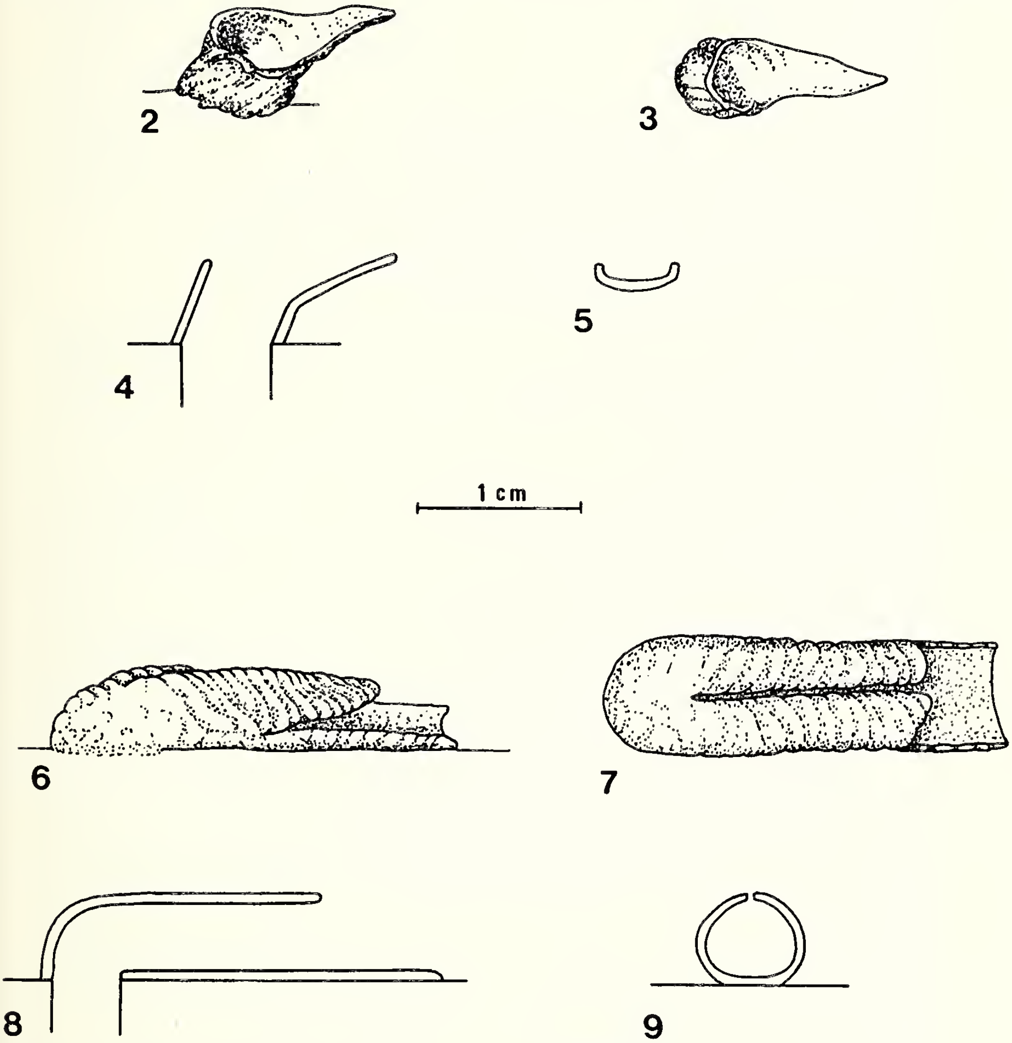
It is noteworthy that the situation of the sleeping place was at a considerable distance from the nearest nesting areas and that the soil near the watercourse was sandy and thus unsuitable for nesting. It appears that the members of the sleeping cluster were drawn from a wide area as the number present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

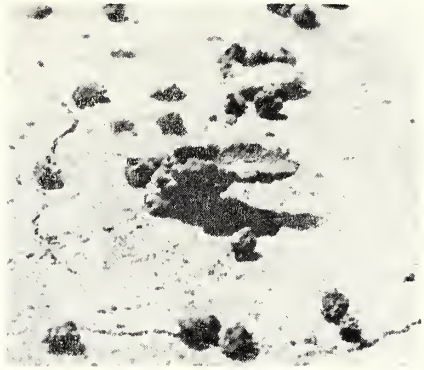
At all times the absence or presence of wasps at the tussock could be correllated with the reverse situation at the nesting sites.

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)

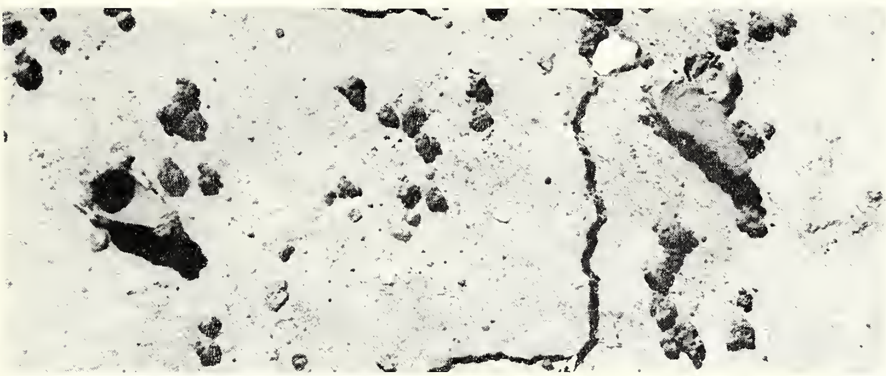


Plate 9. Hilton, 8 iii.1974. Nest turrets of *B. oxydorcus* (Handl.) from above. That on left open, that on right sealed. (x1,3)

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).

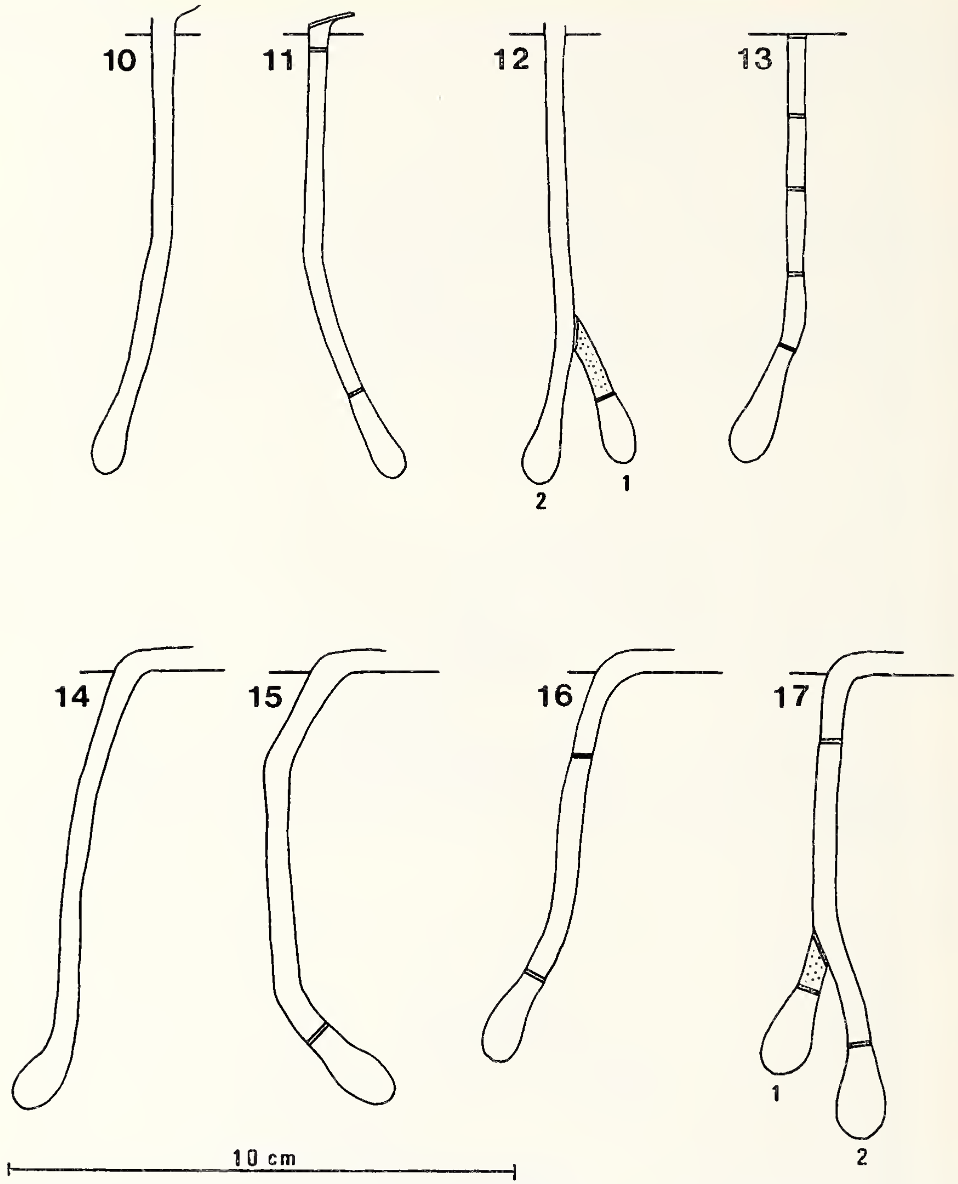
DESCRIPTION OF THE SUBTERRANEAN BURROW

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 1 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 atypieal, 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 aeute 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 speeies 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 eonnection 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 speeies 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 suecessful 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 eonditions 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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