Wasps and bees in southern Africa

Sarah K. Gess and Friedrich W. Gess

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by
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Pretoria
2014

SANBI Biodiversity Series

The South African National Biodiversity Institute (SANBI) was established on 1 September 2004 through the signing into force of the National Environmental Management: Biodiversity Act (NEMBA) No. 10 of 2004 by President Thabo Mbeki. The Act expands the mandate of the former National Botanical Institute to include responsibilities relating to the full diversity of South Africa's fauna and flora, and builds on the internationally respected programmes in conservation, research, education and visitor services developed by the National Botanical Institute and its predecessors over the past century.

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Dedication

For Howard Evans, Karl Krombein and Charles Michener who inspired and encouraged us.

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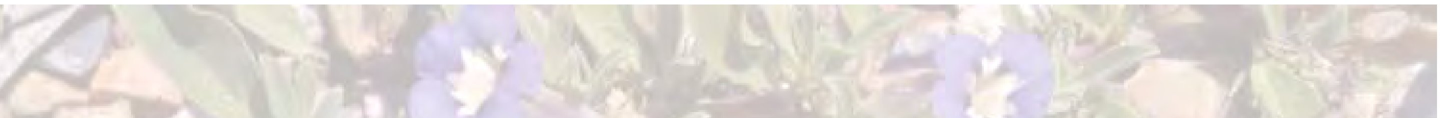

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Introduction

The importance of wasps and bees

What are the perils faced by wasps and bees in the semi-arid to arid areas of southern Africa? How do these perils impact wasps and bees? Why? Why should we be asking these questions?

In the past 20 years there has been mounting awareness that, with the increasing pressure on the land by people, pollinators worldwide are in decline and that this decline is likely to have an impact on food production and conservation of biodiversity. For many years, it has been known that most plants require pollen vectors to achieve pollination, and that insects from several orders are commonly involved. These include Hymenoptera (most notably bees and wasps), Lepidoptera (butterflies and moths), Diptera (flies) and Coleoptera (beetles). However, the requirements for their survival are diverse and to a large degree poorly understood.

Furthermore, there is increasing awareness and discussion of the imbalances caused by the loss of predatory birds and mammals but, undoubtedly because of their small size, insect predators, which are of no less importance, do not attract as much attention.

With this awakening awareness John LaSalle and Ian Gauld organised a symposium on Hymenoptera and biodiversity for the 1990 congress of the International Society of Hymenopterists. The presentations were gathered together in a single volume (LaSalle & Gauld 1993) published by the Commonwealth Agricultural Bureau International. It was for this symposium that we presented the first evaluation of the effects of increasing land utilisation on species representation and diversity of wasps and bees in the semi-arid areas of southern Africa.

The International Pollinator Initiative (IPI) was instituted by the Convention on Biological Diversity (CBD) in 1996 in order to generate understanding, promote conservation and build the requirements of pollinators into land management. Regional initiatives followed. One such, the African Pollinator Initiative (API), came into being in 1999. Much has been said to popularise the cause. It is said that we can thank a pollinator for one out of every three bites of food. Although many staple foods are cereals (wind-pollinated grasses), most other food plants eaten by humans and stock require animal pollination. Thus, we depend on diverse pollinators not only for the fruit and vegetables we eat, but also in considerable measure for meat. In this regard, two invited articles on the Karoo, its insect pollinators and the perils they face were prepared (Gess 2001, 2002).

In order to maintain essential populations of plants and animals, it is necessary to have an understanding of their requirements. With the institution of the Conservation Farming Project in South Africa by the South African National Biodiversity Institute (SANBI) (Donaldson 2002) the scarcity of this understanding is being emphasized (e.g. Donaldson *et al.* 2002).

About this book

This book is divided into two sections.

In Section I we present, as an example, the diverse requirements of wasps and bees—important pollinators and, in the case of wasps, predators—in the semi-arid to arid areas of southern Africa. This has been the subject of our own research for the past 40 years. It has been our aim to obtain a knowledge and understanding for wasps and bees, principally solitary species (which form the vast majority), regarding their:

- Diversity.
- Distribution.
- Roles in the ecological system.
- Flower and, where applicable, prey preferences.
- Importance as pollinators and, where applicable, predators.
- Nests and nesting requirements.

Furthermore, it has also been our goal to:

- Formulate guidelines for maintaining essential populations in areas utilised for farming, conservation and ecotourism.
- To generate an awareness and appreciation of the diversity and value of aculeate wasps and bees at all levels of society.

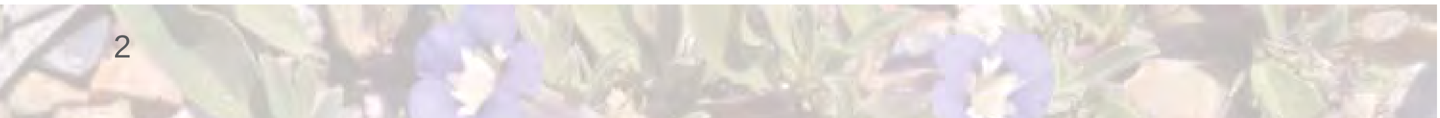
Our approach has been to:

- Sample wasps and bees to establish alpha, beta and gamma diversity.
- Sample wasps and bees together with all other insects visiting plants in flower.
- Observe the behaviour of flower visitors to establish relationships between flowers and insects.
- Observe nesting leading to the establishment of the nature of nests and nesting requirements.
- Discover the nature, identity and provenance of provision required for rearing young—in the case of provision being pollen and nectar, the degree of specificity.
- Investigate parasites, nest parasites and usurpers.
- Investigate the manner of water collection (when water is required for nesting) and what human activities make water unavailable.

In Section II we present a synthesis of what is known of nesting, provisioning and associates of bees, pollen wasps and hunting wasps in southern Africa. It is inevitable that, in an undertaking of this nature, some observations have been overlooked, not only those of others but of ourselves.

Classifications of wasps, bees and plants

The wasps and bees make up part of the insect order Hymenoptera, a group of enormous size with more than 100 000 described species (Goulet & Huber 1993). The Hymenoptera are classified into two major groups, the Symphyta, commonly known as sawflies, with free living



phytophagous larvae and the Apocrita subdivided into Parasitica, including parasitic, gall and fig wasps, and Aculeata, including 'true' wasps, ants and bees. The Aculeata are so named because the ovipositor has been modified to become a sting. For ease of reading the true wasps will be referred to hereafter as wasps.

In the present work the classification of wasps and bees at superfamily level and of wasps at family level follow that used by Goulet & Huber (1993). Below superfamily level more recent works have been followed:

- For the bees, Apoidea, Apiformes, we followed Michener (2007), Eardley *et al.* (2010) and Eardley & Urban (2010).
- For the wasps, Masarinae (pollen wasps) we used Carpenter (2001).
- For the wasps, Eumeninae we used Carpenter *et al.* (2009, 2010a, 2010b).
- For Apoidea, Spheciformes we used Pulawski (2010).

With active ongoing phylogenetic research it has proved difficult to keep abreast of all the changes. Indeed, one finds lack of consistency between publications within superfamilies published in the same year. For example, Eardley *et al.* (2010) and Eardley & Urban (2010) show considerable variance.

The classification of the flowering plants followed is that of the Angiosperm Phylogeny Group (APG 1998). With active ongoing phylogenetic research on flowering plants there is a continuous shift in understanding the family boundaries. These changes can be followed on the Angiosperm Phylogeny Website at http://www.mobot.org/MOBOT/research/APweb.

The classifications of flowering plants as used in Leistner (2000) and Germishuizen & Meyer (2003) in the main but not in all instances follow APG (1998) and do not in all instances agree with each other.

Hartmann's (1991) collective term Mesembryanthema is used for all Aizoaceae which have petaloid staminodes, in fact for those plants commonly termed 'mesembs', formerly Mesembryanthemaceae. All other Aizoaceae are referred to as Aizoaceae, non-Mesembryanthema.

Identification of bees, pollen wasps and wasps

A number of references to literature useful for identifying southern African aculeate wasps and bees are provided in the APPENDIX.

Flower visiting records

Our analyses of flower visiting are mainly based on our own records and those of others whose material is housed in the Albany Museum. The database for this collection is included in this book enabling more detailed access to the specimen data. This includes determinations of the wasps and bees to species level, the full details of collecting localities, collecting times, collectors and in many cases more detailed determinations of the plants.

Morphology and life history of wasps and bees

Morphology of the adult

The complex structure of an adult wasp or bee, like that of all insects, has been built up by the modification of a simple segmented creature. An unmodified segment would basically have a dorsal and a ventral hard plate (the sclerites) joined by membranes and equipped with a pair of jointed appendages. The segments are grouped to form three distinct regions—the head, the thorax and the abdomen.

Head

The head is encased in a strongly sclerotized capsule in which the sclerites are fused. It is attached to the thorax by the flexible neck which makes it possible for the head to be turned freely, increasing the usefulness of eyes and jaws. The head bears a pair of antennae, jointed mouthparts, a pair of compound eyes, and usually three ocelli.

The compound eyes are generally large and composed of a great number of facets or retinal elements. The ocelli are grouped together centrally on the top or back of the head. Each consists of a group of visual cells beneath a common lens. It is known that they are light-sensitive but their exact function is not fully understood. They may have some relevance in the regulation of daily activity rhythms.

An antenna is composed of a basal segment, the scape, a one-segmented pedicel, and a flagellum. As a general rule in bees, wasps (including pollen wasps), other than Bethyloidea, a flagellum is composed of ten flagellomeres in females and eleven in males. The number of flagellomeres in the Bethyloidea, as a whole, ranges from eight to more than 17. In the Chrysididae there are 11 in both males and females. The antennae bear a wide variety of sensory cells derived from epidermal cells. They are for the reception of tactile and olfactory stimuli, and possibly of temperature and humidity. In appearance the antennae show considerable variation. Those of Pompilidae (Vespoidea) are long and thin, those of Scoliidae (Vespoidea) and spheciform Apoidea generally of moderate length and those of the Vespidae, particularly the Masarinae, have a tendency to be short and clubbed. Those of apiform Apoidea are short and markedly elbowed. The scape is relatively long compared with the flagellum.

The most noticeable mouthparts are the mandibles, or 'jaws'. These are heavily sclerotized, curved appendages of considerable strength. They articulate with the head capsule below the eyes and can only move in one plane, like a pair of pincers. They are variously toothed depending on their function, which may be biting, cutting, scraping, chewing or carrying, or a combination of these activities depending on the nature of nest construction and provisioning.

The maxillae and the labium are lightly sclerotized and bear segmented palps. Bees and wasps (including pollen wasps) use these structures principally for the uptake of liquids such as nectar and water, and in the case of hunting wasps, haemolymph (blood) from their prey.

Not to be confused with the above two sclerites are the clypeus and the labrum which surmount the mouth. The clypeus is strongly convex often having a beak-like appearance. The labrum is articulated on the lower surface of the clypeus and is extended to form a dorsal lip to the mouth. It bears numerous sensory setae.

It has been misleadingly stated that in the Aculeata it is only among the bees that long proboscises are found (Kevan & Baker 1983). This statement has often been repeated, however, although a short proboscis is characteristic of the majority of wasps, elongation of the proboscis has taken place in several wasp taxa, e.g. *Bembix* (Crabronidae, Bembicinae, Bembicini), *Ammophila* (Sphecidae, Ammophilinae) and *Raphiglossa* (Vespidae, Eumeninae). In pollen wasps (Masarinae) there has been little elongation of the mouthparts other than the glossa (the 'tongue' part of the labium). In some, most notably *Priscomasaris*, the glossa is relatively short. However, in the majority the glossa is markedly elongated, in many species of *Quartinia* being considerably longer than the wasp's length from the frons to the tip of the abdomen. Consequently, pollen wasps have the potential to obtain nectar from a wide range of flower forms including many in which the nectar is not readily accessible.

Thorax

The thorax consists of three segments, the prothorax anteriorly, mesothorax centrally, and metathorax posteriorly. As in all Hymenoptera the first abdominal segment is fused with the metathorax and is termed the propodeum.

As a general rule the meso- and metathoracic segments each bear a pair of wings. Apterous (wingless) females occur in the Mutillidae and Tiphiidae. The wings of insects are thin plate-like expansions of the integument which are strengthened by a framework of hollow sclerotized tubes known as veins. The arrangement of the veins is an important taxonomic character. The hind wings are smaller than the forewings and show considerable reduction in venation. The fore- and hind wings are strongly coupled in flight being held together by a row of hamulae (hooks) on the anterior margin of the hind wing which engage with the down-curved fold of the posterior margin of the forewing. In most species, when at rest, the wings uncouple and are folded one over the other across the insect's back. However, in many Vespidae the wings do not uncouple and in order for the wings to be folded, the forewings themselves fold longitudinally. The wings can be vibrated at astonishing speeds with 117 to 247 beats per second having been recorded (Sotavalta 1947 as quoted in Spradbery 1973).

Each of the three thoracic segments bears a pair of jointed legs. The legs are composed of the coxa which articulates with the thorax, trochanter, femur, tibia and generally five tarsal segments (tarsomeres), the most distal one bearing a pair of claws usually with a pad (the arolium) between them. The tibia bears one or two spurs at the apex. The spur of the forelegs is generally knife-like and fits against a setate or comb-like invagination at the base of the first tarsomere. Together these form an apparatus for cleaning the antennae, which are passed through it during preening. Preening takes place particularly frequently during nest building. The hind legs are equipped with a dense brush of setae on the inner surface of the tibia and sometimes on the basitarsus. This is used to clean the abdomen, wings, mid-legs and hind legs themselves.

Another development of setae has resulted in legs variously adapted to perform a variety of functions connected with nest construction and provisioning. The most obvious and best known are the pollen baskets on the hind legs of honeybees. Not all bees collect pollen on their hind legs but in those that do the hind tibia and basitarsus are dilated and clothed in a dense covering of setae or bear a fringe of setae surrounding a concavity. Another common modification is a development of setae on the outer margin of the tarsus of the foreleg to form a rake—a condition usual in species which dig with their forelegs in friable soil.

Abdomen

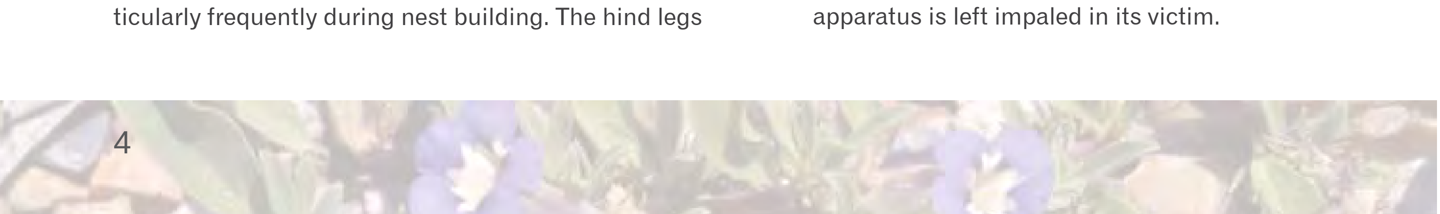
The basic number of abdominal segments in the Hymenoptera is ten. However, in bees and wasps (including pollen wasps) the number of visible abdominal segments is variable but is, in addition to the propodeum, generally six in females and seven to eight in males. The propodeum is followed by a marked constriction, the petiole, which separates it from the main portion of the abdomen, known as the gaster. The petiole gives the abdomen considerable manoeuvrability, making possible accurate placement of stings and eggs. The petiole ranges in length from very short in bees and some wasps, such as *Bembix* (Crabronidae), to extremely long in wasps, such as *Sceliphron*, *Chalybion* and *Ammophila* (all Sphecidae).

A pair of spiracles occurs on each abdominal segment. In most groups, the number is reduced. However, in all there is a pair of spiracles on the propodeum.

In the male, the external parts of the genitalia consist of a basal ring often partly divided longitudinally, a pair of two-segmented forceps, the inner end of which is attached to a plate, and a pair of valves connected by membranes to form a tube acting as an intromittent organ.

The ovipositor in the wasps (other than the Chrysidoidea) and the bees no longer has a reproductive function, having become a sting. The eggs are ejected from an opening of the genital chamber at the base of the sting. The sting consists of a pair of stylets grooved along their entire length and enclosed in a stylet sheath or a pair of stylet sheaths. In structure the sting is very little different from the ovipositor except in the development of valves on the bases of the stylets for driving the poisonous liquid through the channel. When not in use the sting is withdrawn into a sting chamber and is not visible.

In hunting wasps the sting is used primarily to subdue the prey and the stylets bear one to a few serrations shortly behind their tips. In bees, pollen wasps and social wasps, the sting is for defence only. In the honeybee workers the serrations are more numerous and more pronounced and barb-like. In all other bees and all wasps, the sting can be withdrawn and the stinger is therefore able to sting an unlimited number of times. However, the honeybee worker can only sting once as its whole sting apparatus is left impaled in its victim.



Alimentary canal

As mention will be made of a ‘crop’ in connection with the transport of water and of nectar a brief outline of the layout of the alimentary canal seems appropriate.

The mouth cavity leads into the pharynx, which is moved by powerful dilator muscles and is an organ of suction. Following the pharynx is the oesophagus, which is dilated in the anterior portion of the abdomen into a thin walled crop that serves as a reservoir for imbibed liquid. The crop is followed by a short narrow proventriculus leading into the true stomach, the ventriculus. It may be the largest part of the gut, as in *Apis* (Apidae) and *Vespula* (Vespidae), or reduced to a small elliptical chamber in some spheciform Apoidea. There follows the ileum and finally the rectum. A whirl of Malpighian tubules arises at the base of the ventriculus.

Life history

The species covered in this book exhibit a wide variety of parental strategies, particularly with regards to the level of parental investment given each offspring. However, there are commonalities in life history strategies that will be covered in this section. The life cycle of wasps and bees is divided into four phases—egg, larva, pupa and adult (Figures 0.1.a–e and 0.2.a & b). The immature stages of the majority are passed in a protected situation within a cell in a nest either constructed by the mother or by another wasp or bee. In the Scoliidae and Tiphiidae development is not within a nest, it is nevertheless in a relatively protected situation being subterranean.

Oviposition as a general rule takes place within the cell or the situation in which development will take place. The egg is therefore protected from rapid desiccation or accidents caused by physical impact. It need not therefore be heavily armoured as are the eggs of many insects which deposit them in exposed situations. The egg is in fact protected only by a delicate pellicle. It is generally sausage-shaped and large in comparison with the size of the mother, especially in nest provisioning species with low fecundity (O’Neill 2001). There is little variation in colour and eggs of most species are white to yellowish.

Figure 0.1.—*Isodontia pelopoeiformis*: a. egg; b. young larva; c. large larva; d. fully fed larva; e. resting stage larva in cocoon; f. adult.

The majority of wasps and bees lay only one egg per cell or per provision mass. The sex of an egg is determined by whether or not it is fertilised. Fertilised (diploid) eggs are

Figure 0.2.—*Tricarinodynerus guerinii* (de Saussure): a. pre-pupa; b. young pupa; c. mature pupa; d. adult.

female producing, whereas unfertilised (haploid) eggs are male producing. This extraordinary arrangement by which females are produced by normal sexual reproduction and males parthenogenetically is characteristic of the entire order Hymenoptera. Parthenogenesis is in fact more frequent among the Hymenoptera than in any other order in the animal kingdom.

Before mating has taken place eggs laid by a female are male producing. After mating, sperm are retained in the spermatheca, a sac-like organ within the abdomen of the female and linked to the vagina by a slender duct surrounded by a muscular sheath. When an egg that will produce a female is laid, sperm is released onto the egg as it passes from the oviduct into the vagina. When an egg that will produce a male is laid no sperm is released. Little is known of the factors determining whether or not an egg will be fertilised. When one prey only is used for provisioning the size of the prey seems to determine whether the egg will be fertilised or not; female-producing eggs being laid on large prey and male producing eggs on small prey. Where a cell is provisioned provisioning is with multiple prey and oviposition takes place before or during provisioning, the amount of available provision cannot be a determining factor. In species constructing cells in linear series, the cells towards the inner end of the nest produce females, whereas those towards the outer end produce males.

The majority of wasps oviposit directly onto the provision and the egg is firmly attached. However, all Vespidae and some Bembicini (Crabronidae) lay their eggs into empty cells before provisioning takes place. Bees, on the other hand, lay their eggs in fully provisioned cells. Thus, there is a striking difference between the pollen and nectar provisioning pollen wasps (Vespidae, Masarinae) and the bees in the timing of egg laying—the former laying an egg in a cell prior to provisioning and the latter laying an egg into a fully provisioned cell. The other subfamilies of Vespidae, the Eumeninae and social paper wasps, represented in southern Africa by the Polistinae, generally do not lay an egg loosely into a cell as do most pollen wasps. The polistine egg is firmly glued to the cell wall and, most usually, the Eumenine egg is suspended from the cell wall by means of a filament.

The position of attachment of eggs to the prey of a solitary hunting wasp is usually relatively constant within a species and often within a genus or even a group of genera. Because the egg is attached at some weak point in the integument of the prey, such as at the base of a leg, the tiny newly hatched larva finds an easier starting point for penetrating the body of the prey.

The egg phase, in all but the social species, lasts only a few days. Shortly before the egg hatches segmentation of the larva is visible through the pellicle. As its mother has provided food and shelter for the larva, it requires neither to actively seek food nor to defend itself from predators. Consequently, it is soft bodied with legs either lacking or reduced to fleshy lobes, and its sensory organs are greatly reduced. However, the larval mandibles of hunting wasps are well developed with the muscles that operate them filling up most of the head capsule. The body is segmented and bears ten pairs of spiracles. An anal opening is missing in the larva, so that defecation takes place only once, shortly before pupation.

In order to be able to grow the larva moults. Four moults take place. Feeding is completed during the fifth larval stage when all the food provided by the mother has been consumed. In solitary wasps (including pollen wasps) and solitary bees the time from oviposition to pupation lasts one to two weeks.

The larva of all pollen wasps and many species of wasps, including all pollen wasps, and of many species of bees then spins a cocoon in which pupation will take place. Debris such as uneaten prey remains. Frequently head capsule, wings and other hard parts of the body wall, are pushed into the extremities of the cell prior to spinning. In rare cases, for example *Ampulex* species (Ampulicidae), the larva feeds within the body of the prey leaving most of the prey exoskeleton intact and cocoon spinning takes place within the shell of the prey. In all cocoon making species either the entire cocoon or its basic framework is of silk that is extruded from a spinerette borne on the labium. Most commonly the cocoon is constructed loosely in the cell and is attached to the walls by an open framework of silk threads but in some, for example *Ceramius* species (Masarinae), it is closely attached to the wall of the cell so that it is inseparable from it except at the truncate outer end. Some Crabronidae, for example *Holotachysphex* and *Bembecinus*, incorporate soil particles and an oral secretion into the silken framework to form a hard shelled cocoon with a granular or smooth surface depending on the nature of the soil employed. The cocoons of *Bembecinus* and *Bembix* species have one to several pores situated around the circumference of the cocoon at mid-length (Evans 1966).

After cocoon spinning has been completed the faecal material is voided in the form of a black substance known as the meconium. As at the completion of spinning, the larvae of most species orientate with their heads towards the cell opening, the meconium is usually to be found at the inner end of the cocoon and may in fact form a plug closing the cocoon and cementing it to the inner end of the cell.

Development to the pupal and adult stages may follow immediately in species in which there is more than one generation produced during the course of the summer or in some species such as carpenter bees and paper wasps, which overwinter as adults. Most species of solitary wasps and bees overwinter as pre-pupae in a state of dormancy known as diapause, only pupating and emerging as adults at the beginning of the following summer. Males emerge before females. It is possible for diapause to last even longer, so that, if conditions are unfavourable, a young wasp may not reach adulthood for another year or more.

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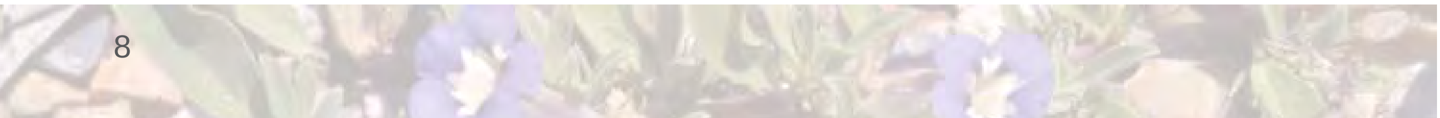

SECTION I:
Wasps and bees in the semi-arid to arid areas of southern Africa

1. Distribution of semi-arid to arid areas of southern Africa

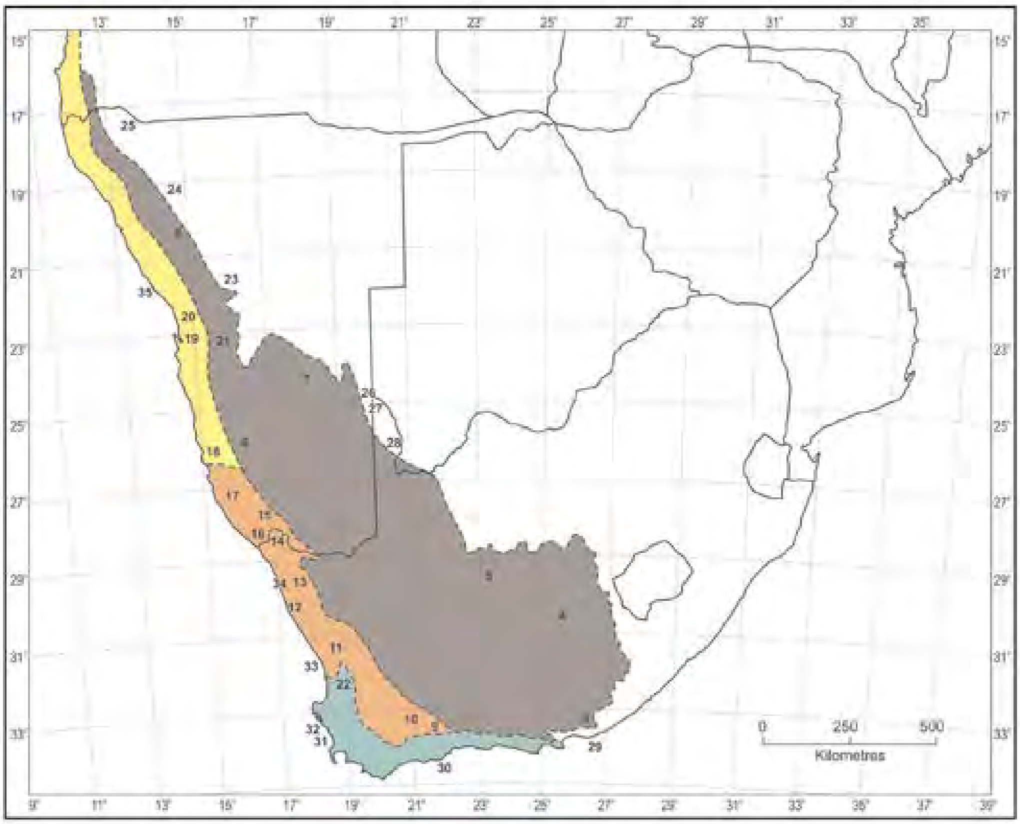

Figure I.1.1.—Southern Africa. The distribution of Fynbos (green), Succulent Karoo (orange), Nama-Karoo (brown), Namib Desert (yellow), Savanna (S), after Rutherford (1977), digits denote areas illustrated in figures I.1.3–35.

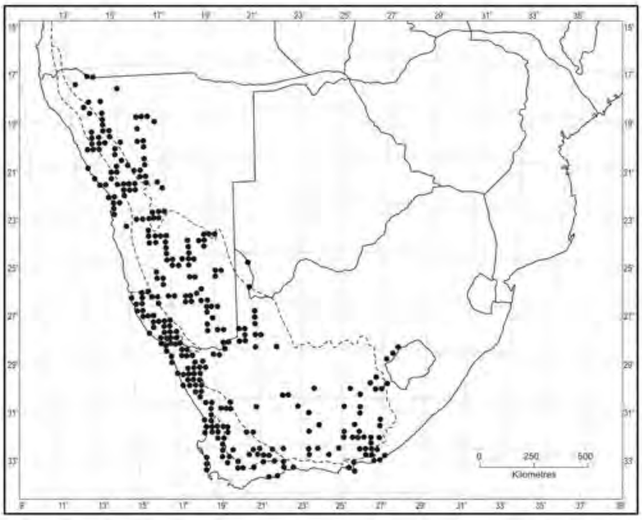

Figure I.1.2.—The distribution of the authors' sampling sites within the semi-arid to arid areas of southern Africa.

The study area for the present work is the semi-arid to arid areas of southern Africa (Figures I.1.1 & I.1.2). Recent delimitations of the biomes represented in southern Africa and comprehensive studies of their ecological patterns and processes have been presented in *The vegetation of Southern Africa* (Cowling *et al.* 1997), and developed further for the Karoo in *The Karoo: ecological patterns and processes* (Dean & Milton 1999). The vegetation of each of the biomes is by no means uniform throughout the biome and can be divided into vegetation types related, amongst other factors, to latitude, altitude, geology and rainfall patterns. However, some generalisations can be made. The core of the area is known as the Karoo-Namib Region.

The Nama-Karoo (Figure I.1.3–8) is the largest of the three biomes included in the Karoo-Namib Region. Its annual rainfall varies but as a generalisation can be said to decrease from east to west with the areas of very low precipitation being in the rain shadows of major mountain ranges. Rainfall is bimodal or strongly seasonal and, for some areas, relatively high in summer. Soils are variously sandy and friable or clayey and non-friable with variable nutrient gradients relating to the geological strata from which they are derived. The vegetation is characterised as dwarf open shrubland dominated by Asteraceae, grasses, Aizoaceae (both Mesembryanthema and non-Mesembryanthema), Liliaceae (*senso lato*) and Scrophulariaceae. The composition of the vegetation varies across rainfall and soil gradients. The Nama-Karoo does not appear to have a species-rich or unique flora. Many of the species are shared with the Savanna, Grassland, Succulent Karoo and Fynbos biomes.

Figure I.1.3.—Extreme southeastern Nama-Karoo, Hilton Farm.

Figure I.1.4.—Southeastern Nama-Karoo, Van Wyksfontein Farm.

Figure I.1.5.— Central Nama-Karoo, between Natuurskroon and Pampoenpoort, Victoria West.

Figure I.1.6.—Southern Namibian Nama-Karoo south of Helmeringhausen.

Figure I.1.7.—Southern Namibian Nama-Karoo south of Mariental.

Figure I.1.8.—Northern Namibian Nama Karoo, northwest of Khorixas.

The Succulent Karoo (Figure I.1.9–15) is characterised by predominantly winter rainfall, a remarkably high diversity of leaf succulents, an unusually high diversity of geophytic and leaf-succulent, petaloid monocots and a general lack of tall shrubs, trees and grasses. Most noticeable among the leaf succulents are the Aizoaceae: Mesembryanthema. This is the most species-rich plant taxon in southern Africa with its greatest species diversity in this biome. The Succulent Karoo is renowned for the diversity of succulent species, unparalleled elsewhere in the world (Cowling & Hilton-Taylor 1997; Cowling *et al.* 1998).

Figure I.1.9.—Succulent Karoo, southwestern Little Karoo.

Figure I.1.10.—Succulent Karoo, southeast of Laingsburg.

Figure I.1.11.—Succulent Karoo, Namaqualand, Knersvlakte.

Figure I.1.12.—Succulent Karoo, Namaqualand Sandveld, looking east from Hondeklip Bay.

Figure I.1.13.—Succulent Karoo, Namaqualand, Klipkoppe, Goegap.

Figure I.1.14.—Succulent Karoo, Namaqualand, Richtersveld, Koeroegabvlakte.

Figure I.1.15.—Succulent Karoo, southeastern Namibia, north of Rosh Pinah.

The Namib Desert (Figure I.1.16–21) stretches for 2 000 km in a north-south direction. It is adjacent to the Nama-Karoo and Succulent Karoo biomes and may be considered from many perspectives to comprise the most arid portions of these biomes. Landscapes in the Namib Desert range from areas devoid of any vegetation to areas where there is a relatively dense ground cover of herbs and dwarf shrubs with taller shrubs and even small trees at sites with a better water regime. There is, in parts, a rapid change in vegetation over short distances, owing to extremely steep ecological gradients. There is a north-south climatic gradient from tropical to temperate. The southern extremity is within the winter rainfall region and represents the most arid part of the Succulent Karoo. The northern extremity is within the summer rainfall region and is characterised by low humidity and high potential evapotranspiration. The coast-inland gradient is characterised by mild temperatures, high humidity, low rainfall but high fog incidence giving way to higher temperatures, lower humidity but higher rainfall. As in all deserts, annuals (seasonal plants which germinate only when rain falls at a specific time of year) and ephemerals (plants which germinate whenever there is sufficient moisture, irrespective of season) are notable. In the Namib Desert the annual and ephemeral flora differs greatly between regions. Some habitats such as the zones of minimum vegetation support only annual and ephemeral species. In the Succulent Karoo portion of the Namib Desert geophytes are also fairly frequent.

Figure I.1.16.—Southern Namib, Sperrgebiet as seen from Skilpad looking north.

Figure I.1.17—Southern Namib, Sperrgebiet, Klinghardtberge.

Figure I.1.18.—Southern Namib, southern end of dune desert northwest of Lüderitz.

Figure I.1.19.—Kuiseb River between Dune Desert (Southern Namib) and Gravel Plains (Central Namib).

Figure I.1.20.—Central Namib.

Figure I.1.21.—Central Namib, drainage channel, east of Walvis Bay.

The limits and regions of the Namib Desert, in particular the Southern Namib have been variously defined (e.g. Giess 1971; Irish 1994; Jürgens *et al*. 1997; Mannheimer *et al*. 2008). The readily available *Atlas of Namibia* (Mendelsohn *et al*. 2003) follows a similar pattern to that of Giess (1971), naming areas as follows:

- The area extending northwards of a line between the Huab and Koigab Rivers into southern Angola, north of the Kunene River, as the Northern Namib Desert.
- The area to the south stretching north from the Kuiseb River as the Central Namib Desert.
- The term Southern Namib Desert is applied to the area south of the Kuiseb River and does not include the

area in the extreme south which lies within the Succulent Karoo, extending south of the Orange River. This is somewhat different to the area as defined by Giess (1971).

For the purposes of this book Mendelsohn *et al*. (2003) will be followed except that the term Southern Namib will follow Giess (1971). The dune desert in the northern Southern Namib will be referred to as the dune desert and the area to the south of the dune desert mainly to the south of the Aus/Lüderitz road, mostly within the area known as the Sperrgebiet, will be referred to as the winter rainfall area.

The Fynbos Biome (Figure I.1.22) is typified in the main by a mediterranean climate with warm, wet, winters with westerly winds and hot dry summers. In the southeast the rainfall regime changes to non-seasonal. The biome includes not only fynbos but also two other major vegetation types, renosterveld and a mosaic of fynbos and strandveld. Fynbos is an evergreen, fire-prone shrubland, confined largely to sandy infertile soils and characterised structurally by the universal presence of restioids, a high cover of ericoid shrubs and the common occurrence of an overstory of proteaceous shrubs.

Strandveld is found on nutrient-poor acidic and alkaline sands of aeolian and marine origin, principally associated with fynbos along the coast but is in addition represented as an 'island' in the Succulent Karoo in southern Namaqualand.

Renosterveld is found on moderately fertile, shale derived soils. It too is an evergreen, fire-prone vegetation type, dominated by small-leaved, asteraceous shrubs—especially *Elytropappus rhinocerotis*, the renosterbos—with an understory of grasses and geophytes.

Savanna (Figure I.1.23–25) is a tropical biome with the vegetation co-dominated by woody plants and grasses. The grass layer may be temporarily absent or replaced with dicotyledonous herbs during periods of drought or disturbance. In southern Africa the wet season is unimodal, during the summertime from October to April. Savanna grades into the arid shrublands of the Nama-Karoo in the Eastern and Northern Cape and Namibia. Across these gradients the trees become progressively sparser, lower, shrubby and more restricted to drainage lines. Many species are shared between the two biomes.

Figure I.1.22.—Dry Fynbos west of Olifants River Valley.

Figure I.1.23.—Thorn Savanna, between Karibib and Omaruru, Erongo Mountains in the distance.

Figure I.1.24.—Mopane Savanna, 67 km north of Palmwag.

Figure I.1.25.—Mixed Savanna, Swartbooisdrif on the Kunene.

The Kalahari 'desert' (Figure I.1.26–28) does not constitute a separate biome but to the south is considered to be arid Nama-Karoo and to the north arid Savanna. The Kalahari basin is characterised by its infilling being the single largest body of wind-blown sand in the world. Over much of its area it is furthermore characterised by linear dunes of which the crests of the majority are stabilised with a permanent vegetation cover.

The sandy coasts from the Kunene River in the northwest to the Riet River (Figures I.1.29–35) in the south east are included in the present work as arid areas. The nature of the dune vegetation varies according to the rainfall regime and the nature of the vegetation inland from the immediate coast.

Figure I.1.26.—Kalahari fringe, southeastern Namibia.

Figure I.1.27.—Kalahari fringe, southeastern Namibia, wet year.

Figure I.1.28.—Kalahari, southern Nossob Valley.

Figure I.1.29.—Southeast coast, Boknes.

Figure I.1.30.—South coast, Stilbay.

Figure I.1.31.—Southwest coast, Melkbosstrand.

Figure I.1.32.—Southwest coast, Yzerfontein.

Figure I.1.33.—Southwest coast, Donkinsbaai north of Lambert's Bay.

Figure I.3.34.—West coast, Port Nolloth.

Figure I.3.35.—Northwest coast, north of Cape Cross.

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2. Geographical affinities of wasps and bees in the semi-arid to arid areas of southern Africa

An attempt has been made to address the subject of the geographical affinities of the wasp and bee fauna of the Karoo Biome within South Africa (Gess & Gess 1993). At that time four principal study sites were chosen: the farm Hilton at the southeastern extension of the Nama-Karoo near Grahamstown, the farm Onverwacht near Oudtshoorn in the Little Karoo, the farm Tierberg near Prince Albert in the southern Great Karoo and Goegap Nature Reserve near Springbok in Namaqualand (Figures I.2.1–4).

Figure I.2.1.—Hilton Farm, southeastern Nama-Karoo.

Figure I.2.2.—Onverwacht Farm, Oudtshoorn, Little Karoo.

All sampling areas were chosen to include the full range of nesting situations—horizontally presented ground (areas of both friable and non-friable soil), vertical banks, plants and stones.

Species representation in the four communities was compared by calculating percentages of similarity using Sørensen's coefficient (Figure I.2.5 & 6), and of uniqueness (Figure I.2.7) using for any one community the number of species not represented in any of the other communities over the total number of species. We concluded the following:

- There are considerable differences in species composition between sites.
- The wasp and bee fauna of the southern Karoo is polarised into two main faunal groups, one centred in the west and the other in the east, as represented by Goegap and Hilton.
- Between the two extremes lies a transition of overlapping subtraction margins of the eastern and western faunas, within which lie the Tierberg and the Onverwacht communities.
- The species composition of the community at Tierberg lying at the southern edge of the Great Karoo, inland of both the Outeniqua and the Swartberg mountain ranges shows greater affinity with that of Goegap than that of Hilton whereas that of Onverwacht in the Little Karoo lying between these mountain ranges shows greater affinity with that at Hilton than with that at Goegap.
- The species composition of the community at Tierberg shows greater uniqueness than that at Onverwacht.

The greater uniqueness of the species composition of the community at Tierberg compared with the other three sites might be explained by the presence of species derived from a northern fauna which probably does not extend south of the Swartberg Range. A preliminary sampling of the wasp and bee fauna of the southern Kalahari at the interface between the Karoo and the Savanna biomes lends support to this hypothesis.

Figure I.2.3.—Tierberg Farm, Prince Albert, southern Great Karoo.

Figure I.2.4.—Goegap Nature Reserve, Springbok, Namaqualand.

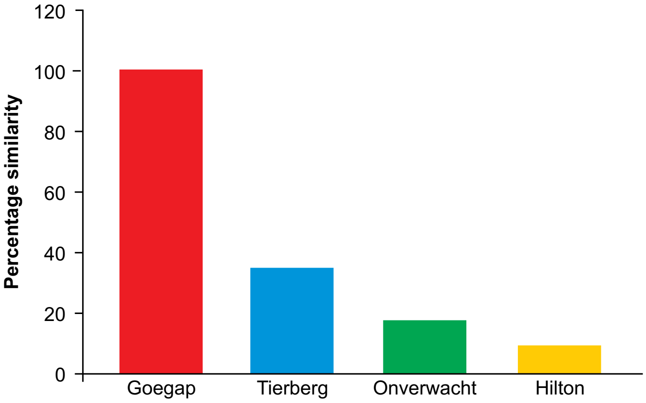

Figure I.2.5.—A bar graph comparing the percentage species similarity of the major community of bees, pollen wasps and wasps of Goegap Nature Reserve, Tierberg Farm, Onverwacht Farm and Hilton Farm compared with that of Goegab Nature Reserve.

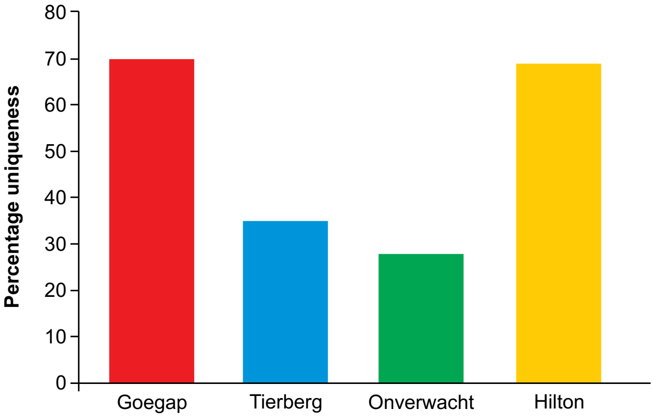

Figure I.2.7.—A bar graph comparing the percentage species uniqueness of the major community of bees, pollen wasps and wasps of Goegab Nature Reserve, Tierberg Farm, Onverwacht Farm and Hilton Farm.

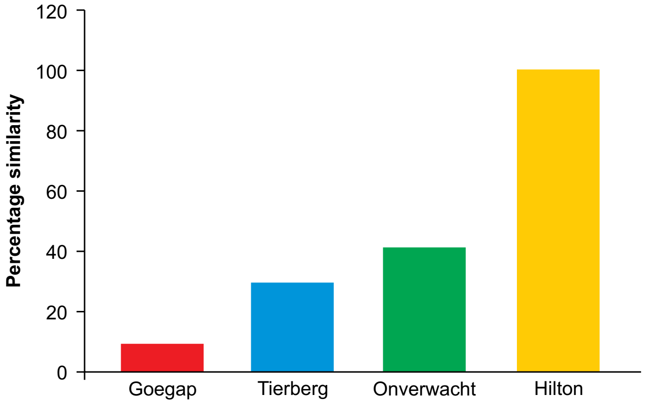

Figure I.2.6.—A bar graph comparing the percentage species similarity of the major community of bees, pollen wasps and wasps of Goegab Nature Reserve, Tierberg Farm, Onverwacht Farm and Hilton Farm compared with that of Hilton Farm.

We noted that species of the western bee, pollen wasp and wasp fauna do not have extensive northern distributions. This is contrary to the distributions of some species of the eastern fauna that extend north into Kenya or even Ethiopia. There is, therefore, a much lower level of endemism in the eastern fauna. However, from a consideration of known distributions of species it is probable that there are some eastern Karoo endemics.

The bipolarity of the faunas is supported by the findings of Kuhlmann (2005, 2009) resulting from his analysis of bee diversity patterns in southern Africa. He noted a bipolar pattern for bees with the highest species diversity located in the arid west of South Africa and the relatively moist east of the country. He noted that an exceptionally high number of endemic species are strictly confined to the winter rainfall area. He furthermore drew attention to the fact that the semi-arid and arid west of South Africa, the Cape Floral Kingdom (CFK), is the only place on Earth where a centre of bee diversity coincides with a plant diversity hotspot, noting that the CFK is the only centre of plant diversity in a semi-arid to arid environment. This is the kind of environment where bees are generally most diverse (Michener 1979, 2000, 2007).

Pollen wasps and bees, provisioning with pollen and nectar, fill the same general behavioural niche, so a comparison of their distributions is of particular interest. Whereas the bees have a worldwide distribution including a broad range of biomes the pollen wasps, although present in five zoogeographical regions, are within those regions markedly restricted to a narrow range of biomes. The majority of the pollen wasps are found in areas with a Mediterranean climate and in the associated semi-arid to arid areas with the greatest diversity of genera and species found in southern Africa. All species of pollen wasps found in southern Africa are endemic to the region, with, like the bees, an exceptionally high number of narrowly endemic species in the winter rainfall regions. *Ceramius*, *Jugurtia*, *Celonites* and *Quartinia* have distributions similar to that of the pollen wasps as a whole, with *Quartinia* being the most desert-adapted. The distributions of *Masarina* and *Priscomasaris*, both genera endemic to southern Africa, are more limited. *Masarina* is only known from the winter rainfall region and *Priscomasarina* only from the Namibian Nama-Karoo.

Species diversity of the pollen wasps is greatest in the semi-arid areas of the southwest, whereas the species diversity of the social vespids is greatest in the subtropical areas of the northeast. The only three genera of social paper wasps represented are the polistines *Belonogaster*, *Polistes* and *Ropalidia.* They appear to be more species-rich in the tropical parts and in southern Africa display a northeast to southwest gradient of decreasing species numbers.

The Masarinae has a principally southwestern distribution and the Polistinae a principally eastern distribution. The other vespid subfamily present in southern Africa, the Eumeninae, occurs throughout the region. Worldwide the Eumeninae is widespread.

There has been no separate analysis of the distributions of the hunting wasps of the same nature as those for bees and pollen wasps. However, it is clear from our analysis which includes bees, pollen wasps and hunting wasps that the hunting wasp faunas show a similar degree of bipolarity as do the bees. Genera for which species distributions are sufficiently well documented can be used to support this conclusion. In his revision of the diverse and widespread wasp genus *Tachysphex* (Crabronidae, Crabroninae, Larrini), Wojciech Pulawski (2007) lists five species as western South African endemics and four eastern South African endemics. From known distribution records it is clear that the widespread and diverse genera *Bembix* and *Bembecinus* (Crabronidae, Bembicinae, Bembicini) exhibit a similar bipolarity in that some of the species occur only in the west and others only in the east. The small genus *Tachytella* (Larrini), known only from three species is entirely western in distribution with one species from South Africa, one from Namibia and one shared between northwestern South Africa and southwestern Namibia (Pulawski 1995). *Ampulex* (Ampulicidae), a widespread largely tropical genus, has a predominantly eastern distribution in South Africa.

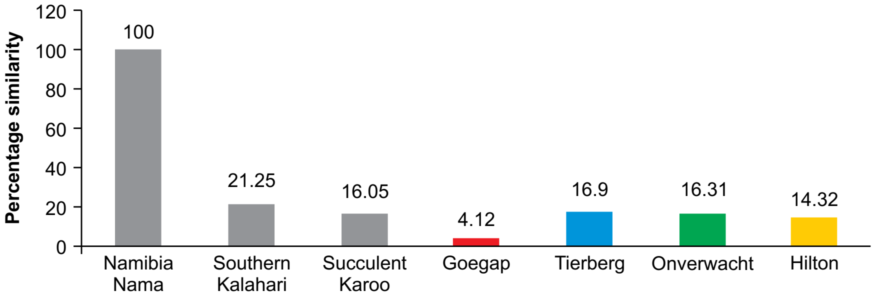

Figure I.2.8.—A bar graph comparing the percentage species similarity of the major community of bees, pollen wasps and wasps of Nama-Karoo in Namibia, southern Kalahari, Succulent Karoo, Goegab Nature Reserve, Tierberg Farm, Onverwacht Farm and Hilton Farm compared with that of the Nama-Karoo in Namibia.

Since our 1993 study was undertaken we have sampled wasps and bees throughout the semi-arid to arid areas of Namibia using hand nets. Due to the nature of the fieldwork no fixed study sites were selected and Malaise trapping and trap-nesting were not employed. However, thorough sampling of wasps and bees visiting flowers, on the ground, at water, and at light sources at night was undertaken. The samples were then correlated variously to the different bioregions, namely Nama-Karoo, Savanna, Succulent Karoo, Kalahari, Desert and Coast. Taking all species attributed to the Nama-Karoo in Namibia and using Sørensen's coefficient of overall similarity some indication was obtained of the degree of similarity between the wasps and bees of this area and the four study sites (Figure I.2.8).

Some indication of the degree of similarity of the complex of wasps and bees found in the Nama-Karoo Biome to the north of the Orange River and that to the south was obtained. The lowest degree of similarity was with Hilton. This can be accounted for by the presence of a relatively high representation of species with northeastern distributions in the Hilton community and a very low representation in the Namibian Nama-Karoo of species with such distributions. Though still low, the degree of similarity with Tierberg in the southern Great Karoo was highest, supporting our earlier suggestion that the Tierberg community includes species with more northern, but not northeastern, distributions.

The degree of similarity between the Goegap site, which is entirely isolated from the Nama-Karoo, and the Namibian Nama-Karoo was minimal. However, when species collected in the Richtersveld and the Succulent Karoo to the north of the Orange River are combined with those from Goegap, a higher degree of similarity with the Namibian Nama-Karoo, which in the southwest shares an interface with the Succulent Karoo, is obtained. Namibian Nama-Karoo showed the highest degree of similarity with the southern Kalahari. These two regions share an interface in the southeast.

The percentage species uniqueness for all species sampled in the semi-arid to arid areas of Namibia was calculated as 73%. This represents the percentage of those species from the Namibian sample not present in our four study sites south of the Orange River. This compares well with the percentage species uniqueness obtained for the Hilton and the Goegap sites in our original study.

To some degree this high percentage results from the extensive interface between the Namibian Nama-Karoo and the Savanna which results in the inclusion of a number of taxa with distributions extending eastwards across Namibia into the Limpopo Province (formerly known as the Northern Transvaal Region). Similarly the long interface with the Namib Desert results in the inclusion of species shared with the desert, including narrowly endemic species. Furthermore in the north there is penetration by taxa with more northerly distributions, for example an undescribed species of *Trachusa* (*Massanthidium*), in Africa otherwise known only from Kenya and Ethiopia (Michener 2000, 2007; Gess & Gess 2007; Eardley *et al.* 2010).

Little is known concerning the wasps and bees of the dune desert of the southern Namib. It is safe to say that the level of diversity is low and that narrow endemics are represented. The dominant plants are grasses. Succulents are generally uncommon, but the woody-stemmed leaf succulent *Trianthema hereroensis* (Aizoaceae) is co-dominant with a grass, *Stipagrostis sabulicola*, in the coastal part of the main dune field. Amongst the insects associated with the minute flowers of *T. hereroensis* are two narrowly endemic sand-coloured species of *Quartinia* (Masarinae), namely *Q. femorata* Gess (average 6.3 mm in length) and *Q. albopicta* (Richards) (average 2.5 mm in length). Also a feature of the dune desert is the much publicised narrowly endemic spider hunting wasp *Schistonyx aterrimus* Arnold (Pompilidae), which specialises in hunting the equally narrowly endemic spider, *Carparachne alba* Lawrence. Both the masarines and the pompilid nest in sand and do not require water or large quantities of nectar, making them successful dwellers in dry sand dune desert.

Little is known of the wasps and bees of the plains of the central and northern Namib and the northern dunes.

Twelve rivers rise inland of the central and northern Namib, with the Kuiseb in the south and the Kunene in the north, cross the desert and enter the sea on the desertic west coast. Apart from the Kunene and the Kuiseb, the rivers in their course across the desert flow beneath the surface except after major rainfall events. However, due to the presence of underground moisture they and their tributaries do support a greater diversity of plants and insects than do the plains. The wasps and bees found in these drainage channels are principally species that penetrate the desert from inland or from the coast.

The communities of wasps and bees of sandy coasts are made up of species that are restricted to the coast, coastal species that penetrate inland and species with inland distributions that reach the coastal dunes. As stated above, inland penetration along drainage channels is a feature of the central and northern Namib. In the southern Namib there is little inland penetration with the only river crossing the Namib being the Orange in the south and the vegetation being sparse. The coast south from the Orange River to Cape Town is associated to a large degree with relatively well but not densely vegetated sandveld, sometimes allowing considerable inland penetration from the coast and coastal penetration from inland. Along the southern and southeastern coast the vegetation and the wasp and bee faunas are very much more distinct from those inland.

Characteristic of truly coastal aculeate wasps and bees, as with coastal plants, are species with very narrow, but lengthy distributions, e.g. *Quartinia poecila* von Schulthess, which is found from Swakopmund in the north to Hondeklip Bay in the south. The colouration of this wasp shows increased melanism from north to south.

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3. Plants as a direct and indirect energy resource for wasps and bees with comments on the payback services rendered to plants

Wasps and bees are directly dependent on nectar from flowers or extra-floral nectaries for adult nourishment. Furthermore, at least some females require additional small amounts of pollen as a protein source in egg production, and all bees and pollen wasps require pollen and nectar for the rearing of larvae. Some bees have forelegs especially modified for oil collection. In addition to visiting flowers for nectar and pollen, they visit oil-secreting flowers to collect oil. Hunting wasps are directly and indirectly dependent on plants—directly as an energy source for adults, and indirectly through their prey as an energy source for the larvae.

No wasps or bees are totally polyphagous in their flower visiting. Some restrict their visits to a small range of related plants and are therefore oligophagous. Monophagy (dependence on one species of plant) is rare.

Similarly, no hunting wasps are totally polyphagous in their choice of prey. Predation is restricted to spiders or insects and within these larger groupings further restrictions are apparent. Insect hunters generally restrict their hunting to a single order of insects and within the order to a particular family or genus. Monophagy is rare.

A second category of aculeates that depend indirectly on plants as an energy source for their larvae are those which do not collect provision for their larvae but seek out the nests of host wasps and bees and insert an egg into a cell where the larva will develop at the expense of the host. The larvae of most chrysidids feed on the egg or larva and provision, those of sapygids on the egg and provision or the fully grown larva, and most mutillids feed on the diapausing larva or pupa. Some chrysidids and some mutillids are not ‘parasites’ of other aculeates. In the Chrysididae, the larvae of Amisginae feed on stick insect (phasmid) eggs, and the larvae of some mutillids feed on the puparia of flies, beetles or moths.

This chapter gives a comparative overview of the flowers visited by wasps and bees and of the spiders and insects hunted by wasps. Comments are given on the potential of the flower visitors as pollinators and the benefits to plants of predation by the hunters of phytophagous insects.

Plants as a direct source of energy for wasps and bees

It has not been possible for us to gather all the known flower visiting records for wasps and bees. This is currently being undertaken by Jonathan Colville of SANBI. Presented here are the results of our own survey and analysis of flowers visited by wasps and bees in the semi-arid to arid areas of southern Africa (Gess & Gess 2003, 2004a, 2004b, 2006). These areas include the Karoo Biome and associated dry fynbos, arid savanna and desert fringes.

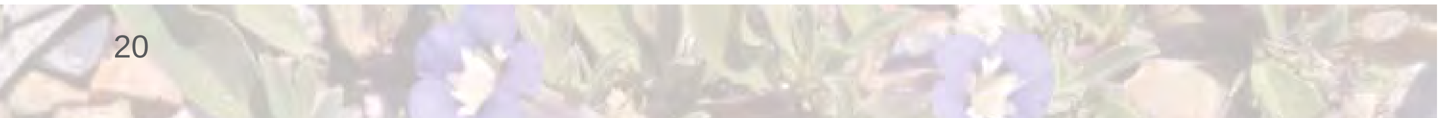
Flowers of 36 plant families, represented by around 600 species (approximately 400 identified to species and the remainder only to generic or familial level), were recorded as visited by wasps and bees. Visitation of flowers according to plant family was examined and discussed, based on 16 229 records for visits by 927 species of solitary wasps and bees (129 species of pollen wasps, 375 species of wasps and 423 species of bees). Differences in assemblages of visitors between families, within families between taxa and across geographic gradients were noted. The dependability or lack of dependability of visitors based on the degree of polyphagy or oligophagy exhibited was discussed. The potential of visitors as pollinators is suggested where sufficient records and observations on flower fit and visitor behaviour were available.

The database for the analysis is *A catalogue of flower visiting records for aculeate wasps and bees in the semi-arid to arid areas of southern Africa* (Gess & Gess 2003). Of the records, 98.2% were derived from our purposeful sampling (assisted at various times and sites by David Gess, Harold Gess and Robert Gess). The remaining records were assembled from label data from the Albany Museum collection, mostly concurrently collected material from the eastern karroid areas (Charles Jacot Guillarmod, 219 records; Jason Londt, 66 records; Alan Weaving, 30 records). An update of the 2003 catalogue in the form of a searchable relational database on CD is provided at the back of this book.

Voucher specimens for all wasps and bees were deposited in the terrestrial insect collections of the Albany Museum. Voucher specimens for many, but not all, plants were deposited in the Selmar Schönland Herbarium, Albany Museum. Duplicates of specimens from Namibia are in the National Herbarium of Namibia, Windhoek.

Published records by other authors and sampling after the closure of the catalogue were taken into account in subsequent discussions but were not included in the database for analysis. The present chapter has been similarly updated and also includes data on oil-secreting Scrophulariaceae and Orchidaceae from Whitehead & Steiner (2001), who made a special study of the oil-collecting bees *Rediviva* (Melittidae). In their paper, Whitehead & Steiner present a review of the history of the study of oil collecting bees.

The database included the sex of insect specimens, but females and males were combined in the analysis. When collecting specimens, distinction between pollen and nectar collection was not always made and thus, except where specifically referred to, the discussion encompassed both types of visits indiscriminately. Those species visiting flowers of taxonomically diverse plants were termed polyphagous (Struck 1994). Degrees of polyphagy from narrow to broad were recognised. The term oligopha-



gous was limited to species visiting flowers of plants all belonging to a single family, subfamily, tribe or genus. Few monophagous species, i.e. those restricted to single species of plants, were encountered.

The bees included in the analysis are all bee taxa excluding the social Apinae. Honeybees and meliponines taken in samples are referred to in the text. The term aculeate, used here as a noun and not an adjective, includes wasps and bees, but not ants (Formicidae).

It should be noted that, apart from the area in which we are resident, it has not been possible to sample areas throughout the year. Seasonal timing of sampling has been based on experience and the gross rainfall and temperature patterns of different areas. The distribution and magnitude of rainfall events, and therefore of flower patches in the semi-arid and arid areas of southern Africa, is unpredictable. Thus, although general sampling areas and sampling times have been purposefully selected, the choice of sampling sites has of necessity been opportunistic.

In the southeast and south the highest rainfall months are September and March and the summer is rarely excessively hot and dry. Thus, sampling has been principally from late October through to March. In the winter rainfall region of the southwest, north to Lüderitz and Aus, sampling has been from August, when temperatures start to rise, through to December, when most flowering is over and in most years the land becomes parched. North of the Orange River in the southern Kalahari, southeastern Namibia and in western Namibia to the north of the winter rainfall area, sampling has been in March and April, which is when rains are expected and the extreme heat of summer is past.

Wasps and bees visiting flowers were collected using a hand net. At all of the study sites there was a mixture of plant taxa in flower and all of these plants were observed for flower visitors and, when possible, were sampled over periods throughout the day. In effect, wasps and bees in an area were all being offered the choice of visiting all available flowers. Each site sampled therefore represented a 'choice chamber', in which all the wasps and bees were offered the same choice of flowers.

Specific flower visitors show varying degrees in diversity of choice, i.e. of oligophagy and polyphagy. In order to make comparisons between groups of flower visitors constituted of unequal numbers of species, an Index of Diversity of Choice at the specific level was developed using the formula:

$D = a - b/b \times 100$, where a = the sum of the number of species of a selected taxon recorded visiting each of the flower families, and b = the total number of species of flower visitors of that taxon (Gess 1992, 1996).

This is an index used to compare the degree of oligophagy or polyphagy exhibited by taxa of differing numbers of species. Clearly, if each species only visited one species of plant, D would equal 0.

The values of D obtained by applying this formula to the database (Gess & Gess 2003) for a comparative overview of flowers visited by wasps and bees (Gess & Gess 2006) and for flowers visted by non-*Apis* bees (Gess & Gess 2004) were: wasps 141.60; pollen wasps 88.37; and bees 144.21. These values indicate a markedly narrower diversity of choice for pollen wasps overall than for non-masarine wasps overall and bees overall (Table 1).

Marked variations in diversity of flower visiting between families of bees are apparent (Table 2 and Gess & Gess 2004b). Diversity of choice for individual bee families are: Andrenidae 177.77; Colletidae 50.00; Halictidae 202.90; Melittidae 70.00; Megachilidae 117.81; Apidae (excluding honeybees) 195.93. These values indicate a similarly low diversity of choice for Colletidae and Melittidae and a greater diversity of choice for Megachilidae, Andrenidae, Apidae and Halictidae, in that order. The low diversity of choice for Colletidae and Melittidae is comparable with that, 88.37, obtained for pollen wasps.

These values were higher, except for Colletidae, than those obtained in an earlier analysis (Gess 1992), even if recalculated using the presently used classifications. Taking into account that the 1992 database excluded the Richtersveld National Park and the southern and western arid areas of Namibia, this could indicate an overall higher degree of polyphagy, a higher degree of opportunistic foraging to the north where rainfall is more unpredictable, or in widely distributed species a shift in plant families visited across range, or a combination of these factors (Gess & Gess 2004a).

Our comments on the potential of wasps and bees as pollinators are made with due circumspection. All too frequently all insects visiting flowers, particularly if they are bees (especially honeybees) are referred to loosely as pollinators. It cannot be emphasised too often that not all insects seen visiting flowers are pollinating them, furthermore not all insects seen collecting pollen are pollinators. For an insect to be a pollinator it must, when visiting a flower with ripe pollen, receive pollen in such a way that, when it visits another flower of the same species, which has a receptive stigma, the pollen is transferred from itself to the receptive stigma. This is usually achieved by insects visiting flowers to obtain nectar, the pollen being deposited on them due to their positioning within the flower. The pollen deliberately collected for provisioning by bees and pollen wasps, packed away, held by special hairs on legs or the underside of the abdomen or swallowed and carried in the crop, is not available for pollination. However, that bees and pollen wasps provision their nests with pollen and nectar enhances their potential as pollinators because they undertake more visits to flowers than do the majority of wasps which provision their nests with insects or spiders.

It must be emphasised that there are no truly generalist pollinators. No bees, not even honeybees, visit all flowers and not all bees seen visiting flowers are pollinating them. For example, although honeybees visit legumes with 'pea flowers' as a general rule, they are not their pollinators but are 'thieves', imbibing nectar without servicing the flowers. Thus, to maintain pollination services, the requirements of all wasps and bees should be taken into account.

Table 1.—Numbers and percentages of species of wasps, pollen wasps and bees recorded visiting flowers of the listed plant families, including the Index of Diversity of Choice (Gess & Gess 2006)

Plant taxon	Wasps (Total: 375 spp.)		Pollen wasps (Total: 129 spp.)		Bees (Total: 423 spp.)		Total number of wasps, pollen wasps and bees (Total: 927 spp.)	Percentage of wasps, pollen wasps and bees
	Number of species	% of species	Number of species	% of species	Number of species	% of species	Number of species	% of species
MONOCOTS								
Asparagales								
Asparagaceae	10	2.67					10	1.08
Asphodelaceae			1	0.78	12	2.84	13	1.40
Iridaceae			2	1.55	12	2.84	14	1.51
EUDICOTS								
Proteaceae	15	4.00			8	1.89	23	2.48
CORE EUDICOTS								
Caryophyllales								
Aizoaceae*	76	20.27	60	46.51	98	23.17	234	25.24
Amaranthaceae	42	11.20	1	0.78	24	5.67	67	7.23
Molluginaceae	46	12.27	5	3.88	19	4.49	70	7.35
Nyctaginaceae	2	0.53	2	1.55	3	0.71	7	0.76
Plumbaginaceae	3	0.08	3	2.33	2	0.47	8	0.83
Portulacaceae	3	0.08					3	0.32
Saxifragales								
Crassulaceae			2	1.55	7	1.65	9	0.97
ROSIDS								
Zygophyllaceae*	51	13.6	17	13.18	71	16.78	139	14.99
Geraniales								
Geraniaceae	5	1.33	8	6.20	6	1.42	19	2.05
EUROSIDS I								
Celastraceae	40	10.67			7	1.6	47	5.06
Cucurbitales								
Cucurbitaceae					7	1.65	7	0.76
Fabales								
Fabaceae*	147	39.2	11	8.53	164	38.77	322	34.74
Polygalaceae					9	2.13	9	0.97
Malpighiales								
Euphorbiaceae	15	4.0	1	0.78	3	0.71	19	2.05
Rosales								
Rhamnaceae	35	9.33			1	0.24	36	3.88
EUROSIDS II								
Brassicales								
Brassicaceae	2	0.53	3	2.33	32	7.57	37	3.99
Malvales								
Malvaceae	5	1.33	8	6.20	54	12.77	67	7.23
Neuradaceae	1	0.27	1	0.78	10	2.3	12	1.29
Sapindales								
Rutaceae	1	0.27			1	0.24	2	0.22
ASTERIDS								
Cornales								
Loasaceae					2	0.47	2	0.22
EUASTERIDS I								
Boraginaceae	13	3.47	5	3.88	50	11.82	68	7.34
Vahliaceae	1	0.27	1	0.78	7	1.65	9	0.97
Gentianales								
Apocynaceae	48	12.80			31	7.33	79	8.52
Lamiales								
Acanthaceae	14	3.73	2	1.55	52	12.29	68	7.34
Lamiaceae	10	2.67	2	1.55	65	15.37	77	8.31
Pedaliaceae					9	2.13	9	0.97
Scrophulariaceae*	27	7.20	33	25.58	38	8.98	98	10.57
Solanales								
Convolvulaceae					1	0.24	1	0.08
Solanaceae	8	2.13			11	2.60	19	2.05
EUASTERIDS II								
Apiales								
Apiaceae*	161	42.93			27	6.38	188	20.28
Asterales								
Asteraceae*	116	30.93	56	43.41	157	37.12	329	35.49
Campanulaceae	9	2.40	19	14.73	33	7.80	61	6.58
% diversity of choice	**141.60**		**88.37**		**144.21**			

* = These six plant families attract >10% of the bee, wasp and pollen wasp species.

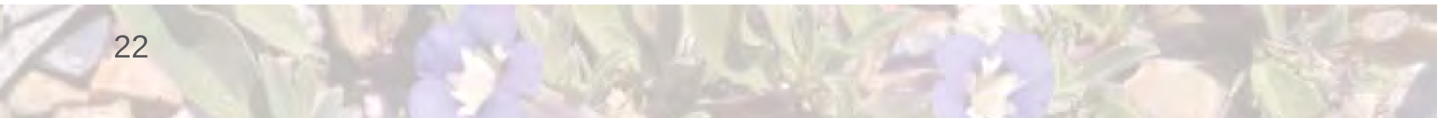


Table 2.—Numbers and percentages of species of bees, by family, recorded visiting flowers of the listed plant families (Gess & Gess 2006)

Plant taxon	Andrenidae (9 spp.)	Apidae (123 spp.)	Colletidae (46 spp.)	Halictidae (69 spp.)	Megachilidae (146 spp.)	Melittidae (30 spp.)
MONOCOTS						
Asparagales						
Asparagaceae						
Asphodelaceae		2	1	1	8	
Iridaceae		3	1	4	2	2
EUDICOTS						
Proteaceae		3	3	1		1
CORE EUDICOTS						
Caryophyllales						
Aizoaceae	4	35	10	21	21	7
Amaranthaceae		5	3	10	5	1
Molluginaceae	4	7		4	2	2
Nyctaginaceae	1			1	1	
Plumbaginaceae		1		1		
Portulacaceae						
Saxifragales						
Crassulaceae		2		2	2	1
ROSIDS						
Zygophyllaceae	3	22	10	23	10	3
Geraniales						
Geraniaceae		3	1		2	
EUROSIDS I						
Celastraceae		1	1	5		
Cucurbitales						
Cucurbitaceae		4		1	1	1
Fabales						
Fabaceae	6	41	3	22	80	12
Polygalaceae		2			7	
Malpighiales						
Euphorbiaceae			1	2		
Rosales						
Rhamnaceae				1		
EUROSIDS II						
Brassicales						
Brassicaceae		17	1	6	7	1
Malvales						
Malvaceae	1	21		10	19	3
Neuradaceae		2	1	2	4	1
Sapindales						
Rutaceae				1		
ASTERIDS						
Cornales						
Loasaceae				1	1	
EUASTERIDS I						
Boraginaceae	2	29		6	13	
Vahliaceae		4		1	2	
Gentianales						
Apocynaceae		9	1	5	15	1
Lamiales						
Acanthaceae		28		4	20	
Lamiaceae	2	31		7	25	
Pedaliaceae		4		2	3	
Scrophulariaceae	1	12	4	15	4	2
Solanales						
Convolvulaceae		1				
Solanaceae		8		3		
EUASTERIDS II						
Apiales						
Apiaceae		8	6	9	4	
Asterales						
Asteraceae	1	51	19	29	53	4
Campanulaceae		8	3	7	7	8
% diversity of choice	**177.77**	**195.93**	**50.00**	**202.90**	**117.81**	**70.00**

Table 3.—The ten plant families receiving visits from the highest percentages of species for wasps, pollen wasps and bees

Wasps (Total: 375 species)	**Pollen wasps (Total: 129 species)**	**Bees (Total: 420 species)**
Apiaceae 42.9%	Aizoaceae 46.51%	Fabaceae 38.77%
Fabaceae 39.2%	Asteraceae 43.41%	Asteraceae 37.12%
Asteraceae 30.93%	Scrophulariaceae 25.58%	Aizoaceae 23.17%
Aizoaceae 20.27%	Campanulaceae 14.73%	Zygophyllaceae 16.78%
Zygophyllaceae 13.6%	Zygophyllaceae 13.18%	Lamiaceae 15.37%
Molluginaceae 12.27%	Fabaceae 8.5%	Malvaceae 12.77%
Apocynaceae 12.08%	Geraniaceae 6.20%	Acanthaceae 12.29%
Amaranthaceae 11.20%	Malvaceae 6.20%	Boraginaceae 11.82%
Celastraceae 10.67%	Molluginaceae 3.88%	Scrophulariaceae 8.98%
Rhamnaceae 9.33%	Boraginaceae 3.88%	Brassicaceae 7.57%

Diversity of plant taxa visited by wasps and bees for obtaining floral resources

Cowling & Hilton-Taylor (1999, Table 4.1) list the ten largest plant families from each of five domains (Namaqualand-Namib semi-arid, Namaqualand-Namib arid, Southern Karoo, Eastern Karoo and Damaraland-Kaokoveld) of the Karoo-Namib Region amounting to an overall of 15 families, namely Asteraceae, Aizoaceae, Acanthaceae, Asclepiadaceae (included in Apocynaceae in APG 1998), Chenopodiaceae, Capparaceae (included in Brassicaceae in APG 1998), Crassulaceae, Euphorbiaceae, Fabaceae, Geraniaceae, Scrophulariaceae, Sterculiaceae (included in Malvaceae in APG 1998), Iridaceae, Liliaceae and Poaceae. The 36 families recorded in our survey as visited by solitary wasps and bees include all the listed families except Poaceae and Chenopodiaceae.

When considering the ten families receiving visits from the highest numbers of species of wasps, pollen wasps and bees (Table 1), one finds six of the Cowling & Hilton-Taylor (1999) families included, namely Asteraceae (329), Fabaceae (322), Aizoaceae (234), Scrophulariaceae (98), Asclepiadaceae (included in Apocynaceae) (79) and Acanthaceae (68). The remaining four, Apiaceae (188), Zygophyllaceae (139), Lamiaceae (77) and Boraginaceae (68), though not amongst the ten largest families, are nonetheless amongst the families that characterise the Karoo-Namib Region.

It is of interest to list separately for non-masarine wasps (for ease of reading referred to for the analyses as ‘wasps’), pollen wasps and bees the ten flower families receiving visits from the highest percentage of species (Table 3). It is of note that only four plant families, Fabaceae, Asteraceae, Aizoaceae and Zygophyllaceae—the top four families visited by bees—are common to all three lists. Three further subfamilies, Scrophulariaceae, Malvaceae and Boraginaceae, are common to both bees and pollen wasps. The equivalent percentages for Fabaceae for wasps and bees are misleading; most Fabaceae visited by bees are of the subfamily Papilionoideae whereas those most visited by wasps are of the Mimosoideae (Figure I.3.11). The high percentage of bees visiting Fabaceae contrasts with the low percentage of pollen wasps.

Plant families and their wasp and bee visitors

The Dicot plant families discussed below are grouped on the percentage of aculeates visiting the flowers—20% (four families); between 10% and 20% (two families); between 5% and 10% (eight plant families excluding Molluginaceae which is grouped together with Aizoaceae); fewer than 5% (19 families) (Table 4). The Monocots are discussed separately. The plant families are listed and discussed alphabetically per group.

Dicots

The four families receiving visits from more than 20% of the wasps and bees

Aizoaceae and Molluginaceae (formerly included in Aizoaceae)

Aizoaceae

The family Aizoaceae has been variously delimited. We follow the assessment by Bittrich & Hartmann (1988). The family is seen to consist of five subfamilies arranged in two groups. Mesembryanthema (Figures I.3.1–4), composed of the Ruschioideae and Mesembryanthemoideae. Non-Mesembryanthema (Figure I.3.5), composed of Aizooideae, Sesuvioideae and Tetragonioideae.

The distribution of Mesembryanthema is centred in south-western Africa (Hartmann 1991) whereas non-Mesembryanthema is cosmopolitan.

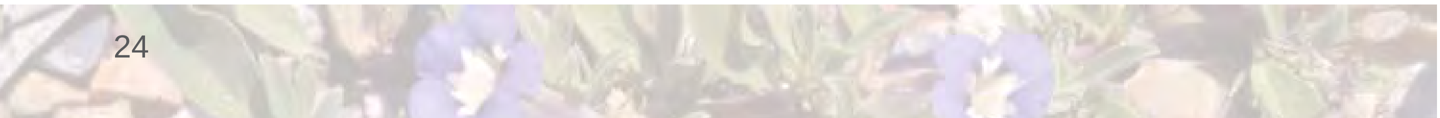


Table 4.—Dicot plant families listed alphabetically based on the percentage of bees and wasps recorded visiting their flowers; following on Table 1

Four families receiving visits from >20%	**Two families receiving visits from 10–20%**	**Eight families receiving visits from 5–10%**	**19 families receiving visits from <5%**
Aizoaceae with Molluginaceae	Scrophulariaceae	Acanthaceae	Brassicaceae
Apiaceae	Zygophyllaceae	Amaranthaceae	Combretaceae
Asteraceae		Apocynaceae	Convolvulaceae
Fabaceae		Boraginaceae	Crassulaceae
		Celastraceae	Cucurbitaceae
		Campanulaceae	Ebenaceae
		Lamiaceae	Euphorbiaceae
		Malvaceae	Geraniaceae
			Loasaceae
			Neuradaceae
			Nyctaginaceae
			Pedaliaceae
			Plumbaginaceae
			Portulacaceae
			Polygalaceae
			Proteaceae
			Rhamnaceae
			Solanaceae
			Vahliaceae

The Aizoaceae sampled for insect visitors were in the main shrubby or semi-prostrate species. None of the ‘miniature’ or ‘cryptic’ species was included. The flowers of the species of Mesembryanthema were either of the carpet (Figure I.3.1.a–d) or cone (Figure I.3.2.a–c) forms of Hartmann (1991) or of the cup form (Figure I.3.3.a & b) of Gess (1996). Recess flowers were not represented. However, Struck (1995) noted that the concealed flowers of Dactylopsis digitata (Ait.) N.E.Br. (Figure I.3.4) in the Knersvlakte, Namaqualand, are visited by Quartinia (Vespidae, Masarinae).

Over the entire study area 234 species (98 bees, 60 pollen wasps and 76 wasps, i.e. 25.2% of the species recorded visiting flowers) were collected on flowers of Aizoaceae. Of these, 183 species were on Mesembryanthema and 80 species on non-Mesembryanthema. Less than 10% were visiting both Mesembryanthema and non-Mesembryanthema. A south–north shift is apparent. In the south 143 species were recorded visiting Mesembryanthema but in the transition (northern Succulent Karoo, north and south of the Orange River) and the north only 31 species were recorded. By contrast, only 21 species were recorded visiting non-Mesembryanthema in the south and transition (northern Succulent Karoo to the south and north of the Orange River) but 57 species were recorded in the north. Thus, although there is a marked decline in the number of species visiting Mesembryanthema on a south–north gradient, there is an increase in the number of species visiting non-Mesembryanthema.

Of the bee species for which flower visiting records were obtained, 23.2% were collected on Aizoaceae. Species recorded from flowers of Aizoaceae, both Mesembryanthema and non-Mesembryanthema, represented all bee families (4 Andrenidae, 35 Apidae, 10 Colletidae, 21 Halictidae, 21 Megachilidae, 7 Melittidae). Some of these species show a considerable range of dependence on Aizoaceae and therefore a considerable range of dependability as visitors to flowers of this family. *Othinosmia* (*Othinosmia*) sp. A (Megachilidae) has been collected from flowers of these plants from eastern Nama-Karoo, southern Great Karoo, the Olifants River Valley and Namaqualand through to northern Richtersveld. The only other record for this bee was of one casual visit to *Grielum* (Neuradaceae). The flower preference of this species is in contrast to that of eight other species of *Othinosmia* (*Megaloheriades*), which restrict their visits almost entirely to Asteraceae. Several species of Colletidae in the southwest, Melittidae in the northern Richtersveld and Fideliinae (Megachilidae) in the southwest and northwest appear to be restricted to Aizoaceae, in particular Mesembryanthema. Unlike *O.* (*Othinosmia*) sp. A, these species have very limited distributions that are narrowly endemic.

Other species of bees visiting Mesembryanthema are polyphagous and therefore neither dependent on the plants nor dependable visitors. A notable example is *Amegilla niveata* (Friese) which we collected visiting flowers of 20 plant families. This species, widespread throughout the entire area, is therefore almost as unbiased in its flower visiting as the honeybee.

As a group, pollen wasps show an exceptionally high preference for Mesembryanthema with 46.5% of species having been recorded from these flowers. They are associated with Mesembryanthema throughout their range and that of these plants. However, the majority of masarine/mesemb associations are found in the southern region of the study area (Gess & Gess 2004a). Eight species of *Ceramius*, variously distributed south of the Orange River, are dependent on Mesembryanthema and are therefore dependable visitors to a wide range of mesembs. Five species of *Jugurtia* have been recorded from Aizoaceae. Two of these species are apparently dependent on Mesembryanthema and the other three species visit a limited range of additional families. Thirty-eight species of the *Quartinia* (*Quartinia*/*Quartinioides*/*Quartiniella*) visit Mesembryanthema and 65% of these species have been collected only

Figure I.3.1.—Aizoaceae, Mesembryanthema, examples of carpet flowers: a. and b. *Malephora* sp.; c. *Drosanthemum* sp.; d. *Prenia pallens* (Ait.) N.E.Br.

Figure I.3.2.—Aizoaceae, Mesembryanthema, examples of cone flowers: a. and b. *Brownanthus kuntzei* (Schinz) Ihlenf. & Bittrich; c. *Ruschia* sp.

Figure I.3.3.—Aizoaceae, Mesembryanthema, examples of cup flowers: a. and b. *Conicosia* sp.; c. *Carpobrotus* sp.

Figure I.3.4.—Aizoaceae, Mesembryanthema, example of concealed flower, *Dactylopsis digitata* (Ait.) N.E.Br.

or predominantly from these flowers. Three species of *Celonites* have been recorded from Mesembryanthema but these plants are not their primary forage plants.

South of the Orange River there appears to be no pollen wasp species dependent on non-Mesembryanthema. However, north of the Orange to the Kunene *Ceramius damarinus* Turner, (the only species of *Ceramius* found in Namibia) by prefence provisions with pollen and nectar from these flowers but, where they are in short supply, visits flowers of other families to obtain nectar.

Amongst the wasps excluding pollen wasps, 20.3% of the species collected on flowers were recorded from Aizoaceae. Most of these were from non-Mesembryanthema and included representatives of all families. All of these species are polyphagous. Some species of scoliids are common and expected visitors to certain large flowered mesembs.

Although the overall number of species visiting Mesembryanthema is large, at any one time and at any one place the number of species visiting these is usually small. Most of the bee visitors are polyphagous and few species are ever numerous visitors. Specialist species, however, when present, are often numerous. Similarly the specialist pollen wasp visitors, when present, are often very numerous. The most dependable and frequent pollinators can be expected amongst the specialist bees and pollen wasps. It is likely that a back up service is provided by the polyphagous bees. Of the wasp visitors only scoliids are likely pollinators.

A minority of Mesembryanthema, particularly those with dark colours are not attractive to bees, pollen wasps or wasps. These generally attract monkey beetles (Scarabaeidae, Hopliini) of the genera *Anisonyx* and *Peritrichia*, which are likely pollinators both in the west and east.

Molluginaceae

The genera presently grouped in the family Molluginaceae have previously been variously included in Phytolaccaceae and Aizoaceae (non-Mesembryanthema). Though present and sampled throughout the study area, Molluginaceae, like Aizoaceae (non-Mesembryanthema) are a more dominant element of the flora and are more frequently visited by wasps, pollen wasps and bees in the northern region. In the present study the visitors to flowers of four genera, *Limeum* (Figure I.3.6.a & b), *Gisekia* (Figure I.3.6.c & d), *Coelanthum* and *Corbichonia* were sampled. The flowers are small and open, unspecialised in structure and mostly grouped to form heads. Visits by 71 species (19 bees, 5 pollen wasps, 46 wasps and infrequently honeybees), i.e. 7.35% of the species recorded visiting flowers, were collected from flowers of Molluginaceae. Because the quantity of nectar obtainable from a single flower is small visitors requiring nectar are likely to move from flower to flower making them potential pollinators of these small unspecialised flowers.

Amongst the bees, no specialisations, expected visitors or dependable visitors were found although some taxa were relatively widely recorded from Molluginaceae. Panurgines (Andrenidae) were recorded from *Limeum*, *Gisekia*

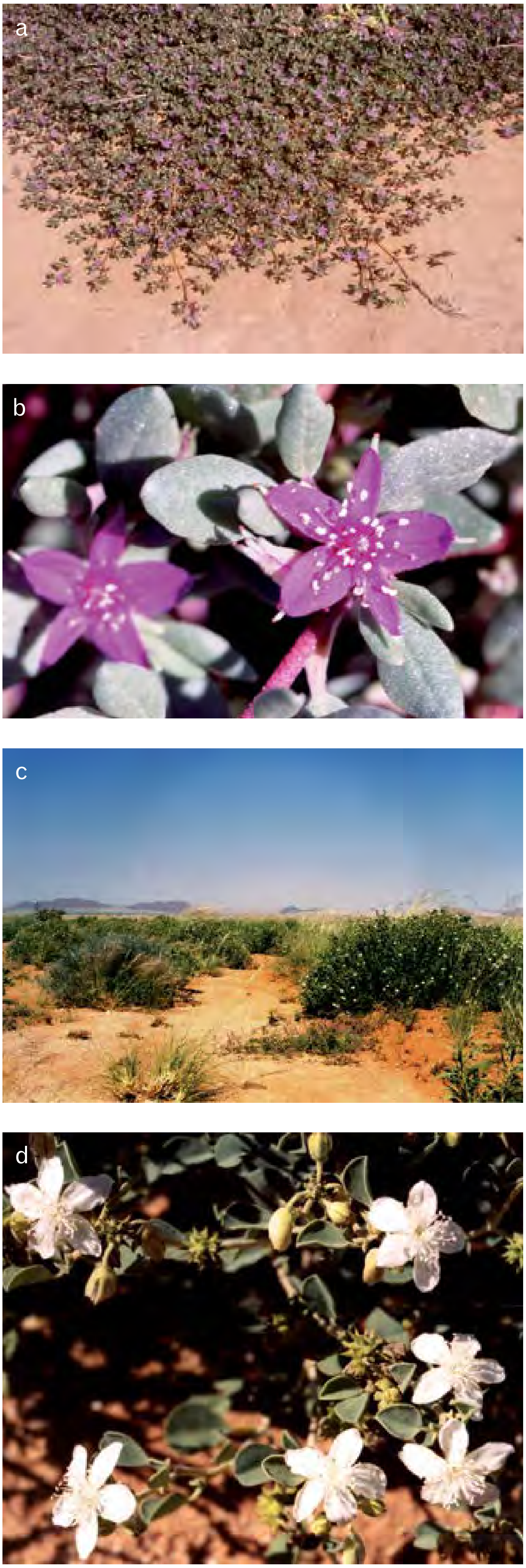


Figure I.3.5.—Aizoaceae, non-Mesembryanthema, examples: a. and b. *Sesuvium sesuvioides* (Fenzl) Verdc.; c. and d. *Tribulocarpus dimorphanthus* (Pax) S.Moore; e. and f. *Trianthema hereroensis* Schinz; g. *Galenia papulosa* (Eckl. & Zeyh.) Sond.

and *Corbichonia* in Namibia and from *Limeum* in southern Kalahari, and nomiines (Halictidae) from *Limeum* and *Gisekia* in western Namibia and from *Limeum* in the extreme southeast of the Nama-Karoo and in southwestern Namibia.

In northwestern Namibia two species of pollen wasps are expected visitors. *Priscomasaris namibiensis* Gess and a *Quartinia* species were repeatedly found only in association with *Gisekia* and *Limeum*. A third species, *Ceramius damarinus* Turner, most commonly visits Aizoaceae (non-Mesembryanthema) but, when its favoured flowers are in short supply, occasionally visits other flowers, including those of Molluginaceae.

Figure I.3.6.—Molluginaceae, examples: a. *Limeum argute-carinatum* Wawra & Peyr.; b. *Limeum myosotis* H.Walter; c. and d. *Gisekia africana* (Lour.) Kuntze.

In the southwest between Clanwilliam and Graafwater, two pollen wasps, *Celonites wahlenbergiae* Gess and *Celonites bergenwahliae* Gess, that show a preference for *Wahlenbergia* (Campanulaceae), but are not restricted to these plants occasionally visit flowers of *Coelanthum* in the afternoon—the time when they are open.

The wasps were represented by 26 Crabronidae (*sensu lato*) (10 Nyssonidae, 9 Crabronidae and 7 Philanthidae following an earlier classification of the sphecoid wasps), 6 Pompilidae, 6 Chrysididae, 2 Sphecidae, 2 Scoliidae, 2 Tiphiidae and 1 Vespidae (Eumeninae). These wasps are all polyphagous and none can be said to be dependent on Molluginaceae. Yet, *Limeum* species are undoubtedly an important nectar source for the Crabronidae, in particular Bembicini and Larrini, throughout the study area and in all probability these wasps provide a pollination service.

Apiaceae

Apiaceae is not species diverse in the Karoo Biome but some species form large stands. Samples taken of the visitors to the flowers were of three species; two indigenous species, *Berula erecta* (Huds.) Coville in the southeast and *Deverra denudata* (Viv.) Pfisterer & Podlech in drainage channels in the southern Kalahari, western Richtersveld and the Namib fringe north of Aus (Figure I.7.a & b); and one alien invasive species, *Foeniculum vulgare* Mill., a common roadside weed in the southeast. All have small, simple, shallow, nectar-producing, yellow flowers arranged in umbels.

Apiaceae, represented by these three species, was the family receiving the fourth highest number of flower visitors. Whereas Asteraceae, Fabaceae and Aizoaceae, the three families receiving larger numbers of visitors, are widespread and were widely sampled, Apiaceae was limited to a small number of sites. Of all families sampled, Apiaceae received visits from the greatest percentage (42.93%) of wasp species. These 161 species included 13 Chrysididae, 2 Bradynobaenidae, 1 Mutillidae, 31 Pompilidae, 12 Scoliidae, 8 Tiphiidae, 15 Vespidae (Eumeninae), 67 Crabronidae (*sensu lato*) (previously as 1 Astatidae, 27 Crabronidae, 21 Nyssonidae, 2 Pemphredonidae and 16 Philanthidae following an earlier classification of the sphecoid wasps) and 12 Sphecidae. By comparison only a small percentage (6.38%) of bee species and no pollen wasps visited Apiaceae. The 27 bee species included 8 Apidae, 6 Colletidae, 9 Halictidae and 4 Megachilidae.

Visitation of these plants by such a wide range of visitors of suitable size and behaviour is likely to ensure pollination, particularly where, as is usually the case, Apiaceae form considerable monospecific stands.

More recently a semi-prostrate species of Apiaceae, *Capnophyllum africanum* (L.) Koch (Figure I.3.7.c), in the Koeberg Reserve was found to be visited by several species of *Quartinia* (Vespidae, Masarinae).

Asteraceae

Asteraceae is the largest family in the Karoo-Namib Region and the largest in four of the five domains listed by Cowling & Hilton-Taylor (1999), being exceeded only in the Namaqualand-Namib Domain by Aizoaceae. Not only are

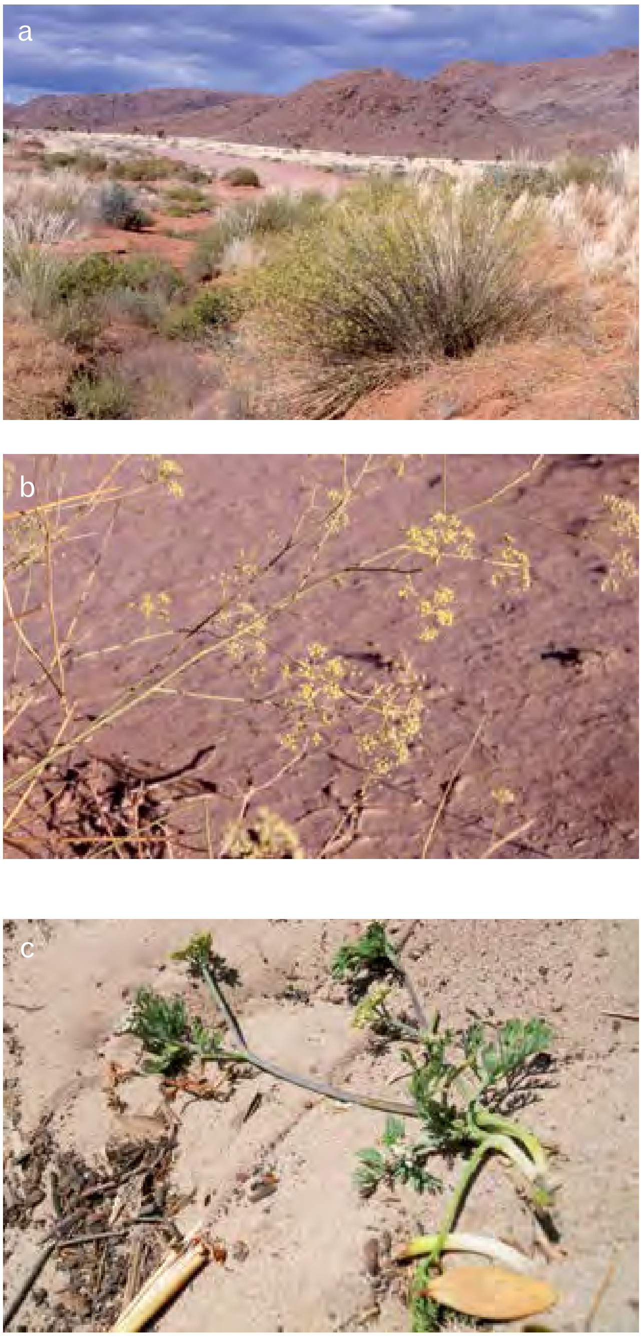


Figure I.3.7.—Apiaceae, examples: a. and b. *Deverra denudata* (Viv.) Pfisterer; c. *Capnophyllum africanum* (L.) Koch.

Asteraceae notable for their species diversity, but they are also amongst the dominant plants in most karroid areas.

Asteraceae sampled include woody, shrubby species and annual and perennial herbs (Figure I.3.8). The flower heads are simple or compound, loose or compact, deep or shallow, with or without ligulate florets. All six tribes characteristic of the semi-arid areas of southern Africa were represented and the number of species was in excess of 75. Together they were recorded as receiving visits from the largest number of species. Over the entire study area 329 species (157 bees, 56 pollen wasps and 116 wasps), i.e. 35.49% of the species recorded visiting flowers, were collected on flowers of Asteraceae.

Of the bee species collected on flowers, 37.12% visit Asteraceae. All bee families were included (1 Andrenidae, 51 Apidae, 19 Colletidae, 29 Halictidae, 53 Megachilidae and 4 Melittidae). Most species visiting Asteraceae are broadly polyphagous. However, some specialisations are apparent. In the Colletidae at least seven species of *Scrapter* and in the Fideliinae, *Fidelia braunsiana* Friese, show a

Figure I.3.8.—Asteraceae, examples: a. *Felicia dubia* Cass.; b. *Leysera tenella* DC.; c. *Tripteris microcarpa* Harv.; d. *Berkheya fruticosa* (L.) Ehrh.; e. *Geigeria pectidea* (DC.) Harv.; f. *Geigeria acaulis* Benth. & Hook.; g. *Athanasia trifurcata* (L.) L.; h. *Pteronia*; i. *Helichrysum herniariodes* DC.

marked preference for Asteraceae, having been collected from flowers of this family only. Furthermore a preference, based on numbers of records for Asteraceae, is exhibited in the Halictidae by some species of *Halictus* and *Patellapis* (some previously known as *Lasioglossum*), in the Megachilidae by many of the Osmiini, and in the Apidae especially by the subgenus *Anthophora* (*Heliophila*) which shows a strong preference for Asteraceae (Gess & Gess 1996).

Of the pollen wasps collected on flowers 43.4% visit Asteraceae. Of these, 21 species specialise in Asteraceae, seven species of *Ceramius*, three species of *Jugurtia*, and approximately 12 species of *Quartinia* (*Quartinia/Quartinioides/Quartiniella*). The remaining 29 species visit a limited range of other families. In areas where pollen wasps specialising in Asteraceae are common, they are probably important potential pollinators of the plants they visit and in some areas are probably their most important potential pollinators.

Amongst the wasp species collected on flowers 30.93% visit Asteraceae. Most families were represented. The distribution of species was 49 Crabronidae (*sensu lato*) (previously as 18 Crabronidae, 21 Nyssonidae, 1 Pemphredonidae and 9 Philanthidae following an earlier classification of the sphecoid wasps), 18 Chrysididae, 14 Vespidae (Eumeninae), 12 Sphecidae, 7 Pompilidae, 8 Scoliidae and 8 Tiphiidae. Most species are broadly polyphagous. Exceptions include some species of Chrysididae, most notably three species of *Allocoelia* which were repeatedly collected solely on Asteraceae, and Eumeninae, most notably species of *Raphiglossa*.

Some species of Asteraceae are widely distributed and are common to a range of vegetation and soil types. Whereas some of the visitors are similarly able to make a living in such diverse situations, most are more restricted in their distributions and their habitat requirements. This results in different complexes of visitors being present at different sites. For example, at some sites *Athanasia trifurcata* (L.) L. (Anthemideae) (Figure I.3.8.g.), is mainly visited by pollen wasps with the species varying between sites—*Ceramius braunsi* Turner to the south of Clanwilliam, *Ceramius metanotalis* Richards to the north of Clanwilliam and *Ceramius toriger* Schulthess in the southern Tankwa Karoo. At other sites no pollen wasps are present and it is visited by a diverse complex of wasps and bees.

Similarly, *Berkheya fruticosa* (L.) Ehrh. (Arctoteae) (Figure I.3.8.d.) is visited by *Ceramius braunsi* Turner at Clanwilliam, by *Ceramius nigripennis* Saussure in Namaqualand and by *Ceramius toriger* Schulthess to the east of Nieuwoudtville where it was visited by a much larger range of bee visitors than elsewhere. A similar picture emerges for other species of *Berkheya* throughout the karroid areas.

Vogel (1954) considers that South African composites are generally Hymenoptera-flowers, though flies and certain beetles may also play a large part in the pollination of some. The suitability of most Asteraceae as a floral resource for aculeates and the suitability of aculeates as pollinators has been discussed Gess (1996). The authors' observations of beetles and flies as visitors suggest that generally beetles are destructive visitors but some do exhibit the requirements for pollinators and that flies are generally of less importance than aculeates but in some instances are specialist pollinators. Examples of probable beetle and fly pollination are given by Picker & Midgley (1996) and Johnson & Midgley (1996) respectively.

Fabaceae (Leguminosae)

Fabaceae is one of the largest plant families in the Karoo-Namib Region (Cowling & Hilton-Taylor 1999).

The flowers of Fabaceae (including all three subfamilies) were found to receive visits from 322 species of aculeates (164 bees, 11 pollen wasps and 147 wasps), i.e. 34.74% of species visiting flowers, were collected on Fabaceae. This number is second only to Asteraceae. Due to distinct differences in flower morphology and therefore of flower visitors the three subfamilies, Mimosoideae, Papilionoideae and Caesalpinioideae, will be considered separately.

Mimosoideae

Mimosoideae, shrubs to small trees, mostly associated with drainage channels, are common in all but the winter rainfall areas (Figure I.3.9). They are visited by a great diversity of wasps. Our samples include 114 species, i.e. 30% of the wasp species collected from flowers. Of the bees, only 28 species, i.e. 7%, were represented in our samples. That is a ratio of wasps to bees of 4:1. One individual male pollen wasp, *Jugurtia confusa* Richards, has been recorded visiting Mimosoideae. This was clearly a casual visit.

The wasps were from a wide range of families—30 Crabronidae (*sensu lato*) (previously established as 7 Crabronidae, 7 Nyssonidae and 16 Philanthidae following an earlier classification of the sphecoid wasps), some Vespidae, 27 Eumeninae, 16 Pompilidae, 14 Scoliidae, 14 Sphecidae, 7 Tiphiidae, 5 Chrysididae and 1 Ampulicidae. The bees were from families showing a relatively high overall diversity of choice—12 Megachilidae, 11 Apidae, 4 Halictidae and 1 Andrenidae. Colletidae and Melittidae, which show a markedly lower overall diversity of choice, were absent.

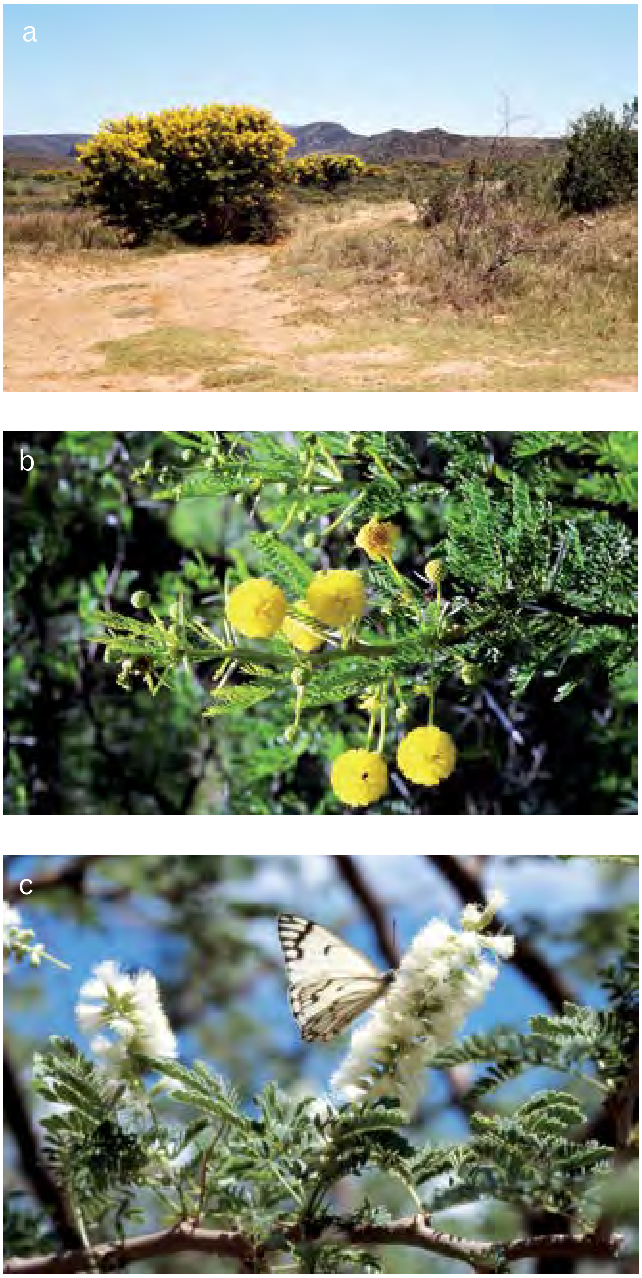


Figure I.3.9.—Fabaceae, Mimosoideae, examples: a. and b. *Acacia karroo* Hayne; c. *Acacia senegal* (L.) Willd.

The flowers of Mimosoideae also attract a great diversity of other insects, notably butterflies and beetles, though wasps are the most species diverse and numerous visitors.

Papilionoideae

Shrubby and herbaceous, perennial and annual species of Papilionoideae occur throughout the study area. They are represented in our survey principally by species of *Crotalaria* (Figure II.4.27), *Lotononis*, *Melolobium* (Figure I.3.10.j & l), *Aspalathus* (Figure I.3.10.c.), *Lebeckia* (Figure I.3.10.d & e), *Wiborgia* and *Rafnia* (all Crotalarieae) (Figure I.3.10.f), and species of *Indigofera* (Indigofereae) (Figure I.3.10.g–i). Also included are species of *Tephrosia* (Tephrosieae), *Otoptera* (Phaseoleae), *Lessertia* (Galegeae) (Figure I.3.10.j), and *Cullen* and *Psoralea* (both Psoraleae).

A greater diversity of bees, 138 species, i.e. 32.62% of the species collected from flowers, than of wasps, 64 species, i.e. 17.0%, were collected from flowers of Papilionoideae. That is a ratio of bees to wasps of 2:16, a reverse of the pattern obtained for Mimosoideae (Figure I.3.11). Furthermore, 10 species of pollen wasps were collected from Papilionoideae.

Despite the much lower number of wasp species recorded, the family representation is the same. Family representation for bees is very different since all seven families were recorded.

In an analysis of the visitors to Cape Crotalarieae, *Aspalathus*, *Lebeckia*, *Wiborgia* and *Rafnia* (all yellow flowered), all assemblages from the western, northern (Namaqualand) and eastern Cape were characterised by the presence of Megachilinae (Megachilidae) and Xylocopini or Anthophorini (Apidae) and those from the west, including Namaqualand (excluding those from *Rafnia*) by the additional presence of Masarinae (Vespidae) (Gess & Gess 1994a). Although not restricted to Polhill's Cape Group, the Megachilinae, Xylocopini and Anthophorini were considered to be potential pollinators. Two species of *Masarina* (Masarinae) are apparently restricted to *Aspalathus*, *Lebeckia* and *Wiborgia*, and are potential pollinators of the smaller flowered species of these genera. Two species of *Ceramius* (Masarinae), apparently restricted to *Aspalathus*, are potential pollinators and, within their distribution ranges, the most dependable visitors of this genus. Honeybees and Vespidae, Eumeninae visit all four genera but are probably of little importance as pollinators. Honeybees are able to obtain nectar from the smaller flowered species without tripping the flowers. Flower structure and visitor behaviour are dealt with in some detail by Gess (1996).

Although *Crotalaria* is the most widespread genus of Crotalarieae, the Karoo and Cape regions support a negligible representation (Polhill 1982). The genus was sampled, however, wherever it was encountered throughout the study area. All species were yellow flowered only. Stands of appreciable numbers of plants were found only in Namibia. These were of three erect annual to short lived perennial species:

- *C. podocarpa* DC., a species of dry open sandy places, growing where a little additional water collects, widespread with a distribution extending well east and north of Namibia to the Sahel.
- *C. damarensis* Engl., a semi-arid to desert species extending from the Namib Desert across to Mozambique.
- *C. argyraea* Welw. ex Baker, a semi-arid to desert species extending from Namibia into southern Angola.

These three species, superficially very similar in habit, were sampled for flower visitors wherever they were encountered from southern Namibia through the semi-arid and arid west to south of Opuwa in the Kaokoveld. At all sites they were visited frequently by a range of large Megachilini, nine species of *Megachile* being recorded. In the area bounded by Omaruru, Palm and Khorixas additional abundant visitors were *Meganomia gigas* Michener (Melittidae), an exceptionally large bee, and *Nomia* (*Crocisaspidia*) *maculata* (Friese) (Halictidae). Occasional visitors of particular interest were *Fidelia* (*Parafidelia*) *ornata* Cockerell (Fideliinae) and a species of *Anthidium* (Anthidiini). To the south west of Helmeringhausen further occasional visitors were *Pseudapis cinerea* (Friese) (Halictidae) and *Serapista rufipes* (Friese) (Anthidiini). Throughout the area the larger *Megachile* species, though polyphagous, are potential pollinators. Additional infrequent visitors were Apidae of which species of *Xylocopa* (Xylocopini) and *Amegilla* (Anthophorini) would certainly be able to pollinate the flowers. Though not as widespread, *Meganomia gigas* is a potential pollinator and is probably more dependable in the areas where it occurs, as it has not been recorded from any other flowers.

Flowers of a fourth erect species, *Crotalaria virgultalis* Burch. ex DC., broom-like in habit, were sampled for visitors at several sites in the southeast of Namibia where it was flowering abundantly on the red sands of the Kalahari. It was visited mainly by a large species of *Megachile*, which is a potential pollinator.

Other Crotalarieae sampled in Namibia and Namaqualand were semi-prostrate, mat forming species. These were also visited mainly by Megachilidae. Flowers of *Crotalaria dinteri* Schinz, growing east of the Gamsberg, were visited by a species of *Megachile*. During two spring seasons flowers of *Lotononis bainesii* Baker growing on the Kamiesberg were being visited repeatedly by *Megachile* (*Chalicodoma*) *murina* Friese. This bee was also frequently represented in samples from flowers of Cape Crotalarieae—*Aspalathus* in southeastern Nama Karoo, to the west of the Olifants River, and westwards, eastwards and northwards through Namaqualand, and *Lebeckia* and *Wiborgia* in the west. It was otherwise recorded from *Polygala* in Namaqualand. A single female was collected from Lamiaceae in the Richtersveld. It seems that this bee is closely associated with Fabaceae and in particular with Crotalarieae regardless of plant form. It is of interest that it also visits the superficially similar flowers of *Polygala* (Polygalaceae).

Two species of Tephrosieae with relatively large, pink flowers were sampled in Namibia. Both were visited solely by a limited number of polyphagous bees:

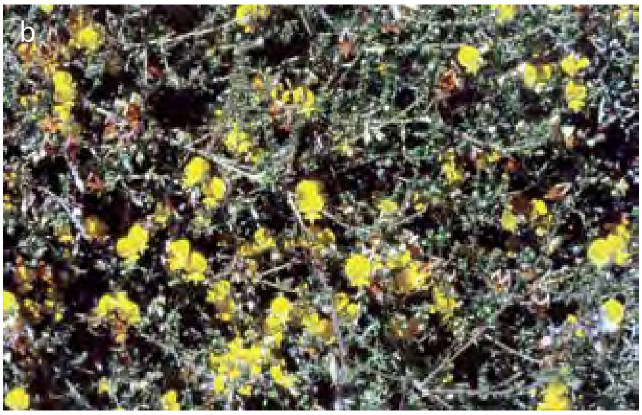
- *Tephrosia burchellii* Burtt Davy in the southeast by *Meliturgula flavida* (Friese) (Andrenidae, Panurginae), *Amegilla langi* (Cockerell) (Apidae, Apinae) and a species of *Ceyalictus* (Halictidae, Nomioidinae).
- *Tephrosia oxygona* Welw. ex Baker in the northwest by two of the same *Megachile* species which commonly visit *Crotalaria* in the same area, *M.* (*Maximegachile*) *maxillosa* Guérin-Méneville and *M.* (*Gronoceras*) *felina cerberus* Friese.

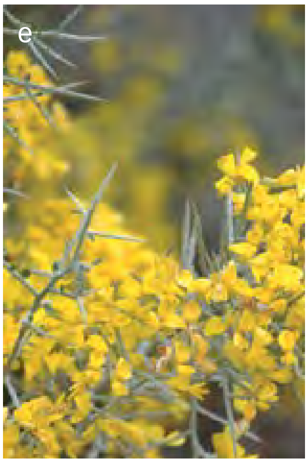
Although not encountered in the present survey it is of interest that *Fidelia* (*Parafidelia*) *ornata* (Cockerell) (Megachilidae, Fideliinae) has been recorded from two species of *Tephrosia* (Whitehead 1984).

The large pink flowers of a single species of Phaseoleae, the desert pea (*Otoptera burchellii* DC.), were sampled for visitors in the Grootberg to the northwest. These flowers were visited by *Amegilla calens* (Lepeletier), *Xylocopa caffra* (L.), *Xylocopa lugubris* Gerstaecker, and *Megachile* (*Gronoceras*) *felina cerberus*, all of which have the capability to pollinate the flowers. It is likely that in other areas it is visited by these and/or other large Apidae and Megachilidae.

The Indigofereae sampled for flower visitors were all species of *Indigofera*. These are erect and mat forming herbs and woody dwarf shrubs with small pink, reddish pink or orange flowers. The principal species were:

- *I. alternans* DC., a pink or pinkish-orange flowered, semi-prostrate, mat forming herb (Figure I.3.10.i), sampled for flower visitors in six areas of southeastern Namibia and one in the southeastern Karoo.
- *I. auricoma* E.Mey., a pink flowered, semi-prostrate herb, sampled for flower visitors at various sites on the desert margin from Aus to the Gaub Pass.
- *I. charlieriana* Schinz, a pink flowered herb, sampled for flower visitors in two areas of southeastern Namibia.
- *I. filipes* Benth. ex Harv., a pink flowered, erect herb, sampled for flower visitors in four areas in southeastern and one in northwestern Namibia.





- *I. longispina* Baker f. ex J.B.Gillett, a pinkish-red flowered, woody dwarf shrub (Figure I.3.10.g & h), sampled for flower visitors in the Richtersveld to the south and north of the Orange River.
- *I. rautaneni* Baker f., an orange flowered dwarf shrub, sampled for flower visitors in the Grootberg Pass in northwestern Namibia.

The representation of bee taxa overall was 24 Megachilidae (all Megachilinae—16 Anthidiini, 5 Megachilini and 3 Osmiini), 8 Halictidae (all Nomiinae), 5 Melittidae, 3 Andrenidae and 3 Apidae. Only one species of pollen wasp, a species of *Quartinia*, was collected on an *Indigofera, I. auricoma* E.Mey., at one of the four sites where this species was sampled for flower visitors. Wasp visits were generally uncommon.

Anthidiini were the most species diverse and the most widely encountered except in the southeast where only Megachilini were recorded. In most areas anthidiines can be said to be expected visitors and likely dependable pollinators.

Indigofera longispina sampled for flower visitors in the Richtersveld National Park and north across the Orange River was visited by Anthidiini and abundantly by the two melittids, *Samba* (*Atrosamba*) *gessorum* Eardley, a species recorded widely in the west, and *Samba* (*Metasamba*) *fasciata* Michener. *Samba* (*Atrosamba*) *gessorum* Eardley was also recorded visiting flowers of *Crassula dichotoma* L. at Sors Sors in the Kamiesberg. All were potential pollinators.

In the Kalahari sand areas two other melittids, *Ceratomonia rozenorum* Michener and *Meganomia binghami* Cockerell, are frequent visitors to *Indigofera* species. *Ceratomonia rozenorum* was not found visiting the flowers of any other plants.

Figure I.3.10.—Fabaceae, Papilionoideae, examples: a. and b. *Aspalathus divaricata* Thunb.; c. *Aspalathus linearis* (Burm.f.) Dalg.; d. and e. *Lebeckia psiloba* Walp.; f. *Rafnia* sp.; g. and h. *Indigofera longispina* Baker ex Gillett; i. *Indigofera alternans* DC.; j. *Lessertia diffusa* R.Br.; k. and l. *Melolobium candicans* (E.Mey.) Eckl. & Zeyh.

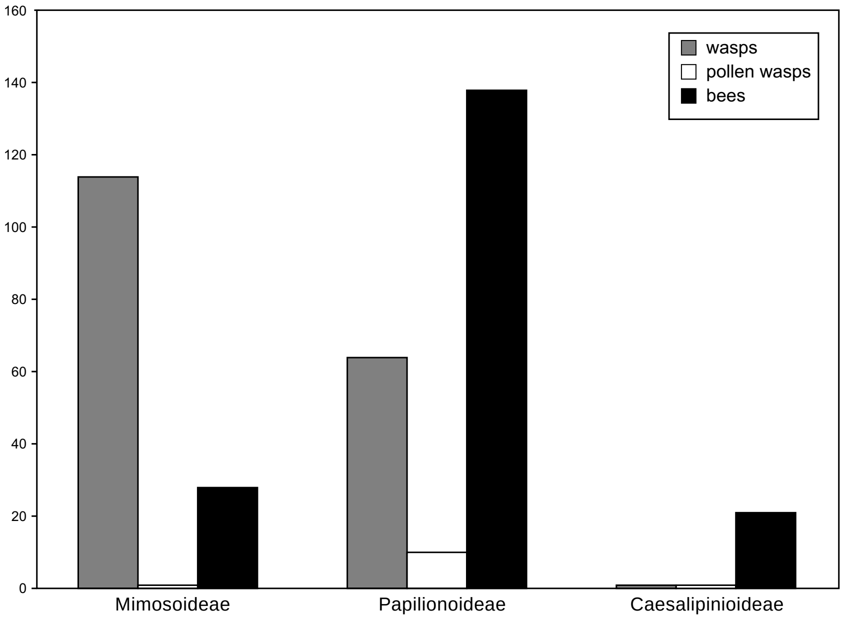


Figure I.3.11.—Differences in the percentages of wasps, pollen wasps and bees visting flowers of Mimosoideae and Papilionoideae.

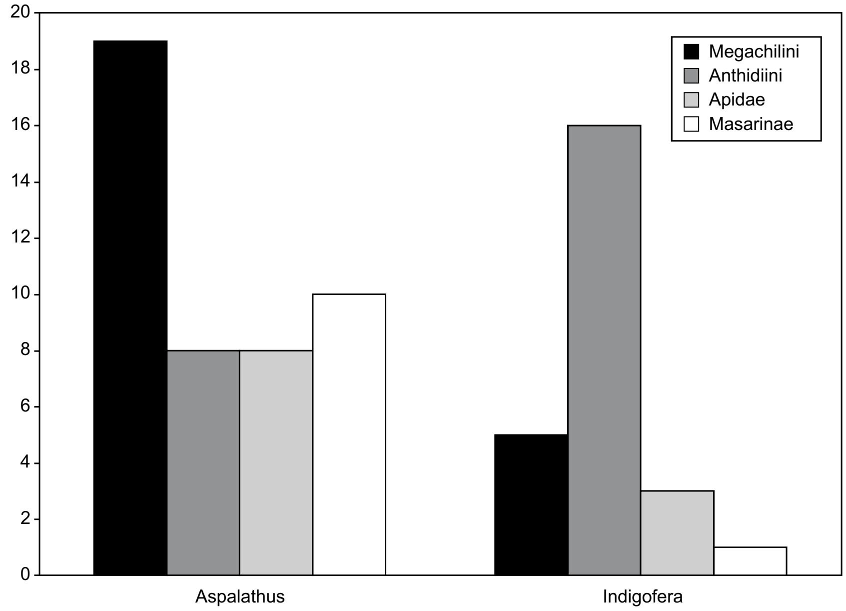


Figure I.3.12.—Differences in percentages of Megachilini, Anthidiini, Apidae and Masarinae visiting flowers of Aspalathus and Indigofera.

The composition of the bee assemblage from *Indigofera* is markedly different from from the Crotalarieae. For example Megachilini is represented by five species whereas 19 of the 27 Megachilidae recorded were from similarly small flowers of *Aspalathus* (Figure I.3.12). Only eight were Anthidiini compared to 16 from *Indigofera* with no Osmiini. However, 16 species of Anthidiini were recorded from *Indigofera* but only eight were recorded from *Aspalathus*. Of the Apidae three were recorded from *Indigofera* and eight from *Aspalathus*. Furthermore, Masarinae, which are important visitors and potential pollinators of *Aspalathus* in the southwest, were absent from the assemblages of visitors to flowers of *Indigofera*, except for one assemblage from the northwest between the Gaub and Kuiseb passes.

Three species of *Lessertia* were sampled. Two of these were from the southwest, *L. diffusa* R.Br. (Figure I.3.10.j) in the Goegap Reserve, Springbok, and *L. cf. spinescens* E.Mey. at Wallekraal. Both were visited only by Anthidiini. Of these, *Afranthidium* (*Branthidium*) *haplogaster* Mavromoustakis also visits *Indigofera* and *Plesianthidium* (*Spinanthidiellum*) *volkmanni* (Friese) also visits *Aspalathus*. The third, *L. macrostachya* DC., a more robust, larger flowered species, sampled in the Kalahari sands area of Namibia was visited principally by large species of *Megachile* and by *Meganomia binghami*.

Only four species of Psoraleae were sampled for flower visitors, namely *Psoralea pinnata* L. and *Psoralea oligophylla* Eckl. & Zeyh. in the southeast, *Psoralea* sp. in the Little Karoo, and *Cullen tomentosum* (Thunb.) J.W.Grimes near Augrabies. The principal visitors were Apidae and Megachilidae.

Caesalpinioideae

Caesalpinioideae were sampled for flower visitors only in the north. Those sampled were yellow and orange flowered *Adenolobus pechuelii* (Kuntze) Torre & Hillc. (Figure I.3.13.a), red flowered *A. garipensis* (E.Mey.) Torre & Hillc. and yellow flowered *Senna italica* Mill. (Figure I.3.13.c).

Adenolobus pechuelii was commonly encountered on rocky banks of relatively deep drainage channels in the northwestern desertic areas. It was mostly sampled for flower visitors between the Gaub and Kuiseb passes and southwest of Büllsport but also sites further north near Palm, Rössing Mountain, to the south between Alexander Bay and Port Nolloth and at one site in southeastern Namibia at Gross Nabas. Sixteen species of bees were recorded (9 Apidae, 3 Halictidae, 3 Megachilidae and 1 Andrenidae). Of these the most likely pollinators are the larger bees, three *Amegilla* spp. (Anthophorini), three *Xylocopa* spp. (Xylocopini), two large anthidiines (species of *Afranthidium* and *Trachusa* Panzer) and *Megachile* (*Maximegachile*) *maxillosa* (Megachilini). All except the anthidiines are broadly polyphagous.

A relatively polyphagous and apparently opportunistic pollen wasp, *Quartinia bella* Gess, was an extremely abundant visitor only at sites between the Gaub and Kuiseb passes. Its small size makes it unsuited to being a pollinator.

No wasps were found visiting *A. pechuelii*, however, the only visitor to *A. garipensis*, which was encountered only at Rooibank on the lower reaches of the Kuiseb River, was a male *Philanthus triangulum* (Fabricius) (Crabronidae, Philanthinae).

Senna italica was found in flower in the southern Kalahari and between Rehoboth and the Gamsberg Pass in Namibia. In all cases visitors were large Apidae. In the southern Kalahari what was taken to be a species of *Xylocopa* was in attendance, however, no voucher specimens were obtained. This sight identification was most probably correct, as *Xylocopa* species are frequent visitors to cultivated *Cassia* species. In Namibia *Amegilla atrocincta* (Lepeletier) and *Anthophora* (*Paramegilla*) *armata* Friese were frequent visitors. The flowers require to be buzzed as the anthers dehisce apically. All of these bees have the size and weight to be pollinators.

Figure I.3.13.—Fabaceae, Caesalpinioideae, examples: a. and b. *Adenolobus pechuelii* (Kuntze) Torre & Hillc.; c. *Senna italica* Mill.

The two families receiving visits from between 10% to 20% of the wasps, pollen wasps and bees

Scrophulariaceae

Scrophulariaceae is listed as one of the ten largest plant families in all five domains of the Karoo-Namib Region (Cowling & Hilton-Taylor 1999). Following APG (1998), Scrophulariaceae here includes Selaginaceae whereas in Gess (1992) Selaginaceae was treated as a separate family. Of the 14 tribes (Smithies 2000) Aptosimeae, Manuleae, Hemimerideae, Cheloneae and Selagineae were represented in the survey.

As a family Scrophulariaceae (*sensu lato*) received visits from 98 species—this is the sixth largest number of species, i.e. 11% of the species recorded visiting flowers. There is little difference in the numbers of species of bees (38), pollen wasps (33) and wasps (27) but marked differences in percentages, 8.98, 25.58 and 7.20 respectively. All families of bees were represented and included 15 Halictidae, 12 Apidae, 4 Colletidae, 4 Megachilidae, 2 Melittidae and 1 Andrenidae. Only half of the wasp families were represented and included 7 Sphecidae, 7 Crabronidae (*sensu lato*) (5 Nyssonidae and 2 Philanthidae following an earlier classification of the sphecoid wasps), 6 Tiphiidae, 3 Pompilidae, 3 Chrysididae and 1 Vespidae (Eumeninae).

Considering the separate tribes of Scrophulariaceae, expected differences linked to flower form and presentation were observed.

Selago (Selagineae) is principally southern African in distribution, widespread but occurring mostly in the Western and Eastern Cape (Smithies 2000). Four species were sampled, namely *S. corymbosa* L. (Figure I.3.14) in the east, northwest of Grahamstown, *S. divaricata* L.f. and *S. verna* Hilliard in Namaqualand, in the Kamiesberg and in the vicinity of Springbok and *S. dinteri* Rolfe in western Namibia to the east of the Gamsberg Pass. The small, erect, nectar producing, tubular flowers, aggregated into corymbs or elongated panicles, are attractive to a diverse range of bees and wasps. In addition two species of pollen wasps, *Jugurtia braunsi* (Schulthess) at the Namaqualand sites and *Ceramius damarinus* Turner in Namibia, have been recorded visiting *Selago*, but only as a secondary resource.

The Manuleae were found to be attractive to aculeates. They all have small, tubular, nectar producing flowers. Those sampled for flower visitors were *Phyllopodium cuneifolium* (L.f.) Benth. in the southeast, *Polycarena* species in Namaqualand and to the west of the Olifants River

Figure I.3.14.—Scrophulariaceae, Selagineae, example: a. and b. *Selago corymbosa* L.

Valley and *Jamesbrittenia canescens* (Benth.) Hilliard in Namibia. The most commonly encountered visitors to violet flowered *P. cuneifolium* were species of Ammophilinae (Sphecidae), which were nesting nearby. Other wasp visitors recorded were three females, two Bembicini and a pompilid. Visits by two bee species, an allodapine and a halictine, and one pollen wasp, *Celonites capensis* Brauns, were also recorded. The two bees visit a wide range of flowers and the pollen wasp is one of the most polyphagous species of pollen wasps, as it has been recorded from flowers of seven families. The *Polycarena* species, all white flowered, were visited as a secondary resource by pollen wasps.

Yellow flowered *Jamesbrittenia canescens* was observed for visitors near Mariental and between Büllsport and Sesriem. At both sites the visitors were polyphagous bees, mainly species of *Amegilla* (Apidae, Apinae, Anthophorini) with *Serapista rufipes* (Friese) (Megachilidae, Megachilinae, Anthidiini) at the second site. By contrast and as predicted, dark-red flowered *J. canescens* observed for flower visitors in the Kamiesberg were ignored by the abundant aculeates visiting other plants in flower nearby. These plants were visited by butterflies.

Oftia africana (L.) Bocq. (Cheloneae) observed near Graafwater, to the west of Clanwilliam, was visited by *Anthophora* (*Heliophila*) *wartmanni* Friese (Anthophorini). This bee mostly visits Asteraceae and less often a wide range of flowers.

Figure I.3.15.—Scrophulariaceae, Hemimerideae, example: a. and b. *Diascia namaquensis* Hiern.

Of the Hemimerideae two genera only, *Nemesia* and *Diascia*, were represented in our survey. For *Nemesia*, only one visit on a single occasion was recorded, that of a female *Ceratina* (Apidae, Xylocopinae, Ceratinini) visiting *Nemesia cf. bicornis* (L.) Pers. near Wallekraal. For *Diascia*, records were obtained for two species, *D. longicornis* (Thunb.) Druce and *D. namaquensis* Hiern (Figure I.3.15), which were visited by *Rediviva longimanus* Michener and *Rediviva emdeorum* Vogel, respectively. In addition flowers of both species were visited by an opportunist, *Patellapis* (*Patellapis*) *montagui* (Cockerell) (previously known as *Lasioglossum* sp. J) (Halictidae).

Vincent Whitehead and Kim Steiner (2001, Appendix) give the known associations of the 15 species of *Rediviva* known from the winter rainfall region. All are recorded

Figure I.3.16.—Scrophulariaceae, Aptosimeae, examples: a. and b. *Aptosimum arenarium* Engl.; c. *Aptosimum spinescens* (Thunb.) Weber; d. *Aptosimum indivisum* Burch. ex Benth.; e. *Aptosimum procumbens* (Lehm.) Steud.; f. and g. *Peliostomum leucorrhizum* E.Mey. ex Benth.; h., i. and j. *Anticharis scoparia* (E.Mey. ex Benth.) Hiern ex Schinz.

from oil-secreting Hemimerideae with five of the species also recorded from Orchidaceae. They record visits to around 22 species of *Diascia* with species of these flowers being visited by more than one species of *Rediviva* and species of *Rediviva* visiting as many as ten species of *Diascia.* In addition to visits by *Rediviva* to *Diascia* they recorded visits for oil collection to other oil-secreting Hemimerideae of the genera *Alonsoa* and *Hemimeris*. They also recorded nectar collection visits by two species to *Nemesia leipoldtii* Hiern.

The Aptosimeae, Karoo violets, are, as their common name indicates, a feature of karroid areas. One of the three genera, *Aptosimum* (Figure I.3.16.a–e), is widespread throughout the karroid and savanna areas of southern Africa, but is most species diverse in the karroid areas. *Peliostomum* (Figure I.3.16.f & g) is not as widespread and *Anticharis* (Figure I.3.16.i & j) is solely desertic but not restricted to southern Africa. Species of *Anticharis* are also found in the Arabian Peninsula and India. The flowers are bluish-violet to purplish, nectar producing, gullet-flowers. Detailed accounts of the structure of the flowers of *Aptosimum* and *Peliostomum* and of the behaviour of visitors to the flowers and their potential as pollinators are given in Gess (1996, 2000). The corolla is tubular over the greater part of its length and very narrow in the basal region, protecting the nectaries from all but long-tongued or minute visitors. There are four stamens in two pairs—a pair with relatively long filaments and a pair with relatively short filaments. In *Aptosimum* the shorter pair of stamens is sterile. The anthers are adpressed in pairs and positioned dorsally in the flower. The style is situated in the dorsal groove. In the freshly opened flower the stigma barely projects from the mouth of the corolla but with time the style elongates and curves downward.

Fourteen species of Aptosimeae (eight *Aptosimum*, three *Peliostomum* and three *Anticharis*) were observed for flower visitors. Throughout their range Aptosimeae were visited predominantly by pollen wasps. Twenty-two species were involved. Of these, specialist *Celonites* species are considered to be the most important pollinators (Gess 1996, 2000; Gess & Gess 1989; Gess *et al*. 1997). The *Quartinia* visitors, with one possible exception, are not specialist visitors and are generally too small to be pollinators except where the flowers are undersized (Gess 1996). The highest number of masarine genera and species visiting Aptosimeae has been recorded from the northern Richtersveld where, in addition to two species each of *Celonites* and *Quartinia*, one species each of *Jugurtia* and *Masarina* are amongst the visitors.

Visits from bees are very uncommon in the south but in Namibia and the Kalahari to the north of the Orange River visits from bees are sufficiently frequent to be expected. Sixteen species of bees were recorded. Most species were uncommon casual visitors, although some were encountered at several sites. These species were *Meliturgula haematospila* Cockerell (Andrenidae, Panurginae), *Nomia* (*Acunomia*) *epileuca* Cockerell and *Pseudapis cinerea* (Friese) (both Halictidae, Nomiinae). All the pollen wasps have long tongues suited to reaching the nectar at the base of the narrow tube, but none of the bees are so equipped. *Meliturgula haematospila* is a small, flattened bee, which would not activate the release of pollen. It is possible that the nomiines might, in forcing themselves into the flowers, do so. All the bees are polyphagous with *M. haematospila* recorded from nine flower families and the two nomiines, *N.* (*A.*) *epileuca* and *P. cinerea*, from 14 and 12 families, respectively.

Apart from a single casual visit by a species of *Meria* (Tiphiidae) to *Aptosimum procumbens* (Lehm.) Steud. in the southeast, no wasp visits to Aptosimeae were recorded.

Zygophyllaceae

Zygophyllaceae are most abundant in the tropics and sub-tropics, mainly in hot, arid, alkaline regions and it is therefore not surprising that in southern Africa the greatest species diversity and the greatest abundance of individual plants is encountered in the western semi-arid to arid areas of this region. Though not one of the ten largest families in the Karoo the genera *Zygophyllum*, *Tribulus*, *Sisyndite* and *Augea* are amongst those genera that characterise the vegetation of these areas (Cowling *et al.* 1997; Dean & Milton 1999). After rain these plants produce an abundance of usually showy, mostly yellow or white flowers, which offer rich rewards to flower visitors. The only species to have been the principal focus of a published study of flower visitors appears to be *Zygophyllum simplex* L. which was the subject of an investigation at the Namib Desert Research Institute, Gobabeb, Namibia (Wharton 1980).

In the present study 139 species of aculeates (71 bees, 17 pollen wasps and 51 wasps), i.e. 14.99% of the species recorded visiting flowers, were collected on flowers of Zygophyllaceae. As a group, the Zygophyllaceae were visited by all bee, pollen wasp and wasp families with the exception of Ampulicidae and Astatidae.

Of the *Zygophyllum* species sampled for flowers, nine were identified. These were:

- *Z. clavatum* Schltr. & Diels, (Figure I.3.17.a) a mound forming species with small, white flowers, sampled in Namibia at Oranjemund and Lüderitz.
- *Z. cylindrifolium* Schinz, a stringy dwarf shrub with small, white flowers sampled in drainage channels in the northern Namib between Usakos and Rössing, Uis and Henties Bay and the Gaub and Kuiseb passes.
- *Z. divaricatum* Eckl. & Zeyh., a lax shrubby species with relatively large, yellow flowers, sampled in Namaqualand in the Kamiesberg and near Springbok.
- *Z. foetidum* Schrad. & J.C.Wendl., a lax shrubby species with relatively large, yellow flowers, sampled in Namaqualand in the northern Richtersveld and by Struck (1994) in the Goegap Reserve near Springbok.
- *Z. cf. morgsana* L., a shrubby species with relatively large, yellow flowers, sampled east of Nieuwoudtville.
- *Z. prismatocarpum* E.Mey. ex Sond. (Figure I.3.17.b), a stringy shrubby species with small, white flowers, sampled in drainage channels in northern Richtersveld and across the Orange River in southern Namibia.

- *Z. retrofractum* Thunb., a compact shrubby species with small, creamy white flowers, sampled in the Little Karoo, southern Great Karoo and by Struck (1994) in the Goegap Reserve, Namaqualand.
- *Z. simplex* L. (Figure I.3.17.c), a succulent annual with small, yellow flowers, forming miniature shrublets which become mat-like or form mounds where sufficient moisture is available, sampled in northern Richtersveld and at numerous sites throughout the area designated as Karoo Biome, on the eastern dry Savanna fringes and across the Namib Desert down to the coast and north along the coast from Swakopmund.
- *Z. stapffii* Schinz (Figure I.3.17.d & e) a mound forming species with relatively large succulent leaves and relatively large, white flowers, sampled at Swakopmund.

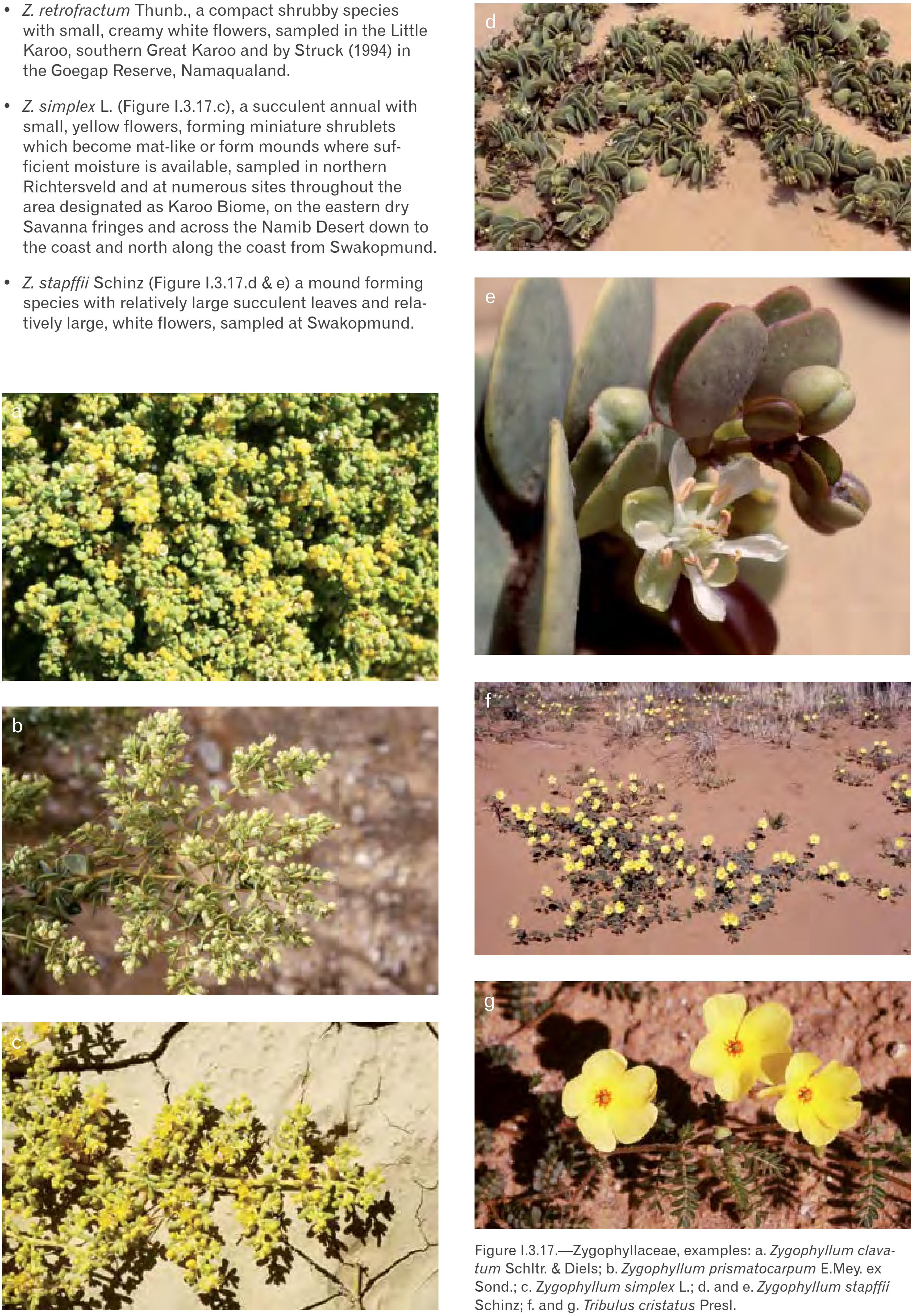


Figure I.3.17.—Zygophyllaceae, examples: a. *Zygophyllum clavatum* Schltr. & Diels; b. *Zygophyllum prismatocarpum* E.Mey. ex Sond.; c. *Zygophyllum simplex* L.; d. and e. *Zygophyllum stapffii* Schinz; f. and g. *Tribulus cristatus* Presl.

In Namaqualand, south of the Richtersveld, the three shrubby species with relatively large, yellow flowers (*Z. divaricatum*, *Z. foetidum* and *Z. cf. morgsana*) were visited only by polyphagous bees, including honeybees. The visitors were species of Anthophorini (Apidae, Apinae), including seven species of *Anthophora* (*Pyganthophora*) but not any other subgenera of *Anthophora*, and Megachilidae, including five species of Anthidiini, and at Springbok and Nieuwoudtville each a single species of *Melitta* (Melittidae). The preference shown by *A.* (*Pyganthophora*) for Zygophyllaceae supports the earlier findings of Gess & Gess (1996). Of the three species, the widespread *Z. foetidum* was also sampled for flower visitors in northern Richtersveld. Here it was visited often and almost exclusively by pollen wasps and colletid bees. Pollen wasps and colletid bees are amongst the visitors to *Zygophyllum prismatocarpum* in this area—a much more commonly visited species which received visits from six species of pollen wasps and around ten species of Colletidae. These associations are particularly interesting because to the south no pollen wasps and only one colletid, *Scrapter nitidus* (Friese), were collected from Zygophyllaceae. *Zygophyllum prismatocarpum* was also visited by three species of melittids (one of which is the species of *Melitta* recorded from *Zygophyllum* in the Nieuwoudtville area), two species of *Parafidelia* (Fideliinae), *Patellapis P. richtersveldi* Timmermann (formerly known as *Lasioglossum* sp. M) (Halictidae) and *Bembecinus hyperocrus* (Arnold) (Crabronidae, Bembicinae). The presence of a species of *Bembecinus*, although polyphagous, is of interest because *Bembecinus rhopaloceroides* (Arnold) was the principal visitor to *Zygophyllum retrofractum* in the Little Karoo and southern Great Karoo and a *Bembecinus* species was the only visitor recorded by Struck (1994) from *Z. retrofractum* at Springbok.

From northern Richtersveld northwards through Namibia the widespread annual *Z. simplex* is an important resource. In the present study 15 species of bees, including the honeybee, five species of pollen wasps and 21 species of wasps from six families were recorded. Although Wharton (1980) recorded a smaller number of flower visitors, wasps, pollen wasps and bees were represented in similar proportions.

The northern coastal and desert perennial species, *Z. clavatum*, *Z. stapffii* and *Z. cylindrifolium*, are similarly attractive to wasps, pollen wasps and bees although they never appear to attract either the diversity or numbers found visiting *Z. simplex*.

Interestingly, at Oranjemund Colletidae are amongst the most frequent visitors just as they are to *Zygophyllum* species in northern Richtersveld, south of the Orange River.

Tribulus species are widespread in the more arid areas and are striking to the north where mass flowering takes place in the more sparsely vegetated areas, particularly where the ground has been disturbed by trampling. They are amongst the plants with staggered germination, not all the seeds produced by an individual are expended in a single attempt at establishment (Van Rooyen 1999). They are ideally suited to areas where opportunistic response to irregular rainfall is a requirement.

Tribulus (Figure I.3.17.f & g) appears to be visited by a far smaller range of aculeates than *Zygophyllum*, particularly when compared to *Z. simplex*, another widespread and often abundant low-growing annual of the northern arid areas. At the family level some noticeable differences were the absence of Colletidae and pollen wasps from *Tribulus*.

North of Sesfontein at several sites on the road to Opuwa, *Tribulus* was mostly visited by a social apid, *Meliponula* (*Meliplebeia*) *beccarii* Friese (Apinae, Meliponini) (Figure II.4.48).

Sisyndite is a monospecific genus, endemic to the Northern Cape and Namibia. In the present study, *Sisyndite spartea* E.Mey. ex Sond. was sampled for flower visitors in the northern Richtersveld south and north of the Orange River and at Vioolsdrif, where it was found to be visited almost solely and repeatedly by Apidae, *Xylocopa* species and honeybees. However, to the south, 70 km east of Port Nolloth, Rozen (1977) recorded that it was visited by *Fidelia* (*Parafidelia*) *pallidula* (Cockerell) (Fideliinae), an association also recorded by Whitehead (1984).

The eight families (excluding Molluginaceae which is grouped together with Aizoaceae) receiving visits from between 5% and 10% of the wasps, pollen wasps and bees

Acanthaceae

Acanthaceae is listed as one of the ten largest families in the Damaraland-Kaokoveld Domain (Cowling & Hilton Taylor 1999). Through the rest of the Karoo-Namib, though not as species diverse, they form a notable element of the flora. Flowering Acanthaceae receiving visits from aculeates were three species of *Blepharis*, four species of *Monechma*, two species of *Petalidium* and one of *Peristrophe*.

Acanthaceae are generally considered to be bee flowers and the results of the present survey are in line with this thinking. Not only were bees the predominant visitors with respect to number of species, 53 species compared to two pollen wasps and 14 wasps, but also in numbers of individuals visiting the flowers.

The three species of *Blepharis* were:

- White flowered *B. capensis* (L.f.) Pers., sampled for flower visitors in the southeastern Nama-Karoo northwest of Grahamstown and east of Waterford.
- Blue flowered *B. obmitrata* C.B.Clarke (Figure I.3.18.a), sampled for flower visitors at numerous sites in Namibia, in the northwestern Nama-Karoo and the associated dry savanna and desert.
- Yellowish white flowered *B. macra* (Nees) Vollesen, sampled between Springbok and Kamieskroon in Namaqualand.

The complexes of visitors to *B. capensis* and *B. obmitrata* were very similar, mainly large species of Apidae and Megachilidae. However, a greater number of species was recorded from *B. capensis* than from *B. obmitrata*—12 apids and nine megachilids from the former and only

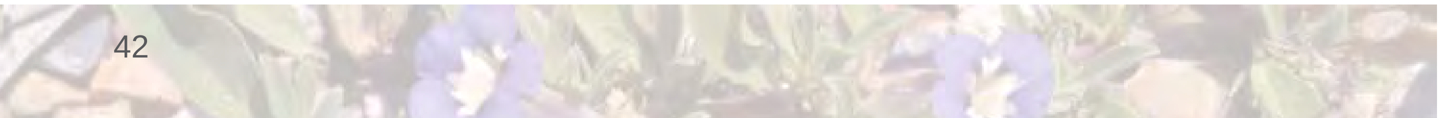


Figure I.3.18.—Acanthaceae, examples: a. *Blepharis obmitrata* C.B.Clarke; b., c. and d. *Monechma mollissimum* (Nees) P.G.Mey., c. pollen presenting, d. pollen receptive; e. *Petalidium lanatum* (Engl.) C.B.Clarke.

six apids and two megachilids from the latter. The apids visiting these two species included six and five species respectively of *Amegilla* of the previously recognised subgenus *Zebramegilla*. The additional apids were two species of *Thyreus* and four of *Xylocopa* from *B. capensis* and *Anthophora* (*Pyganthophora*) *abrochia* Eardley from *B. obmitrata.* Honeybees were occasionally included.

The Megachilidae consisted of nine species from *B. capensis* and two species from *B. obmitrata*. In addition to the apids and megachilids, three species of halictids were recorded from *B. obmitrata*.

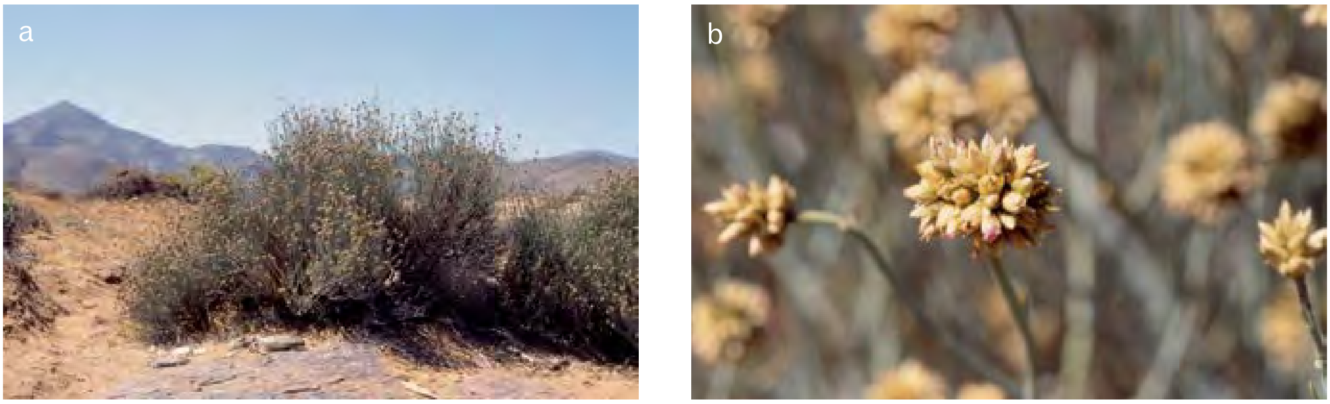
Wasp visitors were incidental, four eumenines and a scoliid from *B. capensis* and a crabronid, *Bembix namibiensis* Gess, from *B. obmitrata*. The only pollen wasp collected from flowers of *Blepharis* was *Ceramius lichtensteinii* (Klug), a mesemb specialist, which occasionally visits *B. capensis* for nectar.

The four species of *Monechma* sampled for flower visitors were:

- Pink flowered *M. mollissimum* (Nees) P.G.Mey. (Figure I.3.18.b–d) in the northern Richtersveld.
- Purplish pink flowered *M. spartioides* (T.Anderson) C.B.Clarke and *M. divaricatum* (Nees) C.B.Clarke in southeastern Namibia.
- Violet flowered *M. genistifolium* (Engl.) C.B.Clarke in northwestern Namibia.

Considered together, the aculeate flower visiting assemblage is similar to that from *Blepharis*. It consists of bees of the families Apidae and Megachilidae and three wasp species of *Amegilla* (two being species of the previously recognised subgenus *Zebramegilla*), one of *Anthophora* (*Paramegilla*), *Thyreus* and *Braunsapis* and two of *Xylocopa*. Six species of Megachilidae were recorded, including *Megachile* (*Maximegachile*) *maxillosa* Guérin.

Two species of *Petalidium*, *P. lanatum* (Engl.) C.B.Clarke (Figure I.3.18.e) and *P. variabile* (Engl.) C.B.Clarke, both associated with drainage channels on the northeastern fringe of the Namib Desert, were sampled for flower visitors. The complex of visitors recorded differed from those from *Blepharis* and *Monechma.* No species of Apidae were



recorded and only two species of Megachilidae, of the genera *Eoanthidium* and *Coelioxys*, not *Megachile*. The only other bee was a halictid, *Pseudapis usakoa* (Cockerell). Two wasps, a sphecid, *Parapsammophila consobrina* (Arnold), and a bembicine, *Bembecinus* sp., were recorded from Usakos only. These are considered to be casual visitors.

The only other identified species of Acanthaceae sampled was *Peristrophe cernua* Nees in the southeastern Nama-Karoo. This species was visited by three bee species—two apids, *Amegilla niveata* (Friese), which is broadly polylectic, *Anthophora* (*Heliophila*) *vestita* Smith, which shows a strong preference for Asteraceae, and one megachilid, *Megachile* (*Eutricharaea*) *stellarum* Cockerell.

When the catalogue closed for analysis, no strong subgeneric preference for Acanthaceae by *Anthophora* had emerged. However, recent records from Namibia do suggest that the subgenus *Paramegilla* has a preference for Acanthaceae comparable with that shown by the subgenus *Heliophila* for Asteraceae and by the subgenus *Pyganthophora* for Zygophyllaceae (Gess & Gess 1996).

Amaranthaceae

Amaranthaceae form a notable component of the vegetation of northern Namaqualand and Namibia. Preliminary palynological evidence from Eksteenfontein in the Richtersveld suggests that they were a previously dominant element before Aizoaceae (Mesembryanthema) took over in the early Holocene (Scott *et al*. 1997).

Several species of *Hermbstaedtia*, most notably *H. glauca* (J.C.Wendl.) Rchb. ex Steud. (Figure I.3.19.a & b) in the Richtersveld and *H. odorata* (Burch.) T.Cooke (Figure I.3.19.c) in Namibia, are attractive to wasps and bees. They were recorded as receiving visits from 7% of the total number of species, 42 wasps and 24 bees. Only one pollen wasp was recorded making occasional casual visits.

Amongst the wasps, the most numerous species are Bembicinae (Crabronidae) of which 17 species were recorded. These are:

- Five species of *Bembecinus* and one each of *Bembix* and *Stizus* from *H. glauca*.
- Three species of *Bembecinus*, six of *Bembix* and one each of *Handlirschia*, *Stizus* and *Stizoides* from *H. odorata.*

Figure I.3.19.—Amaranthaceae, examples: a. and b. *Hermbstaedtia glauca* (Wendl.) Reichb. ex Steud.; c. *Hermbstaedtia odorata* (Burch.) T.Cooke; d. *Calicorema capitata* (Moq.) Hook.f.

The other wasps included seven species of Sphecidae and two species each of Chrysididae, Vespidae (Eumeninae), Crabronidae (Philanthinae) and Scoliidae. All are polyphagous species.

Similarly, the bees are all polyphagous species. All families except Andrenidae were represented. The family with the highest number of species represented was Megachilidae.

Apocynaceae

Apocynaceae is used here in the broad sense (as understood by APG 1998) to include the family Asclepiadaceae. The only species of Apocynaceae (*sensu stricto*) visited by aculeates was the shrub *Carissa bispinosa* (L.) Desf. ex Brenan, flowering in a dry drainage channel in the Karoo Biome experimental plot on Tierberg Farm, Prince Albert in the southern Great Karoo. Single species of Apidae and Megachilidae were recorded—*Thyreus delumbatus* (Vachal) (Apinae, Melectini) and *Megachile* sp.

Three species of Asclepiadaceae were sampled for flower visitors. These were two non-succulent, perennial, bushy species of *Asclepias* with heads of relatively small cream flowers, *Gomphocarpus filiformis* (E.Mey.) D.Dietr. (= *Asclepias buchenaviana* Schinz) (Figure I.3.20.a & b), an *Asclepias* sp. and an erect, succulent, perennial species with heads of relatively small yellow flowers, *Sarcostemma viminale* (L.) R.Br.

Gomphocarpus filiformis was sampled for flower visitors on Tierberg Farm, Prince Albert in the southern Great Karoo and in southern Namibia between Ariamsvlei and Karasburg and Karasburg and Grünau, where it was abundantly visited by diverse polyphagous wasps and bees but not by pollen wasps. The diversity at the southern site was greater than at the northern site. This is not surprising as Prince Albert lies in the transition zone between the eastern and western aculeate faunas and shares some additional species with the northern savanna fauna. The distribution of visitors between groups was 42 wasp and 27 bee species. Wasp species included 12 Crabronidae (*sensu lato*) (7 Nyssonidae, 3 Philanthidae, 2 Crabronidae (Larrinae) following an earlier classification of the sphecoid wasps), 9 Pompilidae, 7 Sphecidae, 4 Tiphiidae, Vespidae, 4 Eumeninae, 3 Scoliidae, 2 Chrysididae and 1 Bradynobaenidae. Bee species included Megachilidae (12 Megachilini and 2 Anthidiini), Apidae (5 Apinae and the honeybee), 3 Halictidae, 2 Xylocopinae, 1 Colletidae and 1 Melittidae.

Gomphocarpus filiformis was recorded as a drainage line specialist in the Namib Desert (Jürgens *et al*. 1997) where, at times, it is probably an important resource for wasps and bees. During the present study it was only once encountered in flower in the northern Namib, namely in a drainage channel near Rössing. During that time it was only visited by *Braunsapis otavica* (Cockerell)/*Braunsapis albipennis* (Friese) (Apidae, Xylocopinae).

The second *Asclepias* species was sampled for flower visitors at Karoo Poort at the southern end of the Tankwa Karoo. At this site the visitors consisted of three species of Pompilidae and one each of Apidae, Crabronidae (Philanthinae), Sphecidae and Tiphiidae.

Figure I.3.20.—Apocynaceae, examples: a. and b. *Gomphocarpus filiformis* (E.Mey.) D.Dietr.; c. *Bembix fuscipennis* Lepeletier carrying pollinia; d. *Stizus dewitzii* Handlirsch carrying pollinia.

Sarcostemma viminale (L.) R.Br. was sampled at Kommadagga in the southeastern Nama-Karoo where the flowers were visited by six species of wasps and four species of bees. The wasps were 2 Crabronidae (*Stizus*), 3 Sphecidae and 1 Vespidae (Eumeninae). The bees were 1 Apidae (Xylocopinae), 2 Megachilidae (Megachilinae) and 1 Halictidae (Nomiinae).

Liede & Whitehead (1991) made a study of the pollination biology of *S. viminale*, sampling plants at several sites in Bushmanland and Namaqualand. In addition to wasps and bees they sampled flies, butterflies, moths, beetles and bugs but concluded that it was only the wasps and bees that successfully transferred pollinia and were therefore pollinators of this plant. They list three wasps, one species each of Crabronidae (*sensu lato*) (Nyssonidae following an earlier classification of the sphecoid wasps), Sphecidae and Scoliidae, and two bees, one each of Megachilidae (Megachilini) and Halictidae (Nomiinae) and in addition honeybees—a similar complex to that from the southeast.

Many of the aculeates, particularly the wasps, collected from the asclepiad species in the present survey bear pollinia and are potentially effective pollinators of these plants (Figure I.3.20.c & d).

Boraginaceae

Boraginaceae is used here in the broad sense (as understood by APG 1998) to include the family Hydrophyllaceae. Representatives of six genera were sampled for flower visitors, the woody genus *Ehretia* and the herbaceous genera *Anchusa*, *Heliotropium* (Figure I.3.21.a & b), *Lobostemon*, *Trichodesma* (Figure I.3.21.c & d) and *Codon* (Hydrophyllaceae) (Figure I.3.21.e–g).

Taking all flower-visiting records for Boraginaceae together, 52 species of bees (1 Melittidae, 2 Andrenidae, 6 Halictidae, 13 Megachilidae and 30 Apidae, including the honeybee), five pollen wasps and 13 wasps were recorded.

Blue flowered *Anchusa capensis* Thunb. was sampled for flower visitors over several years in the southeastern Nama-Karoo, at several sites northwest of Grahamstown and a site near Colesberg, and in Namaqualand at several sites in the Kamiesberg. In total, the bees from these areas consisted of 18 species of Apidae (14 Apinae and four Xylocopinae), ten species of Megachilidae (three Anthidiini, five Megachilini and two Osmiini) and one species of Halictidae. Of these, Apinae were the most numerous, the most abundant and the most characteristic of the visitors. Of the apines, seven were species of *Anthophora* (four of the subgenus *Heliophila*, two of *Pyganthophora* and one of *Paramegilla*), two *Amegilla* and four of *Thyreus* (cleptoparasites and therefore, like wasps, visiting flowers for adult nourishment only). Of the Xylocopinae, two are species of *Allodapula*, one of *Ceratina* and one of *Xylocopa*. No pollen wasps were recorded.

In addition to the bees, ten species of wasps were collected from *A. capensis*. These included three species of *Bembix* (Crabronidae, Bembicinae), three species of *Ammophila*, *Podalonia capensis* (Dahlbom) (Sphecidae) and three species of Scoliidae, all in the category of casual visitors.

Lobostemon is a mainly southwestern Western Cape genus but some species do occur northwards to Namaqualand and eastwards to the Eastern Cape. Several blue or bluish violet flowered species of *Lobostemon*, including *L. trichotomus* (Thunb.) DC., were sampled for flower visitors to the east and west of Clanwilliam. Seven species of Apidae, three Anthophorini (two species of *Anthophora* (*Pyganthophora*) and *Amegilla niveata* (Friese)), three Xylocopini (*Xylocopa* spp.) and the honeybee, were recorded. No other bee families, wasps or pollen wasps were represented.

Two species of *Trichodesma* were sampled for flower visitors. The relatively small purple flowered *Trichodesma cf. africanum* (L.) Lehm. (Figure I.3.21.a) was encountered from northern Richtersveld northwards to the Namib Desert fringe southwest of Uis in northern Namibia in dry drainage channels. The relatively large blue flowered *Trichodesma angustifolium* Harv. (Figure I.3.21.b) was found at a site east of the Gamsberg Pass. Both species were only visited by bees.

Trichodesma cf. africanum was never found to be abundantly visited. Some of the visiting bees included: *Pachymelus peringueyi* (Friese) (Apidae, Anthophorinae), *Afranthidium* (*Immanthidium*) *junodi* (Friese) (Megachilidae, Anthidiini), *Pachyanthidium* (*Ausanthidium*) *ausense* (Mavromoustakis) (Megachilidae, Anthidiini) and *Pseudapis usakoa* (Cockerell) (Halictidae), only at the northernmost site.

Trichodesma angustifolium was visited abundantly, but only by four large Anthophorini, three species of *Amegilla*, (*A. nubica* (Lepeletier), *A. atrocincta* (Lepeletier) and *A. niveata* (Friese)) and *Anthophora* (*Paramegilla*) *basalis* Smith.

White flowered *Heliotropium ciliatum* Kaplan occurs along roadsides in Namibia but only once, between Aus and Helmeringhausen in the southwest on the desert fringe, was it observed receiving visits from aculeates. The only relatively abundant species was a pompilid, *Schistonyx umbrosus* (Klug).

Since closing the catalogue for analysis, a second species of white flowered *Heliotropium*, *H. tubulosum* E.Mey. ex DC. (Figure I.3.21.c & d), an abundant herb in the drainage channels of the Central Namib, was sampled for flower visitors. At several sites it was abundantly visited by two pollen wasps, *Jugurtia namibicola* Gess, and *Celonites heliotropii* Gess, both of which have been recorded only from these plants, of which they seem to be the likely pollinators. The forelegs of the *Jugurtia* show similar modifications (Gess 2004) to those of *Trimeria* (Masarinae) associated with *Heliotropium* in South America (Neff & Simpson 1985).

The flowers of the violet flowered shrub *Ehretia rigida* (Thunb.) Druce are expected to be bee flowers. However, although the flowers were observed on many occasions only one aculeate visitor, *Celonites capensis* Brauns, an unusually polyphagous pollen wasp, was encountered.

Codon with two species, *C. royenii* L. (Figure I.3.21.e–g) and *C. schenckii* Schinz, is a southern African endemic. Both species are found in dry drainage channels in Na-

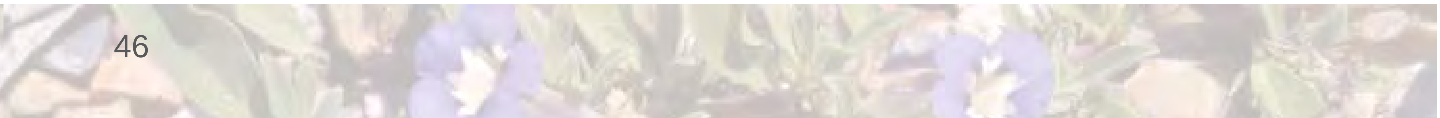


Figure I.3.21.—Boraginaceae, examples: a. and b. *Heliotropium tubulosum* E.Mey. ex DC.; c. *Trichodesma africanum* (L.) Lehm.; d. *Trichodesma angustifolium* Harv.; e–g.; e. plant *Codon royenii* L., f. with *Xylocopa lugubris* taking nectar, g. with *Jugurtia codoni* taking pollen.

maqualand and Namibia and the former somewhat further to the southeast in dry areas. Detailed accounts of the structure of the flower of *C. royenii* and the behaviour of the flower visitors have been given (Gess 1999a; Gess *et al*. 1997). The abundant nectar is not readily accessible, being contained in the base of the relatively large, inverted, bell-shaped flower below tightly adpressed staminal filaments. For nectar to be obtained by a flower visitor, the visitor must be able to insert its glossa between the filaments. A pollinator must be large enough that, when entering a flower to obtain nectar, it comes into contact with ripe anthers or receptive stigmas. The pollinators of both species are considered to be *Xylocopa* species, however, both species are also visited occasionally by a very broadly polyphagous apid, *Amegilla niveata* (Friese) (Anthophorini), and a megachilid, *Eoanthidium* (*Clistanthidium*) *turnericum* (Mavromoustakis) (Anthidiini). The most abundant visitors to *C. royenii* are two species of pollen wasps, *Jugurtia codoni* Gess and *Quartinia codoni* Gess. In the northern Richtersveld both species were commonly present but to the north of the Orange River *J. codoni* was absent. The flowers are clearly an important source of both nectar and pollen for these pollen wasps. However, due to their small size and the nature of their behaviour in the flowers, they are not considered to be pollinators. The only wasp visitor to these flowers was *Philanthus triangulum* (Fabricius), a casual visitor.

Celastraceae

In the Celastraceae, *Gymnosporia* species are a notable component of the taller shrubby vegetation of drainage channels in the Nama-Karoo and, when in flower in the early summer, are immediately apparent as they produce an abundance of small, white, heavily scented flowers. The species are variously attractive to aculeates. For example, northwest of Grahamstown, *Gymnosporia linearis* (L.f.) Loes (= *Maytenus linearis* (L.f.) Marais), characterised by the shape of its leaves, (Figure I.3.22.a) attracts large numbers and a great diversity of aculeates. Recorded were 40 species of wasps (1 Bradynobaenidae; 3 Crabronidae, Crabroninae; 3 Crabronidae, Larrinae; 2

Figure I.3.22.—Celastraceae, examples: a. *Gymnosporia linearis* (L.f.) Loes; b and c. *Gymnosporia buxifolia* (L.) Szyszyl.

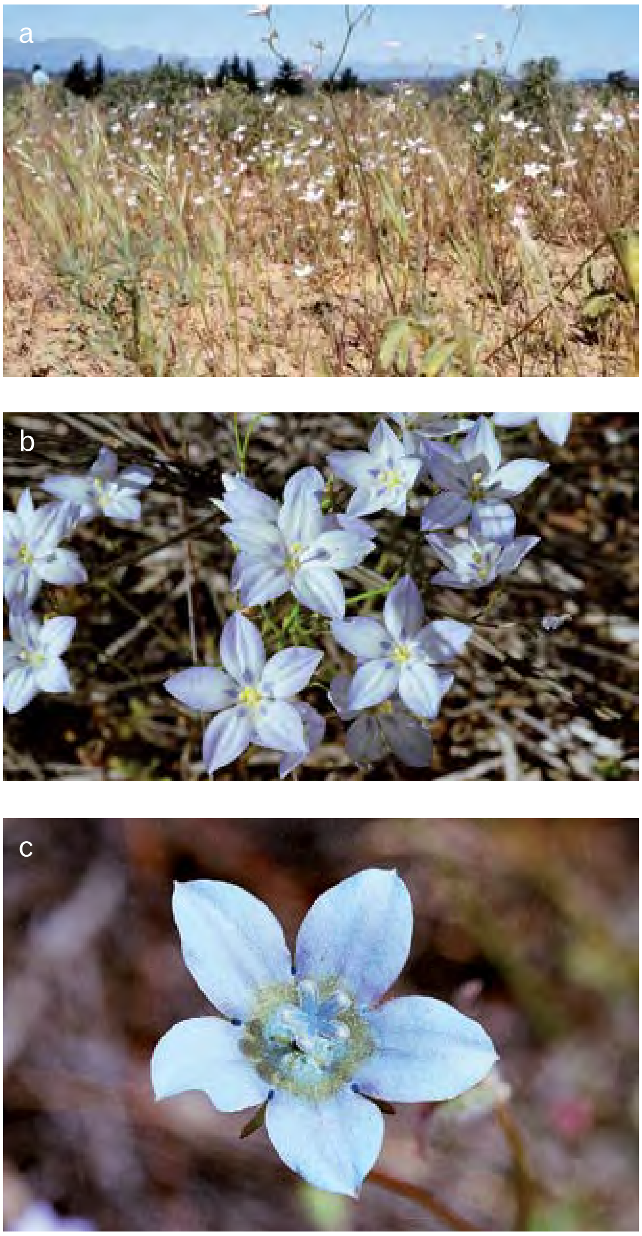


Figure I.3.23.—Campanulaceae, Campanuloideae. Examples of stellate flowers: a. and b. *Wahlenbergia annularis* A.DC.; c. monkey beetle pollinated *Wahlenbergia capensis* (L.) A.DC.; d. *Wahlenbergia namaquana* Sond.; e. *Wahlenbergia nodosa* Buek. Examples of campanulate flowers: f. and g. *Wahlenbergia psammophila* Schltr.; h. *Wahlenbergia pilosa* Buek.; i. *Wahlenbergia* near *polyclada* A.DC.

Mutillidae; 2 Nyssonidae; 8 Philanthidae; 9 Pompilidae; 3 Sphecidae; 4 Tiphiidae and 5 Vespidae, Eumeninae), and seven species of bees (1 Apidae, 1 Colletidae and 5 Halictidae). By contrast, *Gymnosporia buxifolia* (L.) Szyszyl. (Figure I.3.22.b & c), with a rather unpleasant scent, attracts very few aculeates but an abundance of flies.

Campanulaceae

The family Campanulaceae is cosmopolitan in distribution, with members mainly in the temperate and subtropical Mediterranean and southern Africa. There are two

Figure I.3.24.—Campanulaceae, Lobelioideae, examples: a. and b. *Lobelia linearis* Thunb.; c. *Lobelia anceps* L.f.; d. and e. *Monopsis debilis* (L.f.) Presl.

well-marked subfamilies namely the Campanuloideae and the Lobelioideae. Members of the Campanuloideae have regular flowers and anthers free. Members of the Lobelioideae have highly irregular, resupinate flowers and connate anthers. A small group of transitional genera are sometimes treated as a third subfamily, the Cyphioideae.

Visits to flowers of Campanulaceae were recorded for 33 species of bees (7.80% of the bees), 19 pollen wasps (14.73% of the pollen wasps) and only nine wasps (2.4% of the wasps).

The majority of records were for Campanuloideae represented by two genera *Wahlenbergia* (including *Lightfootia*) (14 identified species and several additional species) (examples Figure I.3.23) and *Microcodon* (one species). All of the flower visiting records were from south of the Orange River, mostly from the west where *Wahlenbergia* is most species diverse. The flowers of most of the species sampled are campanulate but four are stellate. In colour, the corolla of all but three of these is violet (bluish to purplish). The exceptions were white, pink and yellow. The structure and pollination strategies of ten species showing various flower forms and the potential of the visitors, based on size and behaviour, to be successful pollinators of the flowers has been investigated in considerable detail (Gess 1996, 1999b; Gess & Gess 1989).

All species together received visits from 30 species of bees (10 Apidae, 7 Melittidae, 6 Megachilidae, 5 Halictidae and 2 Colletidae), 16 pollen wasps and four wasps. In the west the visits of all groups except pollen wasps and melittid bees were infrequent and casual. Bee flies and butterflies occasionally visit the deeply campanulate flowers for nectar, but are not pollinators. Pollen wasps were the most numerous and reliable visitors to the deeply campanulate flowers and amongst these are several specialist *Celonites* species, which are dependable pollinators. Melittid bees are amongst the less frequent visitors. Melittid bees on the other hand were the most numerous and reliable visitors to the stellate flowers and amongst these are specialists, *Capicola danforthi* Eardley, *Capicola gessorum* Eardley (as undescribed species of *Hesperapis* in Gess & Gess 2006) and *Capicola nigerrima* Cockerell, which are dependable pollinators of these flowers. Pollen wasps are less frequent visitors to these flowers and, even when numerous, are unlikely to pollinate them.

Wahlenbergia flowers sampled in the east are shallowly campanulate to stellate. Melittid bees are not available as pollinators as they do not occur in the east and no pollen wasps have been recorded from them. The candidates for pollinators are polyphagous bees, *Ceratina* (*Ctenoceratina*) *armata* Smith (Apidae, Xylocopinae, Ceratinini), which has been collected from these flowers as a not infrequent visitor in two years, two megachilids, *Megachile* (*Eutricharaea*) *semiflava* (Cockerell) (Megachilini) and *Afranthidium* (*Branthidium*) *guillarmodi* (Mavromoustakis) (Anthidiini), less frequently collected, and a colletid *Colletes fascicularis* Cockerell, collected only once.

Only one record was obtained for Cyphioideae represented by the single genus *Cyphia*. This was for a male of a polyphagous species, *Amegilla spilostoma* (Cameron) (Apidae, Apinae, Anthophorinae), collected from *Cyphia* in the southeast—a record of negligible value.

Records were obtained for three species of Lobelioideae. These were the dark, bluish-purple flowered *Lobelia linearis* Thunb. (Figure I.3.24.a & b), pale pinkish flowered *Lobelia anceps* L.f. (Figure I.3.24.c) and purple flowered *Monopsis debilis* (L.f.) C.Presl. (Figure I.3.24.d & e). The visitors to *L. linearis*, growing near Nieuwoudtville, were two similarly sized species, a small relatively polyphagous carpenter bee, *Ceratina* (*Ctenoceratina*) *armata* Smith, and a pollen wasp, *Celonites lobeliae* Gess. Both would be suited to pollinating the flowers.

At the site near Colesberg, *Lobelia anceps* was observed over several days. It was visited by *Celonites andrei* Brauns, halictine and anthophorine bees and a small bombyliid fly (Bombyliidae). The usual forage plants of *C. andrei* are species of *Aptosimum* but at the time when the observations were made, although *Aptosimum* plants were present, they were not in flower.

It is of interest that small carpenter bees (*Ceratina* spp.) have occasionally been observed visiting *Lobelia* in the southeast.

Monopsis debilis forms dense patches in moist areas from Namaqualand south to the Olifants River Valley and to the west. The flowers, like many dark purple flowers, though striking to the human eye, appear to attract few insects. However, they are visited abundantly by a single species of bee, *Samba* (*Haplomelitta*) *ogilviei* (Cockerell) (Melittidae, Dasypodainae). In the present survey, 67 voucher specimens, including both females and males, were taken and visits by many more individuals were observed at various sites in Namaqualand, the Olifants River Valley and to the west. Furthermore, Rozen (1974), when investigating the nesting biology of *S.* (*H.*) *ogilviei* at Velddrif to the southwest of Citrusdal, found *M. debilis* to be the source of most of the provisions. No other visitors have been recorded. Whether or not *S.* (*H.*) *ogilviei* extends throughout the range of *M. debilis* remains to be determined, but it is certainly known from the greater part of its distribution. The evidence so far assembled suggests a mutualistic dependence between *M. debilis* and *S.* (*H.*) *ogilviei*, with the latter apparently the only pollinator of *M. debilis* in the areas investigated and *M. debilis* apparently the principal source of provision of *S.* (*H.*) *ogilviei* (Gess & Gess 1994b).

Samba (*H.*) *ogilviei* is not entirely restricted to *M. debilis*, having been occasionally recorded from Asteraceae and *Wahlenbergia* in the present study and from Asteraceae by Rozen (1974). Eardley also collected three males from Asteraceae in the Biedou Valley (Michez *et al.* 2010). However, these plants are considered minor, secondary resources by us.

Lamiaceae

Lamiaceae, though not species rich in the Karoo, are present throughout the biome, particularly along drainage channels. Flowers of representatives of nine species in six genera were sampled for flower visitors. These included *Acrotome inflata* Benth., *Ballota africana* (L.) Benth., *Leucas capensis* (Benth.) Engl., *Leucas pechuelii* (Kuntze) Guerke, *Ocimum americanum* L., *Ocimum filamentosum* Forssk., *Salvia dentata* Aiton, *Stachys aurea* Benth. and *Stachys rugosa* Aiton.

Lamiaceae are generally considered bee flowers and the results of the present survey are in line with this thinking. Not only were bees the predominant visitors with respect to numbers of species (65 bee species compared to 10 wasp and 2 pollen wasp species), but also in numbers of individuals visiting the flowers. However, representation of bee families was narrow, 31 species of Apidae (21 Apinae; 10 Xylocopinae), 25 Megachilidae (10 Megachilinae, Anthidiini; 1 Lithurgini; 8 Megachilini and 6 Osmiini), seven Halictidae and two Andrenidae. Visits by the andrenids *Melliturga* spp., by the pollen wasps and by the wasps (3 Sphecidae; 2 Vespidae, Eumeninae; 2 Crabronidae, Philanthinae; 1 Crabronidae, Bembicinae; 1 Scoliidae and 1 Chrysididae) were recorded only in the northwest of Namibia on the desert fringe. Visits by the two pollen wasps, *Ceramius damarinus* Turner and *Jugurtia alfkeni* (du Buysson) are of interest, being the only visitors to Lamiaceae recorded in the Afrotropical Region, whereas in the Palaearctic visits to Lamiaceae by some species of pollen wasps are expected (Mauss 1996). The visits by *C. damarinus* and *J. alfkeni* were both opportunistic having taken place only at one site in a mixed patch of flowers, in which their favoured forage plants, *Sesuvium* (Aizoaceae) and *Hermannia* (Sterculiaceae) respectively, were in short supply.

Halictidae were uncommon visitors to Lamiaceae. The four species were all single records, one from west of the Olifants River Valley in the south and the other six from three separate sites in the northeast.

The representation of Apinae was:

- Widespread and broadly polyphagous *Amegilla niveata* (Friese) from the Western Cape, Namaqualand and northeastern Namibia.
- Four other species of *Amegilla* (all of the previously recognised subgenus *Zebramegilla*), variously from the southeastern Nama-Karoo through the Olifants River Valley and Namaqualand in the Succulent Karoo, to the northwestern Nama-Karoo/Desert fringe.
- Two species of *Pachymelus*, *P. festivus* (Dours) from the southeast and *P. peringueyi* (Friese) from Namaqualand.
- Three species of *Anthophora* (all of the subgenus *Heliophila*) variously from the southwest and Namaqualand.

- Four species of *Tetraloniella* variously from the Little Karoo to the northeastern fringe of the Namib Desert.
- Four species of *Thyreus* all from the Little Karoo.
- The honeybee.

The Xylocopinae were represented by four small carpenter bees (*Ceratina* spp.), variously from the southwest through to the northwest, and six large carpenter bees (*Xylocopa* spp.) variously from the southeast to the southwest and north to Namaqualand.

Megachilini were represented in samples from the extreme southeast, southwest and Namaqualand but not from north of the Orange River. Osmiini, by contrast, were recorded from Lamiaceae as far north as the northeastern fringe of the Namib Desert but none were recorded further south than Namaqualand.

Anthidiini were found visiting Lamiaceae only in Namaqualand. Three species of *Afranthidium* (*Immanthidium*), five of *Plesianthidium* (*Spinanthidium*) and one of *Pseudoanthidium* were recorded variously from *Ballota africana* (L.) Benth., *Stachys aurea* Benth. and *Stachys rugosa* Aiton.

Since the compilation of our catalogue (Gess & Gess 2003) we have sampled flowers of *Syncolostemon floccosus* (Launert) D.F.Otieno 5 km south of Palmwag, northwestern Namibia (Figure I.3.25.a.) where it was flowering in abundance and was visited by numerous bees. The flowers were most commonly visited by a polyphagous bee *Nomia* (*Acunomia*) *epileuca* Cockerell (Figure I.3.25.b.) but some were visited by an undescribed species of *Trachusa* (*Massanthidium*) and *Fidelia* (*Parafidelia*) *friesii* (Brauns), the principal visitor to flowers of *Sesamum* (Pedaliaceae) in Namibia.

Figure I.3.25.—Lamiaceae, example: a. and b. *Hemizyga floccosa* Launert: a. plant, 5 km south of Palmwag, northwestern Namibia; b. flower being visited by a female *Nomia (Acunomia) epileuca* Cockerell.

Malvaceae

Malvaceae is used here in the broad sense (as understood by APG 1998) to include Malvaceae, Sterculiaceae, Tiliaceae and Bombacaceae. Members of Malvaceae (*sensu stricto*) were occasionally encountered in flower but were rarely visited by aculeate Hymenoptera. An exception was the purple-violet flowers of a *Hibiscus*, which were visited by *Tetraloniella cf. michaelseni* (Friese) (Apidae, Apinae, Eucerini) near Omaruru on the northwestern savanna fringe. Other exceptions were the white flowers of a 'mallow', which were visited by *Xylocopa caffra* (L.) in the Grootberg Pass in the northwest and the pink flowers of another 'mallow', which were visited by *Podalonia canescens* (Dahlbom) (Sphecidae) at Lamberts Bay on the southwest coast. Red, relatively small flowered *Hibiscus elliottiae* Harv. is widespread in the northwest and, as indicated by the colour of the flowers, is not visited by aculeates but by butterflies.

Sterculiaceae is amongst the ten largest families of the Eastern Karoo and the Damaraland-Kaokoveld Domains (Cowling & Hilton Taylor 1999). Fourteen named species of *Hermannia*, representing both subgenera, *Hermannia* and *Mahernia*, and several unnamed species were sampled across the study area. The flowers of all species are relatively small, downwardly hanging and 'bell-shaped', requiring entry from below.

Overall 40 species of aculeates, 32 bees (13 Apidae including the honeybee, 15 Megachilidae, 2 Melittidae, 1 Andrenidae and 1 Halictidae), six pollen wasps and two wasps, were recorded visiting the flowers of *Hermannia* (examples Figure I.3.26). The bees all exhibited varying degrees of polyphagy with the possible exception of the two melittids. However, the large diversity of bee visitors was not randomly distributed within the families represented. Of the Apidae, seven were species of Anthophorini, four *Anthophora*, all from the subgenus *Pyganthophora* and three *Amegilla* of which two were of the previously recognised subgenus *Zebramegilla*. Of the Megachilidae, nine were Anthidiini.

Visits by pollen wasps, four species of *Jugurtia* and two of *Masarina*, were all from the west, from Ladismith in the south to just south of Opuwa in the north of Namibia. The most widespread species was *Jugurtia confusa* Richards, which has been encountered from northwest of Grahamstown in the southeast to southwest of Windhoek in Namibia. In the Grahamstown district, it is considered to be associated with Mesembryanthema but in Namibia it was abundantly associated with *Hermannia comosa* Burch. ex DC. at a site east of the Gamsberg Pass. At this site, although a range of other plants were in flower, of which some were visited by other species of *Jugurtia*, none were visited by *J. confusa* at any time throughout the day.

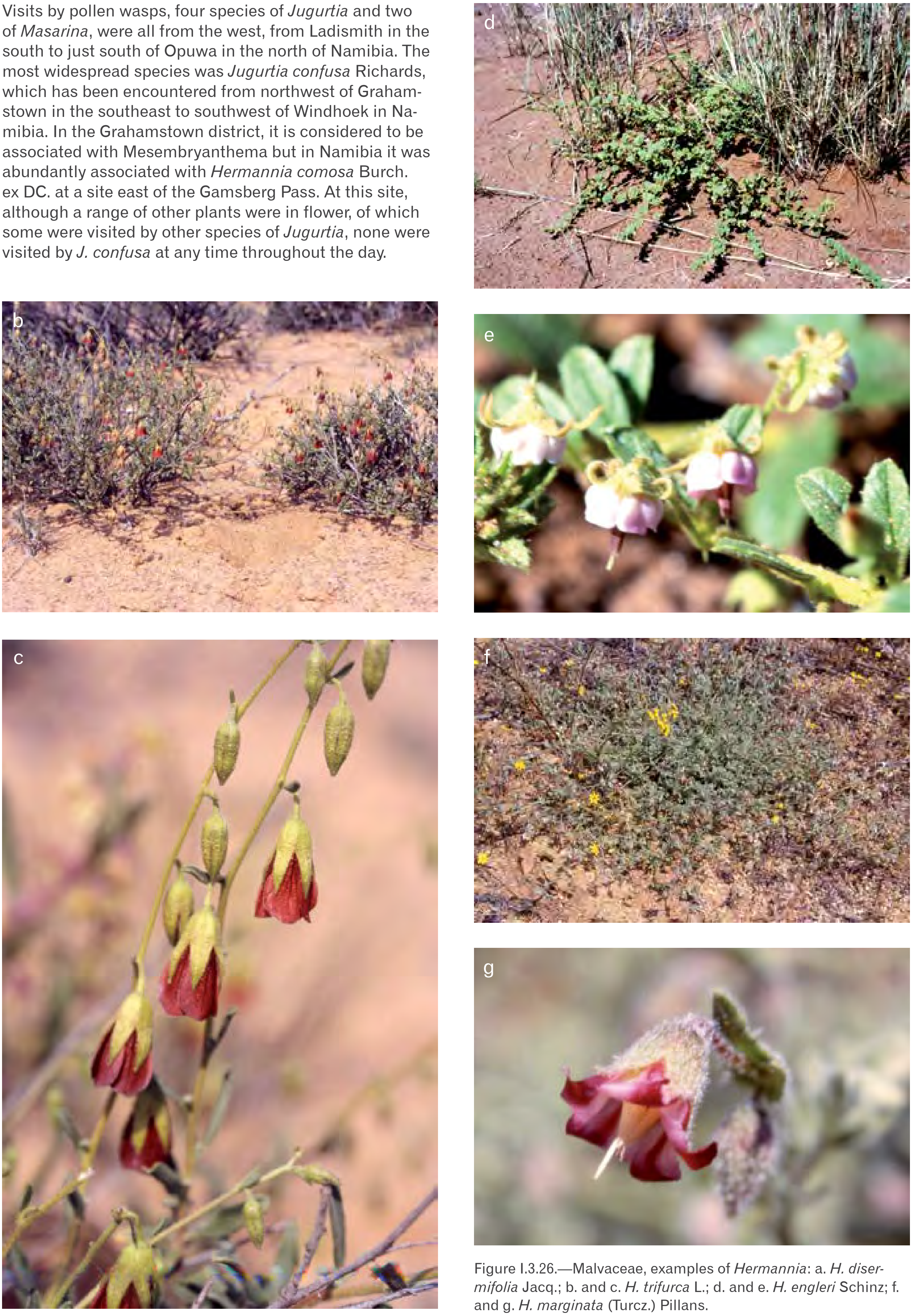


Figure I.3.26.—Malvaceae, examples of *Hermannia*: a. *H. disermifolia* Jacq.; b. and c. *H. trifurca* L.; d. and e. *H. engleri* Schinz; f. and g. *H. marginata* (Turcz.) Pillans.

Jugurtia alfkeni (du Buysson) was encountered abundantly on flowers of two species of *Hermannia* from seven localities in Namibia from Karasburg in the southeast across to the west, south of Maltahöhe, and northwards to north of Sesfontein in the Kaokoveld. This species apparently specialises in *Hermannia* with only three single, probably casual, visits to flowers of other taxa recorded.

Two additional species, *Jugurtia mandibulata* Gess and *J. damara* Gess, were recorded from two species of *Hermannia* from Karasburg to north of Sesfontein. No visits to flowers of any other plants were recorded.

The association between *Masarina strucki* Gess and *Hermannia*, to which it is apparently restricted, was examined (Gess *et al*. 1997). A nest of this species was investigated and the pollen of the provision found to be solely derived from *Hermannia*. There are no records of visits by this species to flowers of any other plants. *Masarina strucki* was abundantly encountered on *Hermannia* in Namaqualand, from Springbok south to the Oilfants River Valley and from east of the escarpment northeast of Nieuwoudtville, and from the western Little Karoo at Ladismith. Other records of flower visiting by *M. strucki*, made available by Struck and Whitehead (label data), are also for *Hermannia*, the former from the Goegap Nature Reserve and the latter from Ladismith.

The remaining pollen wasp is of little significance, being *Masarina mixta* Richards, a species most commonly associated with, but not restricted to, *Wahlenbergia* (Campanulaceae).

The two wasps, *Philanthus capensis* Dahlbom (Crabronidae, Philanthinae) and *Allocoelia quinquedens* Edney (Chrysididae), are casual visitors. The presence of *Allocoelia*, however, is of interest as this genus of cuckoo wasp is a 'parasite' only in the nests of pollen wasps.

In size, behaviour and constancy the *Jugurtia* and *Masarina* species are suited to be pollinators of the *Hermannia* species that they visit. Indeed, where they occur, they are probably the most reliable potential pollinators. However, in the areas where they don't occur, the flowers are certainly adequately serviced by anthophorine and anthidiine bees.

Three species of *Grewia* (Tiliaceae), all shrubs, were observed for flower visitors. The pinkish violet flowered *G. occidentalis* L. was sampled for flower visitors in the southeastern Nama-Karoo northwest of Grahamstown, where it was visited mainly by *Xylocopa* spp. (Apidae). In addition, *Xylocopa* was observed visiting the yellow flowers of *G. flava* DC. in the Kalahari and of *G. bicolor* Juss. in the Namib.

Zietsman (1991) studied the reproductive biology of *G. occidentalis* in the vicinity of Bloemfontein, recording honeybees and two species of *Xylocopa* as the only flower visitors. He studied the behaviour of the honeybees and concluded that as pollinators they are inefficient.

It is concluded that *Xylocopa* species can be considered to be the expected visitors to *Grewia*, and though polyphagous and therefore not dependable, to be the most likely pollinators.

Other visitors to *Grewia* recorded in the present study were a single male each of *Tetraloniella apicalis* (Friese) (Apidae) and *Anthidiellum* (*Pygnanthidiellum*) *spilotum* (Cockerell) (Megachilidae) and a single female *Megachile* (*Pseudomegachile*) *sinuata latitarsis* (Friese) (Megachilidae) to *G. occidentalis*. Single male nomiines (Halictidae), *Lipotriches* (*Macronomia*) sp. and *Nomia* (*Acunomia*) *epileuca* Cockerell were visitors to *G. bicolor*. These all appear to be casual visitors.

The 19 plant families receiving visits from less than 5% of the wasps, pollen wasps and bees

Brassicaceae

Brassicaceae is used here in the broad sense (as understood by APG 1998) to include Capparaceae. Three genera were sampled for flower visitors, *Heliophila* (Brassicaceae *sensu stricto*) in Namaqualand, *Cleome* (formerly Capparaceae and sometimes placed in the family Cleomaceae) (Figure I.3.27.a–c) from the northern Richtersveld through the Nama-Karoo of Namibia and associated arid savanna and desertic areas, and *Maerua* (formerly Capparaceae) (Figure I.3.27.d & e) at Vioolsdrif and Rooivaal south of the Orange River.

Herbaceous annual species of *Heliophila* were observed on numerous occasions at various localities but flower visitors were infrequently recorded. Sampling in the Kamiesberg yielded bees of two families, one each of Megachilidae (Anthidiini) and Colletidae, both polyphagous species. Five species of *Heliophila* were sampled for flower visitors by Struck (1990) in the Goegap Nature Reserve. These species received visits, respectively, from:

- One species of Megachilidae (Megachilini).
- Honeybees and a single species each of Megachilidae (Megachilini) and Colletidae.
- Two species of Apidae both Anthophorini.
- One species of Megachilidae (Anthidiini).

No records of visits by pollen wasps or wasps were recorded.

Four species of the herbaceous genus *Cleome* were sampled for flower visitors. Yellow flowered *C. paxii* (Schinz) Gilg & Gilg-Ben. was sampled for flower visitors in northern Richtersveld and yellow flowered *C. angustifolia* Forssk., yellow flowered *C. suffruticosa* Schinz and purplish pink flowered *C. elegantissima* Briq. at numerous sites in Namibia. Collectively they were visited by 23 species of bees, one species of pollen wasp and one species of wasp. Of the bees:

- 16 species were apids (6 *Amegilla* (Anthophorini), 2 *Anthophora* (Anthophorini), 3 *Tetraloniella* (Eucerini), 4 *Xylocopa* (Xylocopini) and the honeybee).
- Five were megachilids (1 *Eoanthidium* (Anthidiini) and 4 *Megachile* (Megachilini)).
- One was a halictid.
- One was a melittid.

Figure I.3.27.—Brassicaceae, examples: a. and b. *Cleome paxii* (Schinz) Gilg. & Ben.; c. *Cleome angustifolia* Forssk.; d. and e. *Maerua schinzii* Pax.

None of these bees is restricted to *Cleome.* However, it is apparent that this plant is attractive in particular to Anthophorini. Additional records for megachilids are those of Whitehead (1984) who collected two species of *Fidelia* (*Parafidelia*) (Fideliinae) from flowers of *Cleome* in Namibia and of Struck (1990) who collected two species of Megachilidae from an additional species of *Cleome* in the Goegap Nature Reserve, Namaqualand.

The pollen wasp, *Jugurtia koeroegabensis* Gess and a bee-hunting wasp, *Philanthus triangulum* Fabricius, were casual visitors, only encountered on *Cleome* at one site, Pootjiespram, in the Richtersveld National Park. In this area, *J. koeroegabensis* was more commonly seen visiting *Peliostomum* (Scrophulariaceae) and *Zygophyllum* (Zygophyllaceae).

Like *Cleome*, *Maerua schinzii* Pax, a small tree with yellowish white flowers, was favoured mainly by polyphagous bees of the families Apidae and Megachilidae and also received casual visits from *Philanthus triangulum*. The bees recorded were *Amegilla niveata* (Friese) (Anthophorini), *Xylocopa caffra* L., *Xylocopa scioensis* Gribodo (Xylocopini), the honeybee and *Megachile* (*Chalicodoma*) *niveofasciata* (Friese) (Megachilini). Clearly other species of Apidae and Megachilidae can be expected.

Combretaceae

One species of Combretaceae, at a single site, was sampled for flower visitors. *Terminalia prunioides* Laws (Figure I.3.28), a small shrub or tree, was found in full flower on a stoney slope above a dry watercourse to the west of Kamanjab in northwesten Namibia. The clusters of small white flowers were abundantly visited by *Nomia* (*Acunomia*) *epileuca* Cockerell (Halictidae, Nomiinae). This bee, which was encountered throughout the 'karroid' areas of Namibia, is broadly polyphagous having been recorded by us from 12 families of plants, however, most widely and frequently from *Tribulus* (Zygophyllaceae). The only other visitor recorded was, rather surprisingly, a single female of *Jugurtia alfkeni* (du Buysson), which shows a marked preference for *Hermannia*. The probable explanation is that herbaceous and small shrubby plants were almost all dried up, with the exception of a labiate from which one female of *N*. (*Acumonia*) *epileuca* was recorded.

Convolvulaceae

Flowers of Convolvulaceae (Figure I.3.29) are visited by bees, few of which seem to be specialists. However, in northwestern Namibia the sole species of *Mermiglossa*, *M. rufa* Friese (Andrenidae, Panurginae), was found in large numbers in mixed flower patches at two sites in arid savanna. It was only visiting the flowers of two species of Convolvulaceae, *Merremia palmata* Hallier f. and *Ipomoea obscura* (L.) Ker Gawl. These constitute the first and only records of flower visiting by these bees. In the choice of flowers they differ from the other nine members of the tribe Melliturgini.

Crassulaceae

Crassulaceae is listed as one of the largest families in the Karoo Biome (Cowling & Hilton Taylor 1999). In all three genera, the flowers have a tubular perianth and are held either erect or hanging down. Although few cases of bee, pollen wasp and wasp activity on flowers of this family were noted, observations for *Cotyledon* and *Tylecodon* are of interest.

Little has been recorded concerning the visitors to the flowers of *Tylecodon*. The widespread *Tylecodon paniculatus* (L.f.) Toelken has dull red-streaked flowers born horizontally on scarlet, robust inflorescence stems. This is characteristic of bird-pollinated plants and *T. paniculatus* is indeed sunbird-pollinated (Gess *et al*. 1998).

Tylecodon reticulatus (L.f.) Toelken (formerly as *Cotyledon dichotoma* Haw.) (Figure I.3.30.a & b), an erect annual herb, 20–150 mm high, with striking yellow flowers marked with reddish orange at the lip, is commonly found growing together with *Wahlenbergia* in sandy areas from the

Figure I.3.28.—Combretaceae, example: a. and b. *Terminalia prunioides* Laws.

Figure I.3.29.—Convolvulaceae, example: a. and b. *Merremia* sp.

Figure I.3.30.—Crassulaceae, examples: a. and b. *Tylecodon reticulatus* (Toelken) Toelken; c. and d. *Tylecodon hallii* (Toelken) Toelken; e. *Cotyledon campanulata* Marloth.

southwestern Cape to Namaqualand. Flower visitors were only observed on two occasions. At Sors Sors in the Kamiesberg the flowers were repeatedly visited only by *Samba* (*Atrosamba*) *gessorum* Eardley (Melittidae), otherwise recorded visiting flowers of *Indigofera longispina* Baker f. ex J.B.Gillett in the Richtersveld. The second occasion was on the east bank of the Clanwilliam Dam where the flowers were visited for nectar by a nesting female of *Celonites wahlenbergiae* Gess (Masarinae), which is particularly associated with *Wahlenbergia* (Campanulaceae) but does visit flowers of other families for nectar. The nectar is used in provisioning its nests and in cell construction (Gess & Gess 1992). Both the bee and the wasp, in size and behaviour, would be likely pollinators.

Tylecodon hallii (Toelken) Toelken (Figure I.3.30.c & d) a narrowly endemic species of northern Richtersveld and southern Namibia has erect greenish yellow flowers. These were observed in two consecutive years for flower visitors and were found to be visited in large numbers only by a pollen wasp, *Masarina tylecodoni* Gess, which appears to be restricted to visiting these flowers and, in fit and behaviour, to be their pollinators (Gess *et al*. 1997 & 1998).

Visitors to a fourth species of *Tylecodon*, *T. cacalioides* (L. f.) Toelken, were observed in the western Little Karoo by Robert Gess in two successive years. He noted that the bright yellow flowers of this species were not attracting aculeates but a long-proboscid horse fly, *Philoliche* (*Phara*) *tumidifacies* Austen (Tabanidae) (Gess 2001, vouchers in Albany Museum). We were interested in the statement by Jan Vlok and Anne Lise Schutte-Vlok (2010) that an uncommon wasp species pollinates the flowers. In response to a request by us for further details Jan Vlok wrote, "[we] could not capture or photograph them but they did resemble wasps". This leaves the Vloks' observation open to doubt.

The flowers of *Cotyledon* species are mainly pendulous and the length of the tube is variable. For example, the reddish flowers of *C. orbiculata* L. are about 25 mm long whereas those of the yellow flowered *C. campanulata* Marloth are about half this length. The flowers of *C. orbiculata* are visited by long-billed sunbirds but are also visited by *Xylocopa* species (Apidae, Xylocopinae) and a species of *Lipotriches* (Halictidae). The halictid bees are small enough to enter the flowers but even the smaller species of *Xylocopa*, such as *X. sicheli* Vachal, are unable to reach the nectar legitimately and steal it by puncturing the corolla tube near the base. Both bees are, however, legitimate visitors to *C. campanulata* (Figure I.3.30.e) and are amongst its potential pollinators.

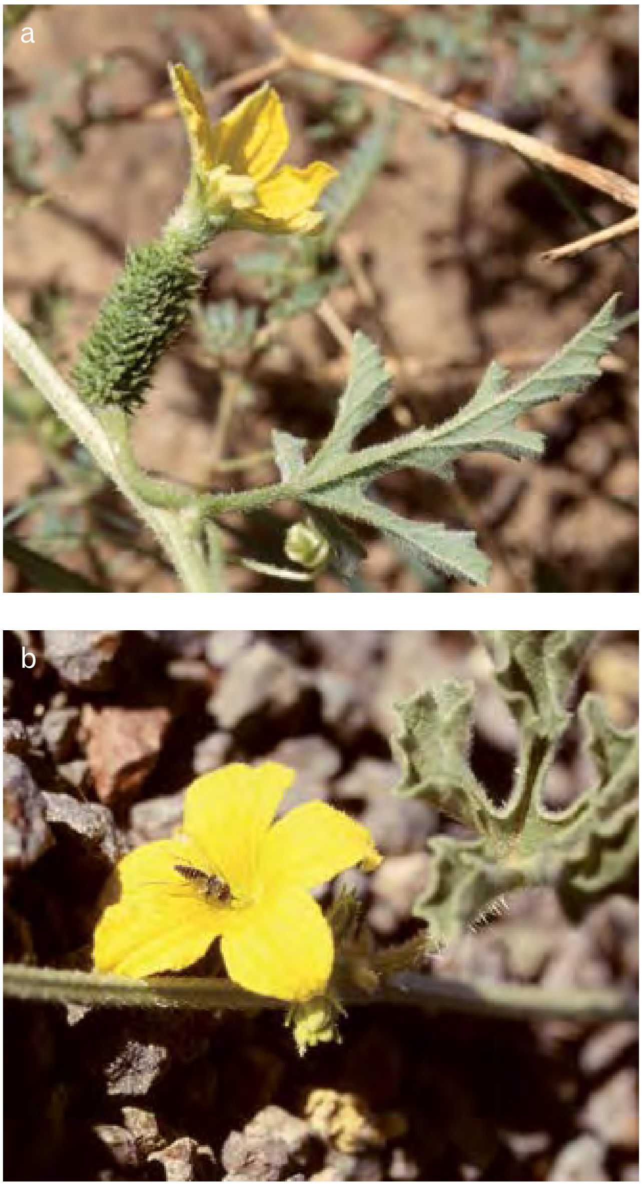


Figure I.3.31.—Cucurbitaceae, example: a. and b. *Cucumis africanus* L.f.

Cucurbitaceae

Cucurbitaceae are a feature of the more arid areas in the north (Figure I.3.31). The flowers attract small numbers of a limited range of aculeates. Only seven bee species were recorded:

- *Amegilla niveata* (Friese), *Amegilla langi* (Cockerell), cleptoparasitic *Thyreus abyssinicus* (Radoszkowski) (Apidae, Apinae), *Braunsapis* sp. (Apidae, Xylocopinae), *Nomia* (*Acunomia*) *epileuca* Cockerell (Halictidae, Nomiinae), all polyphagous species.
- *Fidelia* (*Parafidelia*) *friesei* Brauns, a specialist visitor of *Sesamum* spp. (Pedaliaceae).
- *Meganomia binghami* (Cockerell), a specialist visitor of Papilionoideae (Fabaceae) in the north.

Ebenaceae

Both genera of Ebenaceae, *Diospyros* and *Euclea*, are widely represented in the Karoo, in particular in association with drainage channels. The small greenish or dull cream flowers of these shrubs do not generally attract many wasps and bees.

Euclea crispa (Thunb.) Gürke was sampled at Karoo Poort at the southern end of the Tankwa Karoo on a day when it was seen to be well attended. The sample consisted of 11 species of wasps (five species of Crabronidae, two of Pompilidae and one each of Chrysididae, Vespidae (Eumeninae), Scoliidae and Pompilidae and two species of bees (one each of Colletidae and Halictidae)).

Diospyros was never well attended but was sampled for flower visitors northwest of Grahamstown, where it was visited by one species each of *Allodapula* and *Braunsapis* (Apidae, Xylocopinae), and east of Nieuwoudtville, where its only visitor was the highly polyphagous and widespread eumenine *Delta caffra* (L.). Otherwise, no flower visitors were recorded.

Euphorbiaceae

Euphorbiaceae, a family exhibiting a high degree of endemism, is listed by Cowling & Hilton-Taylor (1999) as the ninth largest family in the southern Karoo and Namaqualand-Namib Domains of the Succulent Karoo and eighth in the Damaraland-Kaokoveld Domain of the Nama-Karoo. Few Euphorbiaceae observed appeared to be attracting visits from solitary wasps and bees although honeybees in the southeastern Nama-Karoo and Namaqualand visited several of the succulent, yellow 'flowered' species. The exceptions, and there are surely others, were an erect, yellow 'flowered' perennial succulent *Euphorbia mauritanica* L. and an annual herb *Euphorbia glanduligera* Pax (formerly known as *Chamaesyce glanduligera* (Pax) Koutnik). In the Olifants River Valley and Namaqualand pompilids are amongst the commonest visitors to *Euphorbia mauritanica* L. which was otherwise only recorded by us as having received a single visit from a male *Chalybion* *tibiale* (Fabricius) (Sphecidae). However, Struck (1994) recorded *Nigranthidium cf. concolor* (Friese) (Megachilidae), *Scrapter* spp. (as *Polyglossa*) (Colletidae) and *Zonalictus* sp. (Halictidae) as visitors in the Goegap Nature Reserve. From the same locality he recorded three solitary bees, *Branthidium cf. nitidorubrum* Pasteels, *Megachile frontalis* Smith (both Megachilidae) and *Hylaeus* sp. (Colletidae) visiting *Euphorbia decussata* E.Mey. ex Boiss.

Euphorbia glanduligera in drainage channels in the Nama-Karoo of Namibia and across the Namib Desert to the coast at Swakopmund receives a much greater variety of wasp visitors. In addition to three species of Pompilidae, *Cryptocheilus morosus* Arnold, *Psammochares decipiens* Bischoff and *Schistonyx umbrosus* (Klug), visits were recorded by *Parapiagetia subtilis* Pulawski (Crabronidae, Crabroninae, Larrini), *Odontosphex damara* Pulawski (Crabronidae, Pemphredoninae), *Handlirschia scoliaeformis* (Arnold) (Crabronidae, Bembicinae), *Ammophila ferruginеipes* Lepeletier (Sphecidae), *Anthobosca* sp. (Tiphiidae) and *Spintharina arnoldi* (Brauns) (Chrysididae). However, only three bees, *Pseudapis cinerea* (Friese), *Pseudapis usakoa* (Cockerell) (Halictidae) and *Hylaeus* (*Deranchylaeus*) sp. (Colletidae) were recorded. Some of these visitors are widespread with distributions extending from the southeastern Nama-Karoo, others have a more northern distribution and yet others appear to be endemic to arid western Namibia. All except *O. damara* were also recorded from flowers of other families.

Southwest of Büllsport, where no other visitors were recorded, *E. glanduligera* received occasional visits from a pollen wasp, *Priscomasaris namibiensis* Gess, which was otherwise abundantly visiting *Limeum sulcatum* (Klotsch) Hutch. (Molluginaceae). This was opportunistic nectar feeding as *P. namibiensis* otherwise favours Aizoaceae (non-Mesembryanthema).

Geraniaceae

Geraniaceae is poorly represented in our study. However, the available information on visitors to the flowers of *Pelargonium*, including some of our records, has been assembled and analysed by Struck (1997), making it possible to comment usefully on additional records from the present study. Struck (1997) examined data for 208 *Pelargonium* taxa (species, subspecies and varieties) enabling him to place them in the pollination syndromes bee, long proboscid hovering fly, butterfly, hawkmoth and bird. The percentages of species attributed to these syndromes were 60, 25, 7, 2–4 and one presumed, respectively. Records subsequently collected and records of Jacot Guillarmod from insect specimen labels add to the knowledge of the association between pollen wasps and Geraniaceae.

Jacot Guillarmod sampled visitors to flowers of *Pelargonium myrrhifolium* (L.) L'Hér. (Sect. *Myrrhidium*) near Oudtshoorn in the Little Karoo and recorded ten polylectic aculeates as flower visitors, four species of bees, one species of pollen wasp and five species of wasps. These were *Colletes fasciatus* Smith (Colletidae), *Hoplitis* (*Anthocopa*) sp. A (Megachilidae, Osmiini), *Epeolus amabilis* Gerstaecker (Apidae, Nomadinae), *Amegilla niveata* (Friese) (Apinae, Anthophorini), *Celonites capensis* Brauns (Masarinae), three species of *Alastor*, *Eumenidopsis baciliformis* (Giordani Soika) and a species of *Stroudia* (all Eumeninae). This adds considerably to the data presented by Struck (1997) which mentioned only a single species of Megachilidae together with a fly (Bombyliidae) attributed to Vogel (1954) and Jacot Guillarmod (label data).

For the present study, two species of *Pelargonium* attracting appreciable numbers of aculeates were sampled for flower visitors. These were *Pelargonium capitatum* (L.) L'Hér. (Sect. *Pelargonium*) (Figure I.3.32.a & b) sampled in spring in two successive years between Clanwilliam and Graafwater to the west and *Pelargonium klinghardtense* R.Knuth in three successive years in northern Richtersveld.

The small pink flowers of *P. capitatum* were visited by:

- Four polyphagous bees, *Amegilla spilostoma* (Cameron) and *Tetraloniella minuticornis* Friese, (both Anthophorini) and *Megachile* (*Chalicodoma*) *karooensis* Brauns (Megachilini) and *Hoplitis* (*Anthocopa*) sp. A (Osmiini).
- Two pollen wasps most closely associated with, but not restricted to, *Wahlenbergia* (Campanulaceae), namely *Celonites wahlenbergiae* Gess and *Celonites bergenwahliae* Gess.
- Bombyliid flies.
- A lycaenid butterfly, which was drinking nectar but also laying eggs, its caterpillars being *Pelargonium* feeders.

The flowers of *P. klinghardtense* (Figure I.3.32.c & d), white with the opening to the 4 mm deep hypanthium red, were visited abundantly and principally by pollen wasps. The only other visitors recorded were a megachilid and a tabanid, *Mesomyia* (*Erodiorhynchus*) *edentula* (Wiedemann), which is commonly and widely found associated with orange and yellow daisies (ligulate Asteraceae, *Didelta*, *Dimorphotheca* and *Osteospermum*). The most abundant pollen wasps were *Jugurtia codoni* Gess, which was also abundant on *Codon* (Boraginaceae) at a different site, and *Masarina mixtoides* Gess which is narrowly polyphagous but most often associated with *Wahlenbergia* (Campanulaceae). Other less common pollen wasp visitors were *Celonites promontorii* Brauns a species most often associated with Asteraceae, and a *Quartinia* species.

Whereas pollen wasps are not important visitors to most species of *Pelargonium*, they may well be of importance as pollinators to some species, for example *P. klinghardtense* which is also of importance to some of its pollen wasp visitors.

Cream and pink flowered *Sarcocaulon* species (Figure I.3.32.e & f) were observed in Namaqualand, in the Springbok area and in northern Richtersveld, and southern Namibia from east of Oranjemund to south of Rosh Pinah. They were rarely abundantly visited. The most widespread visitor appears to be *Hoplitis* (*Anthocopa*) sp. as listed above as an occasional visitor to *P. myrrhifolium* and *P. capitatum*. This bee has also been recorded from Asteraceae from the eastern Nama-Karoo, to the west of Clanwilliam, from Namaqualand and singly from *Homeria* (Iridaceae) from Springbok and *Ballota* (Lamiaceae) from Nieuwoudtville. Petal nests of this bee were found in snail shells from sites north and south of the Orange River. The petals used were from a pink flowered *Sarcocaulon*. The pollen obtained from a nest was examined microscopi-

Figure I.3.32.—Geraniaceae, examples: a. and b. *Pelargonium capitatum* (L.) L'Hér.; c. and d. *Pelargonium klinghardtense* Knuth; e. and f. *Sarcocaulon* sp.

cally and found to match that of *Sarcocaulon* (Gess & Gess 1999).

East of Oranjemund several plants of a cream flowered *Sarcocaulon* were visited by numerous individuals of a *Quartinia* species which, at the same site, was also visiting flowers of Aizoaceae, Asteraceae and occasionally *Aptosimum* (Scrophulariaceae).

Only honeybees have been observed visiting the widespread exotic weed *Erodium cicutarium* (L.) L'Hér.

Loasaceae

Loasaceae is represented in southern Africa by one species, *Kissenia capensis* Endl. (Figure I.3.33). It occurs in northern Namaqualand and Namibia. In the present survey, flower visits were recorded for this plant growing in a dry drainage channel in the Namib Desert southwest of Uis. Here the flowers received visits only from males of *Pseudapis usakoa* (Cockerell) (Halictidae) and *Pachyanthidium* (*Ausanthidium*) *ausense* (Mavromoustakis) (Megachilidae). In the present survey, the halictid was found on flowers throughout Namibia and was recorded from ten families. The megachilid (Anthidiini) was recorded from flowers of five families but most commonly from *Indigofera* (Fabaceae) in the Richtersveld and across the Orange River in Namibia and from *Zygophyllum* (Zygophyllaceae) in Namibia between Palm and Khorixas.

Struck (1990) sampled *K. capensis* at the southern end of its distribution in the Goegap Nature Reserve. He recorded visits from a female *Amegilla velutina* (Friese) (Apidae), *Halictus* (*Seladonia*) *cf. atroviridis* Cameron (Halictidae) and two species of bee flies (Bombyliidae).

Figure I.3.33.—Loasaceae, example: *Kissenia capensis* Endl.

Neuradaceae

Neuradaceae is a small family restricted to semi-arid regions. Two genera are represented in southern Africa and a third genus is found in north Africa across the Middle East to India. They are prostrate herbs with large, regular, open, yellow flowers. Two species of *Grielum*, *G. grandiflorum* (L.) Druce and *G. humifusum* Thunb. were sampled for flower visitors at several sites in Namaqualand and in the sandveld to the west of the Olifants River Valley. *Grielum sinuatum* Licht. ex Burch. (Figure 1.3.34) was sampled for flower visitors in southwestern Namibia. One species, *Neuradopsis austro-africana* (Schinz) Bremek. & Oberm., was sampled for flower visitors in southern Namibia, on the fringe of the Kalahari in the east and on the fringe of the Namib in the west. Visits from 12 species of aculeates were recorded. These consisted of 10 bees (2 Apidae, 1 Colletidae, 2 Halictidae, 4 Megachilidae and 1 Melittidae) one pollen wasp and one wasp.

The most commonly encountered visitor to both species of *Grielum* was *Scrapter chloris* Eardley (Colletidae), which appears to specialise in flowers of this genus having not been collected from any other flowers. In the sandveld, but not further inland, *G. humifusum* was frequently visited by a species of *Fidelia* (*Parafidelia*) (Megachilidae, Fideliinae), which also appears to be a specialist visitor. Visits by the other bees were casual and infrequent.

The species of *Fidelia* (*Parafidelia*) was the most common visitor to *N. austro-africana* on the Kalahari fringe. Visits

Figure I.3.34.—Neuradaceae, examples: a. and b. *Grielum sinuatum* Licht. ex Burch.

by males of *Meganomia binghami* (Cockerell) (Melittidae) were recorded but these were casual in nature as was that of the single wasp species, *Stilbum cyanurum* Förster (Chrysididae).

It would appear that *Scrapter chloris* and the species of *Fidelia* (*Parafidelia*) are the most dependable visitors to, and most likely pollinators of these plants.

A pollen wasp, *Quartinia poecila* Schulthess, has since been found to be one of the most abundant visitors to flowers of *Grielum sinuatum* in the southern Namib. It is not, however, restricted to Neuradaceae, visiting also Aizoaceae, Asteraceae and Zygophyllaceae.

Nyctaginaceae

Although members of Nyctaginaceae are widespread in arid areas, only one species, *Boerhavia deserticola* Codd, was seen in flower. At a single site in northwestern Namibia on the desert fringe, where numerous plants were in flower in a dry drainage channel, these plants received visits from six species consisting of three bees, two pollen wasps and one wasp.

The three bees were polyphagous species, *Meliturgula haematospila* Cockerell (Andrenidae), *Nomia* (*Acunomia*) *epileuca* Cockerell (Halictidae) and *Coelioxys afra* Lepeletier (Megachilidae).

One of the pollen wasps was a species of *Quartinia* (formerly *Quartinioides*) which, however, was most abundantly found visiting the flowers of *Zygophyllum* species, in particular *Z. simplex*. The other was *Celonites michaelseni* Schulthess, otherwise always found in association with *Peliostomum*, *Aptosimum* and *Anticharis* (all Scrophulariaceae) from northern Richtersveld through southern and western Namibia. The visits to *B. deserticola* were casual and occasional in nature and apparently only made by males.

The wasp, *Kohlia cephalotes* Handlirsch (Nyssonidae), was the most abundant of the visitors. However, at the same site and at others on the inland fringe of the desert, it was found more abundantly visiting *Zygophyllum simplex* L. (Zygophyllaceae).

Thus, although flowers of *B. deserticola* are clearly attractive to aculeates, none of those observed showed a marked preference for them.

Pedaliaceae

The Pedaliaceae are principally tropical to subtropical and in southern Africa are found mainly in the more northern arid areas. Only one genus, *Sesamum*, was encountered in flower. All plants sampled were erect annual or perennial herbs with numerous large, pink to pinkish violet gullet flowers. The widespread species, *S. triphyllum* Welw. ex Asch. (Figure I.3.35.a & b), was sampled for flower visitors from the southern Kalahari north of Upington and in Namibia from the Kalahari fringe in the southeast and along the desert fringe in the west from Helmeringhausen in the south to north of Opuwa in the north. In addition, *S. capense* Burm.f. (Figure I.3.35.c & d) was sampled for flower visitors near Helmeringhausen. Whitehead (1984) and Whitehead *et al*. (1987) sampled flower visitors to the two species above, to *S. rigidum* Peyr., and to an undetermined species in the Western Cape.

In our survey, recorded visitors to *Sesamum* were four species of Apidae, three species of Megachilidae and two species of Halictidae.

Along the desert fringe from Helmeringhausen/Spes Bona in the south to Opuwa in the north and in the Kalahari the large, pink gullet flowers of *Sesamum* were visited principally by *Fidelia* (*Parafidelia*) *friesei* (Brauns) (Megachilidae, Fideliinae). This association supports the records of Whitehead *et al.* (1987) except that in addition they also recorded *F.* (*P.*) *ornata* (Cockerell) from *S. rigidum*.

The other species of Megachilidae, both *Megachile* (Megachilinae, Megachilini) were generally casual visitors, though *Megachile* (*Maximegachile*) *maxillosa* Guérin was a somewhat frequent visitor in southeastern Namibia on the Kalahari fringe.

The most frequently encountered Apidae were species of *Amegilla.* In Namibia, these were the widespread and broadly polyphagous *A. niveata* (Friese), *A. langi* (Cockerell) and *A. nubica* Lepeletier. In the Western Cape Whitehead (1984) recorded *A. spilostoma* (Cameron).

There appear to be no bees which are *Sesamum* specialists. However, considering their large size and their

Figure I.3.35.—Pedaliaceae, examples: a. and b. *Sesamum triphyllum* Welw. ex Aschers; c. and d. *Sesamum capense* Burm.

behaviour, entering the flowers deeply and moving from plant to plant on a single foraging trip, both *Fidelia* (*Parafidelia*) and *Amegilla* qualify as pollinators.

Plumbaginaceae

Plumbaginaceae is represented in southern Africa by three genera, *Plumbago* with slender tubular flowers, *Dyerophytum* with more funnel-shaped tubular flowers and *Limonium* with petals separate or only fused for a short distance. Only the flowers of *Limonium* are suited to wasps and bees. The flowers of the other two genera appear to be visited solely by butterflies. Visits by insects to *Limonium* were observed only at Karoo Poort to the south of the Tankwa Karoo. Here, flowers of a violet flowered species of *Limonium* were being visited occasionally. One bee and three pollen wasp species were recorded.

The bee was a single female of *Halictus* sp. A *cf. jucundus* Smith, otherwise recorded from Asteraceae from eastern Nama-Karoo, southern Great Karoo, Little Karoo and Namaqualand and six other families.

During the course of a day, two *Celonites promontorii* Brauns females visited. This was surprising, as this wasp appears otherwise to specialise in Asteraceae, having been recorded from flowers of this family from the eastern Nama-Karoo, southern Great Karoo, Little Karoo and Namaqualand. The other two pollen wasps were a female *Quartinia niveopicta* Schulthess, otherwise recorded by Turner (1939) from Mesembryanthema, and five females of *Quartinia* sp. (*Quartinioides* sp. J), which is also otherwise associated with Mesembryanthema. More recently (since closing the catalogue for analysis) we have found *Quartinia capensis* Kohl visiting flowers of *Limonium scabrum* (Thunb.) Kuntze (Figure I.3.36) on the south coast to the west of Mossel Bay. However, it was also visiting flowers of mesembs at this site and on the coast at Port Elizabeth.

Figure I.3.36.—Plumbaginaceae, example: a. and b. *Limonium scabrum* (Thunb.) Kuntze.

Portulacaceae

The only records of aculeate visits to Portulacaceae were for the succulent shrub *Portulacaria afra* Jacq., a dominant shrub in some areas of the southeast. The small, massed flowers appeared to receive few visits from aculeates, as only three visits, all by eumenines, *Antepipona* Saussure and *Zethus* were recorded.

Polygalaceae

In the 1998 classification of the Angiosperm Phylogeny Group, Polygalaceae was placed together with Fabaceae in the Fabales. Unlike Fabaceae, Polygalaceae is not one of the families that characterises the Karoo Biome either in number of individual plants or in number of species. Indeed, of the southern African biomes, it is only in the Fynbos Biome that many members of Polygalaceae occur (Cowling *et al*. 1997).

In this study flower visitors were collected from only two species of *Polygala* namely, *P. virgata* Thunb. (Figure I.3.37.a) in the Goegap Nature Reserve, Springbok and *P. hottentotta* C.Presl. on a farm near Colesberg in the southeast.

Figure I.3.37.—Polygalaceae, examples: a. *Polygala virgata* Thunb.; b. *Polygala myrtifolia* L.

In Goegap Nature Reserve, *P. virgata* is fairly common in the hills in moist areas where there is water seepage. During spring of two separate years, it was found to be visited only by Megachilidae. These consisted of two species of *Plesianthidium* and three species of *Megachile* (all most often encountered visiting the flowers of Papilionoideae in the Olifants River area and Namaqualand) and a fourth species of *Megachile*, associated with *Crotalaria* in Namibia.

Polygala hottentotta, like *P. virgata*, was associated with an area where there is moisture seepage. It was visited by two species of *Megachile* and *Xylocopa caffra* (Apidae, Xylocopinae).

In the Eastern Cape, a common shrubby species *Polygala myrtifolia* L. (Figure I.3.37.b) is similarly visited by Megachilidae (Figure IV.2.28.b).

All these bees qualify as suitable pollinators for these flowers.

Proteaceae

Proteaceae are not well represented within the study area, as they are Fynbos rather than Karoo plants. However, in the Clanwilliam and Nieuwoudtville areas at the interface between karroid and fynbos scrub two species of Proteaceae were sampled for flower visitors. One was the dusky-pink flowered *Paranomus bracteolaris* Salisb. ex Knight, growing west of Nieuwoudtville near the edge of the escarpment and in the hills to the west of Clanwilliam. The other was a species of *Leucadendron*, with relatively large brilliantly yellow female ‘cones’ held within broad yellow involucral leaves, growing west of Clanwilliam near Graafwater.

Rebelo (1995) states that some species of *Leucadendron* are visited by a number of beetles; and that most of the genera (of Proteaceae) with smaller flower heads are visited by a variety of beetles, flies and wasps.

In our study, at both sites, bees of the families Apidae and Colletidae and wasps of the family Tiphiidae visited *P. bracteolaris*. Of particular interest are the colletids, *Scrapter erubescens* (Friese) (Clanwilliam and Nieuwoudtville), also recorded from *Leucadendron*, and *Scrapter fuliginatus* Eardley (Clanwilliam). These are the only known records of flower visiting for these bees (Eardley 1996), indicating that there may be an association between these bees and Proteaceae. The apids were honeybees, which were abundant visitors, and uncommonly *Amegilla spilostoma* (Cameron), a polyphagous species (recorded from 15 plant families) with a wide distribution from the eastern limits of the Nama-Karoo through to the west. The tiphiids, four species of *Mesa* Saussure, one of *Tiphia* Fabricius at Nieuwoudtville and one species of *Mesa* at the Clanwilliam site, can be expected to be polyphagous.

In addition to *S. erubescens*, a polyphagous cleptoparasitic bee, *Sphecodes* sp. (Halictidae), and ten wasp species of the families Pompilidae, Crabronidae, Scoliidae and Tiphiidae visited the *Leucadendron*. The crabronid wasps were *Oxybelus peringueyi* Saussure, *Oxybelus ruficaudis* Cameron, *Dasyproctus immitus* (Saussure) and *Dasyproctus ruficaudis* (Arnold). They were probably casual visitors as the last three, at least, are polyphagous and widespread species. The scoliid, *Cathimeris* (*Cathimeris*) *capensis*

(Saussure), and the tiphiids, two species of *Mesa*, shared with *Paranomus bracteolaris*, are expected to be polyphagous. The records of a single male each for the pompilids *Paracyphononyx frustratus* (Smith) and *Psammoderes mimicus* (Haupt) and for a crabronid, *Philanthus capensis* Dahlbom, are probably of little consequence.

Rhamnaceae

The only species of Rhamnaceae sampled for flower visitors was *Ziziphus mucronata* Willd., a shrub to small tree with the greater part of its distribution outside the Karoo Biome to the east and north. However, it is present in the extreme southeast and northwest. It was sampled for flower visitors near Adelaide in the southeast over a period of three days during which time the flowers were abundantly visited by wasps. The sample was made up of 13 species of Eumeninae, seven species of Pompilidae, six species of Crabronidae (Bembicinae), four species of Sphecidae and three species of Crabronidae (Crabroninae)—all polyphagous species. For wasps it is clearly an important source of nectar.

Solanaceae

Solanaceae are widespread in the Karoo Biome but are not highly species diverse. *Lycium* (Figure I.3.38), *Solanum* and *Nicotiana* were observed for flower visitors. Overall, 11 species of bees and eight species of wasps but no pollen wasps were recorded. All were visited by bees of the family Apidae, all by species of *Xylocopa*. *Lycium* was additionally visited by three species of Anthophorini and one species of Eucerini. Less commonly *Lycium* and *Solanum* were visited by Halictidae. Only *Lycium* was visited by wasps which included four species of Eumeninae, two species of *Ammophila* (Sphecidae, Ammophilinae), *Sphex decipiens* Kohl (Sphecidae, Sphecinae) and *Campsomeriella* (*Campsomeriella*) *caelebs* (Sichel) (Scoliidae).

These findings support larger bees being the pollinators of Solanaceae but suggest that wasps may be contributory pollinators of *Lycium* which provides them with readily accessible nectar.

Vahliaceae

The monogeneric family Vahliaceae is represented in southern Africa by a single species containing several infraspecific taxa. *Vahlia capensis* (L.f.) Thunb. is widespread in the drier west. The flowers are small, regular, open with free petals. This erect herb, was sampled for flower visitors on the banks of drainage channels at Rooibank, on the lower reaches of the Kuiseb River in the Namib Desert, and in the Karas Mountains in southeastern Namibia. At Rooibank the flowers were visited by an apid, *Amegilla niveata* (Friese) (Anthophorini), and a megachilid, *Afranthidium* (*Branthidium*) *minutulum* (Brauns) (Anthidiini). In the Karas Mountains it was visited by two apids, *Ctenoceratina bilobata* (Cockerell) and *Braunsapis otavica* Cockerell/*Braunsapis albipennis* (Friese) (Xylocopini)), and a megachilid, *Pseudoheriades moricei* (Friese) (Osmiini). An additional visitor at the site in the Karas Mountains was a pollen wasp, a female *Quartinia propinqua* Schulthess. This was probably a casual visit as this species was otherwise recorded only from yellow flowered Asteraceae at sites in the southern Great Karoo, Bushmanland and east of the escarpment in Namaqualand.

Figure I.3.38.—Solanaceae, examples: *Lycium* spp. a. and b. Eastern Cape; c. Swakopmund, Namibia.

Monocots

In the study areas, at the times of year when sampling took place, relatively few monocots attracting solitary wasps and bees were encountered. Indeed, many of the showy species forming spectacular expanses which are a feature of marshy ground and 'rock gardens' in spring and early summer in the southwest are not patronised by aculeate wasps and solitary bees but by flies and beetles (Goldblatt *et al*. 1995, 2002; Goldblatt & Manning 2000a, 2000b; Manning & Goldblatt 2001).

Despite the small number of monocot species sampled in this survey, visits were recorded for all bee families except Andrenidae, which are, however, known to visit some *Gladiolus* (Goldblatt *et al*. 1998a, 1998b). No species were found to be restricted to monocots.

Goldblatt and his co-workers have established that solitary bees contribute to the pollination of some Iridaceae including species of *Moraea* (Goldblatt *et al*. 1989; Goldblatt & Bernhardt 1999), *Nivenia* (Goldblatt & Bernhardt 1990), *Romulea* (Goldblatt *et al*. 2002), *Lapeirousia* (Goldblatt *et al*. 1995) and *Gladiolus* (Goldblatt & Manning 1998; Goldblatt *et al*. 1998a, 1998b).

The few species recorded from *Moraea* (example Figure I.3.39.a & b) in this study, in addition to honeybees, include:

- Species of Melittidae, *Rediviva longimanus* Michener, which otherwise obtains oils from the long spurs of *Diascia longicornis* (Thunb.) Druce (Scrophulariaceae) and an undescribed polyphagous species of *Melitta*.
- Halictidae, species of *Patellapis*, which were more commonly visiting *Herrea* (Aizoaceae, Mesembryanthema).
- Apidae, *Anthophora* (*Heliophila*) *wartmanni* Friese (Anthophorini), which was most commonly visiting Asteraceae.
- Two polyphagous Megachilidae, *Plesianthidium* (*Spinanthidium*) *neli* (Brauns) (Anthidiini) and a species of *Hoplitis* (*Anthocopa*) (Osmiini).

One of the most widespread bee-pollinated species of nectar producing *Gladiolus* in the study area is *Gladiolus orchidiflorus* Andrews (Figure I.3.39.c), which is found from the Cape Peninsula in the south to southern Namibia in the north and eastwards across Bushmanland and the Karoo to Kimberley and Fauresmith, but not in the south-east (Goldblatt & Manning 1998). During our study, at a site in Namaqualand, it was found to be repeatedly visited by females of two polyphagous species of *Amegilla*, *A. obscuriceps* (Friese) and *A. spilostoma* (Cameron) (Apidae, Anthophorini). Both species recorded by Goldblatt *et al*. (1998b) to be visitors to *Gladiolus* but not *G. orchidiflorus*, for which they recorded only *Anthophora* (*Pyganthophora*) *diversipes* Friese (Anthophorini). Struck (1994) made observations on visitors to *G. orchidiflorus* near Springbok, Namaqualand, where he recorded *Amegilla niveata* (Friese) (Anthophorini) and *Plesianthidium* (*Spinanthidium*) *calvini* (Cockerell) (Anthidiini). It seems likely that a wide range of *Amegilla* and *Anthophora* can be expected to visit this species of *Gladiolus* to obtain nectar.

Figure I.3.39.—Monocots, examples: a. and b. *Morea* sp.; c. *Gladiolus orchidiflorus* Andr.; d. *Ferraria variabilis* Goldblatt & Manning; e. *Ferraria kamiesbergensis* M.P.de Vos.; *Trachyandra divaricata* (Jacq.) Kunth.

Other monocots visited by bees are:

- Some *Albuca* spp. (Hyacinthaceae) by polyphagous Megachilidae.
- *Wachendorfia* spp. (Haemodoraceae) by polyphagous Apidae.
- *Bulbinella latifolia* Kunth (Asphodelaceae) by honeybees.
- *Bulbine frutescens* (L.) Willd. (Asphodelaceae) by polyphagous Megachilidae, most frequently *Megachile* (*Creightonella*) *dorsata* (Smith).

Visits by pollen wasps to monocots are unusual, in fact only *Aloe striata* Haw. (Asphodelaceae) and two species of *Ferraria* (Iridaceae) were recorded as receiving visits from these wasps. *Aloe striata* in the southern Great Karoo was visited abundantly by *Quartinia antigone* (Richards) (a sample of 24 females and five males were taken in 30 minutes), a species for which no other flower visiting records are known.

Ferraria was generally considered to be attractive only to flies (Scott-Elliot 1891; Vogel 1954; Cowling & Pierce 1999; Manning & Goldblatt 2001) or flies and small beetles (De Vos 1979). However, in our study we found that some species of *Ferraria* were being visited repeatedly and solely by Masarinae (Vespidae). We recorded female *Jugurtia koeroegabensis* Gess, a narrowly endemic species, visiting *F. variabilis* Goldblatt & J.C.Manning (as *F. cf. divaricata* M.P.de Vos in Gess & Gess 2006) (Figure I.3.d) in the Richtersveld and *Celonites capensis* Brauns, a widespread Karoo species, visiting *F. kamiesbergensis* M.P.de Vos (as *F.* cf *divaricata* in Gess & Gess 2006) (Figure I.3.e) in the foothills of the Kamiesberg. Neither of these is restricted to *Ferraria*. Both are unusually polyphagous for pollen wasps, *C. capensis* have been recorded from flowers of six additional families and *J. koeroegabensis* from four. More recently, Goldblatt *et al.* (2009) confirmed that flowers of some species of *Ferraria*, those that produce large quantities of nectar with a low sugar content, do attract aculeates. They recorded visits to *F. variabilis* and *F. divaricata* Sweet, solely by Eumeninae (Vespidae) at a time when bees and flies were active on co-blooming flowers. These eumenines, two species of *Delta* and *Allepipona erythrospila* (Cameron), like the two pollen wasps, are polyphagous.

Few wasp species were found to visit any monocot species, apart from *Asparagus suaveolens* Burch. (Asparagaceae), which they visit abundantly in the southeast. Five species of pompilids, three species of tiphiids, and one species each of scoliid and sphecid were recorded.

Oil collecting visits by five of the 15 winter rainfall area *Rediviva* species to oil-secreting Orchidaceae, of the genera *Ceratandra*, *Corycium*, *Disperus*, *Pterygodium* and *Satyrium* are listed by Vincent Whitehead and Kim Steiner (2001, Appendix)*.* All but one of the *Rediviva* species have been recorded from more than one orchid genus and all have additionally been recorded from Hemimerideae (Scrophulariaceae) (see above).

They record pollen collection by *Rediviva gigas* Whitehead & Steiner from two localities from two species of *Watsonia* (Iridaceae), and nectar collection by both females and males from *Watsonia*, *Wachendorfia* (Haemadoraceae) and *Moraea* (Iridaceae)*. Moraea* is represented amongst the nectar flowers of many species, and appears to be preferred by *R. longimanus* Michener having been recorded repeatedly from *Moraea.* Our findings also support these records.

Recent collecting of visitors to flowers of *Trachyandra divaricata* (Jacq.) Kunth (Figure I.3.39.f) (Asphodelaceae) along the southwest coast has indicated that it is an important resource for some Masarinae (Gess & Gess 2010).

Final remarks on pollinators and plants

Although a relatively small number of the plant species of the study area were sampled for flower visitors, sufficient evidence has been provided to conclude that:

- The flowers of some plants receive visits from a very large range of aculeates. However, there are no flowers that are visited by all aculeates present at any one site.
- The flowers of plants of some subfamilies, tribes or genera are consistently visited by particular complexes of a limited number of aculeate taxa throughout the study area.
- The flowers of other taxa show marked differences in their assemblages of flower visitors along east/west, south/north gradients.
- The flowers of relatively few species of plants are visited by just a single species of aculeate.

Solitary bees are the most species-diverse of the aculeates visiting flowers in the semi-arid to arid areas of southern Africa. They are also without question the most likely pollinators of the broadest range of plant taxa. They range from broadly polyphagous to narrowly oligophagous. High diversity of choice, i.e. high incidence of polyphagy, is exhibited by most Megachilidae, Apidae, Halictidae and Andrenidae whereas low diversity of choice, i.e. high incidence of oligophagy, is exhibited by Colletidae and Melittidae. However, within the Megachilidae and Apidae some taxa appear to be oligophagous.

Pollen wasps are sufficiently species-diverse, widespread and abundant for it to be essential that they be included with bees in any study of bee/flower associations as they are equivalent in behaviour. For some plants, they are probably the sole pollinators and for others they form part of a complex with bees. The diversity of choice of pollen wasps is similar to that of Colletidae and Melittidae, indicating a high incidence of oligophagy.

Non-pollen wasps recorded visiting flowers are almost as species diverse as bees but visit a narrower range of plants. They are important as flower visitors and for some plants are their most abundant potential pollinators. It has been suggested that wasps are not effective pollinators because their low nectar requirements do not require them to move much between flowers and plants. However, considering that many of the flowers they favour are low nectar producers, this reasoning falls away.

Plants as an indirect source of energy for wasps

Hunting wasps

It was possible to conduct a survey of flowering plants visited by wasps and bees, plants being static and readily visible. On the other hand, insects and spiders are neither static nor, as a rule, make themselves readily visible. Therefore, a survey of prey taken by wasps was not possible. Recording of prey had perforce to be opportunistic. By gathering together records (our own and those of others) of wasps captured carrying prey and of prey from nests, some indication of the insects and spiders hunted by wasps in the semi-arid to arid areas of southern Africa has been assembled. These are grouped according to the wasps' feeding behaviour (Tables 5 & 6). Assessment of the impact of the predators on the populations of their prey has not been possible. Considering that the populations of some wasps, judged by the sizes of their nesting aggregations, are significant, it is believed that, as do all predators, they must contribute to the population size control of their prey. Most female wasps provision numerous cells during their lifetime and in most instances, these cells are provisioned with several to many prey.

Orthoptera (examples Figures 40–45)

Six families of grasshoppers are known to be hunted by wasps in southern Africa. The wasps concerned are all members of the Sphecidae and Crabronidae. Within the Sphecidae, three genera of Sphecinae, *Prionyx*, *Sphex* and *Isodontia*, specialise in hunting grasshoppers (examples of prey transport Figures II.3.13.b. & II.3.14c). *Prionyx* always takes Acrididae, and *Sphex* and *Isodontia* mainly longhorned grasshoppers (Tettigoniidae), although tree crickets (Gryllidae) are also taken.

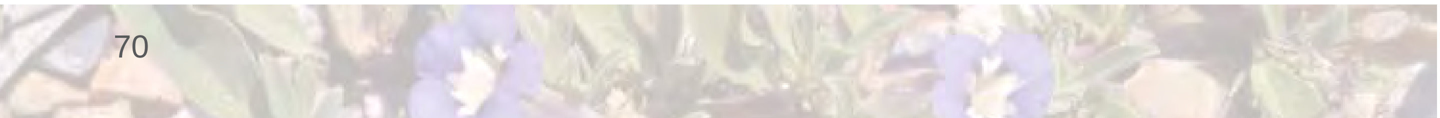
Whereas only two of the six families of grasshoppers are known to be hunted by Sphecids, all six are hunted by Crabronidae of the subfamilies Crabroninae and Bembicinae. Within the Crabroninae hunting grasshoppers is confined to four larrine genera, all species of *Holotachysphex* and *Prosopigastra* and most *Gastrosericus* and *Tachysphex* (example of prey transport Figure II.3.33), and in the Bembicinae to most species of *Stizus* (example of prey manipulation Figure II.3.31). Of these, *Stizus* is the most unbiased, taking grasshoppers of at least four families.

Table 5.—Phytophagous insects (grouped according to their feeding behaviour) hunted by southern African wasps

Prey role	**Prey order**	**Prey family**	**Aculeate wasp family**	**Aculeate wasp subfamily**	**Aculeate wasp genus**
Sap feeders	Hemiptera	Membracidae	Crabronidae	Bembicinae	*Bembecinus* spp., *Hoplisoides aglaia*
		Cicadellidae	Crabronidae	Bembicinae	All *Bembecinus* spp.
		Fulgoridae (s.l.)	Crabronidae	Bembicinae	All *Bembecinus* spp.
		Aphididae	Crabronidae	Pephredoniae	*Diodontus* spp.
		Cercopidae	Crabronidae	Bembicinae	*Gorytes* spp.
		Pentatomidae	Crabronidae	Astatinae	*Astata* and *Dryudella* spp.
			Crabronidae	Crabroninae	*Prosopigastra* spp, e.g. *P. creon*
		Miridae	Crabronidae	Crabroninae	*Dasyproctus westermanni* (in exceptional cases)
Gum feeders	Dictyoptera	Blattidae e.g. *Bantua dispar*	Ampulicidae	Ampulicinae	e.g. *Ampulex bantuae*
Foliage feeders	Lepidoptera	Psychidae	Vespidae	Eumeninae	*Aethiopicodynerus* (= *Parachilus*) spp.
		Tortricidae	Vespidae	Eumeninae	various genera
		Pyralididae	Vespidae	Eumeninae	e.g. *Antepipona*, *Pseudepipona* and *Rynchium* spp.
			Sphecidae	Ammophilinae	*Ammophila conifera*
		Geometridae	Vespidae	Eumeninae	various genera
			Sphecidae	Ammophilinae	Some *Ammophila spp.*
		Lasiocampidae	Sphecidae	Ammophilinae	*Ammophila dolichodera*
		Noctuidae	Vespidae	Eumeninae	*Paravespa mima*
		Arctiidae	Sphecidae	Ammophilinae	*Ammophila dolichodera*
		Pieridae	Sphecidae	Ammophilinae	*Ammophila ferrugineipes*
		Lycaeinidae	Sphecidae	Ammophilinae	*Ammophila ferrugineipes*
		Other undetermined	Vespidae	Eumeninae and Polistinae	
	Coleoptera	Chrysomelidae	Vespidae	Eumeninae	e.g. *Tricarinodynerus guerinii*, occasional secondary prey
			Crabronidae	Philanthinae	Some *Cerceris* spp. (see Table 11)
		Curculionidae	Crabronidae	Philanthinae	Some *Cerceris* spp. (see Table 11)
	Orthoptera	Acrididae	Sphecidae	Sphecinae	All *Prionyx* spp.
			Crabronidae	Crabroninae	*Tachysphex* spp. e.g. *T. panzeri*
		Lentulidae	Crabronidae	Crabroninae	*Tachysphex* spp. e.g. *T. fugax*
		Gryllidae	Crabronidae	Crabroninae	*Liris* spp.
			Sphecidae	Chloriontinae	*Chlorion maxillosum*
			Rhopalosomatidae		
		Gryllidae, Oecanthinae	Crabronidae	Crabroninae	*Kohliella alaris*
		Tettigoniidae	Sphecidae	Sphecinae	All *Isodontia* and *Sphex* spp.
		Tetrigidae	Crabronidae	Crabroninae	*Parapiagetia* spp.
		Pyrgomorphidae	Crabronidae	Crabroninae	e.g. *Holotachysphex turneri*
			Crabronidae	Bembicinae	e.g. *Stizus imperialis*
		Pamphagidae	Crabronidae	Bembicinae	e.g. *Stizus imperialis*
		Grasshoppers and crickets	Crabronidae	Crabroninae	*Gastrosericus* spp., one or other depending on species
Flower/inflorescence feeders	Coleoptera	Phalacridae	Crabronidae	Philanthinae	Some *Cerceris* spp. (see Table 11)
		Scarabaeidae	Crabronidae	Philanthinae	Some *Cerceris* spp. (see Table 11)
Pollen and nectar feeders	Hymenoptera	Apidae	Crabronidae	Philanthinae	Some *Cerceris* spp. (see Table 11) and all *Philanthus* spp.
			Crabronidae	Crabroninae	All *Palarus* spp.
		Halictidae	Crabronidae	Philanthinae	Some *Cerceris* spp. (see Table 11)
		Vespidae, Masarinae	Crabronidae	Crabroninae	*Palarus* spp. e.g. *P. latifrons*
Stem and root feeders	Coleoptera	Buprestidae	Crabronidae	Philanthinae	Some *Cerceris* spp. (see Table 11)
		Scarabaeidae	Crabronidae	Philanthinae	Some *Cerceris* spp. (see Table 11)
			Scoliidae	Scoliinae	Most species (some hunt *Curculionidae*)
	Lepidoptera	Noctuidae	Ammophilidae	Ammophilinae	e.g. *Podalonia canescens*
Decaying plant matter: palms	Coleoptera	Scarabaeidae, Dynastinae	Scoliidae	Scoliinae	*Scolia ruficornis*
		Curculionidae	Scoliidae	Scoliinae	*Scolia ruficornis*

Table 6.—Non-phytophagous insects and spiders hunted by wasps in southern Africa

Prey role	**Prey order**	**Prey family**	**Aculeate wasp family**	**Aculeate wasp sub-family**	**Aculeate wasp genus**
Predators	Dictyoptera	Mantidae	Crabronidae	Crabroninae	*Tachysphex* spp. e.g. *T. albocinctus*
	Hymenoptera	Tiphiidae	Crabronidae	Bembicinae	*Palarus* spp.
			Crabronidae	Philanthinae	Some *Cerceris* spp. (see Table 11)
		Scoliidae	Crabronidae	Bembicinae	*Palarus* spp.
	Diptera	Asilidae	Crabronidae	Bembicinae	Some *Bembix* spp.
	Coleoptera	Cicindelidae	Tiphiidae	Methocinae	*Methoca* spp.
	Araneida	Argiopidae	Pompilidae	Pompilinae	see Table 8
			Sphecidae	Sceliphroninae	*Sceliphron* and *Chalybion* spp.
			Crabronidae	Crabroninae	Some *Trypoxylon* spp.
		Clubionidae	Pompilidae	Pompilinae	see Table 8
			Pompilidae	Pepsinae	see Table 8
		Ctenizidae	Pompilidae	Ctenocerinae (Claveliinae)	see Table 8
		Gnaphosidae	Pompilidae	Pompilinae	see Table 8
		Lycosidae	Pompilidae	Pompilinae	see Table 8
			Pompilidae	Pepsinae	see Table 8
			Crabronidae	Crabroninae	Some *Trypoxylon* spp.
		Pisauridae	Pompilidae	Pompilinae	see Table 8
			Pompilidae	Pepsinae	see Table 8
			Crabronidae	Crabroninae	Some *Trypoxylon* spp.
		Salticidae	Pompilidae	Pompilinae	see Table 8
			Pompilidae	Pepsinae	see Table 8
			Crabronidae	Crabroninae	Some *Pison* spp.
		Sparassidae	Pompilidae	Pompilinae	see Table 8
			Pompilidae	Pepsinae	see Table 8
		Theraphosidae	Pompilidae	Pepsinae	see Table 8
		Theriidae	Pompilidae	Pepsinae	see Table 8
		Thomisidae	Pompilidae	Pompilinae	see Table 8
		Zodariidae	Sphecidae	Sceliphroninae	*Sceliphron* and *Chalybion* spp.
		Zoriidae	Pompilidae	Pompilinae	see Table 8
Blood suckers as adults	Diptera	Tabanidae	Crabronidae	Bembicinae	Some *Bembix* spp.
		Simuliidae	Crabronidae	Crabroninae	*Dasyproctus* spp. e.g. *D. westermanni*
Parasites of insects as larvae	Diptera	Bombyliidae	Crabronidae	Bembicinae	Some *Bembix* spp.
		Conopidae	Crabronidae	Bembicinae	Some *Bembix* spp.
		Tachinidae	Crabronidae	Bembicinae	Some *Bembix* spp.
	Hymenoptera	Bethylidae	Crabronidae	Philanthinae	Some *Cerceris* spp. (see Table 11)
		Pteromalidae	Crabronidae	Philanthinae	Some *Cerceris* spp. (see Table 11)
		Braconidae	Crabronidae	Philanthinae	Some *Cerceris* spp. (see Table 11)
		Mutillidae	Crabronidae	Philanthinae	Some *Cerceris* spp. (see Table 11)
Scavengers as larvae	Diptera	Calliphoridae	Crabronidae	Bembicinae	Some *Bembix* spp.
			Crabronidae	Philanthinae	Some *Cerceris* spp. (see Table 11)
		Stratiomyidae	Crabronidae	Bembicinae	Some *Bembix* spp.
		Muscidae	Crabronidae	Bembicinae	Some *Bembix* spp.
			Crabronidae	Crabroninae	All *Oxybelus* spp.



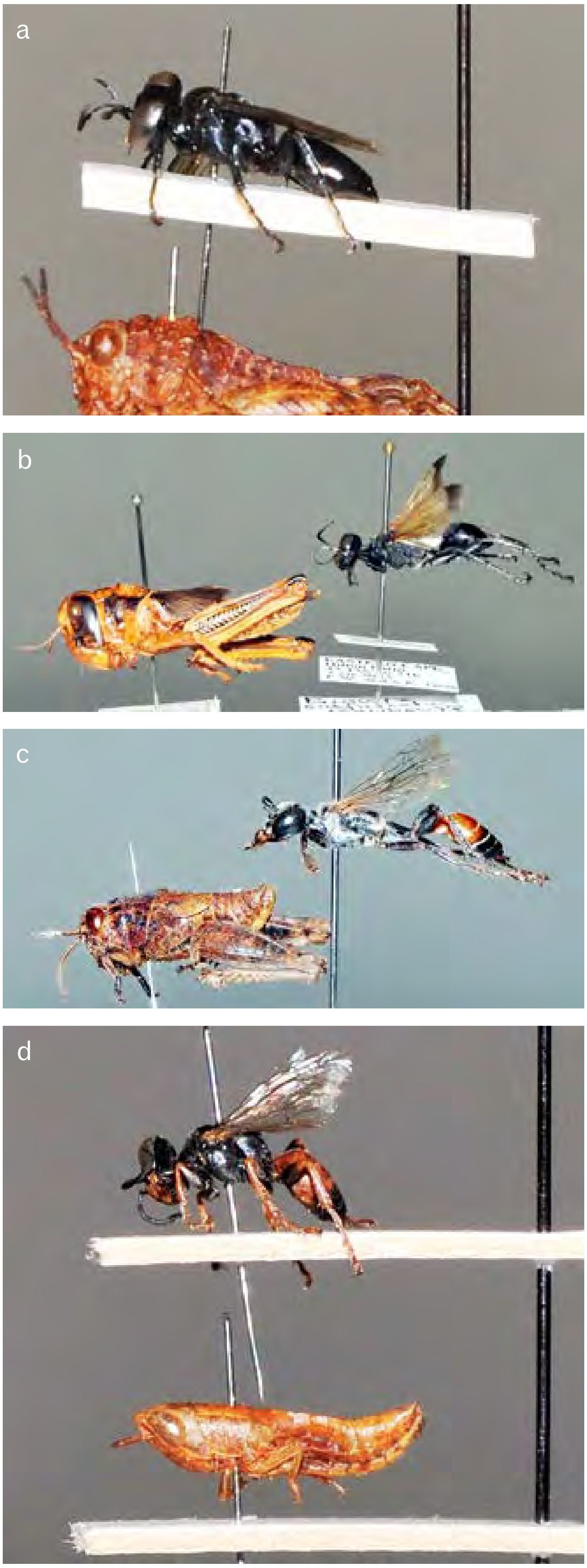


Figure I.3.40.—Orthoptera, Acrididae, examples: a. *Eneremius* sp. (nymph), prey of *Tachysphex vanrhynsi* Arnold (actual length of wasp 9.7 mm); b. *Locustana pardalina* (Walker), nymph, prey *Prionyx subfuscatus* (Dahlbom) (actual length of wasp 18.7 mm); c. nymph, prey of *Prionyx kirbii* (Vander Linden) (actual length of wasp 16.7 mm); d. nymph, prey of *Tachysphex pentheri* Cameron (actual length of wasp 7.5 mm).

Crickets are hunted by Rhopalosomatidae, Sphecidae and Crabronidae. However, being limited in the Sphecidae to the Chloriontinae and in the Crabronidae to the Larrini, species of *Liris*, *Larra*, some species of *Gastrosericus*, and the specialist *Kohliella alaris* Brauns which hunts only tree crickets, Oecanthinae (Gryllidae).

Figure I.3.41.—Orthoptera, Lentulidae, example: *Lentulus* sp., prey of *Stizus imperialis* Handlirsch; (actual length of wasp 20 mm).

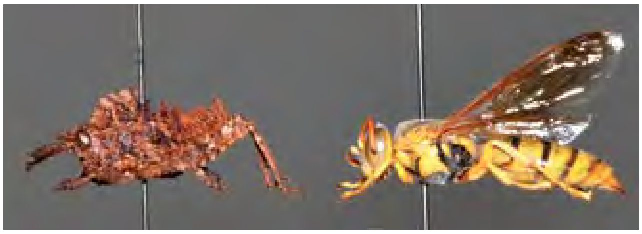


Figure I.3.42.—Orthoptera, Pamphagidae, example: *Hoplolopha* sp., prey of *Stizus imperialis* Handlirsch; (actual length of wasp 20 mm).

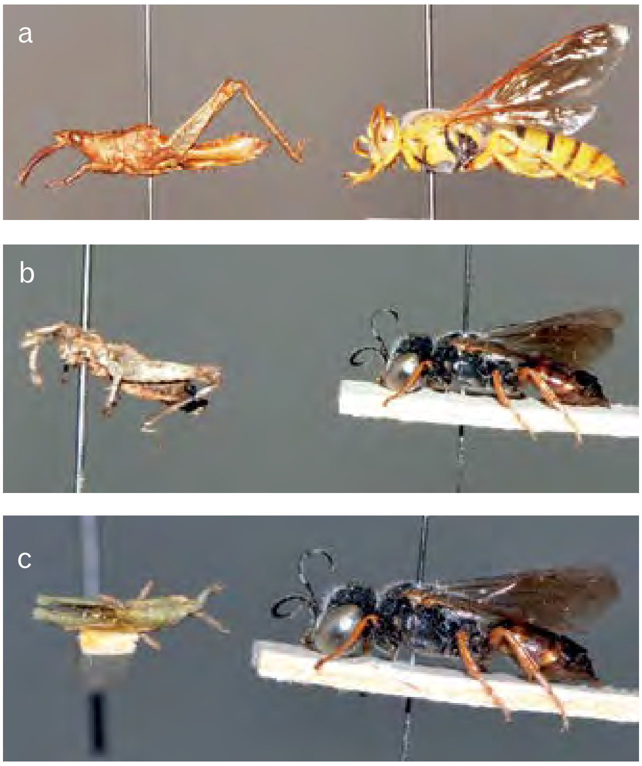


Figure I.3.43.—Orthoptera, Pyrgomorphidae, examples: a. *Pyrgomorpha* sp., prey of *Stizus imperialis* Handlirsch (actual length of wasp 10.8 mm); b. nymph, prey of *Holotachysphex turneri* (Arnold); c. nymph, prey of *Holotachysphex turneri* (Arnold).

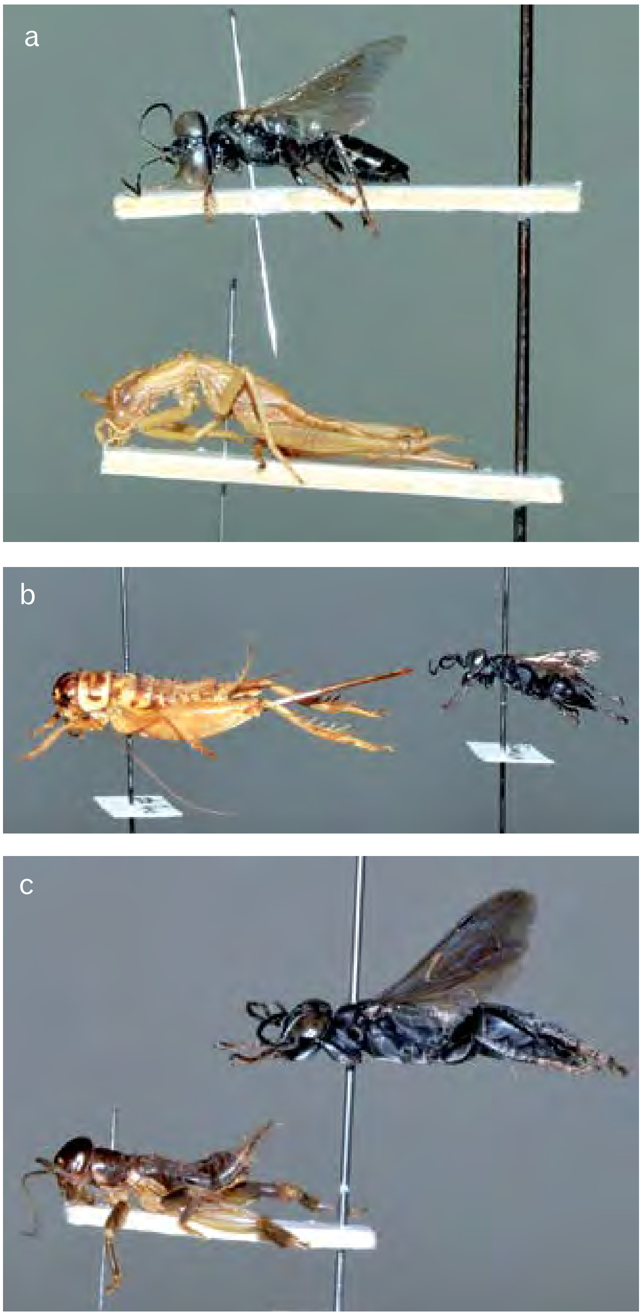


Figure I.3.44.—Orthoptera, Gryllidae, examples: a. Oecanthinae, *Oecanthus capensis* de Saussure (nymph), prey of *Kohliella alaris* Brauns (actual length of wasp 9.2 mm); b. Gryllinae, prey of *Liris* sp. (actual length of wasp 13 mm); c. Gryllinae nymph, prey of *Liris* sp. (actual length of wasp 16.3 mm).

Blattodea (examples Figure I.3.46)

All species of Ampulicidae specialise in hunting cockroaches (examples of prey transport Figures II.3.1.c. and II.2.a & b). Some species are known to specialise in a single species of cockroach. The most fully investigated is *Ampulex bantuae* Gess named for its prey *Bantua dispar* (Burmeister). Both cockroach and wasp are associated with *Acacia karroo.*

Some species of *Tachysphex* (Crabronidae, Crabroninae, Larrini) specialise in provisioning with cockroaches. Generally, though, species of this genus provision with grasshoppers and some with mantids.

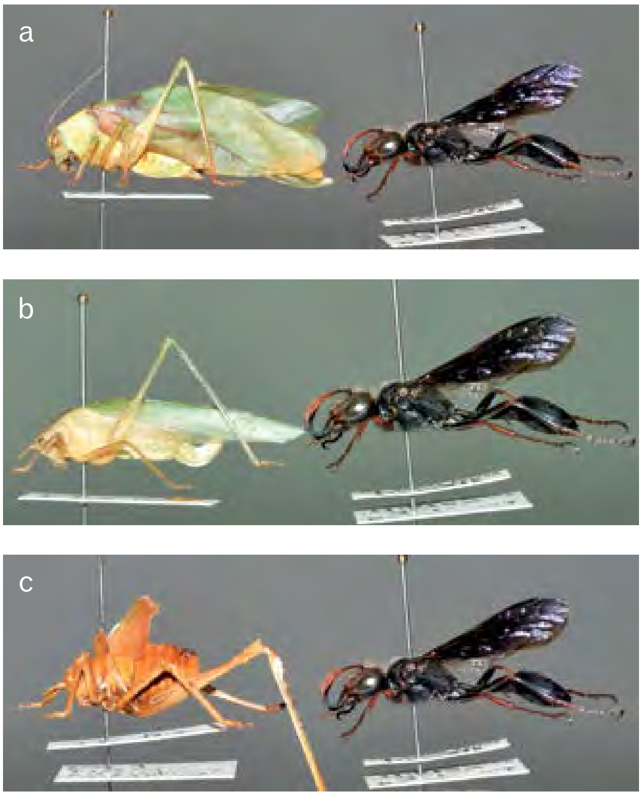


Figure I.3.45.—Orthoptera, Tettigoniidae, Phaneropterinae, examples: a. *Eucorypha prasinata* Stal, b. *Phaneroptera* sp. and c. *Terpnistria zebrata* (Serville) nymph, prey of *Isodontia pelopoeiformis* (Dahlbom) (actual length of wasp 26.7 mm).

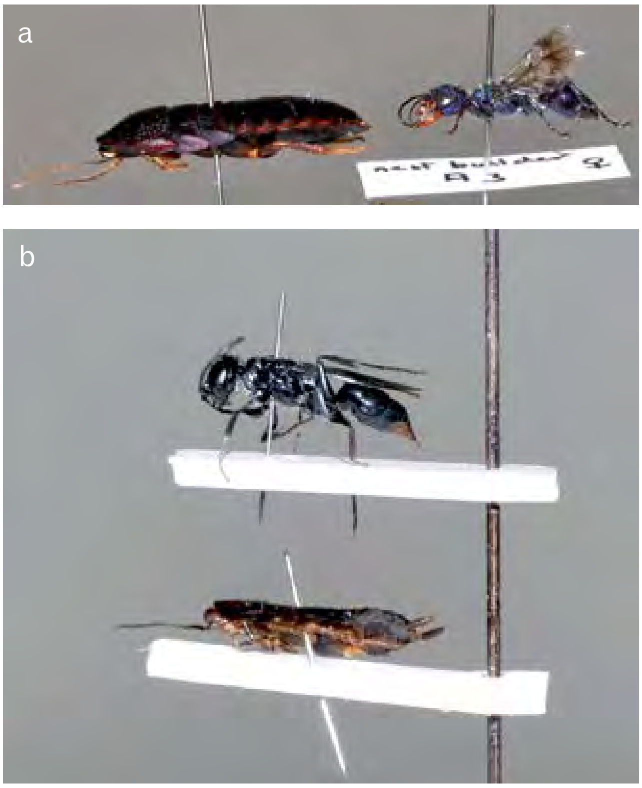


Figure I.3.46.—Blattodea, examples: a. cockroach *Bantua dispar* (Burmeister), prey of *Ampulex bantuae* Gess (actual length of wasp 13.8 mm); b. cockroach nymph, prey of *Dolichurus ignitus* Smith (actual length of wasp 8 mm).

Mantodea (example Figure I.3.47)

Mantids, themselves predators, are hunted by a minority of species of two Crabronidae genera. These are *Tachysphex* (Crabroninae, Larrini) and *Stizus* (Bembicinae).

Psocoptera

Booklice, Psocidae, are uncommonly taken as prey. However, they are the predominant prey of *Nitela* (Crabroninae, Larrini) (Figure I.3.48), which use large numbers of these very small insects to provision their larvae.

Hemiptera

Wasps that provision with bugs specialise in either Heteroptera or Homoptera.

Heteroptera

Heteroptera are less commonly hunted than Homoptera. However, several genera of Crabronidae prey upon these bugs. *Astata* and *Dryudella* (Astatinae) take nymphal heteropterans and at least some species of *Prosopigastra* (Crabroninae, Larrini) are known to provision with heteropterans. For southern Africa, Arnold (1922) investigated the nests of *P. creon* Nurse (as *P. neavei* Turner) and found the provision to be Pentatomidae.

Dasyproctus (Crabronidae, Crabroninae) species as a general rule hunt flies although we found that *D. westermanni* Dahlbom, which usually provisions with flies, occasionally included Miridae in its provision on the farm Hilton.

Homoptera (examples Figures I.3.49–51)

Four families of Homoptera are known to be hunted by Crabronidae in southern Africa.

These are divided between *Hoplisoides*, *Bembecinus* and *Gorytes* (all Bembicinae). *Bembecinus* specialises in hunting small species of the families Cicadellidae, Membracidae and Fulgoridae. Up to 40 individuals are required to make up the provision for a single cell. As some nesting aggregations are several thousand strong and most nests are two-celled, the number of bugs taken must be considerable.

Figure I.3.47.—Mantodea, example: Immature mantid, prey of *Tachysphex albocinctus* (Lucas) (actual length of wasp 12.5 mm).

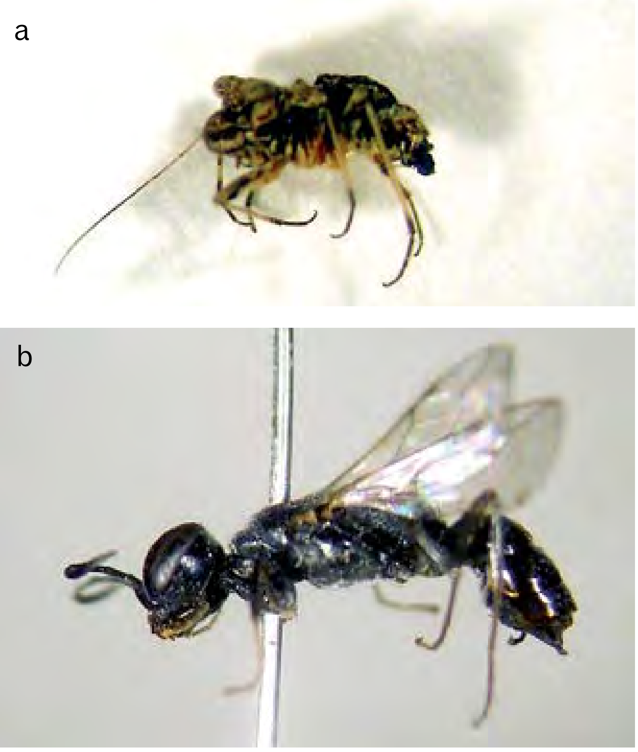


Figure I.3.48.—Psocoptera, example: a. psocid prey of *Nitela ? braunsi* Arnold; b. *Nitela ? braunsi* Arnold., builder of nest from which prey was taken (actual length 5 mm).

Figure I.3.49.—Hemiptera, Cercopidae, example: *Ptyelus grossus* Fabricius prey of *Gorytes natalensis* (Smith) (actual length of wasp 21 mm).

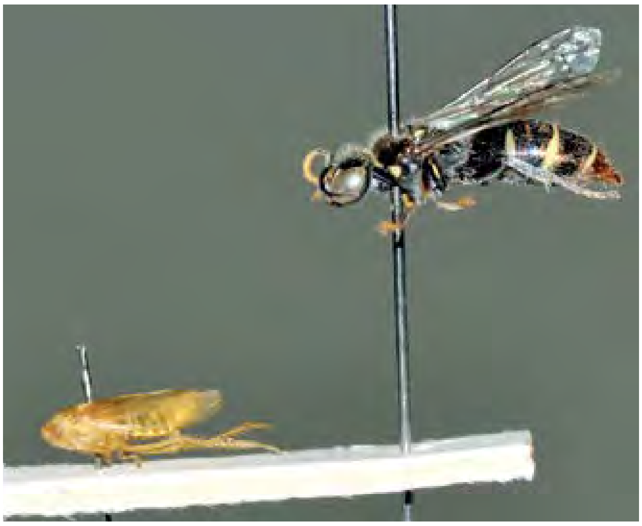


Figure I.3.50.—Hemiptera, Cicadellidae, example: prey of *Bembecinus haemorrhoidalis* (Handlirsch) (actual length of wasp 9.5 mm).

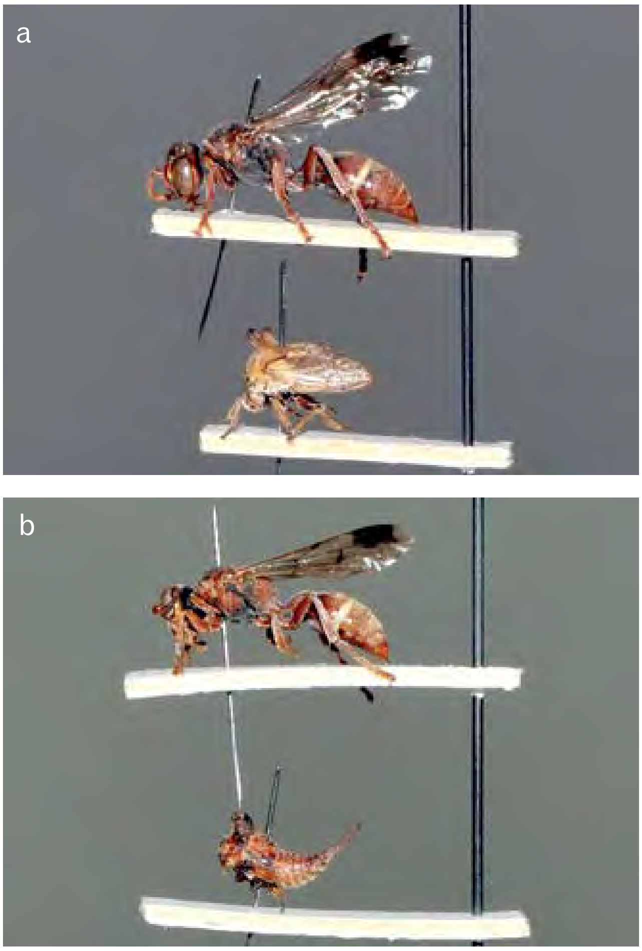


Figure I.3.51.—Hemiptera, Membracidae, example: a. and b. *Beaufortiana cornuta* Distant, a. adult; b. nymph, prey of *Hoplisoides aglaia* (Handlirsch) (actual length of wasps a. 12.0 mm, b. 10.7 mm).

Larger plant sucking bugs of the family Cercopidae are taken by *Gorytes* species (Crabronidae, Bembicinae), at least some of which appear to be specialists. *Gorytes natalensis* (Smith) and *G. effugiens* (Brauns) investigated by us in Grahamstown where they were nesting together took only *Ptyelus grossus* Fabricius and *Poophilus cf. costalis* Walker respectively.

Hoplisoides aglaia (Handlirsch) on the farm Hilton, provisions with Membracidae.

Diodontus (Crabronidae, Pemphredoninae) prey have not been recorded in southern Africa, but elsewhere they are known to provision with aphids.

Cicadas have not been recorded as prey in southern Africa. They are, however, hunted by species of *Sphecius* (Crabronidae, Bembicinae) in North America (Evans & O'Neill 2007). No prey have been recorded for the two species of *Sphecius* represented in southern Africa.

Coleoptera (examples Figures I.3.53–57)

Beetles are hunted in their larval stage by Scoliidae, Tiphiidae. The larvae of Lepidoptera are hunted by some Eumeninae. Most scoliids and tiphiids hunt Scarabaeidae although some species of the former hunt Curculionidae and some species of the latter hunt Cicindelidae.

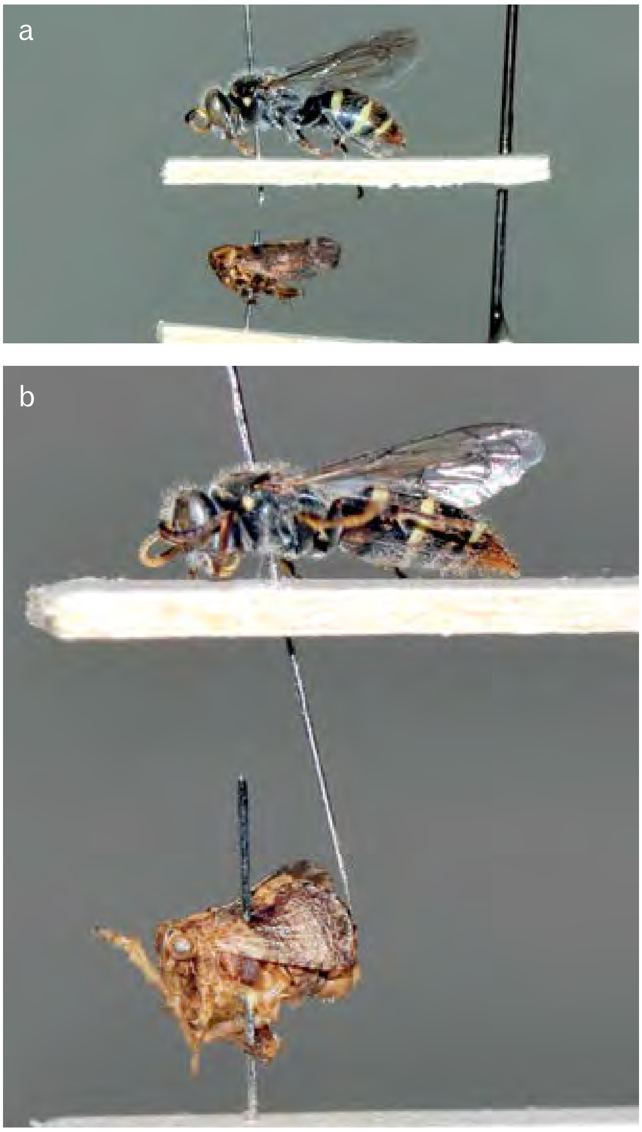


Figure I.3.52.—Hemiptera, Fulgoridae, example: a. and b. prey of *Bembecinus haemorrhoidalis* (Handlirsch) (actual length of wasp 7.9 mm).

Occasionally the larvae of Chrysomelidae were found mixed with the larvae of Lepidoptera (the more usual prey) in nests of *Tricarinodynerus guerinii* (Saussure) (Eumeninae) on the farm Hilton. A nest of *Raphiglossa natalensis* Smith from Namaqualand was found to be provisioned with beetle larvae (Figure II.2.50).

Adult beetles are one of the two specialisations of *Cerceris* (Crabronidae, Philanthinae). A wide range of beetle families is hunted—Curculionidae, Scarabaeidae, Tenebrionidae, Buprestidae, Phalacridae and Chrysomelidae—by the genus as a whole but all species show specialisation.

Hymenoptera (examples Figures I.3.58–66)

Hunting aculeate Hymenoptera is largely restricted to the Philanthinae (Crabronidae). *Philanthus* specialises in provisioning with bees and wasps and those species of *Cerceris* that do not provision with beetles take a wide range of aculeates. For example, *C. holconota* Cameron has been found to take aculeate wasps of the families Bethylidae,

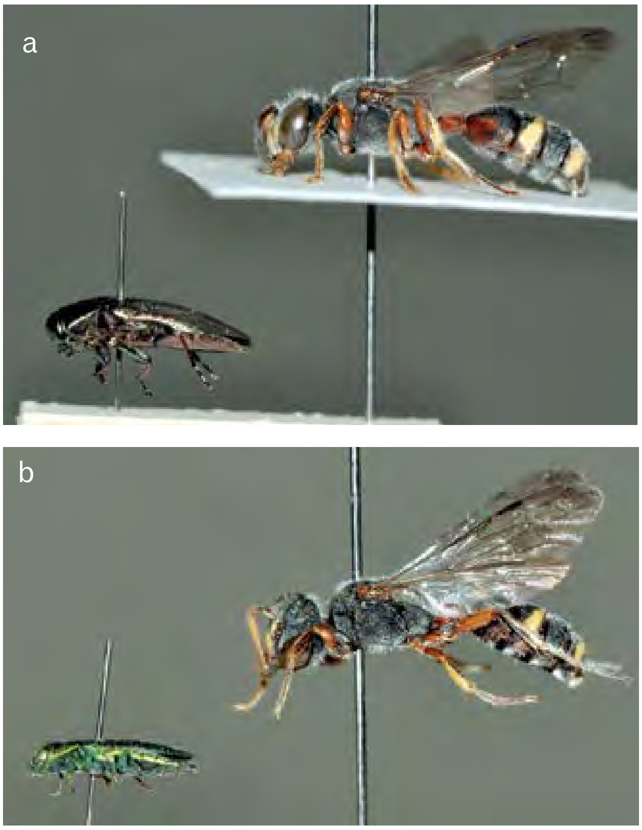


Figure I.3.53.—Coleoptera, Buprestidae, examples: a. *Chrysobothris dorsata* Fabricius, prey of *Cerceris nigrifrons nigrifrons* Smith (actual length of wasp 12.7 mm); b. *Anthaxia sexualis* Obern., prey of *Cerceris nigrifrons nigrifrons* Smith (actual length of wasp 11.5 mm).

Figure I.3.54.—Coleoptera, Chrysomelidae, example: Criocerinae, prey of *Cerceris ruficauda ruficauda* Cameron (actual length of wasp 9.2 mm).

Tiphiidae and Mutillidae, bees of the family Halictidae and Parasitica of the family Braconidae. *Palarus* (Crabronidae, Bembicinae, Palarini) species are known to take Tiphiidae, Scoliidae, Vespidae (Masarinae) and honeybees (Apidae).

In southern Africa, *Philanthus* species appear to specialise in taking bees, most commonly honeybees although some species also take other bees—Halictidae, for example, having been recorded. The most widespread and familiar species is *Philanthus triangulum* (Fabricius), commonly known as the bee pirate by apiarists. North American species of *Philanthus* often include a substantial number of wasps among their prey (Evans and O'Neill 1988).

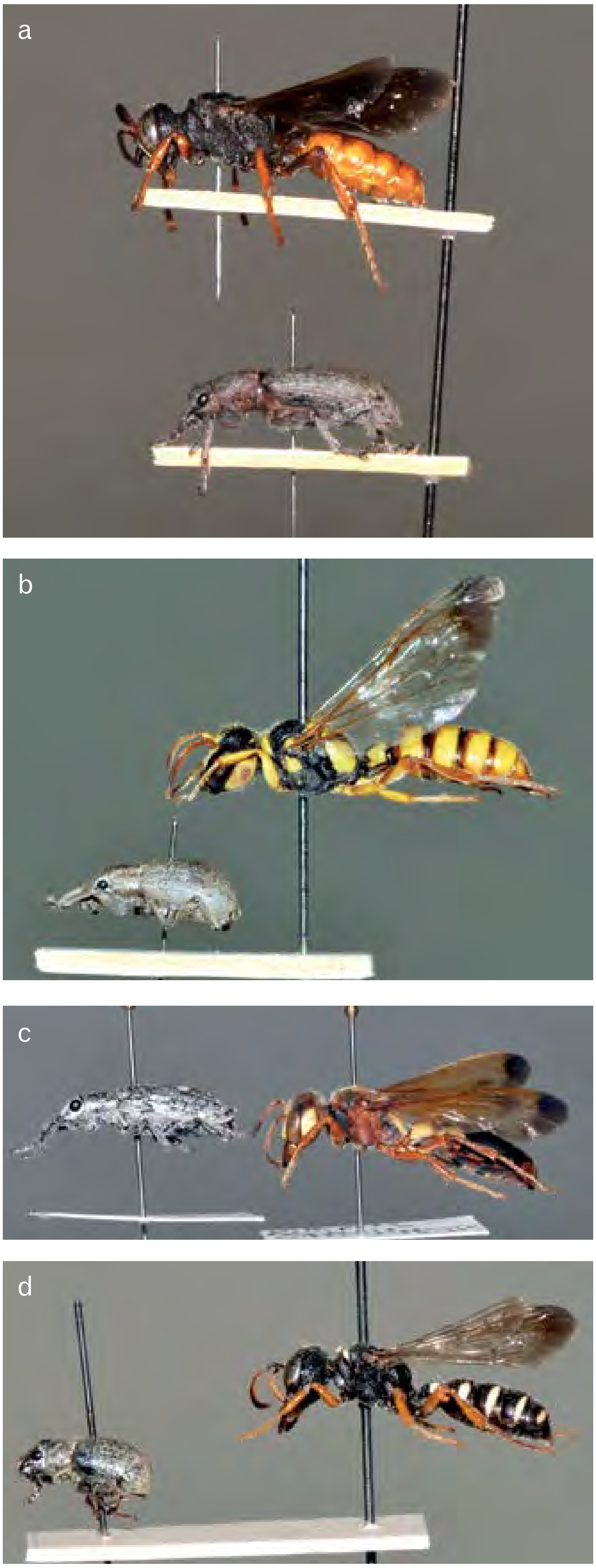


Figure I.3.55.—Coleoptera, Curculionidae, examples: a. *Tanymecus trivialis* Fahraeus, prey of *Cerceris erythrosoma* Schletterer (actual length of wasp 14.3 mm); b. *Protostrophus* sp., prey of *Cerceris oraniensis* Brauns (actual length of wasp 15 mm); c. *Polyclaeis castaneipennis* Hust., prey of *Cerceris multiplicata fuscifacies* Empey (actual length of wasp 24.5 mm); d. *Leurops sublineata* Marshall, prey of *Cerceris bothavillensis* Brauns (actual length of wasp 10.8 mm).

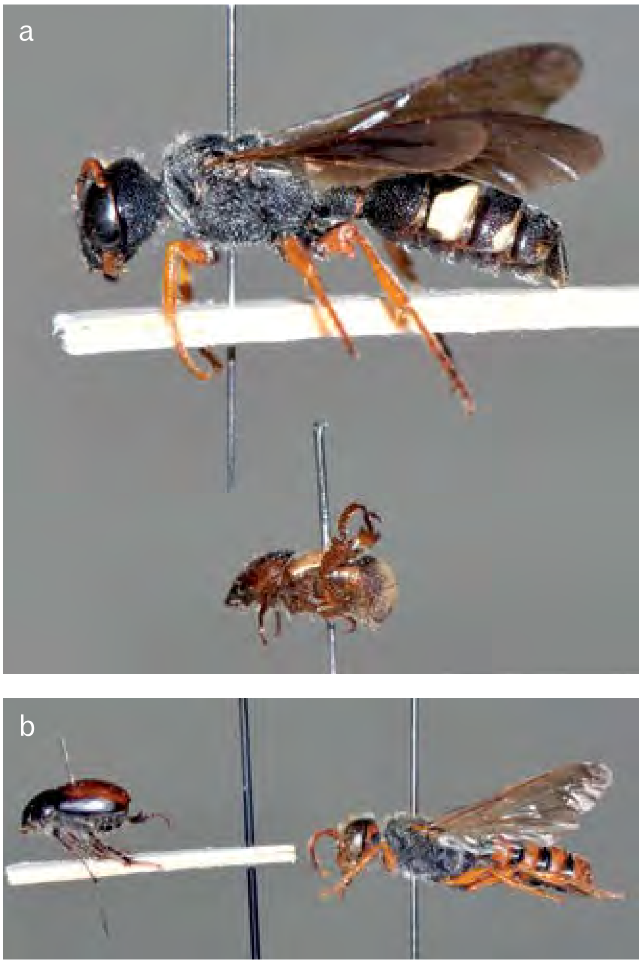


Figure I.3.56.—Coleoptera, Scarabaeidae, Melolonthinae, examples: a. Hopliini, prey of *Cerceris latifrons* Bingham (actual length of wasp 14.8 mm); b. Sericini, *Aldabera splendida* (Fabricius), prey of *Cerceris nasidens obscura* Schletterer (actual length of wasp 16.2 mm).

Figure I.3.57.—Coleoptera, Tenebrionidae, example: *Zophosis* sp., prey of *Cerceris curvitarsis* Schletterer (actual length of wasp 17.3 mm).

Figure I.3.58.—Hymenoptera, Braconidae, example: prey of *Cerceris holconota holconota* Cameron (actual length of wasp 10.8 mm).

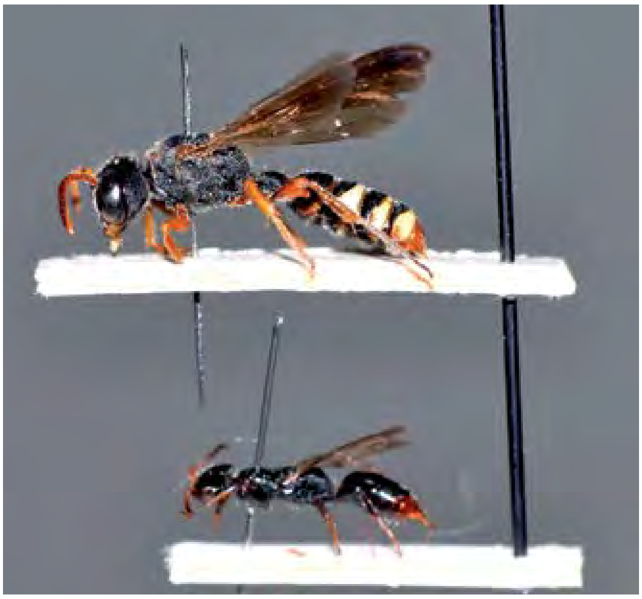
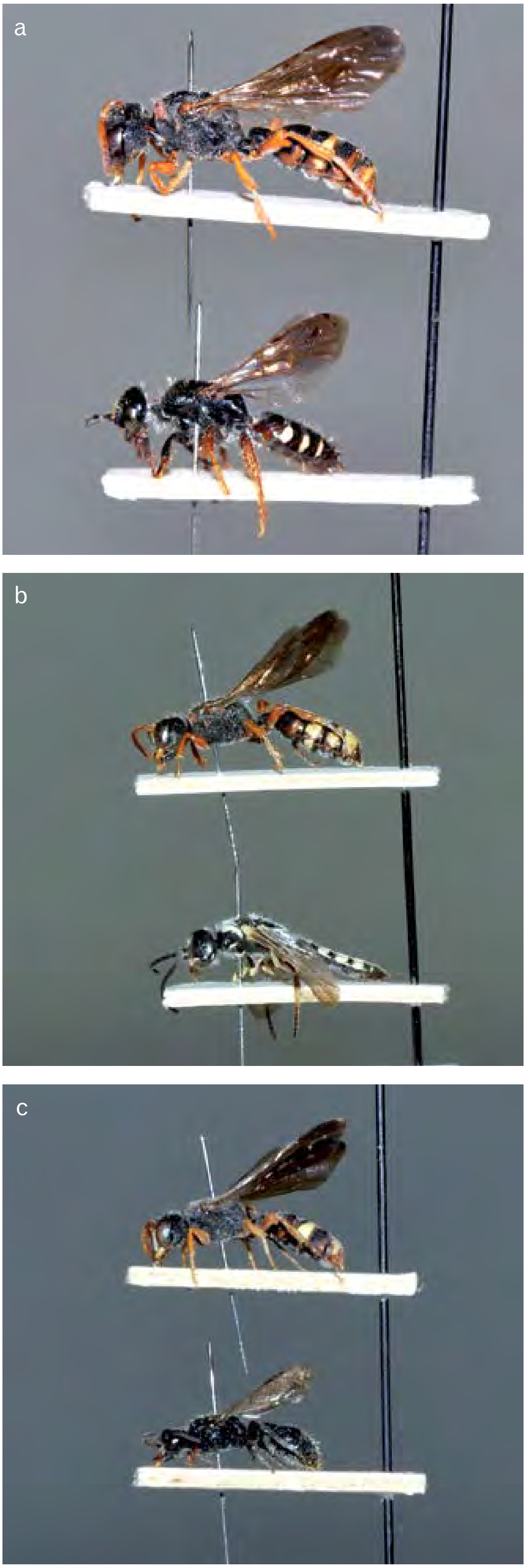


Figure I.3.59.—Hymenoptera, Chrysidoidea, Bethylidae, example: prey of *Cerceris rufocincta polychroma* Gribodo (actual length of *C. r. p.* 11.5 mm).

Hunting of ants (Formicidae), although an abundant resource, is unusual. *Encopognathus* (Crabronidae, Crabroninae, Crabronini) is known to prey on ants of the genus *Tetramorium* and *Cerceris holconota* includes winged male ants in its mix of hymenopterous prey.

Diptera (examples Figure I.3.67–78)

At least 20 families of flies are hunted by wasps, all Crabronidae. Flies are the specialisation of the *Oxybelini* and *Dasyproctus* (Crabroninae) and most of the species of *Bembix* (Bembicinae) (examples of prey transport Figure II.3.26.a–d). None seems to specialise in taking a single family of flies, all taking whatever is available. For example, we recorded that *Dasyproctus westermanni* Dahlbom nesting on the farm Hilton was provisioning with a mix of Simuliidae (black flies), Stratiomyidae (soldier flies), Tabanidae (horse flies), Bombyliidae (bee flies), Empidi-



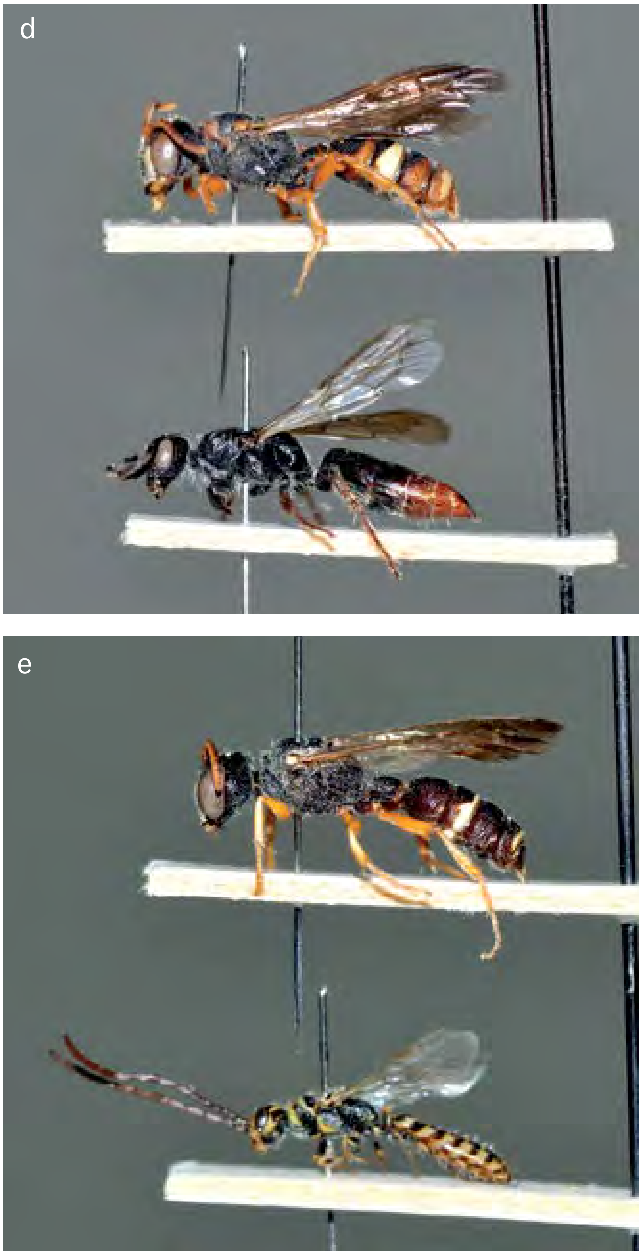


Figure I.3.60.—Hymenoptera, Vespoidea, Tiphiidae, examples: a. *Anthobosca* sp. female, prey of *Cerceris rufocincta polychroma* Gribodo (actual length of *C. r. p.* 12.5 mm); b. *Anthobosca* sp. male, prey of *Cerceris rufocincta polychroma* Gribodo (actual length of *C. r. p.* 11.7 mm); c. *Tiphia* sp. female, prey of *Cerceris rufocincta polychroma* Gribodo (actual length of *C. r. p.* 11.2 mm); d. *Mesa incisa* (Cameron) female, prey of *Cerceris rufocincta polychroma* Gribodo (actual length of *C. r. p.* 11.3 mm); e. *Braunsomeria* sp. male prey of *Cerceris holconota holconota* Cameron (actual length of *C. h. h.* 10.5 mm).

dae (dance flies), Syrphidae (hover flies), Otitidae (picture wing flies) and Chaemyiidae. Similarly, *Bembix albofasciata* Smith takes a mix of Stratiomyidae, Tabanidae, Bombyliidae, Asilidae (robber flies), Conopidae (thick headed flies), Muscidae (the house fly family) and Tachinidae. The limiting factor seems to be suitability of size for transport in flight. Many prey are taken to provision a single cell allowing for prey of varying sizes to be taken. Whereas the *Oxybelini* and *Dasyproctus* are small and are restricted to taking relatively small flies, *Bembix*, though favouring

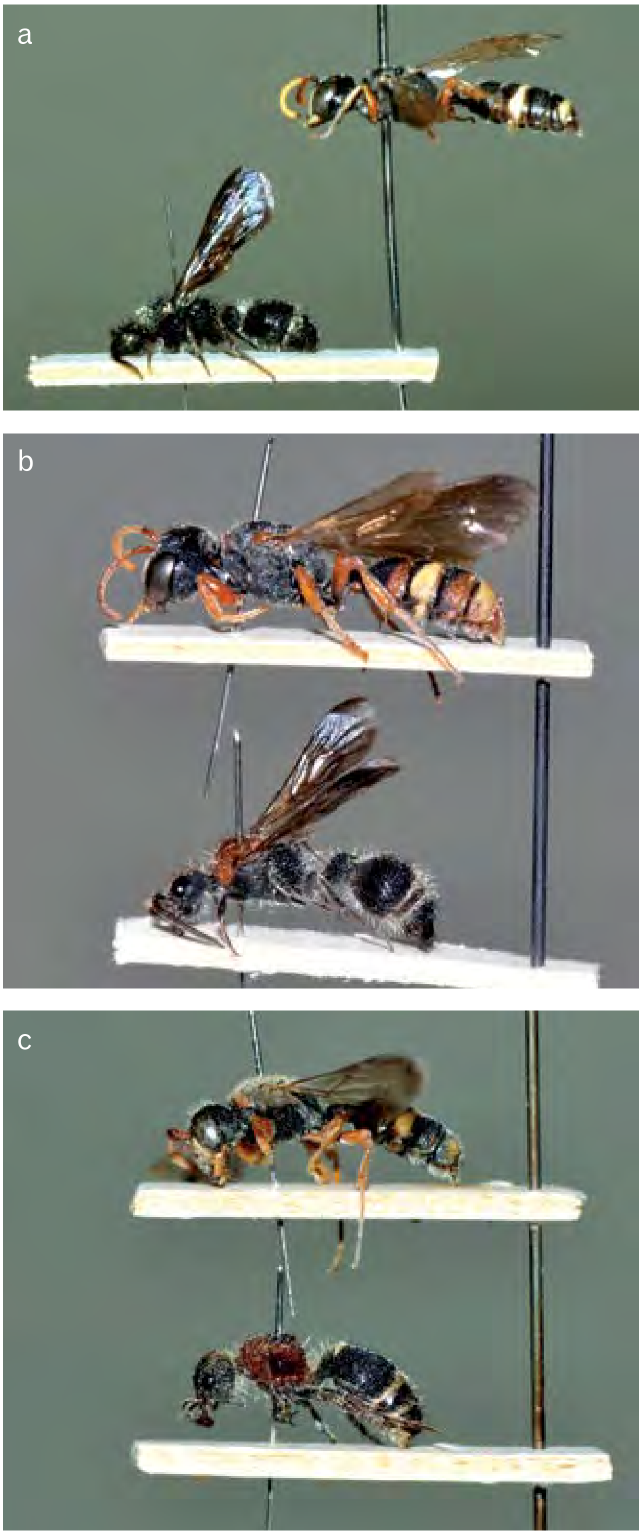


Figure I.3.61.—Hymenoptera, Vespoidea, Mutillidae, examples: a. *Dasylabris* sp. male, prey of *Cerceris holconota holconota* Cameron (actual length of *C. h. h.* 12.3 mm); b. *Dasylabroides caffra* (Kohl) male, prey of *Cerceris rufocincta polychroma* Gribodo (actual length of *C. r. p.* 13 mm); c. *Dasylabroides* sp. female, prey of *Cerceris rufocincta polychroma* Gribodo (actual length of *C. r. p.* 11.3 mm); d. *Psammotherma flabellata* (Fabricius) male, prey of *Cerceris rufocincta polychroma* Gribodo (actual length of *C. r. p.* 12.7 mm).

Figure I.3.62.—Hymenoptera, Vespoidea, Formicidae, example: male ant, prey of *Cerceris holconota holconota* Cameron (actual length of *C. h. h.* 9.3 mm).

medium sized flies, when these are not available takes relatively small flies. *Bembix* most commonly takes Calliphoridae, however, Bombyliidae and Syrphidae are common prey and Asilidae are also taken by some species.

Lepidoptera

Moth larvae are hunted by all species of Ammophilinae (Sphecidae) and Eumeninae (Vespidae) (examples Figures II.2.41.b–d., 44) and are the favoured prey of Polistinae (Vespidae).

The Ammophilinae *Podalonia* and *Ammophila* favour Noctuidae (examples Figures II.3.4.a and b., II.3.6 b and c. and 3.7.b–d) although some species of *Ammophila* take Geometridae (example Figure II.3.7.a), Pyralididae, Lycaenidae, Arctiidae (example Figure I.3.6.a) and Lasiocampidae.

The only account for southern Africa of a wasp hunting adult Lepidoptera is that of Benson (1934) for *Bembix regnata* Parker (Crabronidae, Bembicinae) which provisioned with butterflies of which three families were recorded.

Figure I.3.63.—Hymenoptera, Apoidea, Spheciformes, Crabronidae, example: *Bembecinus cinguliger* (Smith), prey of *Palarus oneili* Brauns (actual length of *P. o.* 14.1 mm).

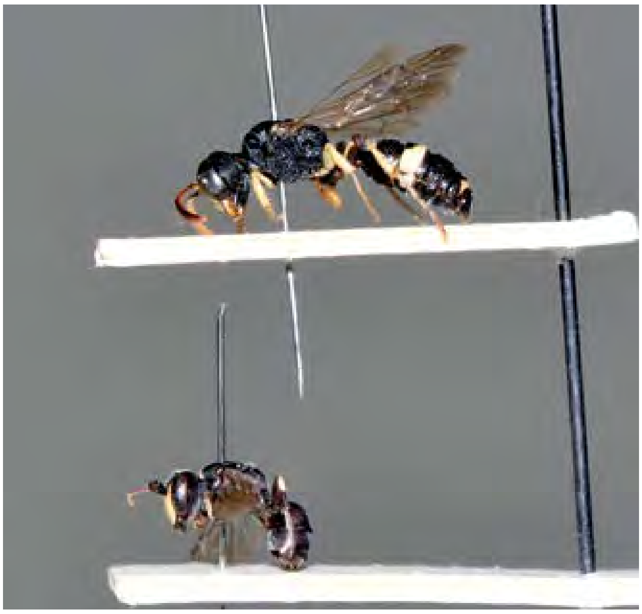


Figure I.3.64.—Hymenoptera, Apoidea, Apiformes, Colletidae, examples: a. *Hylaeus* sp. male, prey of *Cerceris spinicaudata* Cameron (actual length of wasp 8.8 mm).

Odonata

There are no records of Odonata being hunted in southern Africa, however, damselflies are taken by a species of *Bembix* (Crabronidae, Bembicinae) in Australia (Evans & Matthews 1975).

Neuroptera

There are no records of Neuroptera being hunted in southern Africa. However, antlions are taken by one species of *Bembix* (Crabronidae, Bembicinae) in Australia (Evans & Matthews 1975) and another *Bembix* preys on lacewings in North America (Evans 1978).

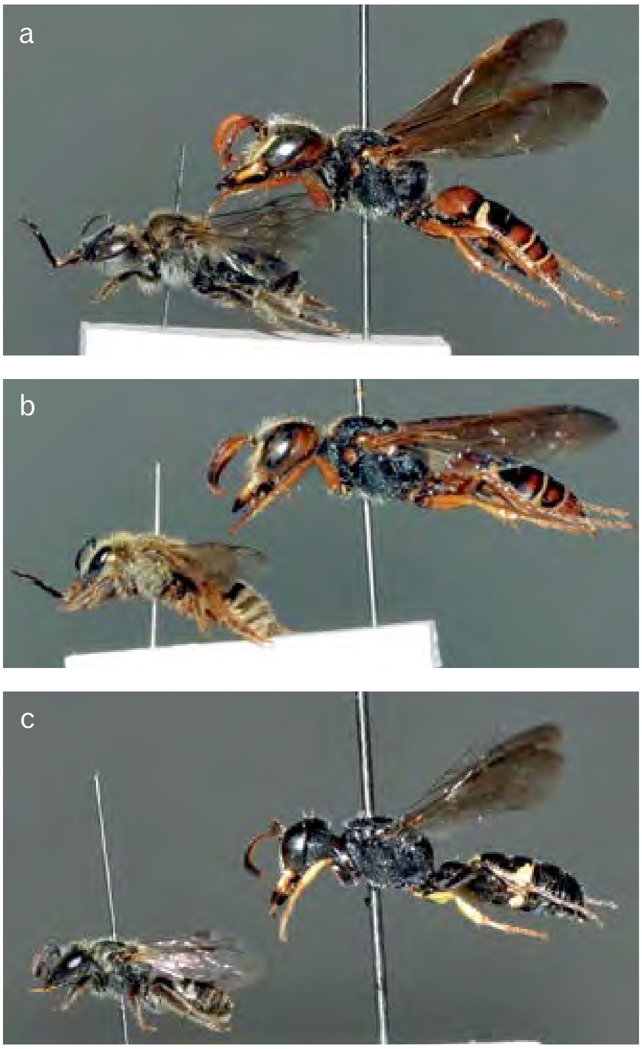


Figure I.3.65.—Hymenoptera, Apoidea, Apiformes, Halictidae, examples: a. and b. *Halictus* spp., prey of *Philanthus histrio* Fabricius (actual length of wasps 14.7 mm); c. *Halictus* sp., prey of *Cerceris spinicaudata* (Cameron) (actual size of wasp 9.8 mm).

Arachnida

Wasps prey upon at least 11 families of spiders. All Pompilidae hunt spiders, all supplying a single suitably sized spider per nest cell, sufficient provision for a single larva (examples Figures II.2.59, 60, 61, 63, 66, 68, 69 and 73). Considerable specialisation, at least at family level, requiring differing hunting techniques, is clear.

Other wasps that hunt spiders are the Sceliphroninae (Sphecidae) and Trypoxylini (Crabronidae, Crabroninae). All species in these taxa provision their cells with a number of spiders, each relatively small compared to the size of the wasp (examples Figures II.3.18.b. and II.3.21.c). In the Sceliphroninae, *Sceliphron* and *Chalybion* (*Chalybion*) take a mix of families, mostly including Argiopidae, but also Theriidae and Zodariidae. *Chalybion* (*Hemichalybion*) *spinolae* (Lepeletier) seems to specialise in Theriidae of the genus *Latrodectus* (Figure II.3.20.d).

A single individual of *Trypoxylon* may take spiders from several different families (Figure II.3.36.b). For example we have recorded Lycosidae, Pisauridae and Araneidae from a single nest.

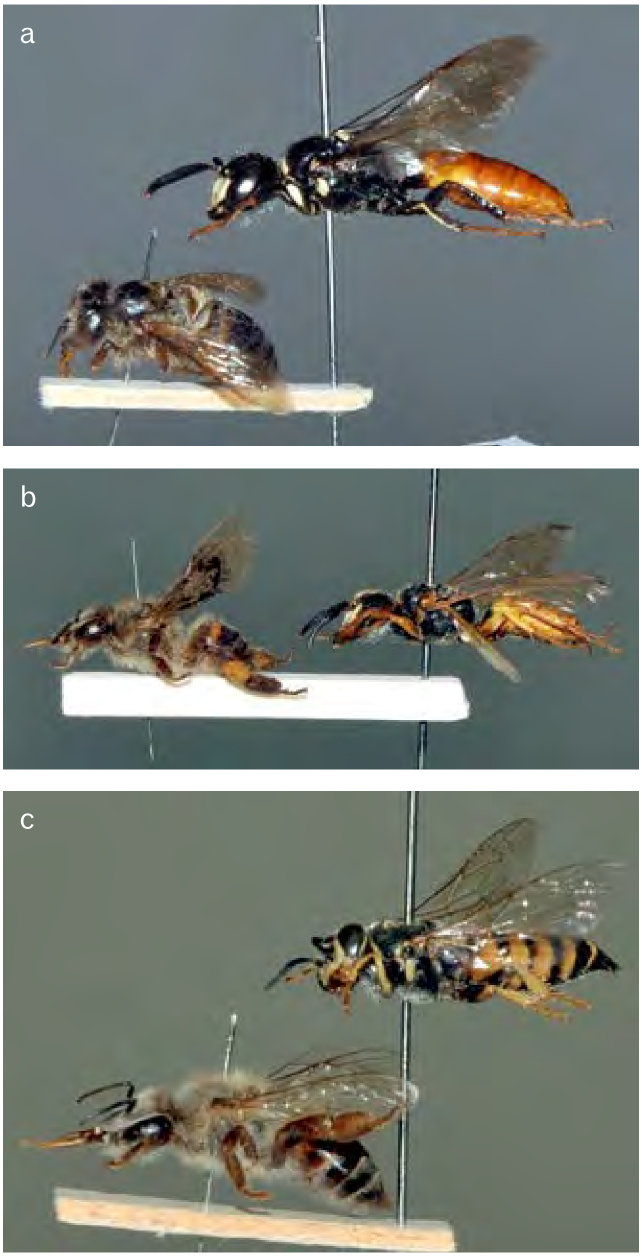


Figure I.3.66.—Hymenoptera, Apoidea, Apiformes, Apidae, examples: a. *Apis mellifera* L., prey of *Philanthus loefflingi* Dahlbom (actual length of wasp 19.0 mm); b. *Apis mellifera* L., prey of *Philanthus triangulum* Fabricius (actual length of wasp 15.7 mm); c. *Apis mellifera* L., prey of *Palarus latifrons* Kohl (actual length of wasp 14.2 mm).

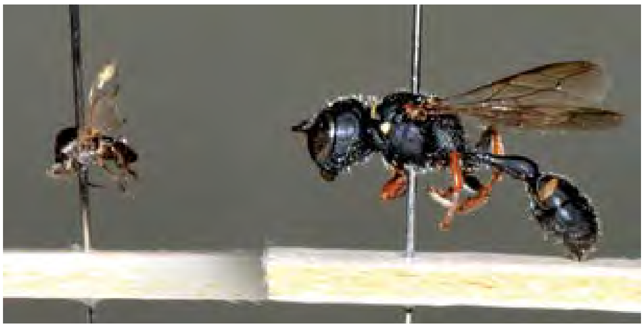


Figure I.3.67.—Diptera, Simuliidae, example: *Simulium adersi* Pom., prey of *Dasyproctus westermanni* (Dahlbom) (actual length of wasp 8 mm).

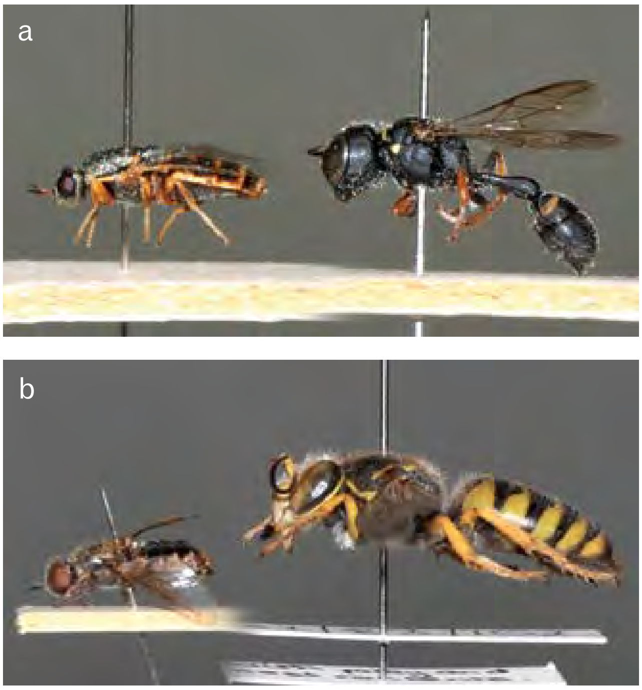


Figure I.3.68.—Diptera, Stratiomyidae, examples: a. stratiomyid, prey of *Dasyproctus westermanni* (Dahlbom) (actual length of wasp 8 mm); b. stratiomyid, prey of *Bembix albofasciata* Smith (actual length of wasp 19.7 mm).

Figure I.3.69.—Diptera, Tabanidae, example: *Philoliche (Phara) flavipes* Macq., prey of *Bembix melanopa* Handlirsch (actual length of wasp 16.7 mm).

Figure I.3.70.—Diptera, Asilidae, example: *Neolophonotus* group, prey of *Bembix albofasciata* Smith (actual length of wasp 19.7 mm).

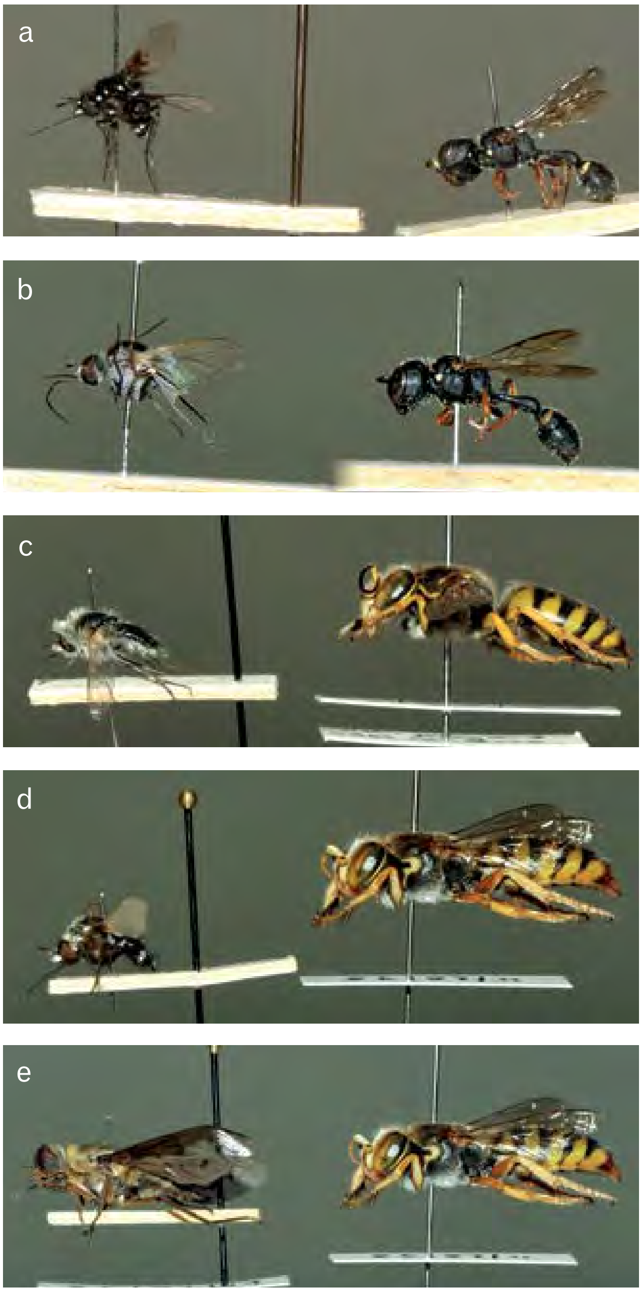


Figure I.3.71.—Diptera, Bombyliidae, examples: a. *Bombylius delicatus* (Wied.) and b. bombyliid, both prey of *Dasyproctus westermanni* (Dahlbom) (actual length of wasp 8 mm); c. *Geron* sp. prey of *Bembix albofasciata* Smith (actual length of wasp 19.7 mm); d. *Bombylius ornatus* Weid. and e. *Exoprosopa* sp., both prey of *Bembix bubalus* Handlirsch (actual length of wasp 23 mm).

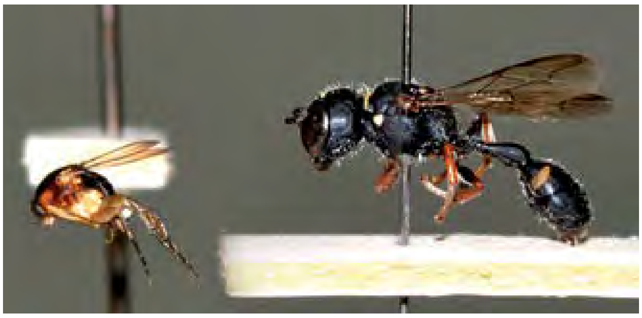


Figure I.3.72.—Phoridae, example: prey of *Dasyproctus westermanni* (Dahlbom) (actual length of wasp 8 mm).

Figure I.3.73.—Diptera, Syrphidae, examples: a. *Eristalis tenax* (L.) and b. *Allograpta calopus* (Loew), both prey of *Bembix bubalus* Handlirsch (actual length of wasps 20.2 mm and 23.0 mm).

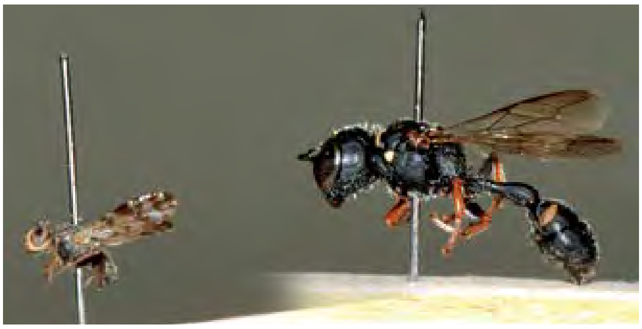


Figure I.3.74.—Diptera, Otitidae, example: prey of *Dasyproctus westermanni* (Dahlbom) (actual length of wasp 8 mm).

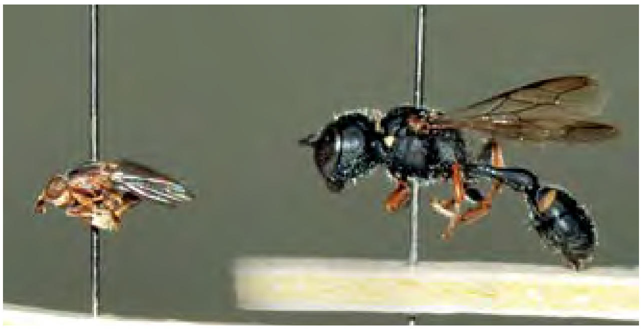


Figure I.3. 75.—Chamaemyiidae, example: prey of *Dasyproctus westermanni* (Dahlbom) (actual length of wasp 8 mm).

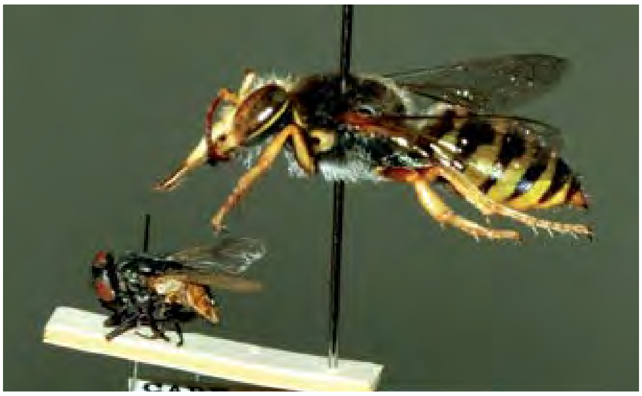


Figure I.3.76.—Diptera, Muscidae, example: prey of *Bembix bubalus* Handlirsch (actual length of wasp 21.8 mm).

Figure I.3.77.—Diptera, Calliphoridae, example: prey of *Bembix albofasciata* Smith (actual length of wasp 19.7 mm).

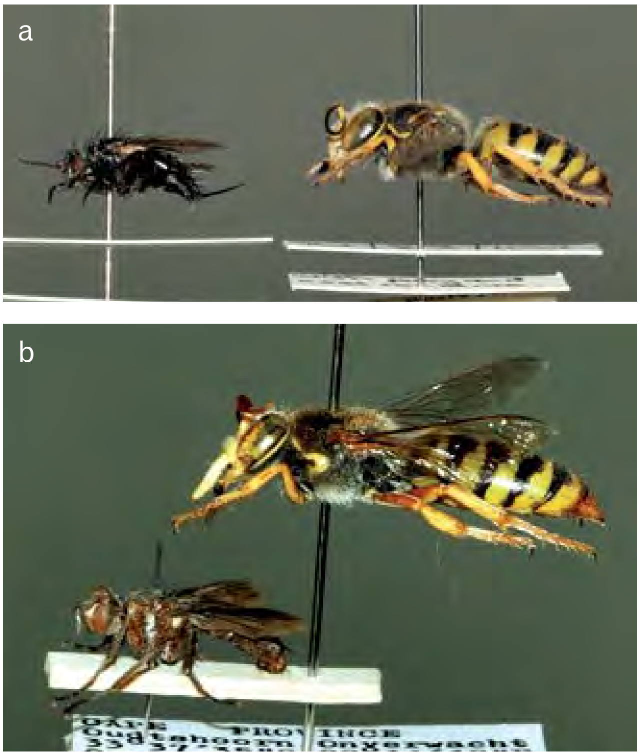


Figure I.3.78.—Diptera, Tachinidae, examples: a. prey of *Bembix albofasciata* Smith (actual length of wasp 19.7 mm); b. prey of *Bembix bubalus* Handlirsch (actual length of wasp 21.7 mm).

‘Parasitic’ wasps

‘Parasitic’ aculeate wasps do not hunt prey to provide provision for their larvae. This category includes Chrysididae, Mutillidae and Ceropalinae (Pompilidae).

The majority of Chrysididae, the Chrysidinae or cuckoo wasps, lay their eggs into the cells of wasps and bees, showing considerable specialisation in their choice of hosts. Most species of *Praestochrysis* are unusual for chrysidines, laying their eggs on resting caterpillars, within their cocoons, of moths of the family Limacodidae. No hosts have been established for the wingless Amiseginae in southern Africa, although it seems likely that these, like the American and Australian species, develop in the eggs of stick insects (Kimsey & Bohart 1990).

Similarly, the majority of Mutillidae, velvet ants, rear their young at the expense of other wasps and bees. They feed on the mature larva or pupa within the host’s nest cell. Those species not ‘parasitising’ aculeates feed on the mature larvae or pupae of flies, beetles or moths.

Amongst the Pompilidae, the Ceropalinae oviposit onto the spider prey of other pompilids. The egg hatches before that of the host, which it kills before feeding on the spider.

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4. Nesting and community structure

A nest is defined as a place or structure in which insects, birds, fishes etc. lay eggs or give birth to young (Anderson *et al*. 2005). Most solitary wasps and bees use a nest entirely or partially constructed by a single female. Relatively few species of wasps and bees construct nests co-operatively. Such species are termed pre-social or social, depending upon the degree of labour sharing. The minority neither constructs nor modifies the shelter that constitutes the nest. These can be divided into two categories:

- Species that, having paralysed the prey and laid an egg on it, leave it within the prey's own burrow. Only some wasp species fall in this category.
- Species that lay an egg in the nest of another and depend upon the host to supply the larval provision. Both wasps and bees fall in this cuckoo-like category.

Constructed nests range from the simplest of shelters to elaborate structures constructed from materials that have been fashioned into 'building bricks'. They may be constructed entirely by the nester or may be a pre-existing cavity modified by the nester.

Nesting behaviour of wasps and bees consists of three major elements: nest building, provisioning and oviposition. These major elements are divisible into sub-elements. Differences in nesting behaviour are brought about by the number of and nature of the sub-elements performed and the sequence of the performance of these sub-elements.

Nest constructed entirely by the nester

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

- Hunting and paralysis of the prey (by stinging).
- Transportation of the prey.
- Excavation of an entrance burrow.
- Excavation of a cell.
- Placement of the prey in cell.
- Oviposition.
- Closing of cell.
- Closing of burrow.

Clearly, this type of nest is restricted to sandy or loose friable soil allowing for rapid excavation.

This basic ethological type is characterised by the fact that hunting precedes nest excavation. There is never any repetition of a behavioural element within a single sequence. Therefore, it follows that not only is a cell provisioned with 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 the excavation of a new nest follows capture of a further prey by the wasp. Clearly there are no pollen wasps and bees in this category.

More specialised nesting is found amongst species that prepare a nest before hunting for prey or collecting pollen and nectar. The change in order of these two elements allows for provisioning cells without the danger of the prey being stolen or parasitised during nest excavation and for provisioning a cell with many, small prey, making transport easier and faster or provisioning with pollen and nectar.

Nest excavation preceding the start of provisioning is the sequence common to the majority of wasps, all pollen wasps and bees that excavate their nests in friable soil. It is also characteristic of all those species that excavate nests in non-friable clayey soil, vertical banks and plant tissue and those that construct aerial nests.

Wasps that 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 expedience but based on its overall suitability. As a consequence there is a tendency for successive nests to be localised in one area which may moreover be removed from the hunting or foraging area.

The change from single-celled to two-celled or to multi-celled nests is brought about within the new sequence of nest excavation before hunting. This is accomplished by a delay in carrying out the final element of the sequence—that is 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 (preparation of a nest).

The behavioural sequence of wasps, pollen wasps and bees, which construct aerial nests, can be similarly expressed with 'construction' being substituted for 'excavation'. The interface of this behavioural change can be seen in the nesting behaviour of some species of pollen wasps, in which mud cells are constructed within excavated cells. Thus with the abandonment of excavation and the construction of the cells above ground, the behavioural change is accomplished.

The simplest behavioural sequence found in species that excavate nests, where hunting takes place before nest construction, is absent from the range of behavioural sequences found in aerial nesters. However, the same range of variations is to be found in the number of cells, the nature of the provision, if prey then the number of prey, and the time of oviposition. If several cells are constructed in a group, they may be enclosed in an envelope, which could be said to represent nest sealing.

In pre-existing cavity modified by the nester

In the behavioural sequences of nesters in pre-existing cavities, there is clearly a considerable reduction in the sub-elements of nest construction. Characteristic of this type of nesting is that, as building materials used in preparing the cavity and in cell closures must be brought into the cavity, they generally differ in nature from the cavity substrate. However, the range of sequences concerning provisioning and oviposition is not reduced.

In pre-existing cavity not modified by the nester

Species that leave the prey in the burrow clearly perform only behavioural sequences that relate to provisioning and oviposition.

In nest constructed and provisioned by another

Species that lay their eggs in nests of others in the construction and provisioning of which they have taken no part are here termed ‘nest parasites’. These species are dependent upon the presence of nests of the aculeate host for their nesting. They can be divided into two groups, one of species belonging to families in which most are nest constructors and provisioners, and the other of species belonging to families in which none are nest constructors and provisioners.

The species of the first group are members of the genera *Nysson* (Crabronidae), *Sphecodes* (Halictidae), *Coelioxys* and *Euaspis* (Megachilidae) and *Epeolus* and *Thyreus* (Apidae). With these is included *Ceropales* (Pompilidae) which, however, differs in that the egg is laid not in the nest of the host but into the book lungs of the spider prey of a pompilid host before the prey is taken into the nest.

Ethologically these ‘nest parasites’ are possibly the most interesting, as all are derived from non-parasitic forms. Most species are related to their hosts and in each case, host and nest parasite must therefore have a common origin.

The species of the second group, belong to the families Chrysididae, Mutillidae and Sapygidae—all species of which are ‘parasites’. Although most chrysidids are ‘nest parasites’ of aculeates, some oviposit into moth cocoons and others into the eggs of stick insects. Similarly, although most mutillids are ‘nest parasites’ of aculeates some are parasites of the puparia of flies, beetles and moths.

Oviposition

Although there is considerable variation in the number of prey placed in each cell by wasps, females always lay one egg per cell. However, 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 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 or may be into an empty cell. The pollen wasps, like all other vespids, oviposit into an empty cell whereas the bees oviposit into a fully provisioned cell.

Among the bees, the egg is always laid on the completed pollen and nectar mass. But, exceptional amongst the bees are the Allodapini which do not construct partitions between their cells. The eggs are attached to the inner wall of the nest burrow in a pattern distinctive for each species (Michener 2007).

Ecological-behavioural classification and community structure

Gess (1981) constructed an ecological-behavioural classification of the wasps and bees of the study area on the farm Hilton, in the eastern extension of the Nama-Karoo. This classification was based on:

- Nest situation.
- Nature of the substrate required for nesting.
- Whether the nest is constructed in or on the substrate.
- The degree of participation by the nester in the construction of the nest, that is whether the nesters:
    - i. Construct their nests entirely by themselves.
    - ii. Use pre-existing cavities which they modify.
    - iii. Use pre-existing cavities which they do not modify.
    - iv. Use a nest constructed and provisioned by another.

This classification later applied to three further study sites: Tierberg near Prince Albert in the southern Great Karoo, Onverwacht near Oudtshoorn in the Little Karoo and Goegap Reserve near Springbok in Namaqualand (Figures I.2.1–4). It was established that the community structure based on nest substrate obtained for Hilton (Figure I.4.1) is typical of semi-arid areas in southern Africa (Figure I.4.2) (Gess & Gess 1993).

Furthermore, the community structure based on nest substrate obtained by us for a comparable site at Portal in the northern Chihuahuan Desert, Arizona, (voucher specimens in the Albany Museum) is very similar to that established for our four sites in the semi-arid areas of southern Africa. It seems probable that this basic community structure is typical for semi-arid areas lying between 30° and 34° north and south of the equator. That it is not typical for all climates and latitudes can be demonstrated by comparison between the percentage of species nesting in or on plants in these areas with percentages for three areas in Europe having climates ranging from humid temperate to tundra and lying between latitudes ranging from 43° to 71° north.

Subsequent investigations drew attention to the importance of snail shells as nesting sites for wasps and bees in the sandy arid areas of the Richtersveld and Sperrgebiet, in the sandveld along the west coast and in southern Knersvlakte, and in the coastal dunes along the west and southern to eastern coasts (Gess & Gess 1999, 2008).

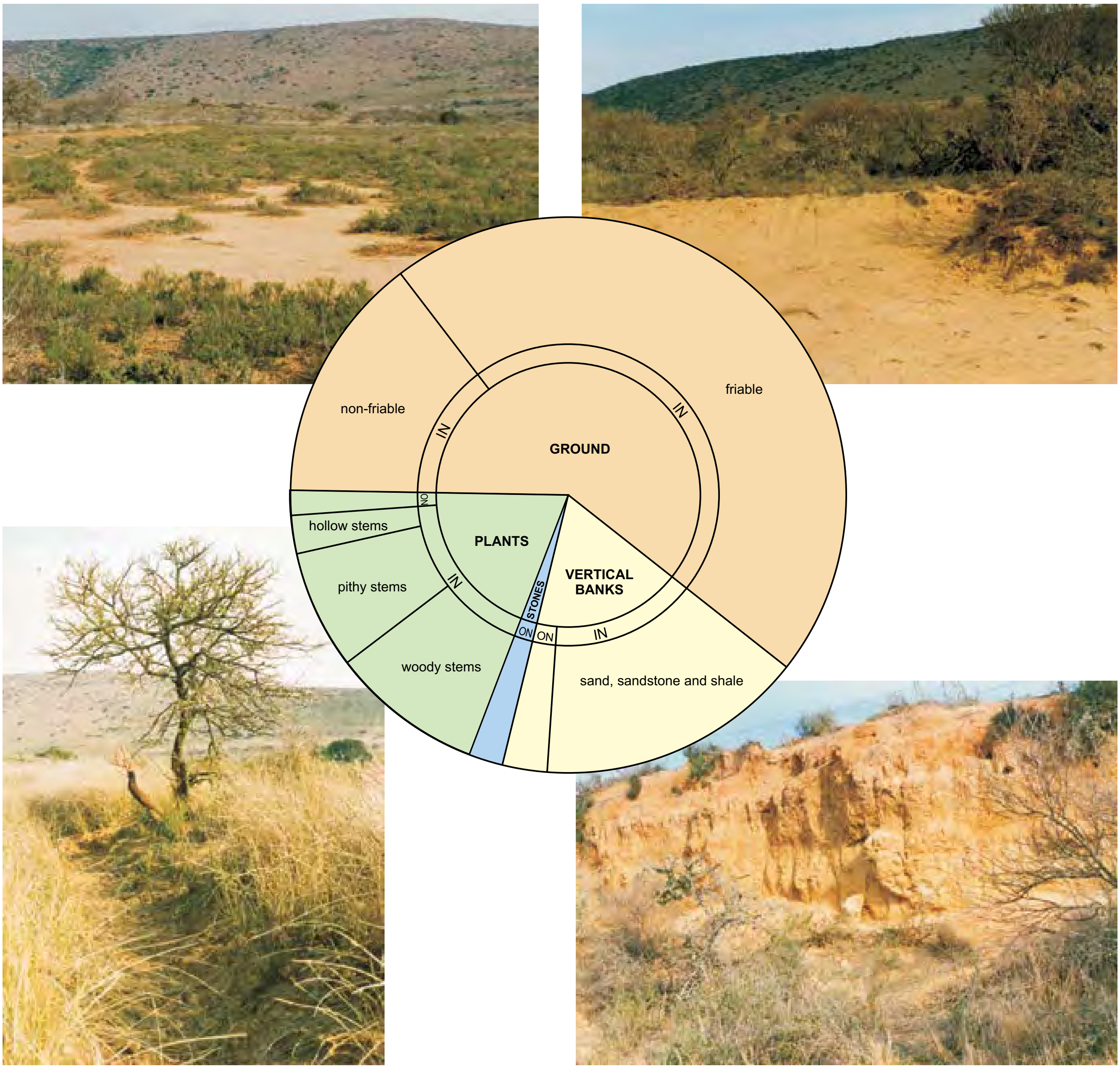


Figure I.4.1.—Diagram showing the structure of the classification of the aculeate wasps and bees of the farm Hilton, Grahamstown, Eastern Cape, on the basis of their nesting situation. The magnitude of the segments is in proportion to the number of species involved.

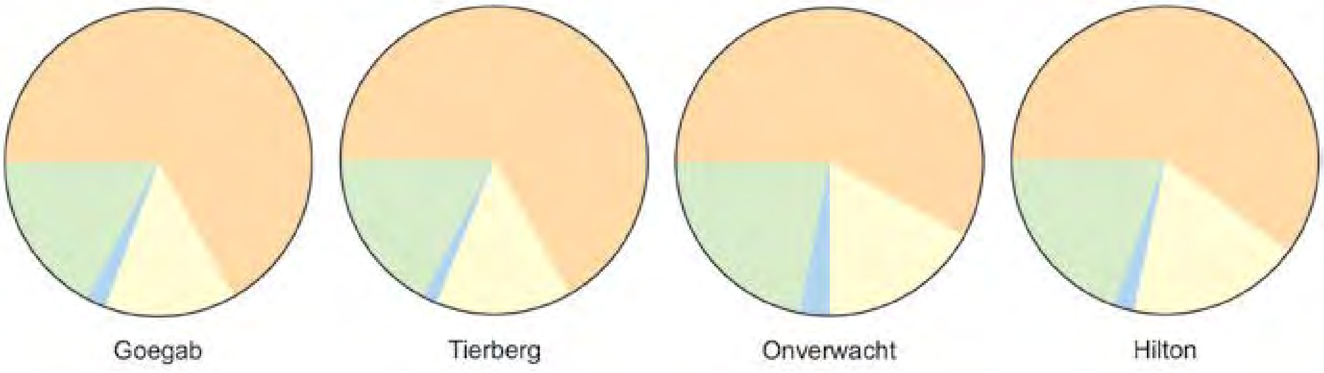


Figure I.4.2.—Diagramatic representations of the structure of the communities of wasps and bees on the basis of nest situation at: Goegab Nature Reserve, Tierberg Farm, Onverwacht Farm, and Hilton Farm. The magnitude of the segments is in proportion to the numbers of species involved. Horizontal ground (orange); vertical banks (yellow); stones (blue); and plants (green).

Here we present a revised classification categorised as follows:

I. NESTING IN THE GROUND

- *a. In friable soils* (typically sandy or disturbed soils).
  - 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.
  - iv. In nest constructed and provisioned by another.
- *b. In non-friable soils* (typically compacted clayey soils).
  - 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.
  - iv. In nest constructed and provisioned by another.

II. NESTING IN OR ON VERTICAL BANKS

- A. IN VERTICAL BANKS
  - 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.
  - iv. In nest constructed and provisioned by another.
- B. ON VERTICAL BANKS
  - 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.
  - iv. In nest constructed and provisioned by another.

III. NESTING ON STONES

- 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.
- iv. In nest constructed and provisioned by another.

IV. NESTING IN SNAIL SHELLS

- A. IN SAND FILLED SNAIL SHELLS
  - 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.
  - iv. In nest constructed and provisioned by another.
- B. IN EMPTY SNAIL SHELLS
  - 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.
  - iv. In nest constructed and provisioned by another.

V. NESTING IN OR ON PLANTS

- A. IN PLANTS
  - *a. Within woody stems.*
    - 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.
    - iv. In nest constructed and provisioned by another.
  - *b. Within pithy stems.*
    - 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.
    - iv. In nest constructed and provisioned by another.
  - *c. Within hollow stems.*
    - 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.
    - iv. In nest constructed and provisioned by another.
- B. ON PLANTS (irrespective of whether plants are woody, pithy or hollow-stemmed).
  - 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.
  - iv. In nest constructed and provisioned by another.

A guide to the representation of taxa falling into these categories is given at the end of this chapter

I. NESTING IN THE GROUND

More species nest in the ground (horizontally presented soil) than in any other situation and all other nesting is derived from ground nesting. Bare areas are favoured. These occur naturally, for example, where sheet erosion has taken place, where silt has been deposited on flood plains, where plant cover is sparse, where large mammals have worn paths to drinking holes and around termite heaps. Activities such as quarrying, particularly for building sand, road building, building of earthen dams and cultivation, provide additional nesting sites. However, use of such sites is hazardous as renewal of such activities often completely extirpates the nests resulting in catastrophic elimination of populations that have built up in such situations.

Soils can be divided into two 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 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 it contains, a wet non-friable soil being more easily worked than a dry one. Sand is the most obvious friable soil. Inland sands are basically derived from the weathering of sandstones and quartzites. Other soil types become friable when disturbed, for example by human activities and burrowing animals. Compacted clay soils are the most obvious non-friable soils. Clays are derived from the weathering of shales, mudstones and tillite. However, any soil that has become compacted or cemented is non-friable.

The construction of nests in the two very different soil types clearly demand different excavation techniques and therefore differences in the structure and behaviour of the wasps involved. Nest sites may be isolated or grouped in aggregations resulting from successive generations of females initiating their nests in close proximity to their natal nest.

Typically, nest excavators in both soil types construct cells with single terminating shafts. A cell is generally of greater diameter than the shaft leading to it. The simplest nest structures consist of a short shaft terminating in a single cell. More complex nests are two- to multi-celled. A lateral shaft including a cell may be little longer than the cell itself or of considerable length.

Nesting burrows of bees, wasps and other insects are used by nesters in pre-existing cavities. In non-friable soil the number of species nesting in pre-existing cavities approximates the number of species nesting in original nests. However, in friable soil the number nesting in pre-existing cavities is much lower. This is all the more striking considering 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 a short time. This is of particular relevance to old burrows from which wasps or bees have emerged.

For most species making use of pre-existing cavities in the ground, such behaviour is obligatory but for some it is facultative.

a. *In friable soils* (typically sandy or disturbed soils)

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 achieved through digging, the 'tools' involved being the mandibles, the forelegs 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, these are aided in their work by the manipulation of the flight mechanisms that produce vibrations transmitted by the mandibles to the substrate. Evidence of this method of loosening the soil is a very noticeable buzzing sound that can frequently be heard being made by excavating females of some sphecids. Often this buzzing sound emanating from the ground is the first indication that nest excavation by one of these species is under way in the immediate vicinity.

Removal of the loosened soil may be effected in several ways. This is the basis on which species excavating nests in friable soil may be divided into so-called 'rakers', 'pullers', 'carriers' and 'pushers' (concepts defined by Olberg 1959, the German terms translated into English and used by Evans & Eberhard 1970 and adopted by Gess 1981).

The 'rakers' are characterised by having a strongly developed series of stout spines on the front tarsus, forming a sand-rake (Figure I.4.3 & 4). The foretarsi, which are bent towards the midline of the body, are moved repeatedly backwards and forwards, each backstroke throwing back a load to 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 (Figure I.4.5) because it is not possible to rake or sweep loose sand vertically upwards, the burrows of 'rakers' are inclined, often at a fairly small angle with the horizontal (e.g. Figures II.3.26 & 28).

The 'pullers', like the 'rakers', use the forelegs to remove the loosened soil from the excavation. However, instead of raking out the soil, it is gathered together to form a load held between the underside of the head and the prothorax and the basal parts of the forelegs, and, the wasp walking backwards, this soil is then pulled out of the excavation and deposited at its entrance. Soil 'pullers' may use the raking technique to level and disperse this deposit.

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 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. The distance from the nest may be very short and exits from the nest be

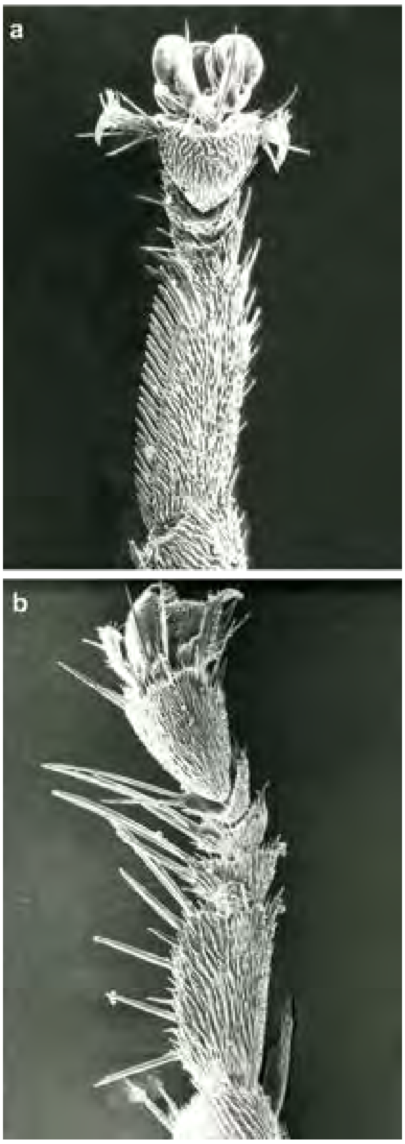


Figure I.4.3.—a and b: a. left foretarsus of *Bembecinus cinguliger* (Smith), showing dense row of short spines; b. left foretarsus of *Bembecinus haemorrhoidalis* (Handlirsch), showing long spines forming 'sandrake'.

Figure I.4.4.—a and b: left foretarsus of *Dichragenia pulchricoma* (Arnold), showing very short spines not forming a 'sandrake'; b. left foretarsus (distal four joints only) of *Batozonellus fuliginosus* (Klug), showing long spines forming 'sandrake'.

made in rotation so that a circle of discarded soil develops (Figure I.4.6).

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 forelegs is moved back by the legs to behind the abdomen and is then pushed by the excavator up the shaft in an action comparable to that of a piston in its cylinder. Species of *Cerceris* (Crabronidae, Philanthinae) are probably the best-known 'pushers'. For the purpose of pushing soil with the end of the abdomen, they have a well developed pygidial plate. Characteristic of *Cerceris* burrows is that they are vertical or sub-vertical and that the excavated soil in the form of 'sand sausages' forms a conical heap surrounding and surmounting the nest entrance (Figure I.4.7). 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 timesaving method of excavation and allows the construction of nests of great depth.

A cell constructed in friable soil is sealed with loose soil raked into the shaft leading to the cell. If a lateral shaft is excavated after a cell has been constructed the soil for sealing is derived from that shaft. If no further lateral shaft is excavated, soil is raked in from outside the nest. In final closure, the remainder of the main shaft is generally filled.

The exclusion of at least a certain proportion of parasites by many species excavating their nests within friable soil is effected by the maintenance of a temporary closure at the nest entrance. This is achieved by raking soil into or out of the nest entrance each time the wasp leaves or returns to the nest. Such an easy way of closing and opening a nest is clearly possible only in friable soil.

By far the largest number of nest excavators in friable soil belong to the spheciform Apoidea. For example, on Hilton 67 species of friable soil nesters were spheciform, as compared with six species of apiform Apoidea and three species of Pompilidae (Vespoidea) (Figure I.4.8).

Nesters that use substances for stabilising the sand in friable soil are unusual. *Quartinia* species (Vespidae, Ma-

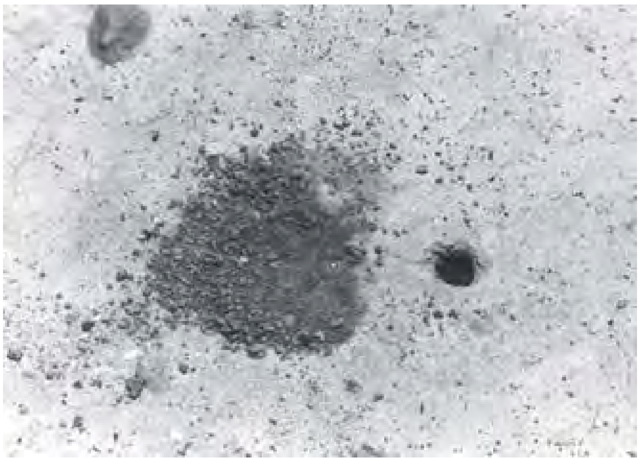


Figure I.4.5.—Example of the nest entrance of a 'raker', *Tachysphex waltoni* (Arnold).

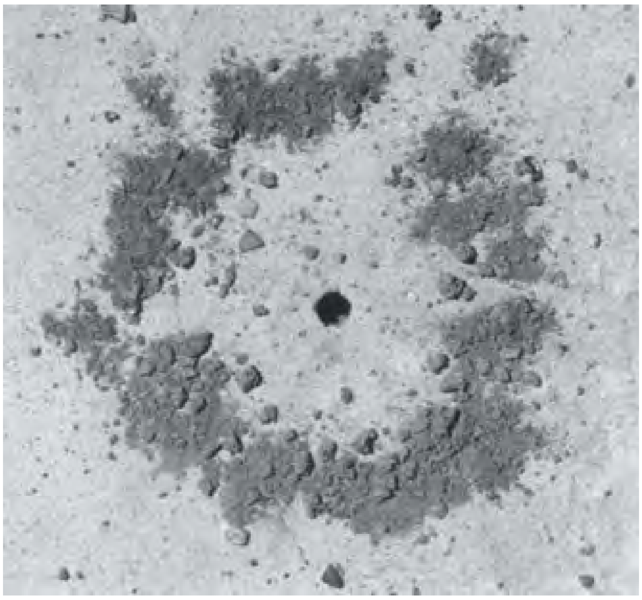


Figure I.4.6.—Example of the nest entrance of a 'carrier', *Prionyx kirbii* (Van der Linden).

Figure I.4.7.—Example of the nest entrance of a 'pusher', *Cerceris oraniensis* Brauns.

sarinae) use self-generated silk to stabilise the walls of the nest turret, shaft and cells. *Hoplitis* (*Anthocopa*) *karooensis* (Brauns) (Megachilinae, Osmiini) uses a resin-like substance to stabilise the walls of the nest turret, shaft and cells. *Celonites latitarsis* Gess (Vespidae, Masarinae), unlike all other species of *Celonites* which do not excavate a burrow, has foretarsal sand rakes used for the excavation of a burrow but like all *Celonites* species uses nectar to stablilise the cell walls.

b. *In non-friable soils* (typically compacted clayey soils)

Most of the nest excavators in non-friable soil are species of Masarinae and Eumeninae (Figure I.4.8). This type of nest excavation is exceptional for Pompilidae and Apoidea, only two species of pompilids, both of the genus *Dichragenia*, and three species of Apoidea, two species of *Bembecinus* (Crabronidae, Bembicinae), a genus which otherwise, worldwide, nests in friable soil, and *Amegilla atrocincta* Lepeletier (Apidae), being known to nest in this way.

Characteristic of species excavating nests in non-friable soils is that excavation is effected by the use of water to soften the soil 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 nesting site in the crop. Excavation is performed by regurgitating a droplet of water onto the working face of the excavation, working this water into the soil by movements of the mandibles, and forming the resultant mud into a pellet, which is carried from the excavation held by the mouthparts. Several such pellets may be formed from a single crop-full of water. When the supply of water is depleted the excavator returns to the water source to refill the crop. In some species, loosening of the substrate is aided by the use of vibrations generated by the manipulation of the flight mechanisms and transmitted by the mandibles to the substrate.

Species excavating in non-friable soil, in marked contrast to those excavating their nests in friable soils, make no use of the forelegs in manipulating the nesting substrate. These limbs are consequently devoid of 'sand rakes'. The difference is particularly striking with respect to *Bembecinus cinguliger* (Smith), *B. oxydorcus* (Handlirsch), *Dichragenia pulchricoma* (Arnold) and *D. neavei* (Kohl).

As in non-friable soil, all manipulation of the substrate and of the mud pellets formed from the excavated material is performed by the mouthparts, principally the mandibles. Therefore, modification of these organs is to be expected. Females of the two *Dichragenia* species possess a brush of long, stiff, forwardly directed bristles emitted from the base of the mentum (Figure I.4.9). It is believed that these bristles may, by supporting it from below, aid the mandibles in holding and manipulating a mud pellet.

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 carrying allowed the construction of vertical burrows. As the species excavating their nests in non-friable soils all remove

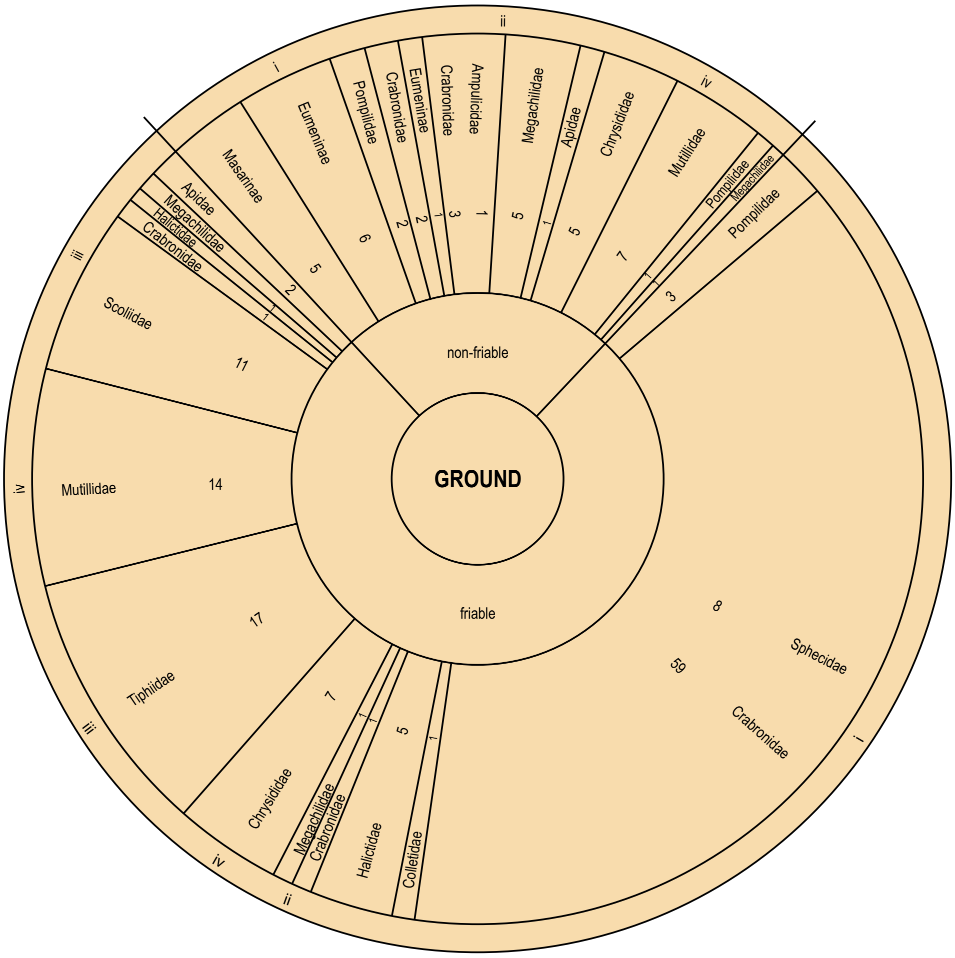


Figure I.4.8.—Diagram showing the structure of the communities of the aculeate wasps and the bees nesting in the ground on the farm Hilton, Grahamstown, Eastern Cape, on the basis of their ethology. Numbers accompanying the family names represent numbers of species. The numbers (i, ii, iii, iv) in the 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 and iv) In pre-existing cavity not modified by the nester and nest constructed and provisioned by another. The magnitude of the segments is in proportion to the number of species involved.

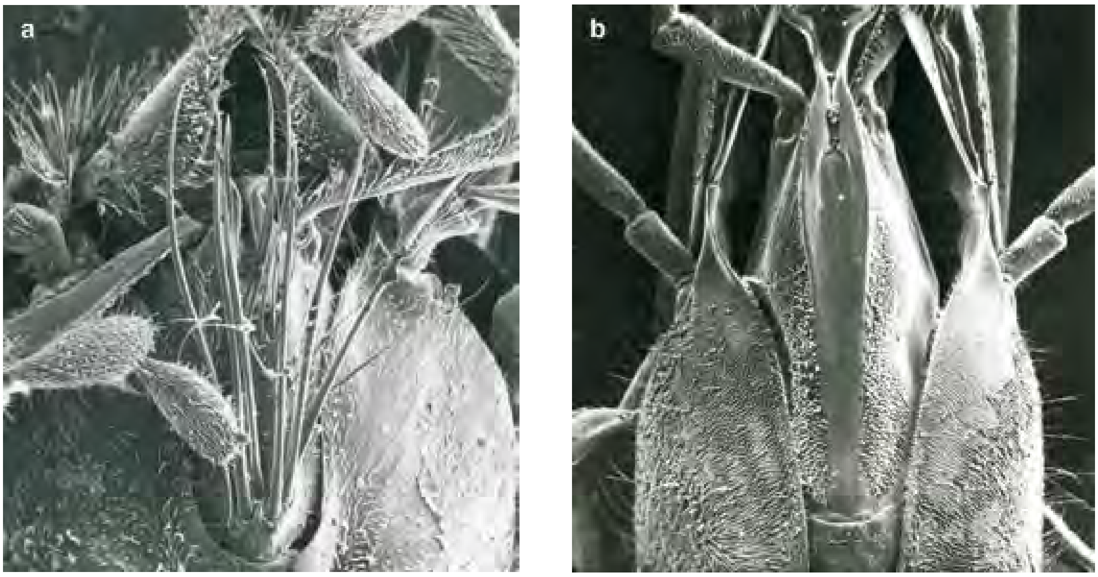


Figure I.4.9.—a and b: a. underside of head of *Dichragenia pulchricoma* (Arnold), showing stiff, forwardly directed bristles emitted from the base of the mentum; b. underside of head of *Batozonellus fuliginosus* (Klug), showing absence of forwardly directed bristles.

Figure I.4.10.—Nest entrance turret of *Dichragenia pulchricoma* (Arnold) with female nest builder.

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 nests excavated are always vertical or sub-vertical. 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 nests of sand-raking species are inclined, the nest shaft of the mud pellet-carrying *B. cinguliger* and *B. oxydorcus* is vertical or sub-vertical. The same picture emerges from a comparison of the nest plan of *Batozonellus fuliginosus* (Klug) with those of the two *Dichragenia* species (Figures II.2.71).

Characteristic of all the species recorded excavating their nests in non-friable clayey soil, is that at least some of the excavated material involved (in the form of mud pellets) is used to build an aerial superstructure encircling and surmounting the nest entrance (Figure I.4.10). 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.

Turret construction developed from pellet dropping in a circle around the nest entrance. It can readily be envisaged that, if the radius of the circle is kept constant and the pellets are moist, a circular ‘wall’ will develop. Such a rudimentary turret is constructed by a species of *Fabriogenia* (Pompilidae, Pepsinae, Ageniellini) observed by us in Western Australia in 1993. These observations were made available for a discussion of the evolution of pompilid nesting (Evans & Shimizu 1998). This ‘turret’, like that of *Dichragenia pulchricoma*, was of greater diameter than that of the nest entrance. The majority of wasp and bee species have reduced the diameter of the circle to equal that of the nest entrance.

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.

That the construction of an aerial superstructure surmounting the nest entrance is of survival value to species excavating their nests in non-friable soils, is evident from the fact that it has evolved independently in the Pompilidae, Vespidae and Apoidea. It is certain that all superstructures, even those consisting only of a low collar surrounding the nest entrance serve to prevent loose powdered soil and other wind-blown debris from entering the nest shafts. The more elaborate of the superstructures serve to protect the nests from flooding by, when soaked by rain or surface run-off, collapsing, thereby blocking the nest entrance. It is highly probable that these more elaborate superstructures also serve to reduce parasitism by concealing the nest entrance from aerial observers such as bombyliid flies that, whilst hovering, oviposit into dark holes.

Temporary closures are not commonly constructed by nesters in non-friable soil. However, they are constructed by *Bembecinus cinguliger* and *B. oxydorcus* (Gess & Gess 1975). These are mud plugs constructed at the end of a working day and removed at the beginning of the next working day. The nest remains open through the duration of the working day.

All cells other than those of some species of pollen wasps are unlined. Those pollen wasp species that line the excavated cell do so by constructing a close-fitting mud cell within the excavated cell. The mud for this purpose is derived from within the nest.

A cell constructed in non-friable soil is sealed with a mud plug, the mud being derived from within the nest. If a lateral shaft is to be excavated after the completion of a cell, the soil is derived from that source. After the completion of a mud plug, further soil excavated from a lateral shaft is used to fill the shaft leading to the completed cell. This filler is in the form of loose crumbs or uncemented pellets. In final completion of the nest before it is abandoned by the nester, the main shaft may or may not, depending upon the species, be filled. Material for filling consists mainly of soil, with in some species the addition of scattered debris, collected from around the nest entrance. Nest superstructures are generally left intact. However, some nesters such as *Aethiopicodynerus* species break down the superstructure and use it in filling the nest.

II. NESTING IN OR ON VERTICAL BANKS

Vertical banks may be of friable or non-friable soil, silicified sand, or stone. All three categories of nesters are able to nest in soil banks or lightly silicified sandstone banks. Clearly, shale and stone are not suited for nest excavation but are used by species that nest in pre-existing cavities. Layered stone, such as shale, is particularly suited to this purpose (for example Figure I.4.11).

A. IN VERTICAL BANKS

Vertically presented soil occurs naturally along watercourses which, due to their flood flow pattern in most parts of southern Africa, at least in part, have deeply cut beds and therefore vertical banks. These beds are often cut into silt laid down in previous years. The vertical soil ranges from friable to non-friable depending upon its

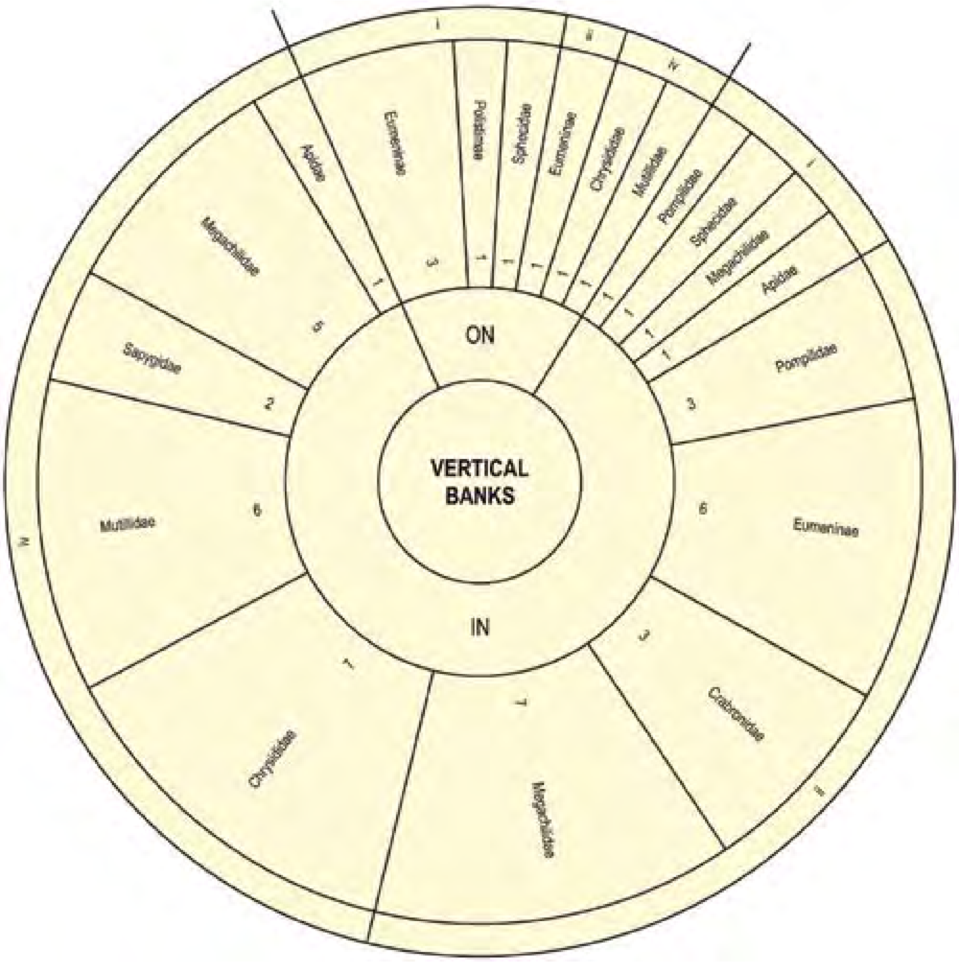


Figure I.4.11.—Diagram showing the structure of the communities of the aculeate wasps and the bees nesting in and on vertical banks on the farm Hilton, Grahamstown, Eastern Cape, on the basis of their ethology. Numbers accompanying the family names represent numbers of species. The numbers (i, ii, iii, iv) 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 and iv) In pre-existing cavity not modified by the nester and nest constructed and provisioned by another. The magnitude of the segments is in proportion to the number of species involved.

origin and degree of mineralisation. Soil is also presented vertically when storms have uprooted trees, the roots of which have brought with them a slab of the soil in which they grew. Human activities have vastly increased the nesting sites available in vertically presented soil. The most obvious sites are road and rail cuttings, quarries and mud walls of buildings.

The difference in the angle of presentation of the soil surface—vertical as opposed to horizontal—has a very pronounced influence upon nesting. Illustrative of this is that there is little or no sharing of species between level ground and vertical banks. Indeed, both nesting situations are characterised 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 proportions of species excavating their nests, to those modifying pre-existing cavities. In level ground, nest excavating species greatly outnumber nest modifying species whereas in vertical banks the opposite is true, nest excavators being outnumbered by nest modifiers.

Characteristic of communities excavating nests in vertical banks is the dominant role played by bees, both in number of species and number of individuals. Most striking are *Anthophora* species (Anthophoridae) which nest in pseudo-colonies in burrows which they excavate with their mandibles.

Of the wasps, only the spheciform Apoidea and Eumeninae appear to be represented in this nesting situation. Some species such as *Stizus imperialis* Handlirsch (Crabronidae, Bembicinae) are dry excavators and, like the bees, nest in pseudo-colonies. Others, such as *Chalybion* (*Hemichalybion*) *spinolae* (Lepeletier) (Sphecidae, Sceliphroninae) and *Antepipona tropicalis* (de Saussure) (Vespidae, Eumeninae), are solitary nesters and fetch water for use in excavation.

Some species that appear to be associated with vertically presented soil are in fact using horizontal ledges. These species are not included here as they are generally found nesting in horizontally presented ground.

B. ON VERTICAL BANKS

Nests situated on the substrate and constructed by the nester are always fashioned from materials brought to the nesting site from elsewhere. The substrate is therefore a support only. The nesters in this category consequently exhibit far less specificity in the choice of substrate than do nesters in a substrate. The requirements are that the substrate should be durable and presented in a way suitable for the attachment of the nest.

Soil is generally unsuitable for the attachment of nests due to the crumbly nature of the surface. Rarely, constructors of paper combs and aerial mud nesters use overhangs on earth banks for the attachment of their nests. However, naturally occurring stone or rock banks, artificial vertical banks and man-made stone and brick walls are well suited to the attachment of aerial nests.

III. NESTING ON STONES

Species constructing nests on stones differ in the placement of their cells. Some build their nests on the underside of large stones lying loose upon the ground and others build on the upper surface of partially buried stones and boulders. Cells built on the upper surface of stones and boulders are potentially subject to extremes of temperature, both high and low. Stones partially buried in the ground will not become as hot or as cold because of heat exchange between them and the ground.

Nests constructed on the underside of stones are generally of fragile, relatively thin, mud walled cells that would be readily damaged if left exposed on the upper surface of stones. Nests built on the exposed surfaces of stones or boulders are more robust in construction. The cells themselves are more robust and are covered with a thick protective layer of mud. The cells and their covering are variously constructed from mud, mud mixed with small pebbles, sand or small pebbles cemented with resin derived from plants.

IV. NESTING IN SNAIL SHELLS

The shells of medium to large terrestrial snails, which are abundantly available, empty and sand-filled, in the desertic winter rainfall areas and the areas of sandy coastal dunes of southwestern Africa, offer abundant secure microhabitats in these areas of sparse low vegetation and unstable, often windswept sand.

Clearly, the marked difference in volume of the large shells of *Trigonephrus* Pilsbry (Dorcasiidae) with a western distribution and the much smaller shells of *Tropidophora ligata* (Müller) (Pomatiidae) with a southern to eastern distribution, makes a difference to the suitability of the cavity offered (Figure I.4.12). This may explain the greater percentages of shells used and the larger number of bee species and *Quartinia* species using shells where *Trigonephrus* shells are available as compared to the south and southeast where they are not available. This possibility is supported by the fact that where the invasive snail *Theba pisana* (Müller) (Helicidae), having shells with a relatively small volume and low spiral, has all but replaced *Trigonephrus*, percentage use of *T. pisana* is very low compared to *Trigonephrus*.

A. IN SAND-FILLED SNAIL SHELLS

The only regular nesters in sand-filled snail shells are seven species of *Quartinia* (Vespidae, Masarinae). Their nests are commonly found in snail shells throughout the winter rainfall desertic areas, at some sites in the sandveld and at many in the coastal dune slacks on the west coast and along the south coast eastwards at least as far as Still Bay. In nest building, self-generated silk is initially used to stabilise sand grains in the excavation of a burrow and the construction of a nest turret. The silk lined burrow reaches far into the shell where cell construction from sand and silk takes place safely in the spiral of the shell where the cells can be securely packed and attached to the shell.

In windswept sandy areas, where the ground is unstable, sand-filled snail shells represent the only microhabitat offering a secure nesting site for *Quartinia*, however, where rock outcrops occur, pockets of sand offer additional secure nesting sites. That snail shell nesters may use such sites was confirmed by the discovery of *Q. refugicola* Gess nesting in sand trapped in calcrete in addition to sand trapped in *Trigonephrus* shells (Gess & Gess 1999). It is therefore clear that for *Q. refugicola*, at least, nesting in snail shells is not obligatory. It seems probable that this will be found to be the case for at least some of the other species collected from nests in snail shells.

The only other wasp found nesting in sand-filled shells was *Tachysphex hermia* Arnold (Crabronidae, Crabroninae).

No bees were found nesting in this situation.

Figure I.4.12.—a and b. Shells (Mollusca, Gasteropoda) of *Theba pisana* (Müller), *Trigonephrus* (Dorcasiidae) and *Tropidophora ligata* (Müller) (Pomatiidae) (actual width of shell of *Trigonephrus* 28 mm).

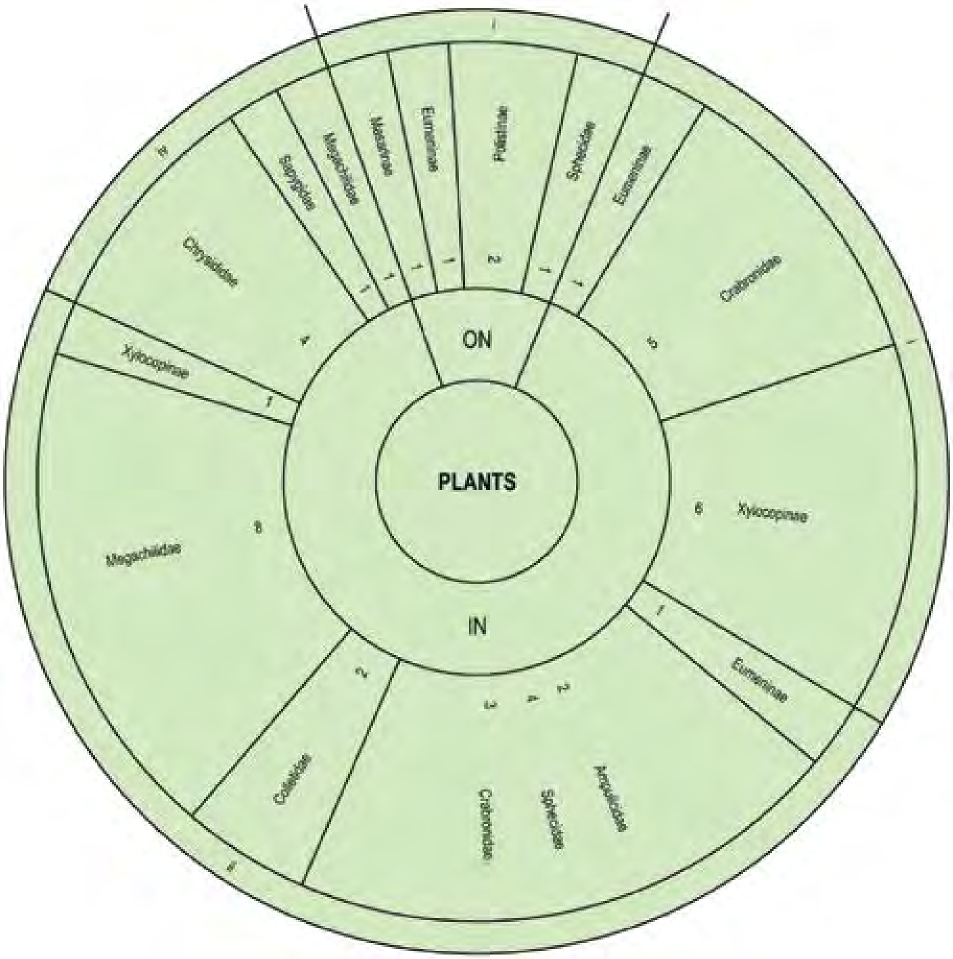


Figure I.4.13.—Diagram showing the structure of the communities of the aculeate wasps and the bees nesting in and on plants on the farm Hilton, Grahamstown, Eastern Cape, on the basis of their ethology. Numbers accompanying the family names represent numbers of species. The numbers (i, ii, iii) in the outermost ring correspond to the same numbers in the classification. (i) In nest constructed entirely by the nester. (ii) In pre-existing cavity modified by the nester. (iii and iv) In pre-existing cavity not modified by the nester and nest constructed and provisioned by another. The magnitude of the segments is in proportion to the number of species involved.

B. IN EMPTY SNAIL SHELLS

Empty snail shells are used as pre-existing cavities for nesting most commonly by species of *Wainia* (Megachilinae, Osmiini) and less commonly by *Alastor ricae* Giordani Soika (Eumeninae), several anthidiine bees (Megachilinae, Anthidiini) and *Hoplitis* (*Anthocopa*) *conchophila* Kuhlmann (Megachilinae, Osmiini).

Nesters of this category were found to be more diverse and more abundant in the winter rainfall desertic areas than they were in the coastal areas.

V. NESTING IN OR ON PLANTS

A. IN PLANTS

Some plant stems offer a suitable substrate for the excavation of nests by wasps and bees. Stems can be roughly characterised as woody, pithy and hollow. The nature of the stem determines which species utilise it for the construction of their nests (Figure I.4.13). A further limiting factor is clearly the diameter of the stem, which must be great enough to accommodate the galleries. An additional requirement is that the stem should retain its form for as long as it takes the species nesting within it to develop from egg to adult and to emerge from the nest.

It is of interest that some points of similarity exist between the community nesting in vertical banks and those nesting in plant tissue. In both situations the original burrow-excavators are most commonly bees and some species that nest in pre-existing cavities are shared. Clearly as the latter do not nest in horizontal ground they are seeking pre-existing cavities above ground level rather than in soil or plant tissue.

The woody stems utilised as a nesting substrate appear invariably to be dead and dry. In the case of resinous species, dry to the point that they are no longer resinous.

Woody stems are the chosen nesting sites of some species of carpenter bees (Apoidea, Xylocopinae). The nest galleries are excavated by the bees using their mandibles. These galleries may be simple or branched. The cells are constructed in linear series and the material used for sealing the cells is obtained by scraping the surface of the gallery walls.

Pithy stems utilised as a nesting substrate are of two distinct groups: green, living inflorescence stems and dry, dead inflorescence stems.

As far as can be ascertained, the only excavators in living tissue are some species of *Dasyproctus* (Crabronidae). The stems utilised are inflorescence stems, mainly those of monocotyledonous plants which offer a good length of internode. It is clearly of survival value for these wasps that the plant stems in which they make their nests are protected in some manner from being eaten by herbivores. This protection may be physiological, as in the case of *Drimia altissima* (L.f.) Ker Gawl. (Hyacinthaceae) stems in which *Dasyproctus westermanni* (Dahlbom) nests. All parts of these plants are toxic to mammals due to the presence of a glucoside having a digitalis action. More commonly, however, the plants utilised are protected from grazing by growing within the cover of spiny or thorny shrubs. The majority of nesters in pithy stems favour dry dead tissue. This appears to be due to the reduced likelihood of the provision being destroyed by fungi.

Excavators in dry pithy stems are predominantly species of carpenter bees, most notably *Xylocopa* and *Ceratina*, and species of *Dasyproctus* (other than those excavating in live stems).

In stands of *Aloe* (Asphodelaceae) with relatively robust inflorescence stems, large populations of some *Xylocopa* species build up so that almost every dry inflorescence stem is occupied. Only the basal parts of the inflorescence offer sufficient thickness of pith for these medium-sized carpenter bees. The upper thinner branches of the inflorescence are suitable only for the small carpenter bees, *Ceratina* species.

Generally, nesters in pithy stems excavate their galleries by first cutting a round entrance hole through the hard outer layers of the stem. When they reach the pith, unbranched upwardly and downwardly directed galleries are excavated. More rarely the gallery may be branched, for example, that of *Xylocopa caffra* (L.) is ‘H’-shaped. Within the galleries cells are constructed serially, each being sealed with a plate constructed from fibres rasped from the gallery walls.

Some carpenter bees that usually nest in *Aloe* inflorescence stems are sometimes found nesting in other pithy inflorescence stems. For example, we found *Xylocopa sicheli* (Vachal), which nests widely in *Aloe* inflorescence stems, nesting in thick pithy inflorescence stems of a species of *Berkheya* (Asteraceae) in Namaqualand.

Some *Allodape* species excavate in pithy stems but never cut holes to obtain access to the pith. They enter through holes cut by other insects, or where stems have been broken. In gardens these little bees with their shiny reddish brown abdomens are a common sight nesting in cut rose stems.

It may be strange to suggest that a nester in a hollow stem is an excavator. However, a nester that actually cuts an access hole into a hollow stem is here considered an excavator.

The most notable example in this category is *Xylocopa scioensis* Gribodo that nests widely in hollow internodes of the culms of the common reed *Phragmites australis* (Poaceae). The culms utilised are dry and the pith, which fills the internodes of young culms, is shrunken to be almost negligible. After cutting an entrance hole, the bee cleans out the remnants of the pith and provisions cells in linear series sealing each with raspings from the gallery walls in the same manner as do carpenter bees nesting in woody and pithy stems.

All nests consisting of cells built within pre-existing cavities in plant tissue may be recognised immediately as such and may be distinguished readily from nests consisting of cells built within a gallery excavated by the nesting wasp or bee itself. This is possible because all cell constructing users of pre-existing cavities in plant tissue introduce foreign materials for the construction of cells or cell partitions and nest closures whereas gallery excavators utilise material rasped from the gallery walls to make cell partitions and nest closures.

Unusual are nesters, for example *Allodape* (Apoidea, Xylocopinae), that do not construct cell partitions although they lay more than one egg per nest.

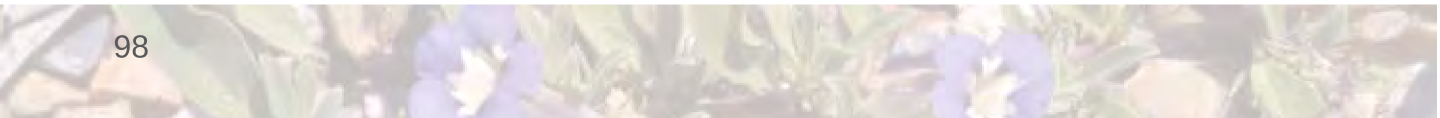
The simplest nests such as those of *Ampulex bantuae* Gess (Ampulicidae) are single-celled. *Ampulex bantuae* nests in *Acacia karroo* (Fabaceae) in abandoned burrows eaten out by the larvae of the cerambycid beetle *Ceroplesis hottentota* (Fabricius). It oviposits on its prey and places it in a cavity. It takes its prey cockroach into an unprepared gallery through the beetles emergence hole, lays an egg on it and then constructs a plug from detritus collected from the ground beneath.

The vast majority of species is behaviourally advanced and commences the nesting process with the search for a suitable pre-existing cavity. Thereafter, some foreign nesting material is introduced in connection with cell construction. 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. Early in nest construction additional material may be brought in to form a temporary cell closure as in the nests of species of *Isodontia* (Sphecidae, Sphecinae).

In addition to the optional preliminary plug most species construct only cell closures which form the partitions between the cells, the side walls of which are those of the gallery. However, some bees construct complete cells variously from pieces cut from leaves or petals, ‘plant fluff’, resin and mud.

If the pre-existing cavity is of a length that allows it, several linearly arranged provisioned cells are constructed, in the nests of some species separated by empty cells. Frequently the nest is completed by the construction near or in the cavity opening of a closing plug and sometimes this is preceded by empty cells.

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. 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 case of dry clods, small pieces of twig, bark and other detritus found lying upon the surface of the ground are also utilised.

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

Plants utilised by species constructing aerial nests are required to offer only a suitable mechanical support for the nest. The type of support selected differs from species to species. Whereas the social vespid species, which construct a downwardly directed stalked comb, require woody branches for nest attachment, those species that construct a single chain of cells require only a slender stem for the support of their nests. Furthermore, a heavily-built mud nest such as that constructed by *Delta caffrum* (L.) (Eumeninae) clearly requires a robust support such as the branches of a woody shrub. The delicate mud cells of *Celonites* species (Masarinae), barely a centimetre long, the mud and dung cells of *Sceliphron quartinae* Gribodo (Sphecidae, Sphecinae) and nests constructed from plant fibres or animal fur by *Serapista* species (Megachilidae), can be supported by slender twigs or grass culms.

A guide to the representation of taxa in the 44 categories of the ethological classification

** indicates known nesting, * indicates circumstantial evidence

Category 1

I. NESTING IN THE GROUND

a. *In friable soils* (typically sandy soils or disturbed soils)

i. In nest constructed entirely by the nester

Vespoidea, Vespidae, Masarinae

** *Celonites latitarsis* Gess: of the known species of *Celonites* exceptional in having tarsal sand rakes on forelegs; burrow excavated in the ground; constructed cell within excavated cell, bonding agent nectar.

Quartinia, about 88 species in study area: ** *Q. vagepunctata* Schulthess, multicellular burrow surmounted by a turret, turret and cell walls stabilised with self-generated silk; seven species found nesting in sand-filled snail shells (Category 21), one of which (*Q. refugicola* Gess) also nests in sand-filled crevices in calcrete, one species at least not restricted to nesting in sand in cavities.

Vespoidea, Pompilidae, Pepsinae, Pepsini

* *Cryptocheilus*, *Cyphononyx*, *Hemipepsis*, *Priocnemis*: all have tarsal sand rakes on their forelegs and can therefore be expected to nest in friable soil.

Vespoidea, Pompilidae, Pompilinae, Pompilini

Batozonellus, *Dicyrtomellus*, *Elaphrosyron*, *Episyron*, *Paracyphononyx*, *Paraferreola*, *Pompilus*, *Tachypompilus*: all have tarsal sand rakes on their forelegs and can therefore be expected to nest in friable soil.

** *Batozonellus fuliginosus* (Klug): single celled burrow in friable soil, situation exposed.

** *Tachypompilus ignitus* (Smith): single celled burrow in friable soil in sheltered situations.

Apoidea, Spheciformes, Sphecidae, Sphecinae

Prionyx species: all have tarsal sand rakes on their forelegs and can therefore be expected to nest in friable soil.

** *Prionyx kirbii* (Van der Linden): excavates nest in friable soil but was also found nesting in abandoned burrows of *Aethiopicodynerus insignis* Saussure (Vespidae, Emeninae) (Category 5).

Apoidea, Spheciformes, Sphecidae, Sphecinae

Ammophila, *Podalonia* and *Parapsammophila consobrina* (Arnold): all have tarsal sand rakes on their forelegs and can therefore be expected to nest in friable soil.

** *Podalonia canescens* (Dahlbom): a simple burrow terminating in a single cell.

** *Ammophila*, eight species: a simple burrow terminating in a single cell.

Apoidea, Spheciformes, Crabronidae, Bembicinae, Bembicini, Bembicina

Bembix species all have sand rakes and typically nest in friable soil; one-celled to multicellular sloping burrow; form aggregations.

** *Bembix albofasciata* Smith, *B. cameronis* Handlirsch, *B. melanopa* Handlirsch, *B. sibilans* Handlirsch and *B. bubalus* Handlirsch.

Apoidea, Spheciformes, Crabronidae, Bembicinae, Bembicini, Gorytina

* *Afrogorytes*: foretarsal rake moderately developed; probably nests in friable soil.

** *Hoplisoides aglaia* (Handlirsch): multicellular nest.

** *Gorytes effugiens* (Brauns): multicellular nest.

** *Gorytes natalensis* (Smith): multicellular nest.

Apoidea, Spheciformes, Crabronidae, Bembicinae, Bembicini, Handlirschiina

Handlirschia scoliaeformis (Arnold) (= *H. tricolor* (Gess)): only species represented in the study area; nesting unknown; has sand rakes and can therefore be expected to nest in friable soil.

Kohlia cephalotes Handlirsch: only species represented in southern Africa; has sand rakes and can therefore be expected to nest in friable soil.

Apoidea, Spheciformes, Crabronidae, Bembicinae, Bembicini, Stizina

Bembecinus and *Stizus* species typically nest in friable soil.

** *Bembecinus*: all but two typical of the genus excavate sloping burrows with one or two cells in friable soil.

** *Stizus chrysorrhoeus* Handlirsch, *Stizus fuscipennis* (F. Smith) and *Stizus atrox* F. Smith: typically multicellular sloping burrow.

Apoidea, Spheciformes, Crabronidae, Astatinae

Astata species all have sand rakes and can be expected to nest in friable soil.

** *Astata fuscistigma* Cameron.

**Dryudella flavoundata* (Arnold).

Apoidea, Spheciformes, Crabronidae, Crabroninae, Oxybelini

Oxybelus species all have sand rakes and can be expected to nest in friable soil.

** *Oxybelus lingula* Gerstaecker.

* *Oxybelomorpha* (seven species) and *Gessus capensis* Antropov: associated with friable soil; have sand rakes and can therefore be expected to nest in friable soil.

Apoidea, Spheciformes, Crabronidae, Crabroninae, Larrini

Gastrosericus, *Tachysphex*, *Tachytella*, *Tachytes*, *Mesopalarus mayri* Brauns, *Palarus*, *Parapiagetia* all have sand rakes and can be expected to nest in friable soil.

** *Kohliella alaris* Brauns: sloping multicellular burrow.

* *Miscophus* species.

** *Palarus*: two species; one or more cells.

** *Tachysphex*: four species; sloping multicellular burrow.

** *Tachytes* species: usually multicellular burrows in friable soil.

Apoidea, Spheciformes, Crabronidae, Pemphredoninae, Odontosphecini

Odontosphex damara Pulawski: single species represented in the study area, known only from northwestern Namibia; has sand rakes and can therefore be expected to nest in friable soil.

Apoidea, Spheciformes, Crabronidae, Pemphredoninae, Pemphredonini

Diodontus species: have sand rakes and can therefore be expected to nest in friable soil.

Apoidea, Spheciformes, Crabronidae, Philanthinae

** *Philanthus*: nesting in friable soil is the norm; sloping burrow.

** *Cerceris*: nesting in friable soil is the norm; vertical multicellular burrows surmounted by a tumulus of sand-sausages.

Apoidea, Apiformes, Colletidae

Colletes: it is possible that some species may nest in friable soil.

Apoidea, Apiformes, Halictidae

Cellariella, *Ceyalictus*, *Lasioglossum*, *Patellapis*, *Pseudapis*, *Lipotriches*, *Nomioides* and *Nomia*: nesting in friable soil appears to be the norm.

** *Nomioides halictoides* Blüthgen.

** *Lipotriches* (*Lipotriches*) sp. (as *Nomia*) in Gess 1981.

Apoidea, Apiformes, Melittidae

** *Samba* (*Haplomelitta*) *ogilviei* (Cockerell): single-celled nest.

** *Capicola braunsiana* Friese: sloping multicellular burrow; cells in linear series.

** *Meganomia*, *M. binghami* (Cockerell) and *M. gigas* Michener: multicellular burrow.

Ceratomonia rozenorum Michener: sole species in the genus, known only from Namibia; presumed to nest in friable soil.

Category 2

I. NESTING IN THE GROUND

a. *In friable soils* (typically sandy or disturbed soils)

ii. In pre-existing cavity modified by the nester

Apoidea, Spheciformes, Crabronidae, Larrinae

** *Liris*: some species.

Apoidea, Apiformes, Megachilidae, Megachilinae, Anthidiini

** *Afranthidium* (*Nigranthidium*) *concolor* (Friese): nest constructed from plant fibres.

** *Serapista denticulata* (Smith): multicellular nest constructed from plant fibres either on plants or in a burrow in the ground.

Apoidea, Apiformes, Megachilidae, Megachilinae, Megachilini

** *Megachile* (*Eutricharaea*) *semiflava* (Cockerell): cells constructed from leaf pieces.

Category 3

I. NESTING IN THE GROUND

a. *In friable soils* (typically sandy or disturbed soils)

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

Vespoidea, Scoliidae

Scoliidae: all provision with scarabaeid larvae *in situ* in the ground.

** Collected in areas of friable soil: *Cathimeris capensis* (de Saussure), *Campsomeriella* (*Campsomeriella*) *caelebs* (Sichel), *Micromeriella atropos* (de Saussure), *M.* sp., *Trielis* (*Heterelis*) *stigma* (de Saussure), *Scolia chrysotricha* Burm., *S. fulvofimbriata* Burmiester and 10 further species of *Scolia.*

Vespoidea, Tiphiidae

Tiphiidae: most provision with scarabaeid larvae *in situ*.

Methoca species: known to provision with burrow-inhabiting larvae of tiger beetles (Cicindelidae) *in situ*.

* *Methoca mosutoana* Péringuéy: almost certainly preys upon the larvae of *Cicindela brevicollis* Wiedemann (Cicindelidae) with which it is found in close association.

Category 4

I. NESTING IN THE GROUND

a. *In friable soils* (typically sandy or disturbed soils)

iv. In nest constructed and provisioned by another

Chrysidoidea, Chrysididae

** *Allocoelia mocsaryi* Brauns: reared from nests of *Quartinia* spp. nesting in sand trapped in snail shells.

** *Hedychrum* spp.: number of species associated with this category not established; *H.* sp. (near *H. comptum* Edney) parasite of *Bembecinus* species.

Chrysidoidea, Mutillidae

** Mutillidae: parasites of wasp and bee larvae—see also non-friable soils. Females from nesting areas in friable soil: *Glossotilla speculatrix* (Smith), *Smicromyrme hecuba* (Peringuéy), *Mimecomutilla renominanda* Bischoff, *Dasylabris* sp. (near *D. cryentocincta* André), *D. simulatrix* (Smith), *D. thais* (Peringuéy), *D. caffra* (Kohl), *Labidomutilla tauriceps* (Kohl), *Psammotherma flabellata* (Fabricius), *Viereckia* sp., *Antennotilla phoebe* (Peringuéy).

Apoidea, Spheciformes, Crabronidae, Bembicinae, Nyssonini

Brachystegus: around five species represented in the study area; probably nest parasites of *Tachytes*.

Nysson: three species represented in the study area; known to be parasitic in the nests of Gorytina.

Apoidea, Spheciformes, Crabronidae, Bembicinae, Bembicini

Stizoides: about three species recorded from the Afrotropical Region; nest parasites of other Spheciformes.

Apoidea, Apiformes, Halictidae

Sphecodes: cleptoparasitic in the nests of other bees.

Apoidea, Apiformes, Megachilidae

Coelioxys species: cleptoparasitic in the nests of other bees, mostly species of *Megachile*.

Apoidea, Apiformes, Apidae, Apinae

Thyreus species: cleptoparasitic in the nests of other bees.

** *Thyreus*, *T. alfkeni* (Brauns) and *T. delumbatus* (Vachal) associated with *A.* (*Z.*) *punctifrons.*

Apoidea, Apiformes, Apidae, Nomadinae

Epeolus species, cleptoparasitic in the nests of other bees.

Category 5

I. NESTING IN THE GROUND

b. *In non-friable soils* (typically compacted clayey soils)

i. In nest constructed entirely by the nester

Vespoidea, Vespidae, Masarinae, Masarini, Priscomasarina

** *Priscomasaris*, the single species *P. namibiensis* Gess: multicellular burrow surmounted by a turret.

Vespoidea, Vespidae, Masarinae, Masarini, Masarina

** *Ceramius*: 20 spp.; multicellular burrow surmounted by a turret; the nest architecture of each species group distinct.

** *Jugurtia*: at least 10 spp.; *Jugurtia confusa* Richards, multicellular burrow surmounted by a turret.

Vespoidea, Vespidae, Eumeninae

** *Antepipona scutellaris* G. Soika: one- or two-celled burrow surmounted by a turret.

** *Aethiopicodynerus*, *A. capensis* (de Saussure), *A. insignis* (de Saussure), *A. major* (de Saussure): one- or two-celled burrow surmounted by a turret.

** *Paravespa* (*Gestrodynerus*) *mima* G. Soika: one- or two-celled burrow surmounted by a turret.

** *Pseudepipona erythrospila* (Cameron): one-celled burrow surmounted by a turret.

Vespoidea, Pompilidae, Pepsinae, Ageniellini

** *Dichragenia*: *D. neavei* (Kohl), multicellular burrow surmounted by a funnel shaped turret; *D. pulchricoma* (Arnold), multicellular burrow surmounted by a retort shaped turret.

Apoidea, Spheciformes, Bembicinae, Bembicini

** *Bembecinus*, *B. cinguliger* (Smith) and *B. oxydorcus*: one- or two-celled burrow surmounted by a turret, the only two species in the world nesting in this way.

Apoidea, Apiformes, Apidae, Apinae, Anthophorini

Amegilla: some species.

** *Amegilla atrocincta* Lepeletier: one- or two-celled burrow surmounted by a turret.

Category 6

I. NESTING IN THE GROUND

b. *In non-friable soils* (typically compacted clayey soils)

ii. In pre-existing cavity modified by the nester

Vespoidea, Vespidae, Eumeninae

** Unidentified: nesting in burrow of *Bembecinus oxydorcus*; own nest entrance turret constructed.

Apoidea, Spheciformes, Ampulicidae

* *Ampulex mutilloides* Kohl: circumstantial evidence suggests nesting in burrow of cockroach, *Pilema* sp.

Apoidea, Spheciformes, Sphecidae, Sphecinae

** *Isodontia simoni* (du Buysson): found nesting in burrows of a cockroach, *Pilema* sp.; would probably use other suitable burrows; introduces plant fluff for cell closures.

** *Prionyx kirbii* (van der Linden): a nester in friable soil (Category 1) also found nesting in abandoned burrows of *Aethiopicodynerus insignis* (Category 5); would probably use other abandoned burrows.

** *Ammophila braunsi* Turner: found nesting in burrows of *Aethiopicodynerus insignis* (Category 5); would probably use other abandoned burrows and may also nest in friable soil.

Apoidea, Spheciformes, Crabronidae, Crabroninae

** *Tachysphex modestus* Arnold and *Tachysphex waltoni* Arnold: found nesting in burrows of *Aethiopicodynerus insignis* (Category 5); would probably use other abandoned burrows and may also nest in friable soil.

* *Pison allonymum* Schultz: strong circumstantial evidence of nesting in old or abandoned burrows of *Bembecinus cinguliger* and *B. oxydorcus* (Category 5).

Apoidea, Apiformes, Megachilidae, Megachilinae

Megachile (*Eutricharaea*) species.

** *M.* (*E.*) *aliceae* Cockerell, *M.* (*E.*) *meadewaldoi* Brauns: found nesting variously in abandoned and sometimes actively usurped burrows of *Ceramius*, *Aethiopicodynerus*, *Paravespa*, *Bembecinus* and *Antepipona* (all Category 5); use petal pieces to construct cells.

** *M.* (*E.*) *semiflava* Cockerell and *M.* (*E.*) *stellarum* Cockerell: found nesting variously in abandoned burrows of *Ceramius*, *Aethiopicodynerus* and *Dichragenia* (all Category 5); use leaf pieces to construct cells.

Megachile (*Creightonella*) species.

** *M.* (*C.*) *dorsata* (Smith), found nesting in abandoned burrows of *Aethiopicodynerus* (Category 5); uses leaf pieces to construct cells.

Apoidea, Apiformes, Apidae, Apinae

** *Tetralonia minuta* Friese: nesting in abandoned burrows of *Bembecinus* and *Aethiopicodynerus* (Category 5).

Category 7

I. NESTING IN THE GROUND

b. *In non-friable soils* (typically compacted clayey soils)

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

No species recorded.

Category 8

I. NESTING IN THE GROUND

b. *In non-friable soils* (typically compacted clayey soils)

iv. In nest constructed and provisioned by another

Chrysidoidea, Chrysididae

** *Allocoelia* spp., *A. bidens* Edney, *A. capensis* Smith, *A. glabra* Edney, *A. latinota* Edney and *A. quinquedens* Edney: parasitic in nests of Masarinae.

* *Chrysis splendens* Dahlbom: in nesting area of *Jugurtia confusa.*

** *Chrysis edwardsi* Buysson: parasitic in nests of *Aethiopicodynerus insignis.*

** *Pseudospinolia ardens* (Mocsary): parasitic in nests of *Aethiopicodynerus insignis.*

Vespoidea, Mutillidae

* *Brachymutilla gynandromorpha* André: females found in nesting area of *Jugurtia confusa.*

* *Dasylabris stimulatrix* (Smith): females found in nesting area of *Jugurtia confusa* and *Aethiopicodynerus insignis.*

** *Dasylabroides caffra* (Kohl): reared from cells of *Ceramius lichtensteinii*; females found in nesting areas of *Dichragenia pulchricoma*, *Aethiopicodynerus insignis*, *Bembecinus oxydorcus*, *Jugurtia confusa* and *Ceramius lichtensteinii.*

* *Glossotilla speculatrix* (Smith): females found in nesting area of *Bembecinus oxydorcus.*

* *Mutilla scabrofoveolata* Sichel & Radoszkowski: females found in nesting areas of *Dichragenia pulchricoma* and *Aethiopicodynerus insignis.*

* *Smicromyrme hecuba* (Péringuey): females found in nesting areas of *Aethiopicodynerus insignis*, *Bembecinus cinguliger* and *B. oxydorcus*; see also friable soils.

* *Smicromyrme* species as in Gess (1981): females found in nesting area of *Jugurtia confusa.*

Vespoidea, Pompilidae

** *Ceropales punctulatus* Cameron: parasitic in nests of *Dichragenia pulchricoma.*

Apoidea, Apiformes, Megachilidae

* *Coelioxys* (*Liothyrapis*) *lativentroides* Brauns: circumstancial evidence suggests that this species is parasitic in nests of Megachilidae (*Megachile* spp.) (Category 6); nesting in old or abandoned burrows of *Aethiopicodynerus insignis* (Category 7).

Category 9

II. NESTING IN OR ON VERTICAL BANKS

a. *In vertical banks*

i. In nest constructed entirely by the nester

Vespoidea, Pompilidae, Pepsinae, Ageniellini

* *Dichragenia jacob* (Arnold): repeated circumstantial evidence.

Vespoidea, Vespidae, Eumeninae

** *Antepipona tropicalis* (de Saussure): turreted nest in mud wall.

Apoidea, Spheciformes, Sphecidae, Sceliphrinae

** *Chalybion* (*Hemichalybion*) *spinolae* (Lepeletier): single-celled nest.

Apoidea, Spheciformes, Crabronidae, Bembicinae, Bembicini

** *Stizus imperialis* Handlirsch: multicellular nest.

Apoidea, Apiformes, Megachilidae, Megachilinae

** *Hoplitis* (*Anthocopa*) *similis* (Friese): single cell containing cell constructed from petal pieces.

Apoidea, Apiformes, Apidae, Apinae

** *Anthophora* (*Heliophila*) *braunsiana* Friese.

** *Anthophora* (*Heliophila*) *praecox* Friese.

** *Anthophora* (*Heliophila*) *rufolanata* Dours.

** *Anthophora* (*Heliophila*) *vestita* Smith.

** *Anthophora* (*Paramegilla*) *epichariformis* Gribodo.

Category 10

II. NESTING IN OR ON VERTICAL BANKS

a. *In vertical banks*

ii. In pre-existing cavity modified by the nester

Vespoidea, Pompilidae, Pepsinae, Ageniellini

Auplopus species.

** *Auplopus* sp.

Vespoidea, Vespidae, Eumeninae

** A species of eumenine as in Gess (1981): linear series of cells separated by mud partitions.

** *Euodynerus* sp.: mud entrance turret.

** *Rynchium marginellum sabulosum* (de Saussure): also in pre-existing cavities in open ended *Arundo donax* inflorescence stems (Category 38); linear series of cells separated by mud partitions.

** *Tricarinodynerus guerinii* (de Saussure): burrow with linear series of cells and with an entrance turret.

Apoidea, Spheciformes, Sphecidae, Sceliphrinae

** *Chalybion* (*Chalybion*) *tibiale* (Fabricius): see also nesting in pre-existing cavities in woody stems.

Apoidea, Spheciformes, Crabronidae, Crabroninae

* *Pison allonymum* Schultz: circumstantial evidence; see also nesting in the ground in pre-existing cavities in non-friable soil.

* *Pison montanum* Cameron: circumstantial evidence, see also nesting in the ground in pre-existing cavities in non-friable soil.

* *Trypoxylon*: at least three species; circumstantial evidence; see also nesting in the ground in pre-existing cavities in non-friable soil.

Apoidea, Apiformes, Colletidae

** *Hylaeus* species: nesting in old burrows of *Antepipona tropicalis* (de Saussure).

Apoidea, Apiformes, Megachilidae, Megachilinae, Anthidiini

** *Anthidiellum* (*Pygnanthidiellum*) *kimberleyanum* Friese.

** *Branthidium braunsi* (Friese).

** *Immanthidium junodi* (Friese): linear series of cells constructed from plant fluff.

Apoidea, Apiformes, Megachilidae, Megachilinae, Osmiini

* *Heriades freygessneri* Schletterer: circumstantial evidence, known also to nest in trap nests.

Apoidea, Apiformes, Megachilidae, Megachilinae, Megachilini

** *Megachile* (*Eutricharaea*) *gratiosa* Gerstaecker: linear series of cells constructed from green leaf pieces.

** *Megachile* (*Paracella*) *spinarum* Cockerell: linear series of cells constructed from green leaf pieces.

** *Megachile* (*Pseudomegachile*) *fulva* Smith.

** *Megachile* (*Pseudomegachile*) *schulthessi* Friese: linear cells, mud cell partitions, nest closure and entrance turret.

Category 11

II. NESTING IN OR ON VERTICAL BANKS

a. *In vertical banks*

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

No species recorded.

Category 12

II. NESTING IN OR ON VERTICAL BANKS

a. *In vertical banks*

iv. In nest constructed and provisioned by another

Chrysidoidea, Chrysididae

** *Chrysis laminata* Mocsáry (= *Octochrysis laminata* (Mocsáry)): reared from nests of *Tricarinodynerus guerinii* (de Saussure) (Category 9).

* *Chrysis laborans* Costa (= *Octochrysis mucronifera* (Mocsáry)): circumstantial evidence.

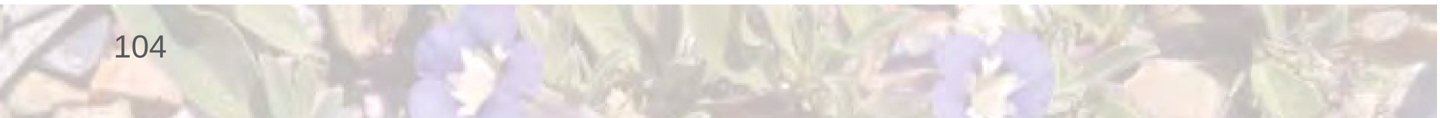
* *Chrysis antiqua* Brauns: circumstantial evidence.

* *Chrysis aurifascia* Brullé: circumstantial evidence.

* *Chrysis capitalis* Dahlbom: circumstantial evidence.

* *Chrysis dira* Mocsáry: circumstantial evidence.

* *Chrysidea pumila* (Klug) (as *C. africana* (Mocsáry) in Gess (1981)): circumstantial evidence; known to be a parasite of *Trypoxylon*; see in woody stems (Category 29).



* *Chrysidea ghilianii* Gribodo: circumstantial evidence.

* *Hedychrum coelestinum* Spinola: circumstantial evidence.

Vespoidea, Mutillidae

* *Antennotilla phoebe* (Peringuéy): circumstantial evidence.

* *Dasylabroides caffra* (Kohl): circumstantial evidence.

* *Mimecomutilla renominanda* Bischoff: circumstantial evidence.

* *Mutilla scabrofoveolata* Sichel & Radoszkowski: circumstantial evidence.

* *Ronisia trispilota* (Radoszkowski): circumstantial evidence.

** *Stenomutilla* species, reared from nest of eumenine as in Gess (1981) (Category 10).

Vespoidea, Sapygidae

* *Sapyga* (*Sapygina*) *simillima* Arnold: circumstantial evidence.

* *Sapyga* (*Sapigina*) *undulata* Gerstaecker: circumstantial evidence.

Apoidea, Megachilidae, Megachilinae, Anthidiini

** *Euaspis abdominalis* (Fabricius): circumstantial evidence that it is associated with nests of *Megachile* (*Chalicodoma*) *schulthessi* (Friese) (Category 10).

Apoidea, Megachilidae, Megachilinae, Megachilini

* *Coelioxys* (*Coelioxys*) *lucidicauda* Cockerell: circumstantial evidence.

* *Coelioxys* (*Lyothyrapis*) *bruneipes* Pasteels: circumstantial evidence; possibly parasitic in the nests of *Megachile* (*Paracella*) *spinarum* (Cockerell) (Category 10).

* *Coelioxys* (*Lyothyrapis*) *lativentris* Friese: circumstantial evidence; possibly parasitic in nests of *Anthophora* species (Category 9).

* *Coelioxys* (*Lyothyrapis*) *lativentroides* Brauns: circumstantial evidence; seen entering nests of *Megachile* (*Chalicodoma*) *schulthessi* (Friese) (Category 10).

Apoidea, Apidae, Apinae, Melectini

* *Thyreus* species: circumstantial evidence; possibly parasitic in nests of *Anthophora* species (Category 9).

Category 13

II. NESTING IN OR ON VERTICAL BANKS

b. *On vertical banks*

i. In nest constructed entirely by nester

Vespoidea, Vespidae, Eumeninae

** *Delta hottentotum concinnum* (de Saussure): single mud cell; ‘pot’ or ‘urn’.

** *Eumenes lucasius* de Saussure: single mud cell; ‘pot’ or ‘urn’; in sheltered positions on shale bank or in groups in cavities (e.g. one with ten and another with nine cells built in trap nests inserted into bank).

** *Pseudonortonia soror* (Kohl): single mud cell with a mud entrance turret.

* *Synagris abyssinica* Guérin: mud nests.

* *Synagris analis* de Saussure: mud nests.

Vespoidea, Vespidae, Polistinae

** *Ropalidia* species as in Gess (1981): ‘paper’ nest; comb; naked.

** *Polistes marginalis* (Fabricius): ‘paper’ nest; regular comb with short central stalk; naked.

** *Polistes smithii* de Saussure: ‘paper’ nest; comb; naked.

** *Belonogaster lateritia* Gerstaecker: ‘paper’ nest; irregular comb; naked.

** *Belonogaster dubia* Kohl: ‘paper’ nest; comb; naked; southeastern fringe of study area.

Apoidea, Spheciformes, Sphecidae, Sceliphrini

** *Sceliphron spirifex* (L.): multicellular mud nest; cells enclosed in a mud envelope.

Category 14

II. NESTING IN OR ON VERTICAL BANKS

b. *On vertical banks*

ii. In pre-existing cavity modified by the nester

Vespoidea, Vespidae, Eumeninae

** Eumenine species as in Gess (1981): nesting in cells of *Eumenes lucasius* (Category 13).

Apoidea, Spheciformes, Crabronidae, Crabroninae

** *Pison transvaalense* Cameron: in abandoned nest of *Polistes* sp.(Category 13).

Apoidea, Apiformes, Megachilidae, Megachilinae

** *Megachile* (*Eutricharaea*) *gratiosa* Gerstaecker: in abandoned nest of *Polistes* sp. (Category 13).

Category 15

II. NESTING IN OR ON VERTICAL BANKS

b. *On vertical banks*

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

No species recorded.

Category 16

II. NESTING IN OR ON VERTICAL BANKS

b. *On vertical banks*

iv. In nest constructed and provisioned by another

Chrysidoidea, Chrysididae

** *Chrysis* species as in Gess (1981): reared from nest of *Eumenes lucasius* (Category 14).

** *Chrysis* sp. (*wahlbergi* group): reared from nests of *Tricarinodynerus guerinii* (Category 10).

Chrysis antiqua (Brauns): possibly.

Vespoidea, Mutillidae

** *Stenomutilla* species as in Gess (1981): parasitic in nests of eumenine (Category 9).

Apoidea, Apiformes, Megachilidae, Megachilinae, Anthidiini

** *Euaspis abdominalis* (Fabricius): parasitic in mud nest of *Synagris* (Vespidae, Eumeninae); found sheltering in mud nest, probably of *Megachile* (*Gronoceras*) *cincta* (Fabricius) (see also reared from nest of *Megachile* (*Gronoceras*) *schulthessi* (Friese) in hollow plant stem).

Category 17

III. NESTING ON STONES

i. In nest constructed entirely by nester

Vespoidea, Pompilidae, Pepsinae, Ageniellini

** *Auplopus rossi nigricornis* (Arnold): group of mud cells attached to underside of rock.

Vespoidea, Vespidae, Masarinae

** *Celonites andrei* Brauns: several mud cells.

** *Celonites michaelseni* von Schulthess: several mud cells.

Vespoidea, Vespidae, Eumeninae

Delta caffrum (L.), multicellular mud nest.

Apoidea, Apiformes, Megachilidae, Megachilinae, Osmiini

** *Othinosmia* (*Megaloheriades*) *jansei* (Brauns): formerly *Hoplitis jansei* (Brauns); groups of cells constructed from tiny pebbles and resin; with or without a covering.

Category 18

III. NESTING ON STONES

ii. In pre-existing cavity modified by the nester

Apoidea, Apiformes, Megachilidae

** *Megachile* (*Eutricharaea*) *gratiosa* Gerstaecker: cells constructed from pieces of green leaf, e.g. in cell of *Othinosmia* (*Megaloheriades*) *jansei* (Brauns) (Category 17); see also vertical banks (Category 10) and woody plants (Category 29).

Category 19

III. NESTING ON STONES

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

Category 20

III. NESTING ON STONES

iv. In nest constructed and provisioned by another

Vespoidea, Mutillidae

** *Antennotilla phoebe* (Péringuey): parasitoid of *Auplopus rossi nigricornis* (Arnold) (Category 17).

Category 21

IV. NESTING IN SNAIL SHELLS

A. SAND-FILLED SNAIL SHELLS

i. In nest constructed entirely by the nester

Vespoidea, Vespidae, Masarinae

** Seven species of *Quartinia*: *Q. australis* Gess, *Q. bonaespei* Gess, *Q. conchicola* Gess, *Q. namaqua* Gess, *Q. namaquensis* Gess, *Q. obibensis* Gess and *Q. refugicola* Gess; turreted, multicellular burrow, stabilised with self-generated silk.

Category 22

IV. NESTING IN SNAIL SHELLS

A. SAND-FILLED SNAIL SHELLS

ii. In pre-existing cavity modified by the nester

No species recorded.

Category 23

IV. NESTING IN SNAIL SHELLS

A. SAND-FILLED SNAIL SHELLS

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

No species recorded.

Category 24

IV. NESTING IN SNAIL SHELLS

A. SAND-FILLED SNAIL SHELLS

iv. In nest constructed and provisioned by another

Chrysidoidea, Chrysididae

** *Allocoelia mocsaryi* Brauns: reared from nests of *Quartinia* spp. nesting in sand trapped in snail shells (Category 21).

Chrysidoidea, Chrysididae

** *Tricholabiodes* species: parasitic in nests of *Quartinia* in sand in snail shells (Category 21).

** Undescribed genus and species: parasitic in nests of *Quartinia* in sand in snail shells (Category 21).

Category 25

IV. NESTING IN SNAIL SHELLS

B. EMPTY SNAIL SHELLS

i. In nest constructed entirely by the nester

No species recorded.

Category 26

IV. NESTING IN SNAIL SHELLS

B. EMPTY SNAIL SHELLS

ii. In pre-existing cavity modified by the nester

Vespoidea, Vespidae, Eumeninae

** *Alastor ricae* Giordani Soika: cell with pebble and matrix closures.

Apoidea, Megachilidae, Megachilinae, Anthidiini

** Two species of anthidiine, *Afranthidium* (*Afranthidium*) *hamaticauda* Pasteels and 'anthidiine sp. 2': cells constructed from plant fluff.

Apoidea, Megachilidae, Megachilinae, Osmiini

** Three species of *Wainia* (*Caposmia*), *W.* (*C.*) *elizabethae* (Friese), *W.* (*C.*) *atrorufa* (Friese) (= Gess sp. A) and *W.* (*C.*) *gessorum* Kuhlmann (= Gess sp. C): cells constructed from sand and resin-like substance.

** *Hoplitis* (*Anthocopa*) *conchophila* Kuhlmann: cells constructed from petal pieces.

Category 27

IV. NESTING IN SNAIL SHELLS

B. EMPTY SNAIL SHELLS

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

No species recorded.

Category 28

IV. NESTING IN SNAIL SHELLS

B. EMPTY SNAIL SHELLS

iv. In nest constructed and provisioned by another

Chrysidoidea, Chrysididae

** *Chrysis grootdermensis* Koch: reared from snail shells, probably from nests of *Alastor ricae* Giordani Soika or *Hoplitis* (*Anthocopa*) *conchophila* Kuhlmann (Category 26).

Category 29

V. NESTING IN OR ON PLANTS

A. IN PLANTS

a. *Within woody stems*

i. In nest constructed entirely by the nester

Apoidea, Apiformes, Apidae, Xylocopinae

** *Xylocopa caffra* (L.): multicellular burrow; cells in linear series.

** *Xylocopa flavicollis* (de Geer): multicellular burrow; cells in linear series.

** *Xylocopa flavorufa* (de Geer): multicellular burrow: cells in linear series.

Category 30

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

Vespoidea, Vespidae, Eumeninae

** *Knemodynerus euryspilus* (Cameron): linear series of cells; mud partitions and closure.

Apoidea, Spheciformes, Ampulcidae

** *Ampulex bantuae* Gess: single celled nest; in abandoned larval galleries of *Ceroplesis hottentota* (Fabricius) (Cerambycidae) in branches of *Acacia karroo*; detritus closure.

** *Ampulex denticollis* Cameron: single celled nest; in trap nests hung in *Acacia karroo.*

Ampulex spp. (other than above): number of species not established.

Dolichurus sp.

Apoidea, Spheciformes, Sphecidae

** *Chalybion* (*Chalybion*) *tibiale* (Fabricius): linear series of cells; mud cell partitions and closure; outer surface of partitions and closure coated with uric acid from bird droppings.

** *Holotachysphex turneri* (Arnold): linear series of cells; cell partitions of coarse detritus and earth; see also hollow stems.

** *Isodontia pelopoeiformis* (Dahlbom): linear series of cells; cell partitions of plant ‘fluff’; preliminary plug and closure a layer of plant ‘fluff’ together with layer of earth and debris.

** *Isodontia stanleyi* (Kohl): linear series of cells; preliminary plug, cell partitions and nest closure grass; see also pithy stems and hollow stems.

Apoidea, Spheciformes, Crabronidae, Larrinae

** *Nitela* sp.: linear series of cells; in boring of *Xylocopa sicheli* in *Berkheya* (Category 29).

** *Pison montanum* Cameron: linear series of cells; mud partitions and closure.

** *Trypoxylon* species as in Gess (1981) and additional species (number not established): linear series of cells; mud partitions and closure.

Apoidea, Apiformes, Colletidae

** *Hylaeus braunsi* (Alfken) and additional species (number not established): linear series of cells; cell partitions and nest closure of very shiny, thin, transparent cellophane-like material.

Apoidea, Apiformes, Megachilidae, Megachilinae, Lithurgini

Lithurge sp.

Apoidea, Apiformes, Megachilidae, Megachilinae, Anthidiini

** *Immanthidium junodi* (Friese): linear series of cells; cell partitions and closing plug of cotton wool-like plant fibre.

Apoidea, Apiformes, Megachilidae, Megachilinae, Megachilini

** *Heriades* (*Heriades*) *freygessneri* Schletterer.

Apoidea, Apiformes, Megachilidae, Megachilinae, Megachilini

** *Megachile* (*Eutricharaea*) *gratiosa* Gerstaecker: linear series of cells constructed from pieces of green leaves.

Megachile (*Pseudomegachile*) *bullata* (Friese).

Megachile (*Pseudomegachile*) *fulva* (Smith).

** *Megachile* (*Pseudomegachile*) *sinuata* Friese (formerly *Chalicodoma sinuata* (Friese), e.g. in abandoned burrows of *Xylocopa* (Category 29)): in linear series; constructed from mud; see also pithy stems (Category 33) and hollow stems (Category 37).

** *Megachile* (*Paracella*) *spinarum* Cockerell: linear series of cells constructed from pieces of green leaves.

Category 31

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

No species recorded.

Category 32

V. NESTING IN OR ON PLANTS
A. IN PLANTS
a. *Within woody stems*
iv. In nest constructed and provisioned by another

Chrysidoidea, Chrysididae

** *Chrysidea africana* Mocsáry: parasitic in nests of *Trypoxylon* (Category 30).

** *Chrysis districta* Buysson: parasitic in nests of *Isodontia pelopoeiformis* Dahlbom (Category 30).

** *Praestochrysis inops* (Gribodo) (formerly *Chrysis inops* Gribodo): parasitic in nests of *Pison* (Category 30).

** *Chrysis* sp. (near *C. purpuripyga* Edney): parasitic in nests of *Trypoxylon* (Category 30).

** *Chrysis lincea* Fabricius: from trap nest.

** *Chrysis hoplites* Mocsáry (= *Octochrysis hoplitis* (Mocsáry)): parasitic in nests of *Knemodynerus euryspilus* (Cameron) (Category 30).

Bethyloidea, Sapygidae

Sapyga (*Sapygina*) *simillima* Arnold: parasitic in nests of *Heriades* (Category 30).

Apoidea, Apiformes, Megachilidae

** *Coelioxys* (*Coelioxys*) *penetratrix* Smith: parasitic in nests of *Megachile* (*Paracella*) *spinarum* (Category 30).

Category 33

V. NESTING IN OR ON PLANTS

A. IN PLANTS

b. *Within pithy stems*

i. In nest constructed entirely by the nester

Vespoidea, Vespidae, Eumeninae

Raphiglossa natalensis Smith: other species of *Raphiglossa*; number of species not established; dry stems.

Apoidea, Spheciformes, Crabronidae, Crabroninae

** *Dasyproctus* species: variously in green stems and possibly dry stems of monocots and dicots; *Dasyproctus bipunctatus* Lepeletier & Brullé in *Watsonia* (Iridaceae) inflorescence stems; *Dasyproctus westermanni* (Dahlbom) in green inflorescence stems of *Drimia altissima* (L.f.) Ker Gawl. (Hyacinthaceae), cells in ascending and descending linear series; *Dasyproctus dubiosus* (Arnold), *D. immitus* (de Saussure), *D. ruficaudis* (Arnold) possibly in *Berkheya* (Asteraceae).

Apoidea, Apiformes, Xylocopinae

** At least four species of *Ceratina*, *C. truncata* Friese, *C. labrosa* Friese, *C. nasalis* Friese and *C. perpolita* Cockerell: variously in dry aloe, *Berkheya* or other dry pithy inflorescence stems.

** *Xylocopa caffra* (L.): in dry aloe inflorescence stems; cells in two ascending and descending linear series within an H-shaped burrow.

** *Xylocopa hottentotta* Smith: in dry aloe inflorescence stems; cells in ascending and descending linear series in an unbranched burrow.

** *Xylocopa sicheli* (Vachal): in dry aloe inflorescence stems; cells in ascending and descending linear series in an unbranched burrow.

Category 34

V. NESTING IN OR ON PLANTS

A. IN PLANTS

b. *Within pithy stems*

ii. In pre-existing cavity modified by the nester

Apoidea, Spheciformes, Sphecidae, Sphecinae

** *Isodontia stanleyi* (Kohl): often in abandoned *Xylocopa* burrows in dry aloe inflorescence stems (Category 33); see also pre-existing burrows in woody stems and hollow stems; cells in linear series; initial plug, cell partitions and nest closure of grass.

Apoidea, Spheciformes, Crabronidae, Larrinae

** *Trypoxylon* species as in Gess (1981): other species number not established; often in abandoned burrows of *Dasyproctus* and *Ceratina truncata* Friese (Category 33); cell partitions and cell closure of mud.

Apoidea, Apiformes, Megachilidae, Megachilinae, Anthidiini

** *Capanthidium capicola* (Friese): often in abandoned burrows of *Ceratina* (Category 33); cell partitions of cotton wool-like plant fibres.

** *Immanthidium junodi* (Friese): often in abandoned burrows of *Ceratina* and *Dasyproctus* (both Category 33); cell partitions and nest closure of cotton wool-like plant fibre; see also in pre-existing cavities in woody stems.

Apoidea, Apiformes, Megachilidae, Megachilinae, Lithurgini

Lithurge sp.

Apoidea, Apiformes, Megachilidae, Megachilinae, Osmiini

** *Heriades spiniscutatus* (Cameron), e.g. in abandoned burrows of *Dasyproctus* (Category 33); cell partitions and nest closure of resin-like substance.

Apoidea, Apiformes, Megachilidae, Megachilinae, Megachilini

** *Megachile* (*Pseudomegachile*) *sinuata* Friese (formerly *Chalicodoma sinuata* (Friese)): often in abandoned burrows of *Xylocopa* (Category 33); in linear series constructed from mud.

** *Megachile* (*Paracella*) *spinarum* Cockerell: often in abandoned burrows of *Xylocopa* (Category 33); cells in linear series, constructed from green leaf pieces.

Category 35

V. NESTING IN OR ON PLANTS

A. IN PLANTS

b. *Within pithy stems*

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

Apoidea, Apiformes, Apidae, Xylocopinae

** *Allodape rufogastra* Lep. & Serv. or *Allodape exoloma* Strand: often in abandoned *Dasyproctus* burrows (Category 33); no cell partitions.

Category 36

V. NESTING IN OR ON PLANTS

A. IN PLANTS

b. *Within pithy stems*

iv. In nest constructed and provisioned by another

Chrysidoidea, Chrysididae

Chrysidea africana Mocsáry: in nests of *Trypoxylon* (Category 33).

Chrysis species (near *C. purpuripyga* Edney): in nests of *Trypoxylon* (Category 33).

Category 37

V. NESTING IN OR ON PLANTS

A. IN PLANTS

c. *Within hollow stems*

i. In nest constructed entirely by the nester

Apoidea, Apiformes, Xylocopinae

** *Xylocopa scioensis* Gribodo: nest exclusively in dry hollow culms of *Phragmites australis* (Graminae); entrance hole cut; cells in linear series, ascending and descending.

Category 38

V. NESTING IN OR ON PLANTS

A. IN PLANTS

c. *Within hollow stems*

ii. In pre-existing cavity modified by the nester

** *Rynchium marginellum sabulosum* (de Saussure): also in pre-existing cavities in vertical banks (Category 10); linear series of cells separated by mud partitions.

Apoidea, Spheciformes, Sphecidae

** *Isodontia stanleyi* (Kohl): often in abandoned *Xylocopa scioensis* (Vachal) burrows (Category 37); see also pre-existing burrows in woody stems (Category 30) and pithy stems (Category 34); cells in linear series; initial plug, cell partitions and nest closure of grass.

** *Holotachysphex turneri* (Arnold): often in abandoned *Xylocopa scioensis* (Vachal) burrows (Category 37); linear series of cells; cell partitions of coarse detritus and earth; see also woody stems (Category 30).

Apoidea, Spheciformes, Crabronidae, Larrinae

** *Trypoxylon* species as in Gess (1981).

Apoidea, Apiformes, Megachilidae

** *Megachile* (*Pseudomegachile*) *sinuata* Friese (formerly *Chalicodoma sinuata* (Friese): often in abandoned burrows of *Xylocopa scioensis* (Category 37); in linear series; constructed from mud; see also woody stems (Category 30) and pithy stems (Category 34).

Category 39

V. NESTING IN OR ON PLANTS

A. IN PLANTS

c. *Within hollow stems*

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

No species recorded.

Category 40

V. NESTING IN OR ON PLANTS

A. IN PLANTS

c. *Within hollow stems*

iv. In nest constructed and provisioned by another

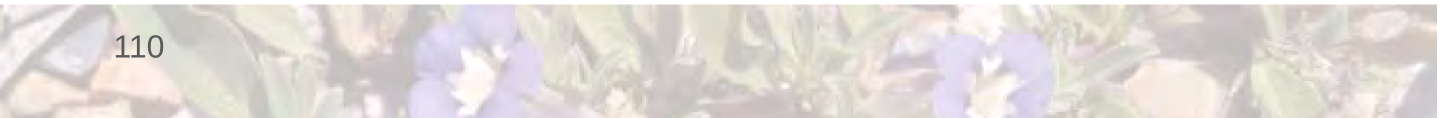
Chrysidoidea, Chrysididae

Chrysidea africana Mocsáry: in nests of *Trypoxylon.*

Trichrysis polinierii (Guérin) (formerly as *Chrysis* near *C. purpuripyga* Edney in Gess (1981)): in nests of *Trypoxylon* (Category 38).

Apoidea, Apiformes, Megachilidae, Megachilinae, Anthidiini

** *Euaspis abdominalis* (Fabricius): parasitic in nest of *Megachile* (*Gronoceras*) *schulthessi* (Friese) (Category 38); see also in mud nest of *Synagris* (Vespidae: Eumeninae) and found sheltering in mud nest, probably of *Megachile* (*Gronoceras*) *cincta* (Fabricius), on vertical bank (Category 13).



Category 41

V. NESTING IN OR ON PLANTS

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

i. In nest constructed entirely by the nester

Vespoidea, Vespidae, Masarinae

** *Celonites capensis* Brauns: putative nest of *Celonites promontorii* Brauns and other; spp. number not established, group of mud cells covered by an envelope.

Vespoidea, Vespidae, Eumeninae

Afreumenes violaceus (Giordani Soika): single mud cell, ‘pot’ or ‘urn’.

Delta caffrum (L.): group of mud cells covered by an envelope.

Delta hottentotum concinnum (de Saussure): single mud cell, ‘pot’ or ‘urn’.

Delta emarginatum (L.) (= *Delta maxillosus* (de Geer)): group of mud cells covered by an envelope.

** *Eumenes lucasius* de Saussure: single mud cell, ‘pot’ or ‘urn’.

Zetheumenidion: some species at least.

Vespoidea, Vespidae, Polistinae

** *Polistes marginalis* Fabricius: naked paper comb.

** *Polistes smithii* de Saussure: naked paper comb.

** *Ropalidia* species as in Gess (1981) and others: naked paper comb.

Apoidea, Speciformes, Sphecidae, Sphecinae

Sceliphron quartinae (Gribodo): multicellular nest constructed from dung.

Apoidea, Apiformes, Megachilidae, Anthidiini

** *Serapista rufipes* Friese: multicellular nest constructed from plant fibres.

** *Serapista denticulata* (Smith): multicellular nest constructed from plant fibres either on plants or in a burrow in the ground.

Apoidea, Apiformes, Megachilidae, Osmiini

** *Othinosmia* (*Megaloheriades*) *globicola* (Stadelmann): multicellular globular nest constructed from minute pebbles and resin attached to stems of small woody shrubs.

Category 42

V. NESTING IN OR ON PLANTS

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

ii. In pre-existing cavity modified by the nester

Apoidea, Spheciformes, Crabronidae, Crabroninae

Pison species: probable; see nesting in *Polistes* nest on vertical bank.

Category 43

V. NESTING IN OR ON PLANTS

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

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

No species recorded.

Category 44

V. NESTING IN OR ON PLANTS

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

iv. In nest constructed and provisioned by another

Chrysidoidea, Chrysididae

** *Chrysis lincea* Fabricius: reared from aerial mud nests of *Delta*, one of which was of *D. caffrum* (L.) (Category 41).

** *Spintharina arnoldi* (Brauns): reared from aerial mud nest of *Celonites*, putative nest of *Celonites promontorii* Brauns (Category 41).

** *Stilbum cynurum* (Förster): reared from aerial mud nest of *Delta caffrum* (L.) (Category 41).

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5. The impact of agricultural land use and coastal exploitation on the diversity of wasps and bees

During the 1980s veld deterioration in South Africa, which had been reported on for at least 100 years, reached such a level that the South African Foundation for Research Development brought into being a National Programme for Ecosystem Research. The semi-arid to arid areas fell primarily within the Karoo Biome Project (Cowling *et al.* 1986; Cowling & Roux 1987), the varied studies of which were synthesised in the book *The Karoo: Ecological patterns and processes* (Dean & Milton 1999). This project stimulated considerable co-operative research and attracted our participation.

Worldwide environmental degradation had reached such an obvious level that in 1992 the United Nations recognised its global nature, bringing together representatives from 179 countries to take part in the Rio Earth Summit at which was formulated the Convention on Biological Diversity (CBD). Various initiatives followed, for example a general examination of land degradation in South Africa (Hoffman & Ashwell 2001) and the SANBI Conservation Farming Project (Donaldson 2002). Another initiative was a cooperative project between Germany, Namibia and South Africa, BIOTA Southern Africa, a sub-project of BIOTA Africa that aimed to feed into the CBD's 2010 goal and the NEPAD (New Partnership for Africa's Development) Environment Action Plan. The latter undertook an in-depth 10 year monitoring of 35 standardised sites forming a transect from the Cape to the Kunene (Jürgens *et al*. 2010).

An overview of historical and present land use in southern Africa, in the context of the impact of agricultural land use on populations of wasps and bees, has been variously presented by us (for example, Gess & Gess 1993 and Gess 2001, 2002 for wasps and bees overall, and Gess 1996 and Gess & Gess 2010 for pollen wasps in particular).

The most notable change in agricultural land use in recent years has been the shift from stock farming to game farming, which is affecting an ever-increasing number of farms in the semi-arid areas, particularly in the Eastern Cape and Namibia. Another notable change is the giving over of farms for so-called development, which increases town sprawl and coastal development. On the positive side, there has been an increase in conservancies created by agreement between neighbouring private landholders and the creation of so-called greater conservation areas.

In Gess & Gess (1993) we concluded that the aspects of agricultural land use adversely affecting bees and wasps in the Karoo are:

- Excessive stocking rates.
- Heavy selective grazing and browsing.
- Excessive trampling.
- Water pollution by stock.
- Large-scale impoundment of water.
- Canalisation of water.
- Extensive replacement of natural vegetation by cultivated pastures.
- Extensive replacement of natural vegetation by crop plants.
- Use of insecticides for crop protection.
- The spread of alien invasive plant species.
- Bush cutting and extensive removal of dry wood.

These conclusions remained unchanged throughout our later considerations of the subject and were popularised through a poster (Gess & Gess 2004), made available to a variety of educational and information centres, and through popular articles (for example Gess 2007). They can be applied to the entire region and were adopted in preliminary documents for South African participation in the African Pollinator Initiative (e.g. Clark & Hawkes 2004).

Excessive stocking rates resulting in heavy selective grazing and browsing, excessive trampling and water pollution by stock

The impact of stock and game farming on the environment is variable. It is well known and accepted that variations in rainfall and vegetation should dictate different choices of breed of goats, sheep or cattle and stocking rates but that all too often unwise choices are made. Often stocking rates are too high and there is a reluctance, for various reasons, to consider reducing numbers to appropriate levels (compare Figure I.5.1 with Figure I.1.8.c; see also Gess & Gess 2010 figures 163–165). As noted by Hoffman & Ashwell (2001), the differences between conditions and farming practices in the commercial and communal areas make the development of a general theory of veld management difficult. A relatively recent cause of overstocking in the northern Kaokoveld has been tourism. The Himba people who were previously nomadic have settled in the area to the south of the Epupa Falls in order to benefit from the visits of tourists to the area. Consequently, this area is no longer rested. Continuous grazing can have long-term effects on the composition of plant communi-

Figure I.5.1.—Overgrazed area south of the Kgalagadi Transfrontier Park.

ties. In addition to removing mature plants, animals eat flowers, thus reducing seed set and furthermore trample and kill young seedlings (Hoffman & Ashwell 2001).

Game farming has given indigenous mammals a commercial value, which is seen as advantageous for their preservation. However, it has also become apparent that to satisfy clients, species inappropriate to an area or a vegetation type are introduced. Furthermore, even in the case of animals suited to an area, due to the inability of the animals to move on when they have exhausted the carrying capacity of the farm, one sees alarming degradation taking place.

The impact of injudicious stock and game farming on diversity is apparent and is being researched. Here we shall confine ourselves to considering the impact on wasp and bee diversity. It has not been possible to quantify the impact, however, we present some observations which give some indication of the magnitude of the impact.

Ground nesting wasps and bees, both those nesting in friable soil and those nesting in non-friable soil, require open patches in which to nest. Such bare areas were historically created by the natural activity of animals, including nomadic humans. Problems have arisen as a result of human settlement and the consequent build up of herds of animals, both domestic stock and game, which no longer leave areas of land when resources become depleted. Attempts have been made to overcome the problem on commercial farms by designing various forms of rotational grazing. Clearly, ground nesting wasps and bees cannot nest successfully where the ground is heavily trampled. Indeed, we have seen established nesting areas destroyed by trampling. In these cases, it is not only the nesters which are displaced but also their associates.

If a species is widespread and such disturbances are patchy, no serious overall drop in the population size of the species will occur. However, if the species has a limited distribution and the disturbance is extensive there may be a serious reduction in the population size or even loss of the species.

Nesters in non-friable clayey soil require water for nest excavation. In a natural system, such water is collected from still water most often in residual pools in drainage channels and from rainwater pools that collect in depressions. Some species always collect water at a shallow sloping edge and others always alight on the water surface. Species collecting mud for nesting come to pools with a shallow muddy edge. Where there is overstocking with domestic stock or game the water and mud become polluted and unsuitable. Additional watering points provided for stock and game are various in nature. Clearly, water in steep-sided troughs is only available to species that collect water from the surface unless there is seepage. Water in man-made earthen dams with a shallow edge is available to species that collect water or mud from the edge of the water body and those that collect water from the water surface provided that the water is not polluted. We have observed that such additional water sources may result in an increase in populations of aculeates requiring water or mud. However, when such a reservoir is damaged, resulting in the water being lost, or is removed, there is a population crash.

Ostriches farmed, as they are, in large numbers in fenced areas, cause total destruction of wasp and bee habitats. The ostrich feather boom was responsible for the establishment of widespread ostrich farming. However, with the decline in the popularity of ostrich feathers in the fashion world, farming of ostriches almost entirely ceased in the northern and eastern areas but remained in the Little Karoo, mainly in the area around Oudtshoorn. The current increasing demand for ostrich leather and ostrich meat has brought about a new expansion in ostrich farming with a return to the farming of ostriches in the Northern and Eastern Cape. Of particular concern is the Richtersveld area.

Changes in the composition of the vegetation of an area resulting from selective grazing and browsing not only bring about changes to pollen and nectar resources and available phytophagous prey for ground nesters, but for all wasps and bees whether they nest in the ground, in or on vertical banks, on stones, or in or on plants. None of these or their associates are therefore exempt and nor are the plants which depend upon them for services.

Furthermore, the use of insecticides for locust control has negative implications for all insect life in the areas where it is used and therefore for the plants which depend on the services of those insects.

Extensive, intensive cultivation leading to canalisation of water, extensive replacement of natural vegetation by cultivated pastures, extensive replacement of natural vegetation by crop plants and use of insecticides for crop protection

Historical cultivation of the land for the production of fodder, fruit and vegetables was on a small scale and had little impact on populations of wasps and bees. In recent years the ever increasing demand for these crops has resulted in ever increasing widespread total destruction of habitats. The extent of the cultivated areas and of the distribution ranges of the wasps and bees affected will govern the overall extent of this loss.

In those areas where small scale dry land cultivation is practised as is the case in Namaqualand there is a mosaic composed of natural communities, areas used for small stock farming in which species diversity has been severely reduced, cultivated areas in which the soil structure has been destroyed and the naturally occurring plants replaced with exotic crop plants, and fallow land with a small number of pioneer plants offering resources to a limited range of insects (Figures I.5.2–5). Recovery of the vegetation on such lands has been shown to be slow. Fields abandoned more than 50 years ago are easily distinguishable from the surrounding vegetation (Van Rooyen *et al*. 2010). Clearly, in much of Namaqualand many species of wasps and bees have been displaced.

In the vast wheat growing areas of the Western Cape only small patches of natural vegetation remain (Figure I.1.6). It is clear that in these extensive areas of monoculture wasps and bees have been almost entirely displaced. Furthermore, the drift of insecticides used to spray wheat lands across to the small remaining patches of natural

Figure I.5.2.—Mosaic of land use west of the Kamiesberg, Namaqualand.

Figure I.5.3.—Dry land wheat farming, Grootvlei Farm, Namaqualand.

vegetation will further impact negatively on any wasps and bees for which all habitat requirements may be present. An attempt to evaluate the effects of fragmentation on pollinator diversity and plant reproductive success in the Renosterveld shrublands of South Africa underlined the need for greater focus on the habitat requirements of pollinators (Donaldson *et al.* 2002).

Similarly, in the wine lands of the Western Cape there is little hope for most wasps and bees (Figures I.5.7a–c).

In those areas where crops are farmed under irrigation, cultivated land is mainly concentrated on the old flood plains and immediately adjacent areas, most notably in the Olifants River Valley (Gess & Gess 2010, Figure 160), and the Little Karoo. These are the same areas that are particularly suited to nesting by a wide range of ground nesting wasps and bees—both those nesting in friable soil and those nesting in non-friable soil with the aid of water. Ploughing, clearing of natural vegetation and replacement with a limited range of fodder and crop plants, application of 'out of season artificial rain' and the use of insecticides results in local extermination of entire communities. Furthermore, the associated construction of dam walls across rivers has resulted in total destruction of some nesting areas and a change in the availability of water in others. Water in steep-sided canals is unavailable to wasps and bees.

Figure I.5.4.—Fallow land with mixed pioneer Asteraceae, Skilpad Farm, Namaqualand.

Figure I.5.5.—Fallow land with pioneer Aizoaceae, Mesembryanthema, *Conicosia*, west of the Olifants River Valley.

Figure I.5.6.—Extensive monoculture, wheat, Western Cape.

Formerly, strip ploughing was general practice in the Sandveld to the west of the Olifants River Valley, in some areas of the Olifants River Valley and some areas to the east of the Cederberg. The strips, depending upon the extent of the cultivated areas and the width of the strips, did offer refuges to ground nesting wasps and bees and their associates. Replacement of strips of natural vegetation with saltbush (Figure I.5.8) and in the Sandveld the more recent extensive clearing of land for the growing of potatoes (Gess & Gess 2010, Figure 162), where practised leads to the elimination of almost all wasps and bees.

Figure I.5.7.—Extensive monoculture, vines: a. Paarl Valley; b. Lutzville, Olifants River Valley; c. west of Ladismith, Little Karoo.

Changes in the composition of the vegetation of an area resulting from extensive, intensive cultivation not only bring about changes to the available pollen and nectar resources and available phytophagous prey for ground nesters, but for all wasps and bees whether they nest in the ground, in or on vertical banks, on stones, or in or on plants. None of these or their associates are therefore exempt. Furthermore, the effects of the use of insecticides for crop protection extends beyond the cultivated areas.

Figure I.5.8.—Extensive cultivation to the west of the Olifants River Valley, lands divided by parallel rows of saltbush.

The spread of alien invasive plant species

The most significant alien invaders of the arid interior are species of the genera *Prosopis* (Mimosoideae) and *Opuntia* (Cactaceae) (Hoffman & Ashwell 2001). The natural species composition of riverine vegetation is being seriously altered over much of the Nama-Karoo by the spread of mesquites (*Prosopis* species), most notably *P. glandulosa* Torrey. Not only is this weed replacing indigenous species, it is also threatening ground water supplies, with estimates that this species collectively extracts about 192 million cubic metres of water each year (Hoffman & Ashwell 2001).

Altering the composition of riverine vegetation not only changes the available flower resources and phytophagous prey species offered, but it also affects nesters in stems. This includes carpenter bees seeking dry wood for burrow excavation and species seeking pre-existing cavities due not only to the affect on carpenter bees, but also due to the affect on wood boring beetles.

Loss of species nesting in woody stems also result in loss of their associates and their services as pollinators and predators extending beyond the limits of the riverine vegetation.

Ten invasive *Opuntia* species are listed in Henderson (2001). Probably the best known is the prickly pear, *Opuntia ficus-indica* (L.) Mill., which is found across most of South Africa but most notably in the east. Attempts to control it are hindered due to the value attached to its fruit. The jointed cactus *Opuntia aurantiaca* Lindl. is spreading rapidly in the east, not only on land farmed for domestic stock but also on game farms and roadsides. Both these species displace the indigenous vegetation.

The destructive effect of the introduction and spread of Australian *Acacias* is well documented.

In a recent survey of the use of snail shells for nesting by aculeate wasps and bees, we drew attention to the affects of the spread of *Theba pisana* along the coast (Gess & Gess 2008). *Theba pisana* was apparently introduced into Cape Town from Europe around 1881. Since then it has spread north along the west coast at least to Port Nolloth and east along the south coast at least as far as East London. In the west, the Agricultural Research Council has investigated its invasion of vineyards and citrus orchards. It has been the subject of considerable study in Southern and Western Australia and California where its explosive reproductive rates are such that in orchards it can be found in densities of up to 3 000 snails per tree! Apart from damaging crops, its copious slime production is considered to make infested plants unpalatable to stock, to other snails and also, notably, to pollinators.

In a recent survey of the use of snail shells for nesting by aculeate wasps and bees, we drew attention to the affects of the spread of *Theba pisana* along the coast (Gess & Gess 2008).

Bush cutting and extensive removal of dry wood

An early well-documented instance of the impact of wholesale injudicious bush cutting for firewood was that which took place on the Cape Flats in the early days of the settlement at the Cape. Not only was the vegetation and its associates lost, but the sandy soil of the entire area became unstable. This led to the introduction of Australian *Acacia* species in order to stabilise the shifting sand. Stabilisation was successfully achieved but the previously existing ecosystem was lost.

The gathering of dead wood for making fires is not new. However, with human settlement and the increase in population size, despite the use of other fuels, there has been an increased demand for firewood which is used not only in the areas where it is gathered but is also supplied to town dwellers for heating of houses and more especially for the currently fashionable braai. Some of the wood sold comes from the clearing of exotic invaders, which is positive. Unfortunately though, much of the wood in the semi-arid to arid areas is collected from the scant supply available along drainage channels—the only places where woody plants with substantial stems are to be found.

The gathering of such wood clearly has a negative impact on the populations of wasps and bees that nest in woody plant stems. This includes species that excavate burrows in dry woody stems, some carpenter bees, and those species that nest in pre-existing cavities that result from the activity of these bees and of beetles such as longhorned beetles (Cerambycidae) the larvae of which feed in the living stems, often resulting in their death. In addition, the populations of parasites and nest parasites, wasps, bees and non-aculeate wasps, beetles and flies, associated with nesters in wood will be affected.

Coastal exploitation

Coastal development has accelerated alarmingly in the past ten years. Particularly disturbing has been destruction of dunes and dune vegetation as the result of stabilisation of dunes and building of roads, parking areas and houses right up to the beach. Clearly, this results in the loss of most habitat specific organisms.

Figure I.5.9.—Strip mining at Hondeklip Bay, Namaqualand.

The effect of coastal diamond mining along the west coast has, and is still, resulting in total habitat destruction (Figure I.5.9).

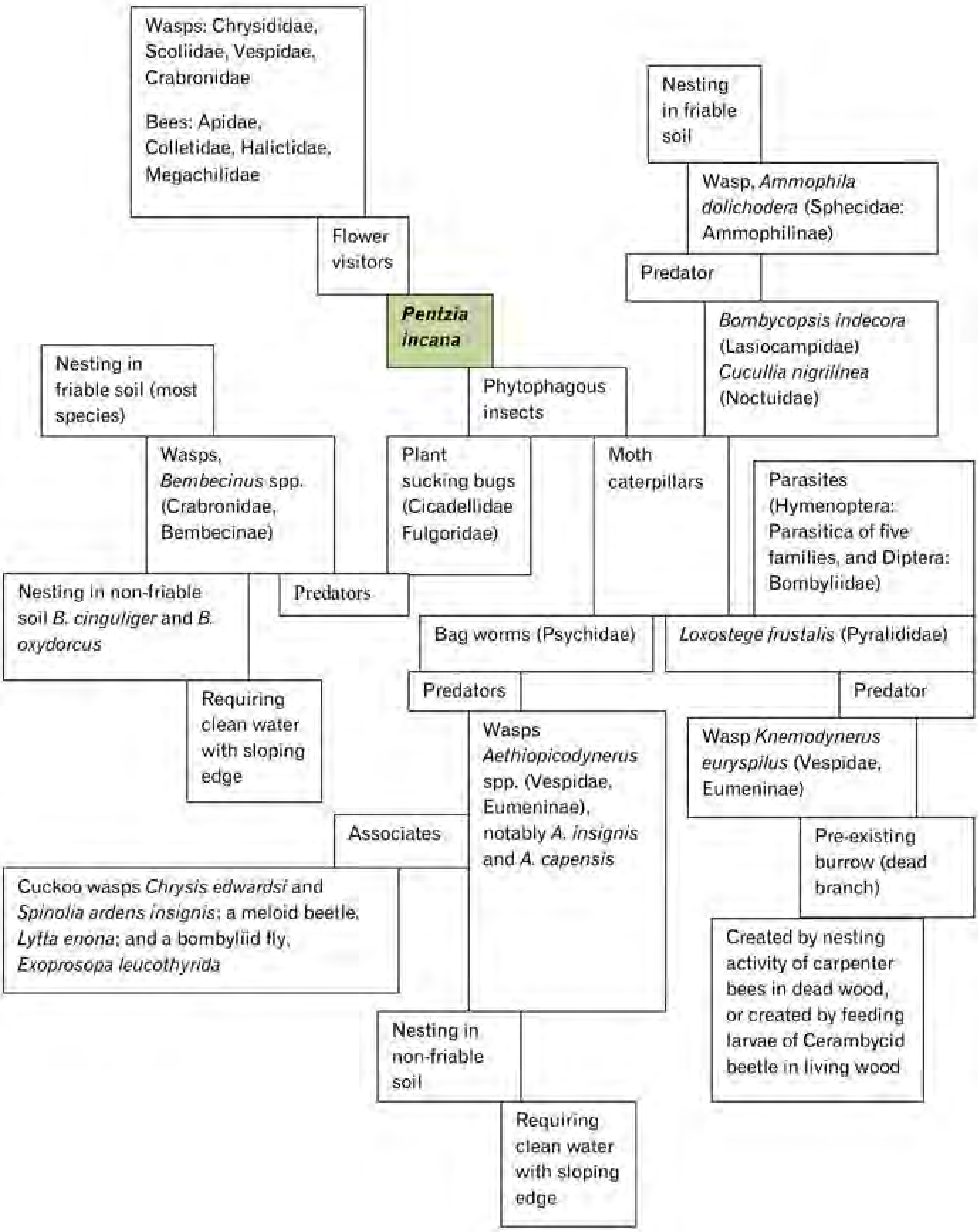
The complexity of evaluating the affects of landuse

The present synthesis of the knowledge of the habitat requirements of wasps and bees offers a step towards the understanding of the complex and interrelated habitat requirements of these and other insects. They are immensely important for the functioning of the ecological systems of the semi-arid to arid areas and may serve as a case study in a wider view of the functioning of ecological systems.

An example of a complex of wasps and bees centered on a widespread dwarf shrub, *Pentzia incana* Kuntze (Asteraceae), is given on page 118.

We suggest that populations of bees and wasps can be maintained, or even enhanced, by:

- Taking into account their diverse nest situation requirements.
- Taking into account their diverse plant resource requirements.
- Taking into account the diverse requirements of the prey of hunting wasps.
- Catering for their water requirements when designing irrigation systems and stock watering points.
- Protecting nesting areas of ground nesting species from trampling by stock.
- Providing suitable ground nesting areas where land is under cultivation.
- Protecting and/or supplementing nesting sites for nesters in pre-existing cavities.
- Protecting and/or supplementing nesting sites for nesters in vertical banks.
- Restricting stabilisation of and building on coastal dunes.


Wasps: Chrysididae, Scoliidae, Vespidae, Crabronidae
Bees: Apidae, Colletidae, Halictidae, Megachilidae
Flower visitors
Pentzia incana
Nesting in friable soil
Wasp, *Ammophila dolichodera* (Sphecidae: Ammophilinae)
Predator
Bombycopsis indecora (Lasiocampidae) *Cucullia nigrilinea* (Noctuidae)
Phytophagous insects
Nesting in friable soil (most species)
Wasps, *Bembecinus* spp. (Crabronidae, Bembecinae)
Plant sucking bugs (Cicadellidae Fulgoridae)
Moth caterpillars
Parasites (Hymenoptera: Parasitica of five families, and Diptera: Bombyliidae)
Nesting in non-friable soil *B. cinguliger* and *B. oxydorcus*
Predators
Bag worms (Psychidae)
Loxostege frustalis (Pyralididae)
Predators
Predator
Requiring clean water with sloping edge
Wasps *Aethiopicodynerus* spp. (Vespidae, Eumeninae), notably *A. insignis* and *A. capensis*
Wasp *Knemodynerus euryspilus* (Vespidae, Eumeninae)
Associates
Pre-existing burrow (dead branch)
Cuckoo wasps *Chrysis edwardsi* and *Spinolia ardens insignis*; a meloid beetle, *Lytta enona*; and a bombyliid fly, *Exoprosopa leucothyrida*
Created by nesting activity of carpenter bees in dead wood, or created by feeding larvae of Cerambycid beetle in living wood
Nesting in non-friable soil
Requiring clean water with sloping edge

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SECTION II:
A review of what is known of nesting, provisioning and associates of bees, pollen wasps and hunting wasps in southern Africa

Chrysidoidea

Family Chrysididae

Chrysidids, commonly called cuckoo wasps, are well represented in southern Africa. Typically they are of brilliant metallic colours such as green, blue, red or combinations of these (Figures II.1.1 & 2). However, *Allocoelia* species are non-metallic brown and black (Figure II.1.3).

All species are 'parasitic'. The majority develops within the cells of wasps and bees, usually first feeding on the host's egg or larva and then on the provision laid in for the latter or in some cases on the host's fully grown larva. The egg of the cuckoo wasp is generally introduced into the host's cell whilst cell provisioning is taking place. Some species are not associated with wasps and bees but with moths, developing upon resting caterpillars within their cocoons. No hosts have yet been established for the wingless or almost wingless African species of the subfamily Amiseginae, however, it seems likely that these, like other species from America and Australasia, develop in the eggs of stick insects (Phasmida). Some known host associations of chrysidids occurring in southern Africa are given in Table 7

The chrysidids 'parasitic' on wasps and bees are commonly seen around the nests of their hosts when these are being worked upon. It is in fact sometimes the brightly coloured chrysidids that attract ones attention to the presence of nests of wasps and bees.

There is generally surprisingly little attempt by the hosts to drive away these intruders. It has been suggested that cuckoo wasps may employ chemical camouflage. The hypothesis was tested for *Hedychrum rutilans* and *Philanthus triangulum* (Crabronidae, Philanthinae) by Strohm *et al.* (2008). They analysed the cuticles of the female beewolves, the female cuckoo wasps and honeybees as well as *Cerceris arenaria* (Crabronidae, Philanthinae) and *Hedychrum nobile* as outgroups*.* They found that behavioural and chemical analysis provided evidence that a specialised cuckoo wasp exhibits chemical mimicry of the odour of its host. This probably allows the cuckoo wasp to enter the nest with a reduced risk of being detected by olfaction and to leave after laying its egg without leaving behind a telltale odour.

Subfamily Chrysidinae

Tribe Allocoeliini

Flower visiting

We have collected seven species of *Allocoelia*, namely *A. bidens* Edney, *A. capensis* (Smith), *A. glabra* Edney, *A.*

Figure II.1.1.—*Chrysis* sp.

Figure II.1.2.—*Chrysis edwardsi* Buysson.

Figure II.1.3.—*Allocoelia capensis* (F. Smith).

latinota Edney, *A. minor* Mocsáry, *A. mocsaryi* Brauns and *A. quinquedens* Edney from flowers. Six species were visiting Asteraceae and/or Aizoaceae (Mesembryanthema and non-Mesembryanthema) and one *Hermannia* (Malvaceae, formerly Sterculiaceae). All plants visited are also visited by their masarine hosts.

Tribe Chrysidini

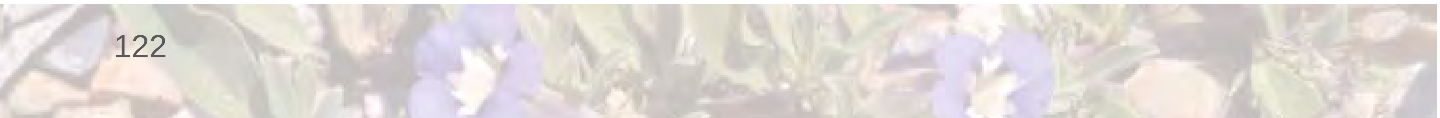
We have collected 24 species of Chrysidini. These included two species of *Brugmoia*, 15 species of *Chrysis*, one species of *Pseudospinolia*, three species of *Spintharina*, two species of *Spintharosoma* and one species of *Stilbum* from flowers. Of these, 52% were visiting Asteraceae,

Table 7.—Some known host associations of Chrysididae in southern Africa

Chrysididae	**Host family**	**Host genus and species**	**Reference**
Allocoelia bidens Edney	Vespidae, Masarinae	*Jugurtia confusa* Richards	Gess & Gess 1980
Allocoelia capensis (F. Smith)	Vespidae, Masarinae	*Ceramius lichtensteinii* (Klug) *Ceramius cerceriformis* de Saussure	Brauns 1910; Gess & Gess 1980 Gess 1996
Allocoelia glabra Edney	Vespidae, Masarinae	*Masarina familiaris* Richards	Gess & Gess 1988a
Allocoelia latinota Edney	Vespidae, Masarinae	*Ceramius capicola* Brauns *Ceramius lichtensteinii* (Klug)	Gess 1973; Gess & Gess 1980
Allocoelia minor Mocsáry	Vespidae, Masarinae	*Ceramius capicola* Brauns *Ceramius clypeatus* Richards	Gess 1973
Allocoelia mocsaryi (Brauns)	Vespidae, Masarinae	*Quartinia vagepunctata* Schulthess *Quartinia* spp. nesting in snail shells	Gess & Gess 1992 Gess & Gess 2008
Allocoelia quinquedens Edney	Vespidae, Masarinae	*Masarina strucki* Gess *Masarina familiaris* Richards	Gess & Gess 1997; Gess 1996
Chrysidea africana Mocsáry	Crabronidae, Crabroninae	*Trypoxylon* sp.	Gess 1981
Chrysis districta Buysson	Sphecidae, Sphecinae	*Isodontia pelopoeiformis* (Dahlbom)	Gess & Gess 1982
Chrysis edwardsi Buysson	Vespidae, Eumeninae	*Aethiopicodynerus insignis* (de Saussure)	Gess & Gess 1976a (as *Octochrysis vansoni* Brauns and *Parachilus insignis* (de Saussure))
Chrysis grootdermensis Koch	Megachilidae, Megachilinae Vespidae, Eumeninae	Possibly *Hoplitis* (*Anthocopa*) *conchophila* Kuhlmann and/or *Alastor ricae* Giordani Soika	Koch 2006 (as *Hoplitis* sp. and/or *Alastor ricae* Giordani Soika)
Chrysis cf. grootdermensis Koch	Megachilidae, Megachilinae		Gess & Gess 2008
Chrysis hoplites Mocsáry	Vespidae, Eumeninae	*Knemodynerus euryspilus* (Cameron)	Gess 1981 (as *Euodynerus euryspilus* (Cameron))
Chrysis laetabilis Buysson	Megachilidae, Megachilinae, Osmiini	*Heriades freygessneri* Schletterer	Taylor 1962
Chrysis laminata Mocsáry	Vespidae, Eumeninae	*Tricarinodynerus guerinii* (de Saussure)	Gess 1981 (as *Octochrysis laminata* Mocsáry)
Chrysis lincea Fabricius	Vespidae, Eumeninae	*Delta caffrum* (L.)	Gess, from nest, unpublished label data
Chrysis mionii Guérin	Megachilidae, Megachilinae	*Afranthidium* (*Immanthidium*) *junodi* (Friese)	Skaife 1950 (as *Tetrachrysis concinna* Mocsáry)
Chrysis lincea Fabricius	Sphecidae, Sceliphrinae	*Sceliphron spirifex* (L.)	Brauns 1911; Krombein & Walkley 1962; Gess & Gess from nest, field-notes and vouchers 1987
Chrysis lincea group	Sphecidae, Sceliphrinae	*Sceliphron spirifex* (L.)	Weaving 1995a
Chrysis oculata group	Vespidae, Eumeninae	*Delta hottentotum* de Saussure	Weaving 1995a
Chrysis sp., near *C. purpuripyga* Edney	Crabronidae, Crabroninae	*Trypoxylon* sp.	Gess 1981
Chrysis succincta group	Sphecidae, Sphecinae	*Isodontia pelopoeiformis* (Dahlbom) *Isodontia stanleyi* (Kohl)	Weaving 1995a Weaving 1995a

Table 7.—Some known host associations of Chrysididae in southern Africa (continued)

Chrysididae	**Host family**	**Host genus and species**	**Reference**
Chrysis wahlbergi group	Vespidae, Eumeninae	*Delta hottentotum* de Saussure	Weaving 1995a
		Proepipona meadewaldoi (Bequaert)	Weaving 1994b; 1995a
		Tricarinodynerus guerinii (de Saussure)	Weaving 1994b; 1995a
		Synagris analis de Saussure	Weaving 1995a
Chrysis wahlbergi group	Pompilidae, Pepsinae	*Auplopus femoralis* (Arnold)	Weaving 1994a; 1995a
		Auplopus vitripennis Smith	
Chrysis wahlbergi group	Sphecidae, Sceliphrinae	*Chalybion* (*Chalybion*) *laevigatum* (Kohl)	Weaving 1994b; 1995a
		Sceliphron spirifex (L.)	Weaving 1995a
Chrysis sp.	Vespidae, Eumeninae	*Eumenes lucasius* de Saussure	Gess 1981
Chrysura schultzei (Mocsáry)	Megachilidae, Megachilinae	*Othinosmia* (*Megaloheriades*) *schultzei* (Friese)	Mocsáry 1910 (as *Chrysis schultzei* Mocsáry and *Osmia schultzei*); Gess & Gess fieldnotes and voucher specimens 1991; Kuhlmann & Timmermann 2002.
Hedychrum coelestinum Spinola	Crabronidae, Philanthinae	*Philanthus capensis* Dahlbom	Brauns 1911
Hedychrum sp., near *H. comptum* Edney	Crabronidae, Bembicinae	*Bembecinus argentifrons* F. Smith	Gess 1981 as *Bembecinus braunsii* (Handlirsch)
		Bembecinus haemorrhoidalis (Handlirsch)	Gess 1981
Parnopes fischeri Dahlbom	Crabronidae, Bembicinae	*Bembix olivata* Dahlbom	Brauns 1911
Praestochrysis inops (Gribodo)	Crabronidae, Crabroninae	*Pison montanum* Cameron	Gess 1981 (as *Chrysis inops* (Gribodo))
Praestochrysis inops (Gribodo)	Crabronidae, Crabroninae	*Pison transvaalensis* Cameron	Taylor 1968 (as *Chrysis inops* (Gribodo))
Primeuchroeus ghilianii group	Pompilidae, Pepsinae	*Auplopus femoralis* (Arnold)	Weaving 1995a
Spinolia ardens (Mocsáry)	Vespidae, Eumeninae	*Aethiopicodynerus insignis* (de Saussure)	Gess & Gess 1976 (as *Pseudospinolia ardens* (Mocsáry) and *Parachilus insignis* (de Saussure))
Spintharina arnoldi Brauns	Vespidae, Masarinae	*Celonites promontorii* Brauns	Gess 1996
Spintharina bispinosa (Mocsáry)	Vespidae, Masarinae	*Celonites andrei* Brauns	Brauns 1913 (as *Sintharsis* (sic) *bispinosa* (Mocsáry))
		Celonites clypeatus Brauns	Gess unpublished label data
		Jugurtia confusa Richards	Gess unpublished label data
Stilbum cyanurum (Förster)	Vespidae, Eumeninae	*Delta emarginatum* (L.)	Brauns 1911 (as *Eumenes tinctor* Christ)
		Delta caffrum (L.)	Reared from nests from two localities Gess unpublished label data
		Delta hottentotum de Saussure	Weaving 1995a
		Afreumenes aethiopicus de Saussure	Weaving 1995a



48% Apiaceae, 17% Fabaceae (only Mimosoideae) and 13% Molluginaceae. These are all flowers visited by a wide range of wasps and bees. The flower families visited by any one species varied from one to eight and therefore the sum of the percentages of species visiting flower families exceeds 100. *Spintharina arnoldi* (Brauns), associated with Masarinae, was found collecting nectar from flowers of *Hermannia* and the extra-floral nectaries of *Euphorbia glanduligera* Pax (Euphorbiaceae) in addition to Molluginaceae. *Stilbum cyanurum* (Förster) was found on the widest range of flower families, namely Aizoaceae (Mesembryanthema), Amaranthaceae, Apiaceae, Asteraceae, Ebenaceae, Fabaceae (Mimosoideae), Molluginaceae and Neuradaceae.

Tribe Elampini

We have collected seven species of Elampini, namely one species of *Elampus*, two species of *Hedychridium*, two species of *Hedychrum* and two species of *Holopyga* from flowers. No particular flower preferences were noted for the tribe as a whole. Some flowering plant families visited were the same while others differed from those listed for Allocoeliini and Chrysidini. The plant families visited are Apiaceae, Apocynaceae (Asclepiadaceae), Asteraceae, Elatinaceae, Fabaceae (Papilionoideae and Mimosoideae), Lamiaceae and Molluginaceae. It is of note that Mesembryanthema were not included but that Papilionoideae and Lamiaceae were.

Tribe Parnopini

Of the tribe Parnopini we have collected only one species, *Parnopes fischeri* Spinola, from flowers. Most of the 19 records were for Asteraceae, followed by Apiaceae (12) with a few from Amaranthaceae, Apocynaceae (Asclepiadaceae) and Molluginaceae.

Family Bethylidae

Bethylids are very poorly known in southern Africa. From knowledge of their behaviour in North America, a generalised picture of their ethology can be drawn up. They prey upon the larvae of beetles and moths in hidden situations such as in soil, burrows in wood, leaf mines and galls (Evans & Eberhard 1970). They are usually much smaller than their prey. The female typically stings the prey a large number of times until it is permanently paralysed. She either leaves it *in situ* or drags it into a crevice, in which case, after oviposition, the crevice is sealed. Several eggs are laid and several larvae develop on a single prey. Govender (1987) recorded an association between an unidentified bethylid and a noctuid moth in Natal.

Family Dryinidae

Dryinids are poorly known in southern Africa. The larvae of North American species are known to feed on nymphs of Homoptera, principally of species belonging to Fulgoroidea, Cercopidae, Membracidae and Cicadellidae (Krombein 1979). The egg is laid externally on the abdomen of the bug, the larva feeds internally initially, later protruding as a cyst. Pupation takes place in a cocoon spun on the bug's food plant or in the soil. The front tarsi of the females are modified to form a trap-like device for capturing bugs.

Family Sclerogibbidae

Sclerogibbids are very poorly known in southern Africa. In North America, the larvae are known to feed externally on the nymphs of Embioptera (web-spinners) (O'Neill 2001).

Family Embolemidae

Virtually nothing is known of the ethology of embolemids in southern Africa or for that matter in any region. The larvae of at least one North American species is known to feed on homopteran bugs, leafhoppers and related species (O'Neill 2001).

Family Plumariidae

Little is known of the ethology of this southern hemisphere family. The larvae are thought to feed on subterranean beetle larvae (Brothers 1985).

Family Scolebythidae

Only one species of scolebythid has been recorded from southern Africa. Its larvae feed on the larvae of wood boring beetles such as Cerambycidae and there are indications that a number of larvae may develop on a single beetle larva (Brothers 1985).

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Vespoidea

Family Vespidae

Three subfamilies of Vespidae are represented in southern Africa, the Masarinae, Eumeninae and Polistinae. The Eumeninae are well represented throughout southern Africa, the Masarinae are most species diverse in the southwest and the Polistinae in the east.

The family Vespidae are distinguished from other wasp families by the characteristic shape of the pronotum and the Masarinae (excepting the extraterritorial tribe Gayellini) from the other subfamilies of the Vespidae by the possession of only two submarginal cells whereas the Eumeninae and Polistinae have three.

All Eumeninae and Polistinae show longitudinal folding of their wings when at rest and in death but in the Masarini only *Celonites* Latreille and *Quartinia* André show longitudinal folding of the wings. Thus, *Priscomasaris* Gess, *Ceramius* Latreille, *Jugurtia* de Saussure and *Masarina* Richards can be readily distinguished from the other Vespidae encountered in southern Africa.

Subfamily Masarinae

A synthesis of the knowledge of the Masarinae up to 1994 and an update for the Masarinae in southern Africa have been presented (Gess 1996; Gess & Gess 2010).

Masarinae (pollen wasps) are found principally in Mediterranean and temperate to hot, semi-arid to arid areas outside the tropics (Gess & Gess 2010, Figures 1 & 2). These areas exhibit a south-to-north and west-to-east macrogradient in which the winter rains diminish and the summer rains increase. Between such areas, there is a broad similarity in the vegetation types that replace each other along the macrogradient from Mediterranean climates to extreme deserts—from a dense evergreen hard-leafed shrubland (termed ‘maquis’ in Mediterranean countries and ‘fynbos’ in South Africa) on the mesic side of the gradient, the vegetation becomes progressively more open, low and sparse.

The masarine wasps number around 350 known species, making them a relatively small group when compared with the eumenines, which number around 3 000 species. Of the masarines, 78% occur in the Afrotropical and Palaearctic Regions combined, with 47% in the Afrotropical Region and 31% in the Palaearctic. The remaining 22% of the species are 10% Australian, 7% Neotropical and 5% Nearctic. Of the 151 species recorded from the Afrotropical Region, 144 are restricted to southern Africa. Most of these species are found in the west, where many are narrowly endemic.

They are represented by six genera—*Priscomasaris*, *Ceramius*, *Jugurtia*, *Masarina*, *Celonites* and *Quartinia* (including *Quartinioides* Richards and *Quartiniella* Schulthess). Masarines differ from all other aculeate wasps in the nature of their provision, which, like that of the bees, is typically composed of pollen and nectar. Unlike most of the bees, none of the masarines is equipped with pollen carrying devices on the legs or abdomen. The pollen and nectar mixture is carried in the crop.

They are important flower visitors and pollinators. Aizoaceae (Mesembryanthema) and Asteraceae, both of which are similarly species diverse, are visited respectively by 45% and 49% of the pollen wasp species. In addition, and of particular interest, are the close associations of some species with other plants of which they are in many instances the sole or most dependable pollinators (Gess & Gess 2010).

In all species oviposition precedes provisioning, the egg being laid at the inner end of the cell, lying loose or attached.

Priscomasaris Gess

Priscomasaris is monospecific and is restricted to western Namibia (Gess 1998, 2001; Gess & Gess 2010, Figure 30).

Flower visiting

Priscomasaris namibiensis Gess, both females and males, forage on flowers of species of *Gisekia* and *Limeum* (Molluginaceae) (Figure II.2.1), for which their short tongues are adequate. We have also observed them drinking nectar from the extra-floral nectaries of *Euphorbia glanduligera* Pax (Euphorbiaceae).

Nest situation

Priscomasaris nests in aggregations in sparsely vegetated areas close to water and with soil malleable when mixed with water.

Nest structure

The nest is a multicellular burrow surmounted by a curved mud turret. Within each excavated cell is a constructed mud cell (Figures II.2.2 & 3; see also Figures 32–36 in Gess & Gess 2010).

Figure II.2.1.—*Priscomasaris namibiensis* Gess on *Limeum sulcatum* (Klotsch) Hutch. (Molluginaceae).

Figure II.2.2.—*Priscomasaris namibiensis* Gess, female on nest entrance turret, holding mud pellet.

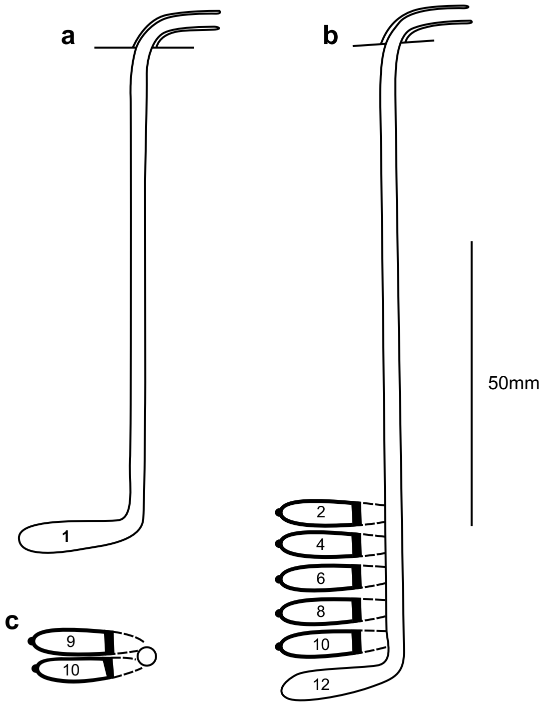


Figure II.2.3.—*Priscomasaris namibiensis* Gess, a. and b. vertical plans of nests: a. nest with first cell only; b. nest with 12 cells; c. transverse in single plane.

Method of nest construction

Nest excavation is performed with the use of water, which is carried in the crop from a water source to the nest site where it is regurgitated. The moistened soil is extracted in the form of pellets that, in the early stage of burrow excavation, are used to construct the entrance turret and at a later stage are discarded at some distance from the nest.

The walls of the shaft are stabilised and smoothed with the addition of water. The diameter of the shaft remains constant at 3 mm for its entire length, that is, there is no turning 'bulb' such as that found in the nests of most species of *Ceramius*. At a depth of 60–80 mm (average 69, n=17) the shaft makes a smooth curve and after about 5 mm is expanded in the excavation of a cell of about 15 mm in length and 5 mm in diameter.

Within the excavated cell, a mud cell is constructed, fitting closely within it but easily removed from it. On the outer surface evidence of deposition of mud pellets is visible. In fact, a faint 'fish scale' pattern, similar to the more marked pattern exhibited by cells of *Celonites* and *Pseudomasaris*, is discernable. The inner surface is perfectly smooth. The closed inner end of the cell is rounded whereas on the outside the tip of the cell is consistently markedly papillate. Apart from the tip, the cells are constant in diameter along their length, cigar-shaped and not ovoid.

A cell in which oviposition and provisioning have been completed is sealed with a mud plug that fits into the neck of the cell, closing but not sealing it. After this plug has been constructed, there is a further addition of mud, which extends across the plug and the rim of the cell, effectively sealing it. The remaining few millimetres of the lateral shaft are filled with soil. Finally, where the shaft curves away from the vertical shaft, mud is used for sealing and plastering so that, when a nest with sealed cells is opened, there is no sign in the walls of the vertical shaft that any lateral shaft other than one leading to an open cell exists.

A first cell having been completed and sealed off, a second lateral shaft leading to a second cell is excavated at the same depth as the first and in the same plane, but at an acute angle from it.

On the completion and sealing off of this cell, a third lateral shaft with cell is excavated almost immediately below the first after a slight deepening of the vertical shaft. A fourth shaft and cell follows almost immediately below the second. Excavation of further lateral shafts with cells follows this pattern so that a double 'stack' of sub-horizontal cells forms to one side of the vertical shaft.

Provisioning and oviposition

After an egg is laid at the inner end of a newly constructed cell, provisioning commences.

The provision obtained from nest-cells consists of a compact, firm, roughly cylindrical mass of pollen and nectar, rounded at the ends and with undulations along its length indicating the deposition of 'loads' of the pollen and nectar mixture. The provision mass or 'pollen loaf' remains loose within the cell. One complete 'pollen loaf' was 8.17 mm in length and 3.0 mm in diameter, that is a diameter of 0.12 mm less than the inner diameter of the cell.

Samples of pollen from provision masses collected on 10, 22 and 31 March, and 2 April were examined microscopically. Four distinct pollen grains of 17.5, 20, 25 and 30 micrometres in diameter were present. These were compared with pollen from flowers visited by *Priscomasaris* and were found to match those of *Trianthema parvifolia*

E.Mey. ex Sond. (Aizoaceae), *Limeum argute-carinatum* Wawra ex Wawra & Peyr. (Molluginaceae), *Gisekia africana* (Lour.) Kuntze (Molluginaceae) and *Sesuvium sesuvioides* (Fenzl) Verdc. (Aizoaceae) respectively. The proportions of the different pollen varied, for example, samples taken on 22 March were mostly of *G. africana* and *S. sesuvioides* and those taken on 31 March and 2 April were principally of *T. parvifolia*.

Sleeping and sheltering

When nests are being worked upon, females spend the night in their nests and shelter in them in inclement weather.

Associates

No instances of any of the categories of associated organisms have been recorded.

Ceramius Latreille

The genus *Ceramius* (Figure II.2.4) has been divided on morphological characters into eight species groups supported by nest structure and forage plant associations. With the exception of groups one and seven, which are endemic to the Palaearctic, all of these species groups are endemic to southern Africa.

Ceramius has been recorded from the Nama-Karoo, from the east across the southern Great Karoo and the Little Karoo, the southwestern Fynbos, north through the Olifants River Valley, and from Namaqualand north to the Kunene (Figure 38, Gess & Gess 2010). Eighteen species are found south of the Orange River and only one species, *C. damarinus*, north of this river in what is seen as the northern tongue of the Nama-Karoo, from Mariental and Maltahöhe in the south to the Kunene River in the north, on the fringes of the Etosha Pan and on the fringe of the arid savanna. *Ceramius* species to the south of the Orange exhibit a variety of distributions from relatively widespread to extremely narrowly endemic (Gess & Gess 2004).

Flower visiting

Flower visiting records are available for all of the 20 described southern African *Ceramius* species (groups 2–6 and 8). Of these, 45% have been recorded from flowers of Asteraceae, 45% from Aizoaceae and 20% from Fabaceae (Papilionoideae). That the percentage of flower families visited is in excess of 100% is explained by records of occasional visits by some species to flowers of families other than that preferred. Such visits appear to be for nectar only.

Flowers of other plant families occasionally visited are *Wahlenbergia* (Campanulaceae) by *C. socius*; *Blepharis* (Acanthaceae) by *C. lichtensteinii* and *C. damarinus*; Zygophyllaceae by *C. brevitarsis* and *C. damarinus*; and Lamiaceae, Molluginaceae and Scrophulariaceae by *C. damarinus.*

Nesting

Nesting has been recorded for 16 of the 20 southern African species of *Ceramius*. These are *C. cerceriformis* (Group 2A); *C. clypeatus* (Group 2B); *C. micheneri* (Group 2C); *C. nigripennis*, *C. jacoti*, *C. braunsi* and *C. toriger* (all Group 3); *C. beyeri* (incomplete nest) and *C. damarinus* (both Group 4); *C. lichtensteinii* (Group 5); *C. rex* and *C. metanotalis* (both Group 6); and *C. capicola*, *C. linearis*, *C. bicolor* and *C. socius* (Group 8) (Gess & Gess 1980, 1986, 1988c, 1990, 2010; Gess 1999).

Figure II.2.4.—a. *Ceramius metanotalis* Richards, female on flower head of *Athanasia trifurcata* (L.) L. (Asteraceae); b. *Ceramius lichtensteinii* (Klug) on mesemb flower.

Nest situation

The nests of all species of *Ceramius* are excavated in aggregations in bare areas close to water, the soil being malleable when mixed with water.

Nest structure

All *Ceramius* nests are multicellular and surmounted by a mud entrance turret (Figures II.2.5–8) and in all but *Ceramius* Group 8, a cell is constructed within the excavated cell. *Ceramius* Group 8 has abandoned cell construction. The six *Ceramius* species groups represented in southern Africa each exhibit a distinctive nest plan.

Figure II.2.5.—*Ceramius braunsi* Turner, female on ground below nest entrance turret.

Figure II.2.6.—*Ceramius metanotalis* Richards, nest entrance turret and discarded pellets.

Figure II.2.7.—*Ceramius jacoti* Richards: nest entrance turret, no discarded pellets, pellet dropping area away from nest.

Key to the southern African species groups based of differences in the architecture of the burrows:

1 Excavated cells not containing constructed cells ... 2
1 Excavated cells containing constructed cells ... 3

2 'Bulb' present in vertical shaft ... Group 8
2 'Bulb' absent ... Group 4

3 No cell terminating the main shaft ... Group 5
3 Cell terminating main shaft ... 4

4 Cells sub-vertical ... Group 3
4 Cells sub-horizontal ... 5

5 'Bulb' short, bottom end well above level of cells ... Group 2
5 'Bulb' long, bottom end level with cells ... Group 6

Method of nest construction

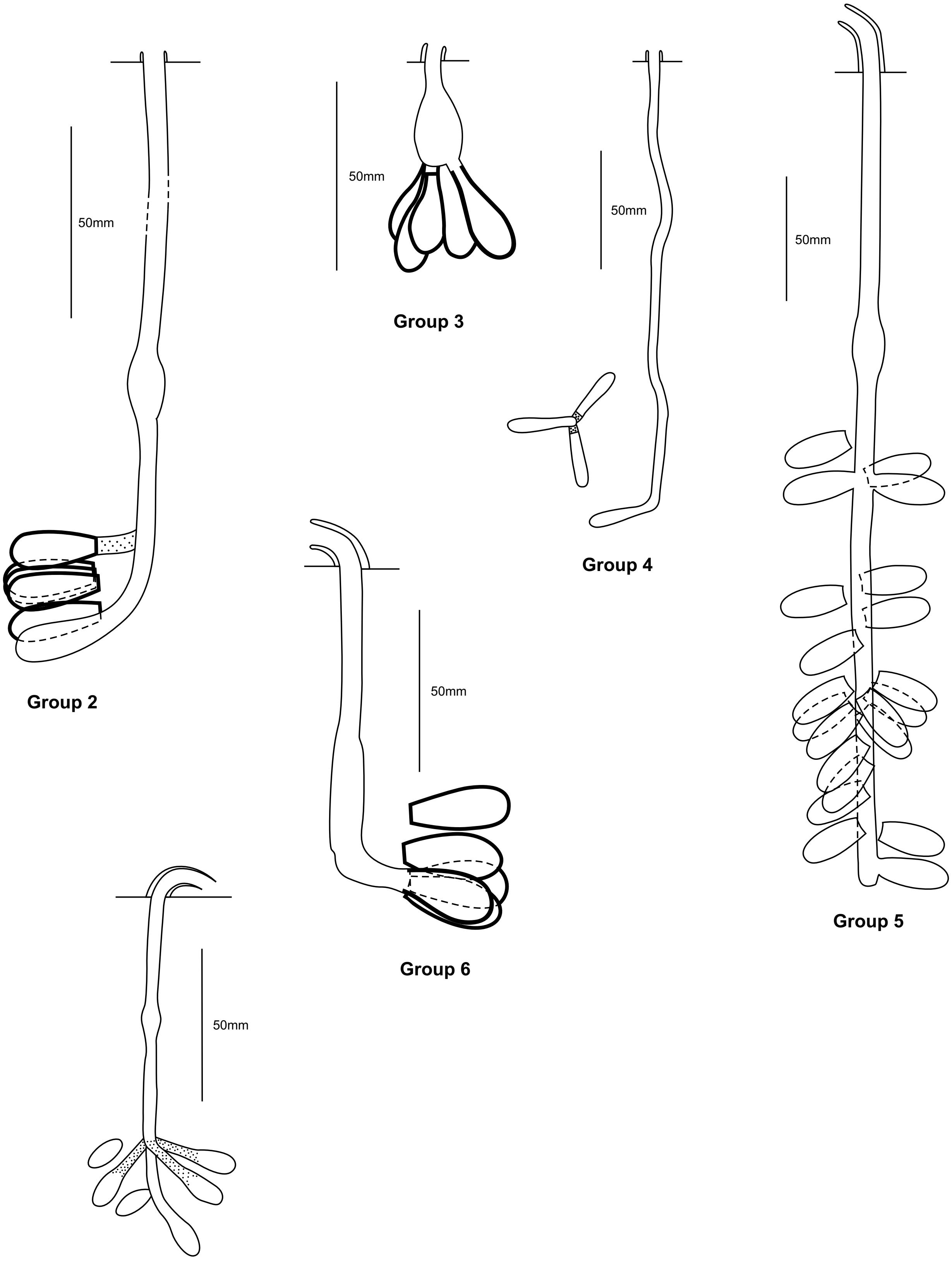
All species of *Ceramius* in southern Africa visit water (Figure 39, Gess & Gess 2010) and all use water as a bonding agent in the construction of nest entrance turrets. Those species that construct cells all use water in cell construction.

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 a 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 even rotating, always 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.

Upon completion of the turret, the wasp continues to excavate the shaft but the pellets then extracted are discarded either in a definite pellet-dropping area in close proximity to the nest or at some distance. In some species whether or not pellets are dropped in close proximity to nests or at some distance varies between populations, both behaviour patterns having been observed for *C. lichtensteinii* but at different localities. The nesting aggregations of one population were littered with discarded pellets whereas that of another was completely free from scattered pellets and the females were observed to fly to the edge of the clearing in which they were nesting and there to drop discarded pellets into the bushes.

After the 'bulb' has been excavated, the wasp is able to turn around in the nest and may emerge from the nest headfirst. Cycles of water carriage and pellet extraction are performed rapidly and without interruption during active nest excavation.

Upon completion of cell excavation, the cells of Group 4 and 8 species, after a variable amount of smoothing and cementing of the cell surface, are ready for oviposition. In the other groups a mud capsule is first constructed within each excavated cell. Mud for the construction of these capsules must be quarried within the nest as these wasps do not fetch mud from elsewhere. It is thought probable that mud used by *C. lichtensteinii* is obtained by deepening the lower end of the main shaft. In the nests of species



Group 2

Group 3

Group 4

Group 5

Group 6

Group 8

Figure II.2.8.—*Ceramius*, diagrammatic vertical plans of nests, showing plan typical for each species group.

of Groups 3 and 6, the diameter of the 'bulb' is greater the larger the number of cells, suggesting that mud for cell construction is probably quarried from the walls of the 'bulb'. The mud cells are constructed in such a way that the outer surface is rough and separate applications of mud are discernable whereas the inner surface is carefully smoothed.

Each cell is sealed with mud after the completion of oviposition and provisioning. The seals of constructed mud-cells are positioned just within the mouth of the cell. The outer surface of the mud plug is generally rough and convex. Those of *C. cerceriformis* (Group 2A) and *C. clypeatus* (Group 2B) are markedly concave.

After a cell is sealed, the shaft above the cell is filled with earth until the vertical section of the shaft is reached. As no earth is carried into the nest, earth for filling must be obtained from within. After filling is completed a mud seal is constructed. This seal is smoothed so perfectly that it is not visible on the surface of the main shaft.

Further cells terminate secondary shafts and are prepared in a similar fashion to the first. The number of cells prepared is probably dependant in part on the availability of water for nest construction and pollen and nectar for cell provisioning, suitability of weather and the constraints imposed by the nest architecture. Clearly, the Group 5 nest plan allows for a greater number of cells to be excavated than does the Group 3 plan. *Ceramius lichtensteinii* differs from the other species for which nest construction is known in that it continuously deepens the main shaft. This is possible because in its nests, unlike those of other species, the main shaft does not terminate in a cell.

Oviposition and provisioning

After an egg is laid at the inner end of a newly prepared cell, provisioning commences. The provision, a pollen and nectar mixture is in the form of a firm pollen loaf positioned at the blind end of the cell, free from the cell walls and filling the cell to about two thirds of its length. Pollen from provision obtained from 15 *Ceramius* species was for each species derived from a single plant family which indicates that the genus *Ceramius* is markedly oligophagous, provisioning with only Aizoaceae, Asteraceae or Cape Crotalarieae according to species group. Foraging records indicate that nectar is almost always derived from the same flowers as pollen.

Associates

Mites, Acarina: All species of *Ceramius* Groups 3 and 6, all of which provision with Asteraceae pollen, carry mites (ectoparasites), but none of Groups 4, 5 and 8, all of which provision with Aizoaceae pollen, carry mites. However, the division based on flower family is not clear-cut as two species of Group 2A, both of which provision with mesemb pollen, carry mites. The two species of Group 2B, both of which provision with papilionate pollen, carry mites. However, mites have not been found on closely allied *C. micheneri*, which also provisions with papilionate pollen.

Most species lack acarinaria, however, a pair of acarinaria are present, positioned laterally, on the metanotum of *C. caffer*, *C. metanotalis* and *C. rex* (Figure 52; Gess & Gess 2010).

All mites found are hypopi of the family Winterschmitiidae—a species of *Zethovidia* was obtained from females of Groups 2, 3 and 6 and a species of *Kennethiella* only from adult females of Group 3.

Flies, Conopidae: Volker Mauss found early instar dipterous larvae, probably Conopidae, in the haemocoel of *C. linearis* and *C. lichtensteinii* in the course of a study of the internal morphology of *Ceramius* (pers. comm.).

Velvet ants, Mutillidae: *Dasylabroides caffra* (Kohl) (Figure II.2.75) has been reared from cocoons of *Ceramius lichtensteinii* (Table 9).

Cuckoo wasps, Chrysididae: three species of *Allocoelia* (*A. capensis*; Figure II.1.3). have been found in association with the nests of *Ceramius* spp. (Table 7).

Blister beetles, Meloidae: *Ceramius lichtensteinii* is host to *Ceroctis groendali* (Billberg) (Lyttinae, Mylabrini) (Figure II.2.9) which feeds upon the provision and larva. The triungulin (first instar) larvae from cells of *C. lichtensteinii* have 'running' legs. Their association with their masarine host is consequently not brought about by chance collection of phoretic triungulins, which wait in flowers for visiting bees.

Leaf cutter bees, Megachilidae: Nests of *Ceramius* are usurped by *Megachile aliceae* Cockerell (Figure II.4.27).

Jugurtia Saussure

Jugurtia (Figure II.2.10) is found in both the Afrotropical Region and in the Palaearctic Region with the greatest species diversity is in southern Africa. No species are common to both zoogeographical regions and the southern African species are all endemic. The genus is represented in most areas of the Karoo Biome and associated dry savanna from the eastern Nama-Karoo across the southern Great Karoo and the Little Karoo, the southwestern Fynbos, north through the Olifants River Valley, and from Namaqualand north to the Kunene (Figure 60, Gess & Gess 2010). Five species bridge the Orange River, 13 species have been found only south and six only north of the Orange. Some species are widely distributed but many are narrowly endemic.

Flower visiting

Flower visiting records are available for 17 of the 24 southern African *Jugurtia* species. Thirteen species, 76%, have been recorded from flowers of Asteraceae, flowers of which are also known to be visited by a Palaearctic species of *Jugurtia.* Of the thirteen, at least four species have been shown to have a strong association with Asteraceae—*J. braunsiella* von Schulthess in the Little Karoo, Robertson Karoo, Tankwa Karoo, Olifants River Valley and Namaqualand; *J. eburnea* (Turner) in southeastern Namaqualand; *J. tibialis* Gess in western Namibia from south to north; and *J. turneri* (von Schulthess) in the southern Tankwa Karoo. *Jugurtia braunsi* (von Schulthess) has been collected widely from Asteraceae but equally commonly from Aizoaceae: Mesembryanthema and less commonly

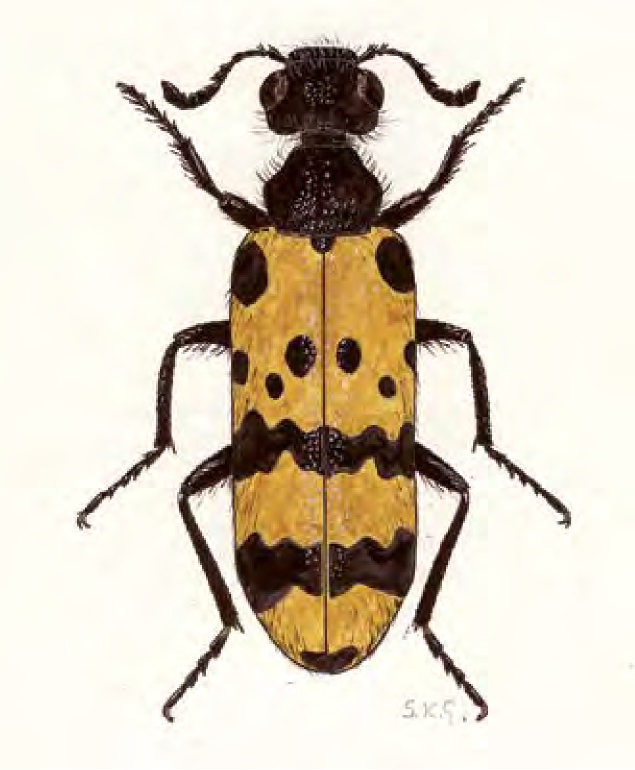


Figure II.2.9.—*Ceroctis groendali* (Billberg) (Meloidae), nest parasite of *Ceramius lichtensteinii* (Klug); actual size 10 mm.

Figure II.2.10.—*Jugurtia codoni* Gess, female ingesting pollen from anther of *Codon royenii* L. (Boraginaceae).

from Campanulaceae and Scrophulariaceae. Four additional species visit Asteraceae infrequently.

Considering the strong overall association of pollen wasps with Aizoaceae in southern Africa, it is of note that only four species of *Jugurtia*, 24%, have been collected from this family. Of these *J. nigrifrons* Gess and *J. braunsi*, endemic to western South Africa, show a strong preference for mesembs throughout Namaqualand, however, *J. braunsi* has also been recorded from four other families, most notably Asteraceae. In the southeastern Nama-Karoo *J. confusa* Richards provisions its nest cells with mesemb pollen and has not been collected from flowers of other families, suggesting oligolecty. However, in Namibia, west of Windhoek, *J. confusa* was found abundantly visiting *Hermannia* (formerly Sterculiaceae, now included in Malvaceae) although mesembs were present. For the fourth species, *J. calcarata* Richards, there are only four flower visiting records, three from mesembs and one from Asteraceae.

Three species show a strong association with *Hermannia* (Malvaceae, formerly Sterculiaceae)—*J. alfkeni* (du Buysson) in the southeastern Nama-Karoo, southern Kalahari, and southern and western Namibia through to the Kaokoveld; and *J. damara* Gess and *J. mandibulata* Gess in western Namibia from south to north. It therefore seems that for *Jugurtia* in some areas *Hermannia* species are important forage plants. *Hermannia* species are also important forage plants for some species of the closely related genus *Masarina.*

Two species, *J. namibicola* Gess and *J. codoni* Gess, are strongly associated with Boraginaceae. *Jugurtia namibicola*, restricted to the desertic areas of northwestern Namibia, has been collected at diverse sites visiting only *Heliotropium tubulosum* E.Mey. ex DC., although at these sites a wide range of flowers was available. *Jugurtia codoni* appears to show a preference for *Codon* (formerly Hydrophyllaceae, now included in Boraginaceae) but also visits *Peliostomum* (Scrophulariaceae) and *Pelargonium* (Geraniaceae). Additionally, *J. codoni* has been recorded, probably as a casual visitor, from four other families.

No species of *Jugurtia* have been found to specialise in visiting Scrophulariaceae. Two species, *J. koeroegabensis* Gess and *J. codoni*, visit *Peliostomum*. *Jugurtia koeroegabensis* shows a possible preference for *Peliostomum* (Scrophulariaceae) but has also been recorded as a casual visitor from Asteraceae, Zygophyllaceae, Iridaceae and Brassicaceae. A third species, *J. braunsi*, is a casual visitor to species of *Selago* and *Polycarena.*

Interesting and unusual records for pollen wasps are those of *J. koeroegabensis* visiting *Ferraria variabilis* Goldblatt & J.C.Manning*. Ferraria* is also occasionally visited by *Celonites capensis* Brauns*.*

Nesting

Nests of *Jugurtia*, though widely sought, have proved to be difficult to discover. Nests of only two species, *J. confusa* and *J. braunsi* were found (Gess & Gess 1980; Gess 1996).

Nest situation

The nests of both species were in bare areas, in horizontal to sloping ground, in areas of karroid scrub, in relatively close proximity to their forage plants and a water source. One nest of *J. confusa* was excavated in a pocket of soil on a ledge of a raised bank. This apparently unusual situation, however, falls within the category of horizontally presented soil.

Figure II.2.11.—*Jugurtia confusa* Richards, female excavating nest.

The nests of *J. confusa* were in sizeable aggregations, whereas those of *J. braunsi* were single. The nests of *J. braunsi* were all recently initiated suggesting that nesting was not yet in full swing. It is probable that this species also nests in aggregations.

The soil at all nesting sites contained a sufficient clay factor to be malleable when mixed with water.

Nest structure

The nests of *J. confusa* and *J. braunsi* consist of a subterranean burrow surmounted by a short cylindrical mud turret (Figures II.2.11–13). The subterranean burrow consists of a vertical shaft of constant diameter for its entire length and from which at its lower end there branches a short sub-horizontal shaft terminating in an excavated cell within which is a constructed mud cell.

Of the nests investigated only one, a nest of *J. confusa*, was at a more advanced stage of construction. In this nest, further sub-horizontal secondary shafts, each terminating in a cell, were present. Each secondary shaft including a cell was barely longer than the cell itself. All completed cells were sealed with a mud plug constructed within the neck of the cell.

Method of construction

Jugurtia confusa and *J. braunsi* use water as the bonding agent. Females of eight additional species, *J. alfkeni*, *J. braunsiella*, *J. damara*, *J. einensis* Gess, *J. mandibulata*, *J. nigrifrons*, *J. eburnea* Turner, and *J. saussurei* (Brauns) have been collected imbibing water from saturated soil near the edge of a water source, suggesting that they also use water in nest construction. However, it is considered possible and even likely that at least some of the other species may have abandoned the use of water in favour of nectar as has *Masarina strucki* Gess. This may well account for the penetration of the desert by at least two species, *J. gariepensis* Gess in the south and *J. namibicola* in the north.

Figure II.2.12.—*Jugurtia*, typical nest entrance turret.

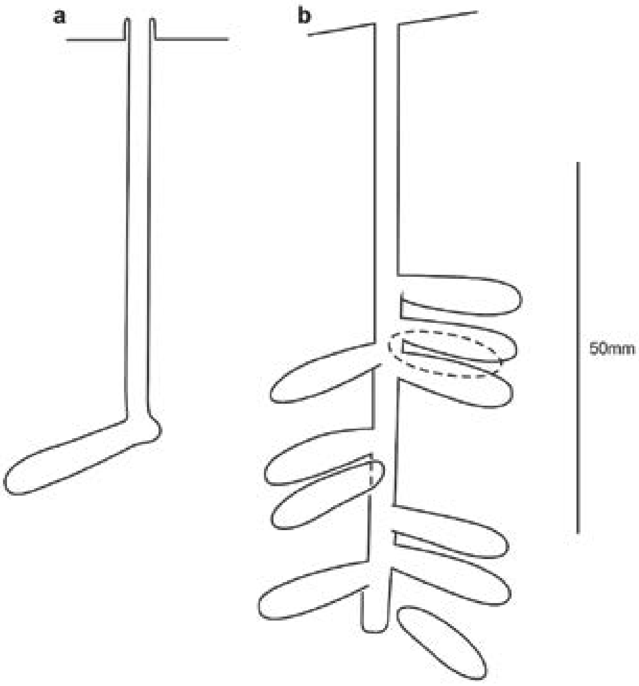


Figure II.2.13.—*Jugurtia confusa* Richards: diagrammatic vertical plans of two nests.

Nest excavation by *J. confusa* and *J. braunsi* is initiated by the female's regurgitating water from her crop onto the ground. Initially the mud pellets extracted from the burrow are used for the construction of the turret. After completion of the turret further pellets extracted are discarded. *Jugurtia confusa* has no clearly defined pellet-dropping area, however, the wasp does confine her arrivals at and departures from the nest to a set quarter segment (90°).

From the bottom of the main shaft, a secondary shaft is excavated in a sub-horizontal plane in such a way that the distal end lies deeper than the bottom of the main shaft and is enlarged to form a cell. A mud cell is constructed within the excavated cell. Mud for the construction of such a cell must be quarried within the nest, as mud is not brought into the nest. 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 soil used in constructing the mud cell is excavated from this source. The mud cell is constructed in such a way that the outer surface is rough and separate applications of mud are discernable whereas the inner surface is carefully smoothed.

After oviposition and provisioning, the cell is sealed with mud. The remaining section of the secondary shaft is filled with earth and sealed off from the main shaft with mud, which is smoothed so that the entrance to the secondary shaft is no longer visible.

Succeeding cells follow in the same manner, the number probably being dependent on the availability of water for nest construction and pollen and nectar for cell provisioning.

Provisioning and oviposition

In a newly constructed cell, oviposition takes place at the closed inner end of the cell after which provisioning takes place. Pollen from provision from cells of *J. confusa* was all of one type that matched those of *Drosanthemum* growing in the vicinity.

Associates

Cuckoo wasps, Chrysididae: the only cuckoo wasp found in association with *Jugurtia* is *Spintharina bispinosa* Mocsáry, which has been found in a nesting aggregation of *Jugurtia confusa* Richards, but not reared from nests. The only rearing of this species was from nests of *Celonites andrei* Brauns*.*

Masarina Richards

Masarina is endemic to and restricted to southern Africa (Figure 65, Gess & Gess 2010). Thirteen species have been described, all from the southwest, that is, almost entirely from the winter rainfall region. Only one species has been found north of the Orange River. Within the area of distribution of the genus some species, for example *M. strucki* Gess and *M. familiaris* Richards, associated with *Hermannia* (Malvaceae) and Cape Crotalarieae (Fabaceae: Papilionoideae) respectively, are relatively widely distributed having being found from Namaqualand south to the Olifants River Valley and east from there in the western Little Karoo and the southern Tankwa Karoo respectively. The most narrowly endemic known species is *M. tylecodoni* Gess which is restricted to the Richtersveld and is associated with an equally narrowly endemic plant *Tylecodon hallii* (Toelken) Toelken (Crassulaceae) which is restricted to a small area in the northern Richtersveld, south and north of the Orange River.

Flower visiting

Flower visiting records are available for all 13 of the known species of the southern African genus *Masarina.* Of these, 10 appear to be specialists. Three species (31%) including *M. ceres* Gess, *M. familiaris* and *M. hyalinipennis* Richards, have been recorded solely from Papilionoideae (Fabaceae).

Four species (31%) have been recorded from *Wahlenbergia* (Campanulaceae). Of these two species, *M. parvula* Gess and *M. namaqua* Gess have been recorded solely from these flowers. However, the other two species have been recorded from flowers of other families, *M. mixta* Richards of Papilionoideae, *Hermannia* (Malvaceae), *Peliostomum* (Scrophulariaceae) and *Athanasia* (Asteraceae) and *M. mixtoides* Gess of *Pelargonium* (Geraniaceae), Asteraceae and Zygophyllaceae.

Nesting

Nests of *Masarina*, though widely sought, have proved to be difficult to discover. Nesting has been recorded for only two species, *M. familiaris* and *M. strucki* (Gess & Gess 1988a; Gess *et al.* 1997).

Nest situation

Masarina familiaris has been recorded nesting at three sites to the west of the Olifants River Valley, all in dry fynbos and in an area of mixed dry fynbos and karroid scrub and in relatively close proximity to a water source. It has been recorded nesting in banks varying in height from 15–100 cm at heights of a few centimetres to half a metre. The soil of the nesting sites varied from a sand coloured clay-sand mixture with a relatively low proportion of clay to a hard non-friable red clay-sand mixture with a relatively high proportion of clay. In all cases, the soil was malleable when mixed with water.

The nests occurred singly and grouped in the vicinity of an old nest, suggesting that there is a tendency for females to initiate nests in close proximity to the nest from which they emerged.

The nest of *Masarina strucki*, situated between two stones, was found in the Kamiesberg in a patch of *Hermannia disermifolia* Jacq. bushes growing, characteristically for that area, in the lee of a large boulder. The soil was sandy and friable.

The nest of *M. familiaris* is a multicellular burrow with at its entrance a downwardly curved tubular mud turret (Figures II.2.14 & 15). The turret is constructed of mud pellets smoothed on the inside but left rough on the outside. A

Figure II.2.14.—*Masarina familiaris* Richards, female at nest entrance.

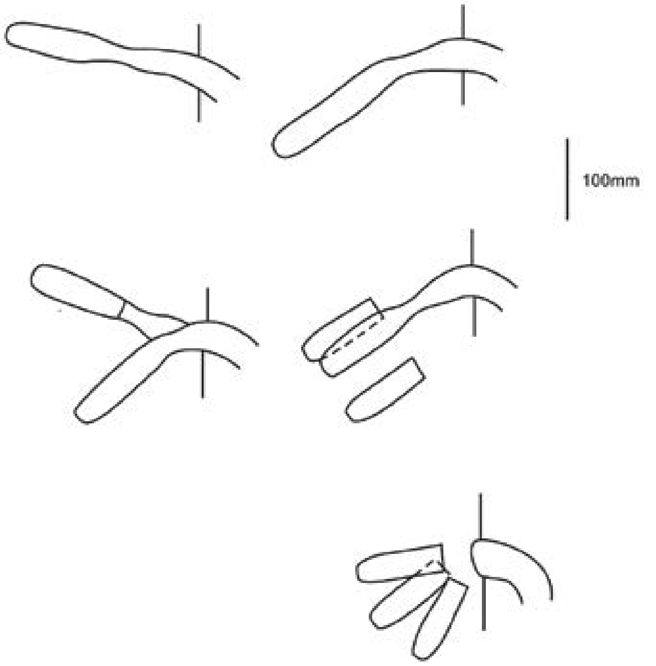


Figure II.2.15.—*Masarina familiaris* Richards: diagrammatic vertical plans of five nests.

large number of interstices are left open so that the turret has a somewhat lacy appearance. The turret and shaft entrance are of the same diameter. There is one or more sub-horizontal to upwardly or downwardly sloping shafts each ending in a cell. All shafts leading to sealed cells are filled with earth and sealed with a mud plate a short distance inside the burrow entrance. A cell is, over most of its length, of the same diameter as the shaft. There is a distinct neck of smaller diameter than that of the cell and shaft. Distally the cell walls slope inwards abruptly to a truncated end wall.

The single nest of *M. strucki* consisted of a sloping burrow terminating in a cell (Figure II.2.16). The cell, unlike that of *M. familiaris* but typical of most other Masarinae, was rounded at the inner end. There was no entrance turret. The seal was concave on the outside and convex on the inside.

Method of nest construction

Water for nest construction is collected by females of *M. familiaris* from saturated soil at the edge of a water source, however, not all species visit water. *Masarina strucki* has not been found at water. The hardness of the cell walls suggests that some bonding agent, other than water, is used for cementing the cell walls and constructing the seal. Analysis of the composition of the freshly completed seal suggested the use of nectar.

At an early stage in burrow excavation by *M. familiaris*, turret construction is initiated using pellets extracted from the excavation. At the commencement of turret construction pellets are laid down around the shaft opening in such a way that the turret will have the same diameter as the shaft. Almost from the start additional pellets are added in such a way that the turret curves over and downwards. After turret construction has been completed, further pellets extracted from the excavation are dropped so that they accumulate in a pile at the base of the bank beneath the nest.

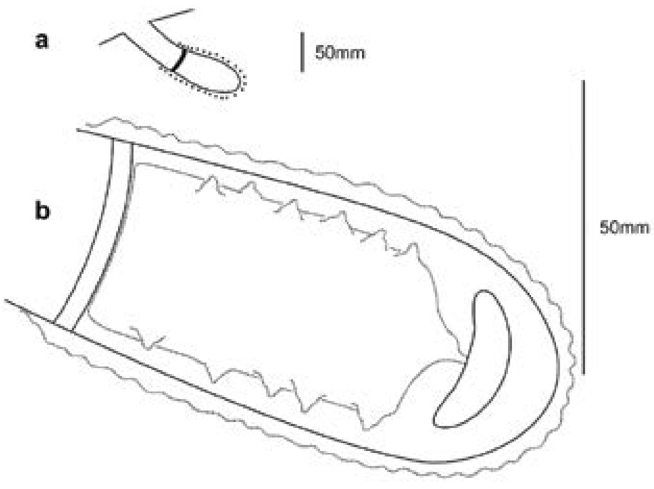


Figure II.2.16.—*Masarina strucki* Gess: diagrammatic vertical plans of a. nest and; b. cell, papillate provision and egg.

The shafts are short and generally slope downwards although they less commonly slope upwards—in a sample of 15 shafts, 13 sloped downwards and only two upwards. The average angle of slope for the sample was 26°. A shaft is extended without change of angle to end in a cell. Cell excavation is preceded by a reduction of 1 mm in the diameter of the shaft over a short distance to form a neck. After the neck is created, the diameter returns to that of the shaft until the inner end of the cell is approached. In this way the cell walls are parallel over most of the length of the cell. Shortly before the end of the cell is reached, there is a rapid reduction in diameter so that the sides slope inwards to the end of the cell which is truncated, not curved.

The excavated cell is very carefully smoothed and shaped so that, although a mud cell is not constructed within it, the walls of the cell are stabilised to such a degree that in nests constructed in relatively friable soils, parts of the cell walls can be separated from the surrounding soil.

After oviposition and provisioning, the cell is sealed with a thin mud plate and the shaft is filled with earth. Several secondary shafts each terminating in a cell may be similarly excavated and completed.

The nest of *M. strucki* was discovered after the burrow had been excavated and the cell walls were being smoothed and stabilised. The friable nature of the soil, the lack of any form of turret, the lack of discarded mud pellets, and the nature of the cell walls and seal suggest that excavation of the nest had taken place without using water, but that some bonding agent, other than water, had been used for cementing the cell walls and constructing the seal. The extreme hardness of the cell walls akin to those of *Celonites* species and the pliable nature of the freshly completed seal suggest the use of nectar.

When observations commenced, final smoothing of the cell walls was in progress. The wasp repeatedly moved backwards until half the body length protruded from the entrance and forward again into the cell. By shining a light into the nest and using a dentist's mirror during the wasp's absence, it was observed that the cell walls were smooth and moist.

The walls of the cell were smoothed on the inside and the surrounding earth was cemented to a depth of 0.5 mm so that the cell could be removed from the surrounding soil as an entity. After oviposition and provisioning the cell was sealed. Soil for sealing was seen to be taken from the walls of the entrance shaft.

Oviposition and provisioning

Oviposition takes place at the inner end of a newly constructed cell.

The provision of both species is a very moist mixture of pollen and nectar. That of *M. familiaris* occupies about two thirds of the cell, is very wet and sticky and has no discrete shape of its own. That of *M. strucki*, however, is jelly-like, pale yellow ochre translucent, adpressed to the cell closure, but along its longitudinal surface is regularly papillate, each papilla ending in a nipple. At the inner end of the provision is a larger central papilla that supports the egg.

In the Clanwilliam district pollen used for provisioning by *M. familiaris* was only derived from flowers of one or more *Aspalathus* species (Papilionaceae), the only flowers on which *M. familiaris* has been observed foraging in that district. It is possible, however, that in other areas pollen from *Lebeckia* and *Wiborgia* (both also Cape Crotalarieae, Papilionoideae) may be used as *M. familiaris* has been recorded foraging on these plants in the Springbok area. From foraging records, it is almost certain that *M. hyalinipennis* similarly obtains its provision from Cape Crotalarieae and possible that *M. ceres* does likewise.

The pollen from the provision of *M. strucki* was all of one kind and matched that of *Hermannia disermifolia*. Undoubtedly, in other areas pollen from other species of *Hermannia* would be used. Judging from foraging records, a second species, *Masarina hermanniae* Gess, most probably obtains its provision from *Hermannia*.

Foraging records indicate that it is probable that the provision of *M. tylecodoni* is derived from *Tylecodon hallii* (Crassulaceae), *M. peliostomi* Gess and *M. aptosimi* Gess from Aptosimeae (Scrophulariaceae) and *M. mixta* from *Wahlenbergia* (Campanulaceae). Although foraging records suggest that most species are oligolectic, they suggest that *M. mixtoides* may well obtain its provision from more than one family of plants.

Associates

Cuckoo wasps, Chrysididae: *Allocoelia quinquedens* Edney is in all probability associated with *Masarina*, having been observed entering the nest of *M. strucki* and inspecting nests of *M. familiaris*.

In addition, *Allocoelia glabra* Edney was observed inspecting a nest of *Masarina familiaris* (Figure II.2.17).

Figure II.2.17.—*Allocoelia glabra* Edney (Chrysididae), female at nest entrance of *Masarina familiaris* Richards.

Figure II.2.18.—*Celonites peliostomi* Gess, female entering flower of *Peliostomum* sp. (Scrophulariaceae).

Leaf cutter bees, Megachilidae: A species of *Hoplitis* usurps the nests of *M. familiaris*.

Celonites Latreille

There are 21 described species of *Celonites* (Figure II.2.18) in southern Africa. They are widely distributed throughout the Karoo Biome, are found in dry fynbos, on the dry savanna fringe and in the Namib Desert in drainage channels (Figure 75, Gess & Gess 2010).

Flower visiting

Flower visiting records are available for 15 of the southern African species of *Celonites.* Together they have been recorded from flowers of ten plant families, namely Scrophulariaceae, Campanulaceae, Asteraceae, Aizoaceae, Geraniaceae, Boraginaceae, Molluginaceae, Nyctaginaceae, Crassulaceae and Iridaceae.

Nine species (60%), including *C. andrei* Brauns, *C. clypeatus* Brauns, *C. kalahariensis* Gess, *C. michaelseni* von Schulthess, *C. peliostomi* Gess, *C. pulcher* Gess and *C. tumidiscutellatus* Gess, are specialist visitors of Aptosimeae (Scrophulariaceae). All visits to Scrophulariaceae are for Aptosimeae. Only two, *C. andrei* and *C. michaelseni*, have been recorded from any other flowers, the former from Nyctaginaceae and the latter from Campanulaceae (Lobelioideae).

Six species (40%) were recorded from Campanulaceae, four from Campanuloideae and two from Lobelioideae. Three species, *C. bergenwahliae* Gess, *C. latitarsis* Gess and *C. wahlenbergiae* Gess, though not restricted to Campanuloideae, show a preference for flowers of *Wahlenbergia* and *Microcodon.*

Five species (30%) have been recorded from flowers of Asteraceae but none of these, except possibly *C. wheeleri* Brauns, is restricted to these flowers.

One species, *C. heliotropii* Gess, has been recorded solely and abundantly from *Heliotropium tubulosum* E.Mey. ex DC. (Boraginaceae).

Visits to the other six families appear to be secondary or casual.

Nesting

Nesting has been recorded for six species of southern African *Celonites.* Aerial earthen cells on rocks, stones or plants are known for *C. andrei*, *C. michaelseni* and putatively for *C. promontorii* Brauns. Earthen cells constructed in a pre-existing burrow in the ground are known for *C. wahlenbergiae*, *C. michaelseni* and *C. arenarius* Gess (Gess & Gess 1992; Gess *et al.* 1997). One species only, *C. latitarsis*, is known to excavate a burrow in which to construct its cells. All use nectar as a bonding agent.

Nest situation

Celonites andrei and *C. promontorii* are wasps of karroid scrub on hard clayey soil. A putative nest of *C. promontorii* was found attached to a dwarf shrub (Aptosimeae) in the southeastern Nama-Karoo near Norvalspont just south of the Orange River.

Celonites michaelseni, widespread in karroid scrub and dry savanna, was found nesting on only two occasions. Firstly in a rock crevice south of the Orange River in the Richtersveld National Park and in the second case somewhat further east, north of the Orange River, near Ariamsvlei, nesting in a cavity in the hard ground.

Celonites arenarius is known only from a sparsely vegetated sandy area southeast of the mouth of the Orange River, where a single instance of nesting was observed.

Celonites wahlenbergiae and *C. latitarsis* are wasps of dry fynbos. The former was found nesting to the east of the Olifants River, Clanwilliam, and the other between Clanwilliam and Graafwater to the west of the Olifants River. The soil in these areas is sandy, relatively coarse and loose on the surface but finer and more compact beneath. The Cape Dune Molerat, *Bathyergus suillus* (Schreber) (Bathyergidae) brings the finer sand to the surface. The molehills stabilise forming ‘hillocks’ of compacted sand in which the wasps nest with *C. wahlenbergiae* in a pre-existing burrow and *C. latitarsis* in a self-excavated burrow.

Nest structure

The only completely exposed aerial nest discovered was a putative nest of *C. promontorii* (Figure II.2.19.a & b). It was on a stem of a dwarf shrub and consists of a group of earthen cells arranged in contact longitudinally and with an earthen covering. The other *Celonites* nests were all in protected situations. The nest of *C. wahlenbergiae* consisted of three linearly arranged earthen cells (Figure II.2.19.c & d) attached to the wall of an apparently pre-existing burrow excavated in sandy soil. The three cells, two completed and sealed and the third in an early stage of construction, were of a diameter appreciably less than that of the burrow. Both nests of *C. michaelseni* consisted of three cells. In each case, the third cell was still under construction and so it is not known how many cells may be constructed in a completed nest. Of the nest in the rock crevice, two cells were complete and attached to each other longitudinally and the third was being constructed with its closed end abutting the seal of one of the completed cells. The three cells of the nest in a cavity in the ground were all attached longitudinally.

The nest of *C. latitarsis* consisted of an arched entrance leading to a short sloping self-excavated burrow terminating in a horizontal excavated cell (Figure II.2.20). Within the excavated cell and of the same diameter was a constructed earthen cell.

The cells of all species were ovoid, rounded at the closed end and somewhat truncated at the open end. Completed cells had a seal positioned just inside the cell opening. Characteristic of all species is the distinct ‘fish scale’ pattern on the outer surface of the constructed earthen cell.

Method of nest construction

It seems likely that the method of cell construction is similar in all species. Whilst building a cell, a wasp makes regular visits to a quarry site. The quarry sites of *C. wahlenbergiae* and *C. latitarsis* were on stabilised molerat hillocks respectively 3 m and 2.5 m from the nests. At the quarry site, the wasp vibrated up and down vigorously whilst scraping up a load of sand, which was held by the mouthparts. The visits to the quarry alternated regularly with periods during which building material was added to the cell. Alternating with a cycle of visits to the quarry and the nest (five to seven observed for *C. latitarsis*) were periods away to collect liquid to mix with the dry sand to make it malleable for cell construction. As the cell walls are harder and more durable than they would be had water been used and, as *Celonites* has never been observed at water, it seems probable that nectar is used. Certainly, between bouts of quarrying and cell construction, *C. latitarsis* and *C. wahlenbergiae* regularly visited flowers of *Wahlenbergia psammophila* Schltr. and *Tylecodon*

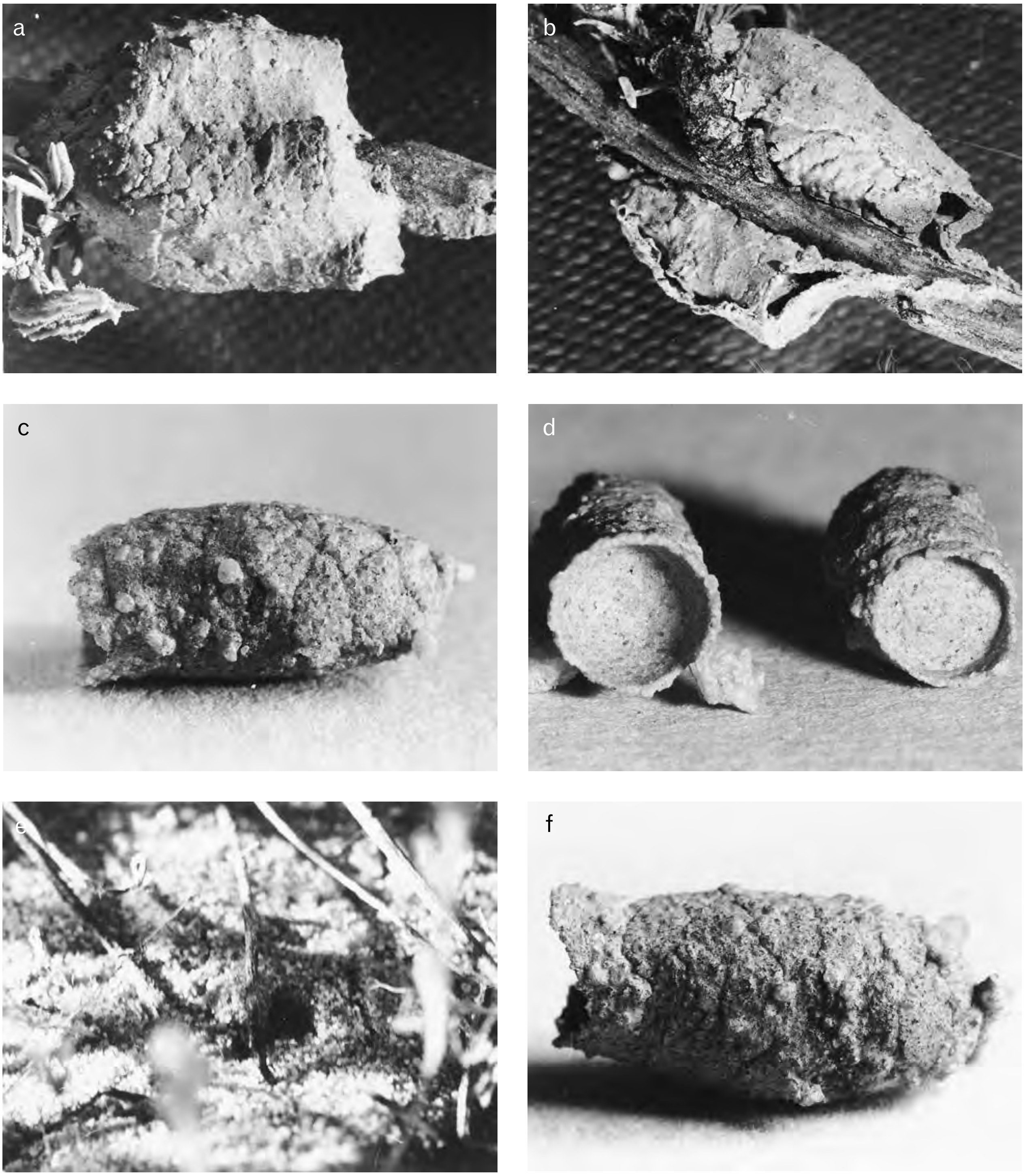


Figure II.2.19.—a.–f. *Celonites* species. a. and b. *Celonites promontorii* Brauns, putative nest (actual length 13 mm); c. and d. *C. wahlenbergiae* Gess, c. incomplete cell with rounded blind end, d. sealed completed cells (actual diameter of seals 3.8 mm); e. and f. *C. latitarsis Gess*, e. nest entrance, f. cell (actual length 11 mm).

reticulatus (L.f.) Toelken (formerly as *Cotyledon dichotoma* Haw.) respectively.

Each load of earth is added to the cell in the form of a semi-circular plate. Cell construction by *C. latitarsis* was monitored from start to finish. It took approximately two hours during which time 36 additions to the cell were made. Each visit to the quarry took 29 seconds (n = 36) and each period in the nest, during which cell construction proceeded, took 48 seconds (n = 37). Absences for liquid collection took 10–20 minutes.

After oviposition and provisioning, the cell is sealed with a plate constructed just inside the lip of the cell from moistened earth laid down in concentric rings.

Further cells may be constructed. After the completion of the construction of a group of aerial cells, the builder may bring further ‘mortar’ for the construction of a covering.

In nest construction by *C. latitarsis*, cell construction is preceded by burrow excavation. The wasp draws out sand excavated from the burrow as she reverses out of the

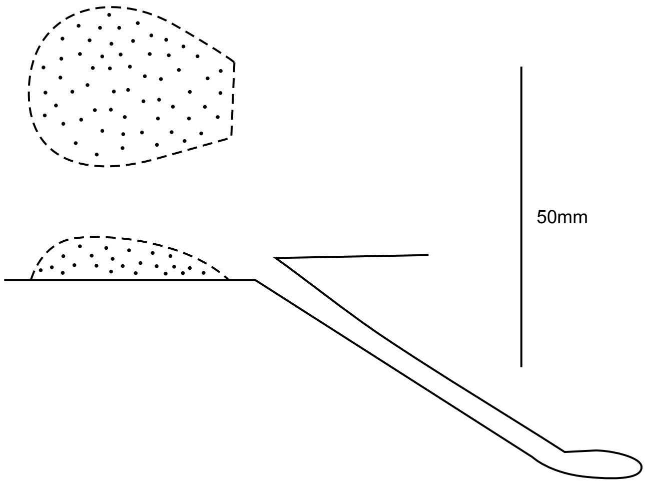


Figure II.2.20.—*Celonites latitarsis* Gess, Nest plan: nest entrance tumulus as seen from above (top); vertical plan (bottom).

burrow. Excavated sand accumulates as a tumulus approximately 20 mm downslope from the burrow entrance. From time to time, a certain amount of raking of the 'path' between the burrow and the tumulus takes place. The burrow entrance is left open while the wasp is away from the nest.

Nest excavation by *C. latitarsis* is linked to the unusual form of its forelegs that differ from those of the other species of *Celonites*. The tarsi are more robust, are markedly expanded and are equipped with unusually stiff setae.

Oviposition and provisioning

The provision from the cells of *C. wahlenbergiae* was olive green, very moist and yet did not adhere to nor wet the cell walls. The pollen, examined microscopically, was of two types, both apparently smooth-walled. On comparison with pollen from plants growing in the vicinity of the nest, one of the pollen types was found to match only that from *Wahlenbergia paniculata* (Thunb.) A.DC. (Campanulaceae) and the other only that from a *Coelanthus* species (Aizoaceae) which was growing mixed with the *Wahlenbergia*. Although the nester visited *Tylecodon reticulatus* (Crassulaceae), there was no pollen from this plant in the sample of provision examined. It is possible that it was visited for nectar only. As provision has only been obtained from Clanwilliam, no comment can be made on whether any of the other plants visited by the wasp in other areas was made use of for obtaining pollen and/or nectar for provision.

Pollen from the provision of *C. latitarsis* was all of one type. On comparison with pollen from plants growing in the vicinity of the nest, it was found to match only that of *Wahlenbergia psammophila* (Campanulaceae).

The provision of *C. michaelseni* from the Richtersveld nest was pale grey, very moist but, having a papillate surface, barely touched the cell walls. Foraging records suggest that *C. michaelseni*, *C. peliostomi*, *C. tumidiscutellatus* and *C. clypeatus* derive their provision from Aptosimeae (Scrophulariaceae).

Celonites heliotropii, which has been found foraging only on *Heliotropium tubulosum*, may well specialise in obtaining its provision from this plant.

Foraging records suggest that not all *Celonites* are specialists, for example *C. capensis* Brauns, which is highly polyphagous, recorded from flowers of seven families, may well prove to be polylectic.

Associates

Cuckoo wasps, Chrysididae: there are only two recorded associations of cuckoo wasps with *Celonites* in southern Africa, both by species of the genus *Spintharina* (Chrysididae, Chrysidini) reared from cells. *Spintharina arnoldi* (Brauns) is reared from the putative nest of *C. promontorii* and *S. bispinosa* Mocsáry from cells of *C. andrei*. The latter species has been recorded as present in a nesting aggregation of *Jugurtia confusa*.

In the Palaearctic Region a third species of *Spintharina*, *S. versicolor* (Spinola), is known as a parasite of *Celonites* sp.

Quartinia Ed André

There are 87 described species of *Quartinia* (Figure II.2.21) with more species described and awaiting publication. *Quartinia* is found throughout the distribution range of Masarinae in southern Africa (Gess & Gess 2010, Figure 81). Throughout the more arid areas, including the true desert, the Namib and southern extensions thereof, *Quartinia* is species diverse, can be considered one of the most common insects, and is often present on flowers in large numbers. This is in contrast with the other pollen wasp genera, which are either absent (*Priscomasaris* and *Ceramius*) or poorly represented (*Jugurtia*, *Masarina* and *Celonites*) in the most arid areas. The number of species associated with the desert and the zonation of these species is currently being determined, however, there are coastal species, coastal and inland desert fringe species which penetrate along drainage channels, Southern Namib species, Namib Dune species, and Central and Northern Namib gravel plains species.

Flower visiting

As with *Ceramius*, Aizoaceae and Asteraceae are of great importance as forage plants. Of the 51 species for which flower visiting records are available, 71% have been recorded from Aizoaceae (including both Mesembryanthema and non-Mesembryanthema) and 53% from Asteraceae. Amongst these, 13 species (25%) visit both Aizoaceae and Asteraceae, with a preference for one, both or neither. An appreciable number of species, 31%, visit *Zygophyllum* (Zygophyllaceae) from just south of the Orange River northwards through western Namibia. Some species are abundant visitors. The number of *Quartinia* species recorded from Geraniaceae, Boraginaceae, Campanulaceae, Malvaceae, Plumbaginaceae, Neuradaceae, Scrophulariaceae, Brassicaceae, Vahliaceae, Amaranthaceae, Cucurbitaceae, Fabaceae and Asphodelaceae is variously one to three. Amongst these species, there are some with apparently definite preferences for flowers of one of these families. *Quartinia codoni* Gess, a species occurring in the Richtersveld, immediately south and north of the Orange River, is frequently present in large

Figure II.2.21.—*Quartinia* sp. visiting flower of white mesemb (Aizoaceae, Mesembryanthema).

numbers in the flowers of *Codon royenii* L. (Boraginaceae). *Quartinia bonaespei* Gess on the Western Cape coast has been recorded almost twice as many times from Asphodelaceae as from its other forage plant family, Aizoaceae. From Namaqualand and the Olifants River Valley there are more records of *Q. persephone* Richards from Campanulaceae than from Aizoaceae and Asteraceae, the other two families from which it has been recorded. *Quartinia poecila* von Schulthess has been recorded from flowers of seven families, Aizoaceae and Asteraceae being most favoured along the Northern Cape coast but in the Sperrgebiet taking second place after Neuradaceae (*Grielum sinuatum* Licht. ex Burch.). In the southwest *Limonium* appears to be an important secondary forage plant for at least one species which is more commonly a mesemb visiting species. *Quartinia tarsata* (Richards) in addition to Aizoaceae and Asteraceae visits Aptosimeae (Scrophulariaceae) in Namaqualand and across the Nama-Karoo in South Africa, which it appears to favour.

Exceptional is the record of a good sample of *Q. antigone* (Richards) from *Aloe striata* Haw. (Asphodelaceae) near Prince Albert in the southern Nama-Karoo.

Nesting

Quartinia species excavate a burrow in friable soil. This they surmount with a turret and within each excavated cell construct another cell. They are unique in that they have retained the larval ability to spin silk, which they use as a bonding agent in the stabilisation of the burrow and construction of the turret and cells. Nesting has been recorded for nine species of *Quartinia*; *Q. vagepunctata* von Schulthess (Gess & Gess 1992), and *Q. australis* Gess, *Q. bonaespei* Gess, *Q. conchicola* Gess, *Q. namaqua* Gess, *Q. namaquensis* Gess, *Q. obibensis* Gess, *Q. poecila* Gess and *Q. refugicola* Gess (Gess & Gess 2008).

Nest situation

Nesting by *Q. vagepunctata* in the Skuinshoogte Pass, northeast of Nieuwoudtville has been described. The nesting aggregation was in a bare patch, approximately 1 metre square, of somewhat uneven level ground between shrubs in an area of karroid scrub. The soil was sandy and friable. Each nest had its entrance to one side of an earth clod or stone.

At least seven species of *Quartinia* nest in sand in the shells of terrestrial snails (Mollusca, Gastropoda). Nests have been recorded from the sand-filled shells of several species of *Trigonephrus* (Dorcasiidae) in the winter rainfall region from Cape Town to the Drachenberg, south of Lüderitz. Up to 70% of available shells were found to have been utilised. At Blaauwberg, Cape Town, *Trigonephrus* shells were found in relatively small numbers, however, shells of an invasive exotic snail, *Theba pisana* (Müller) (Helicidae), which competes with *Trigonephrus* for resources and also preys upon it, are abundant. These shells are much smaller and are lower crowned, but they are also used. Clearly, they are able to house fewer cells and as the crown is low, the nest is less secure. Although historically *Trigonephrus* and *Tropidophora* have been recorded from the western south coast, no shells of these snails were found at the sites investigated but *T. pisana* shells were abundant. Only at Witsand were *T. pisana* shells found to be used for nesting by *Quartinia*. No species of *Quartinia* were found nesting in snail shells at any of the sampling sites from Witsand east to Riet River in the Eastern Cape.

Representation of species from snail shells was as follows:

- In the desertic winter rainfall area north of the Orange River to south of Lüderitz Bay, *Q. obibensis* and *Q. refugicola* either singly or together (and also nesting in sand captured in crevices in calcrete).
- In the desertic winter rainfall area south of the Orange River to Hondeklip Bay, *Q. obibensis*, *Q. refugicola* and *Q. conchicola*.
- In sandveld in the vicinity of Hondeklip Bay and Wallekraal, *Q. namaqua* and *Q. namaquensis* (otherwise known only from the Kamiesberg).
- In the sandveld area north of Vanrhynsdorp, *Q. conchicola*.
- In dune slacks along the coast from Donkinsbaai, north of Lamberts Bay, south to 4 km north of Blaauwbergstrand in the Blaauwberg Conservation Area north of Cape Town, *Q. bonaespei*.
- At Yzerfontein on the southwest coast in addition, surprisingly, *Q. obibensis* and *Q. namaqua*.
- In dune slacks at Witsand on the south coast east of Cape Town, *Q. australis*.

In the area north of Port Nolloth to south of Lüderitz, in addition to *Q. obibensis* and *Q. refugicola*, a third closely related species (*Q. vexillata* Gess) was collected from flowers at several sites but was not collected from snail shells. It is thought that this species most probably also nests in sand-filled snail shells.

Quartinia poecila was found nesting in relatively stable sand at the base of its forage plants on dunes at Port Nolloth. It is suspected that such a nesting situation may be common to some other species of *Quartinia*.

Figure II.2.22.—*Quartinia vagepunctata* von Schulthess, position of nest entrance turret (indicated by arrow).

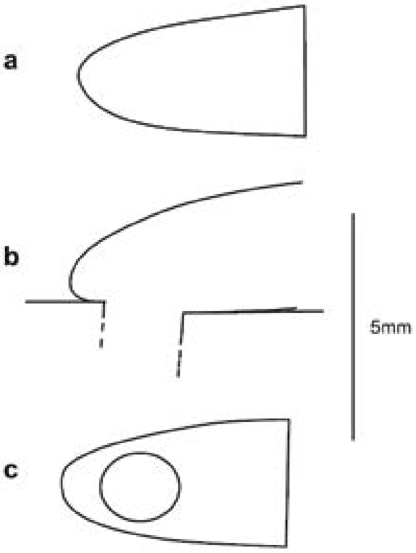


Figure II.2.23.—*Quartinia vagepunctata* von Schulthess, plans of turret: a. from above; b. vertical section; c. from below.

Nest structure

The nests of all nine species found nesting consisted of a subterranean burrow excavated in sandy soil. The nests of *Q. vagepunctata* and the seven species nesting in snail shells consist of a subterranean silk-lined burrow surmounted by a turret constructed from silk and sand, the inner surface being of silk and the outer surface of sand (grain size: 0.16–1.2 mm in nests of *Q. vagepunctata*) held together by the silk.

The turret of *Quartinia* spp. nesting in snail shells was a simple short, erect cylinder of the same diameter as the burrow (Figure II.2.22). That of *Q. vagepunctata* is horizontal, bag-like, approximately circular in cross-section with its diameter greatest at its outer open end and smallest at its closed inner end, with the opening to the burrow entrance at some little distance from the closed inner end of the bag.

Figure II.2.24.—*Quartinia* sp., nest entrance turret to nest in sand-filled shell.

The burrow of all the snail shell nesters is multicellular, with up to 20 or more cells closely packed into the spiral of the shell (Figure II.2.23). That of *Q. vagepunctata* consists of a subvertical shaft that terminates in a sealed, roughly ovoid cell (Figures II.2.23–25). In one of the nests the female was found sheltering in a lateral shaft, suggesting that more than one cell per nest is probably constructed.

The cell walls of all are constructed of sand bonded together with silk and those of *Q. vagepunctata* are in addition cemented with a substance somewhat resinous in appearance.

The nests of *Q. poecila* were in an early stage of construction, each consisting of a short vertical shaft only.

There appear to be no records of nesting by the Palaearctic species of *Quartinia*.

Method of nest construction

Quartinia is unique amongst the Masarinae worldwide in the use of self-generated silk as a bonding agent in the construction of its nest turrets, burrow and cell walls. The silk used in nest construction is spun by the nest-builder. One individual was observed whilst constructing its nest. It was joining together sand grains with silk and whilst so doing was rotating its head, the silk was apparently issuing from its mouth.

Oviposition and provisioning

The provision from each of four nests of *Q. vagepunctata* was in the form of a relatively moist bright yellow nectar and pollen mass almost entirely filling the cell, adhering to the cell walls and therefore not forming a discrete pollen loaf. The pollen from one of the nests was found to be all of one kind and to match that of *Cotula leptalea* (Asteraceae). That from the other three nests matched that of *Relhania* and *Cotula* (both Asteraceae).

Associates

Velvet ants, Mutillidae: Two species, one of the genus *Tricholabiodes* and one of an undescribed genus (both

Figure II.2.25.—*Quartinia refugicola* Gess, nest cells in opened shell of *Trigonephrus* (Dorcasiidae).

Sphaeropthalminae, Dasylabrini) have been reared from nests of *Quartinia* in snail shells from sites in southwestern Namibia and south of the Orange River, east of Alexander Bay. Both are night-flying and pale orange in colour.

Cuckoo wasps, Chrysididae: *Allocoelia mocsaryi* Brauns (Chrysidinae, Allocoelini) (Figure II.2.26.a–c) has been reared from nests of *Quartinia* in snail shells from sites in southwestern Namibia and south of the Orange River, east of Alexander Bay. *Allocoelia* pupates outside the *Quartinia* cell in which it developed so that in nests from which it has emerged its past presence is readily visible in the form of its empty cocoon attached to the outside of a *Quartinia* cell.

Several individuals of *A. mocsaryi* were present in close proximity to the nests of *Q. vagepunctata*.

Bee flies, Bombyliidae: *Apolysis hesseana* Evenhuis & Greathead (Usiinae, Usiini) has been reared from nests of *Quartinia* in snail shells from sites in southwestern Namibia and south of the Orange River, east of Alexander Bay (Figure II.2.27). In nests from which *Apolysis* has emerged, the empty shuck is found attached to the outside of a *Quartinia* cell.

Subfamily Eumeninae

Eumenines are extremely species diverse. More than 3 000 species have been described. The number of genera and species of Eumeninae represented in southern Africa is still to be established. However, for the Afrotropical Region, excluding the Malagasy Subregion, 75 genera and 686 species are listed by Carpenter *et al*. (2009, 2010a, 2010b).

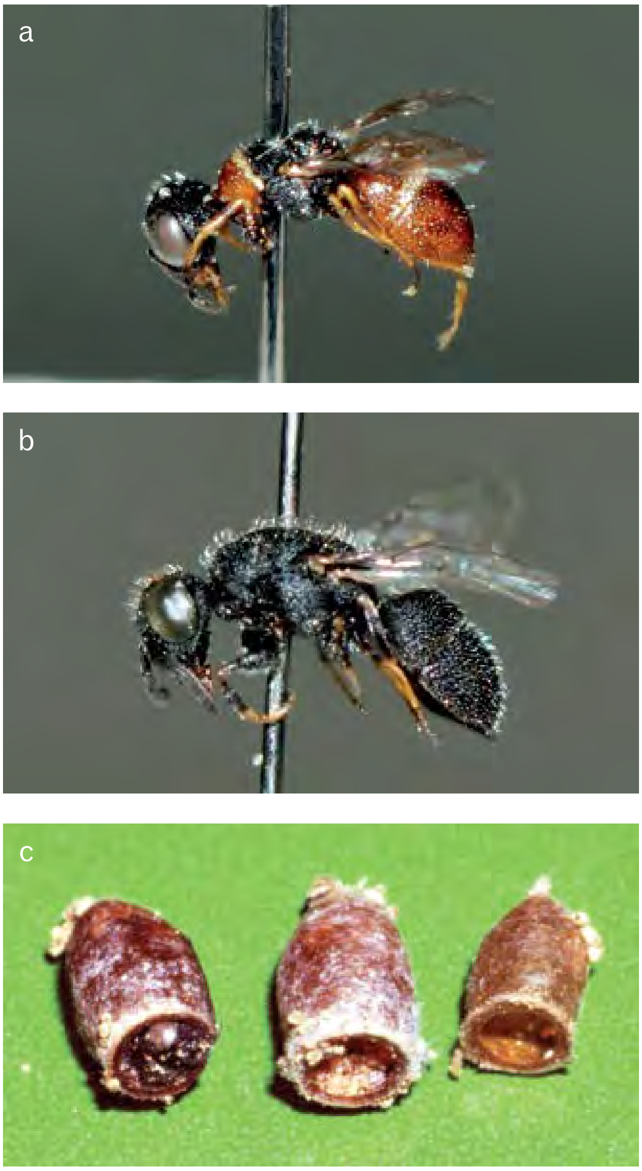


Figure II.2.26.—a.–c. *Allocoelia mocsaryi* Brauns: a. light coloured form; b. melanistic form; c. cocoons from *Quartinia* nest in snail shell.

Figure II.2.27.—*Apolysis hesseana* Evenhuis and Greathead (Bombyliidae) (left), reared from nest of *Quartinia obibensis* Gess in snail shell (female and nest, right) (Actual length of wasp 5.4 mm).

Eumenines are known variously to excavate multicellular burrows surmounted by an entrance turret in non-friable soil and in vertical banks, to nest in pre-existing burrows in horizontal ground, vertical banks and in plants, and to construct aerial mud nests on rocks, stones and plants. In southern Africa, no eumenines have been found nesting in friable soil but this nesting substrate is known for at least one genus, *Pterocheilus* Klug, studied in North America. This genus is unusual in having mouthparts specially adapted for carrying sand.

As a general rule eumenines provision their nests with paralysed caterpillars; in exceptional cases beetle larvae are used. In all species oviposition precedes provisioning. The egg is characteristically attached to the wall of the cell, the position varying according to genus.

The most familiar nests are the aerial mud nests, such as those built by species of *Afreumenes* Lepeletier, *Delta* de Saussure, *Eumenes* Latreille and *Pseudonortonia* Giordani Soika, which have given members of this subfamily the common names of mason wasps and potter wasps. However, species nesting in burrows are more numerous. For southern Africa there are relatively few studies on burrow nesters. Accounts are available for some species of burrow initiators in the genera *Aethiopicodynerus* Gusenleitner (= *Parachilus* Giordani Soika), *Antepipona* de Saussure (including vertical banks), *Paravespa* Radoszkowski and *Raphiglossa* Saunders, and of nesters in a pre-existing cavities in the genera *Knemodynerus* Blüthgen, *Proepipona* Giordani Soika, *Rynchium* Spinola and *Tricarinodynerus* Giordani Soika.

Water is required for nesting by most species. Excavators of nests in the ground and in vertical banks all nest in non-friable soil and use water for burrow excavation and turret construction. Builders of aerial nests and nesters in pre-existing cavities carry water to a quarry site where it is used to mix mud, which is then transported to the nest building site.

Burrow excavation in plant tissue is uncommon.

Flower visiting

Flower visiting records are available for 30 species of Eumeninae identified to species level. At least 16 other species in seven genera await determination. The eumenines, unlike the masarines, but more typically of aculeate wasps in general, visit flowers of a wide range of families. Flower families, with approximate percentages of eumenine species visiting them, included: Fabaceae (Mimosoideae) 49%; Apiaceae 27%; Rhamnaceae 26%; Asteraceae 24%; Fabaceae (Papilionoideae) 16%; Aizoaceae 15%; Acanthaceae 11%; Celastraceae 9%; Geraniaceae 9%; Apocynaceae (including the formerly known Asclepiadaceae) 7%; Solanaceae and Portulacaceae 6% each; Scrophulariaceae (Selagineae) 4 %; Campanulaceae, Capparaceae, Ebenaceae, Salvadoraceae, Anacardiaceae and Boraginaceae 2% each.

Aethiopicodynerus Gusenleitner (= *Parachilus* Giordani Soika)

Aethiopicodynerus, for which 13 species have been described, is endemic to the Afrotropical Region. Six species have been recorded from southern Africa (Carpenter *et al.* 2009). There appear to be published nesting accounts for only three species, *A. insignis* (de Saussure) (Gess & Gess, 1976), *A. capensis* (de Saussure) and *A. major* (de Saussure) (Gess & Gess 1988b), all southern African endemics. The prey consist of larval psychids (bag worms). After capturing the prey, the wasp extracts it from its bag; the 'naked' caterpillars being used for provisioning the cells. The nesting *A. insignis* and *A. capensis* were investigated on the farm Hilton, near Grahamstown in the Eastern Cape and that of *A. major* in the Goegap Nature Reserve, near Springbok, Namaqualand.

Nest situation

The three species of *Aethiopicodynerus* for which nesting has been recorded all nest in the ground in non-friable clayey soil in aggregations in bare areas in karroid vegetation in close proximity to a water source.

Nest structure

The nests of the three species of *Aethiopicodynerus* are all of similar structure, a one- or two-celled burrow surmounted by a mud entrance turret. The nests can be readily distinguished by the design of the turret. That of *A. capensis* is flared, that of *A. major* cylindrical and that of *A. insignis* merely a collar. The remarkable feature of the nests of all three species is that the cell is divided into compartments, suggesting that this is probably typical for the genus *Aethiopicodynerus* (Figures II.2.28–30).

Method of construction, oviposition and provisioning

The wasp, when collecting water for nest excavation, stands on the mud at the edge of the water (Figure II.2.31).

The mud-pellets extracted at the start of burrow excavation are used for the construction of the entrance turret. Further pellets extracted after the turret has been completed are discarded in a definite pellet dropping area. When dropping pellets a female always leaves the nest in the same direction, flies off, drops the pellet, and before returning flies in a wide circle, re-entering the nest facing away from the pellet dropping area. All individuals in a particular nesting aggregation were seen to have their pellet dropping areas in the same direction. Later in the season, the nests were closely crowded and therefore the pellet dropping areas were no longer distinct.

The shaft is initially vertical and later curves to one side to end in a cell of slightly greater diameter than the shaft and with the inner end rounded.

The egg is attached by a thread to the wall in the lowest section of the cell, after which some provision is supplied. A thin mud plate is then constructed to close off this compartment. The greater part of the provision is stored by *A. insignis* and *A. major* in a single pantry compartment separated from the egg compartment by a thin mud partition, 1 mm or less in thickness, and by *A. capensis* in more than one compartment each separated by a thin mud partition. After the upper compartment has been fully provisioned, the cell is closed with a thicker more robust mud plug, about 2 mm thick.

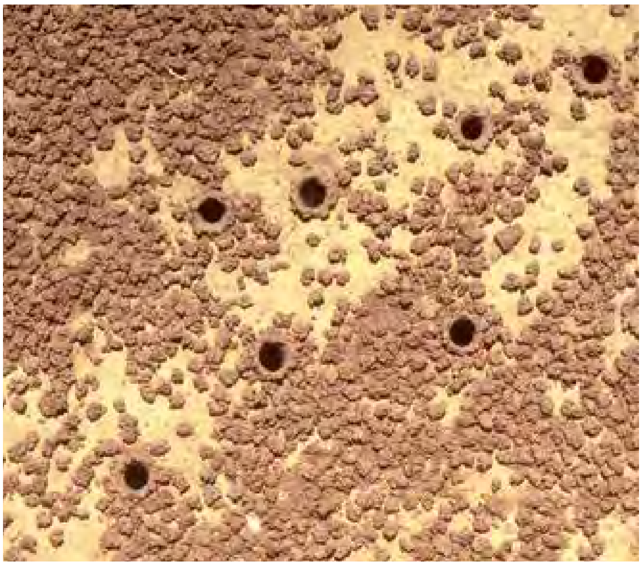


Figure II.2.28.—*Aethiopicodynerus insignis* (de Saussure), nest aggregation.

Figure II.2.29.—*Aethiopicodynerus insignis* (de Saussure), female at nest entrance.

After completion of the cell or cells, the shaft is filled using loose crumbs of earth, scattered discarded pellets and pellets formed with the use of water from the nest collar or turret and from a 'quarry' a short distance (*circa* 300 mm) from the nest. The wasp flies from the quarry to the nest with each pellet and drops it down the shaft. When the shaft has been filled, the wasp seals the opening by cementing together pellets to form a plug, smoothed but somewhat concave so that sealed nests are difficult to distinguish from quarry sites.

Identity of prey and prey transport

All three species apparently provisioned with caterpillars of the same two species of psychid caterpillars. A total of 318 prey of *A. insignis* were examined, 287 were of one species and only 31 of the second species. Unfortunately, neither prey capture nor the extraction of the caterpillars was observed. However, careful search for the caterpillars resulted in the discovery that the more commonly used species feeds on *Pentzia incana* (Burm.) DC. (Asteraceae). Only one individual of the other species was found feeding on a plant, also Asteraceae.

A total of 54 prey of *A. major* were examined, 50 were of the species taken from *P. incana* and only four of the second species. Only 12 prey of *A. capensis* were obtained, 9 of the species taken from *P. incana* and three of the second species.

The prey is carried to the nest in flight. It is held closely beneath the wasp's body by the mandibles and legs, positioned ventral side up and facing the direction of travel. On arrival at the nest, she relinquishes the hold with her legs. Holding the prey with her mandibles, she works it forwards and drops it down the shaft. After several prey have been dropped down the shaft, the wasp enters the nest and arranges them in the cell.

Sleeping and sheltering

The females shelter in their burrows in unfavourable weather and at night. They position themselves head uppermost facing the entrance.

Associates

Two chrysids, *Chrysis edwardsi* Buysson (Figure II.1.2) and *Spinolia ardens* (Mocsáry) were frequently found in association with nests of *Aethiopicodynerus insignis* (Saussure) (Gess & Gess 1976), as *Octochrysis vansoni* Brauns (Figure II.2.32) and *Pseudospinolia ardens* (Mocsáry) in association with *Parachilus insignis* (Saussure).

A meloid beetle, *Lytta enona* Péringuey (Figure II.2.33.a–c), was a common 'parasite' in the nests of *A. insignis* on the farm Hilton. In its larval stage it fed on the stored caterpillars after first destroying its host's egg.

A bombyliid fly, *Exoprosopa leucothyrida* Hesse was commonly found resting on the ground or flying around the nests of *A. insignis* on the farm Hilton where a bombyliid larva was obtained from a nest of this wasp.

During the summer 1973/74 a camponotine ant, *Plagiolepis steingroeveri* Forel, nesting on the edge of a nesting aggregation of *A. insignis*, systematically robbed this wasp's nests of the caterpillar provision, attacking the wasps if they alighted on the ground.

Old burrows were used for nesting by various bees and wasps that nest in pre-existing cavities in the ground.

Afreumenes Bequaert

Afreumenes is Afrotropical in distribution. Seven species are listed (Carpenter *et al.* 2009). Four have been recorded from southern Africa. The nests are single-celled solitary pots.

Alan Weaving (1995a) investigated the nests of *A. aethiopicus* (Saussure) in northern KwaZulu-Natal where this wasp was constructing its pot nests on roof beams, walls and roofing thatch, usually on vertical surfaces (Figure II.2.34). The pots were 12–14 mm in diameter with walls approximately 1 mm thick. Oviposition was into the empty nest and was followed by mass provisioning with caterpillars, the identity of which was not given. The nest remained open during provisioning and was finally plugged

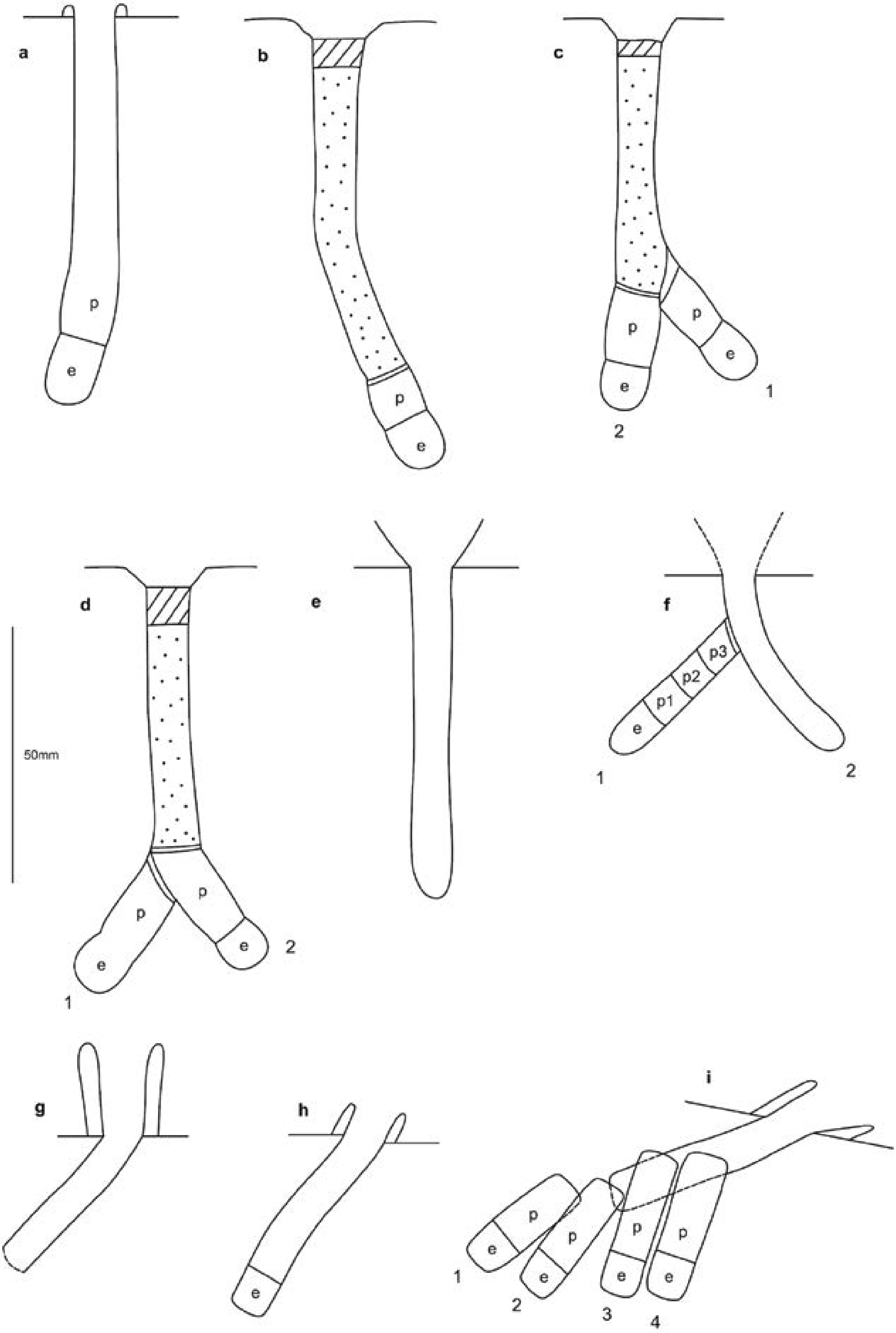


Figure II.2.30.—a.–i. *Aethiopicodynerus*, vertical plans of nests (p = pantry compartment, e = egg compartment): a.–c. *A. insignis* (de Saussure); d.–f. *A. capensis* (de Saussure); g.–i. *A. major* (de Saussure).

Figure II.2.31.—*Aethiopicodynerus capensis* (de Saussure), female imbibing water.

Figure II.2.32.—*Aethiopicodynerus insignis* (de Saussure), female entering nest; female *Chrysis edwardsi* Buysson (Chrysididae) in attendance.

with mud. The lip was not destroyed and there was no daubing of the exterior with mud.

Charles Jacot Guillarmod collected a single pot of *A. violaceus* (Giordani Soika) constructed on a *Protea* leaf on his property, Faraway, on the Highlands road outside Grahamstown, Eastern Cape (specimen in Albany Museum) (Figure II.2.35).

Associates

Alan Weaving reared *Dolichomutilla heterodonta* Bischoff (Mutillidae), *Stilbum cyanurum* (Förster) (Chrysididae), *Osprynchotus* sp. (Ichneumonidae), *Melittobia* sp. (Eulophidae) and a miltogrammine fly, *Amobia africa* Curran (Sarcophagidae) from nests.

Alastor Lepeletier

Alastor is known from the Afrotropical, Palaearctic and Oriental regions. Forty-two species are listed (Carpenter

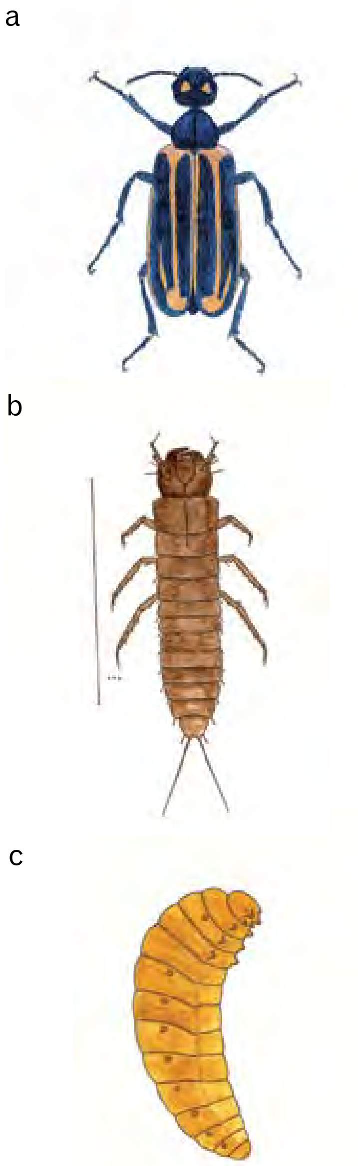


Figure II.2.33.—a.–c. *Lytta enona* Péringuey (Meloidae), nest parasite of *Aethiopicodynerus insignis* (de Saussure):
a. adult, actual size 13 mm; b. triungulin larva, scale bar = 1 mm;
c. coarctate larva, actual size 12 mm.

Figure II.2.34.—*Afreumenes aethiopicus* (de Saussure), female constructing pot nest.

Figure II.2.35.—*Afreumenes violaceus* (Giordani Soika) female and pot nest on *Protea* leaf.

Figure II.2.36.—*Alastor ricae* Giordani Soika, female with nest in *Trigonephrus* (Dorcasiidae) shell.

et al. 2009). All are represented in the Afrotropical Region with at least 37 in southern Africa. Little seems to be known concerning the nesting of this genus.

Alastor ricae Giordani Soika

Nest situation

Alastor ricae nests in empty shells of the desert snail *Trigonephrus* (Dorcasiidae) in the desertic areas of western South Africa immediately north and south of the Orange River (Hesse 1944 as a 'Eumenid wasp' in the shells of *Trigonephrus* as '*Dorcasia rosacea*'; Gess & Gess 1999 as 'a eumenine'; Koch 2006; Gess & Gess 2008).

Nest structure

Even without the nest builders, these nests are readily identified being the only nests in shells with the nest closure constructed from pebbles embedded in a matrix of sand and an unidentified bonding substance (Figure II.2.36).

Figure II.2.37.—*Allepipona perspicax* Giordani Soika, female on nest entrance turret depositing a pellet on the surrounding circular wall of discarded un-worked mud pellets.

Allepipona Giordani Soika

Allepipona is a small genus of seven species, all endemic to the Afrotropical Region (Carpenter *et al*. 2009). All but one of these species is known from southern Africa.

Little has been published on the nesting of *Allepipona*, the only published accounts for southern Africa appear to be those for *A. erythrospila* (Cameron) (Gess & Gess 1991) and *Allepipona perspicax* Giordani Soika (Weaving 1995b).

Nest situation

Two nests of *A. erythrospila* were investigated on the farm Hilton. Both nests were situated in level areas of denuded clayey soil near the edge of shallow rain puddles.

Five nests of *A. perspicax* were investigated in Mkuzi Game Reserve in northern KwaZulu-Natal. These were situated along a hard clayey footpath through riverine bush.

Description of nest

Neither of the nests of *A. erythrospila* was complete. One consisted of a short burrow surmounted by a collar of the same diameter constructed from mud pellets. The second lacked an entrance turret or collar, which appeared to have been present but had been destroyed by the trampling of sheep. The burrow of this nest consisted of a short curved shaft slightly dilated at its lower end to form a cell. Provisioning was still in progress and so it is not known what the nature of the seals would have been or whether further cells would have been excavated.

The nests of *A. perspicax* were reported to consist of a vertical to subvertical shaft terminating in one to three linearly arranged cells. The burrows were surmounted by a short flared turret. Of particular interest was that the turret was surrounded by a circular wall of unworked mud-pellets (Figure II.2.37).

Figure II.2.38.—*Antepipona scutellaris* Giordani Soika, female on nest entrance turret.

Method of construction

Allepipona erythrospila was seen collecting water from the edge of a pool. Discarded pellets were dropped in a distinct pellet dropping area about 1.90 m from the nest.

Initiation of the nests and construction of the turret of *A. perspicax* was not observed, however, the builders were seen adding pellets to the outer circular wall while straddling the gap between the turret and the wall.

Oviposition and provisioning

During burrow excavation *A. erythrospila* always entered the nest forwards but, as she is not able to turn around in the burrow, entered backwards to oviposit. The egg of *A. erythrospila* and *A. perspicax*, typically for eumenines, were laid before provisioning and was suspended from the wall at the outer end of the cell.

After oviposition, provisioning commenced. The single prey of *A. erythrospila* obtained was a caterpillar of the family Pyralididae. The wasp carried the caterpillar in flight, held beneath her, facing forwards, using her mandibles and legs. On alighting next to the nest entrance, the wasp retained her hold on the prey with her mandibles and straddling it entered the burrow facing forwards.

The provision from two cells of *A. perspicax* consisted of six and seven caterpillars, the identity of which was not recorded.

Associates

Miltogrammine flies were observed following *A. perspicax* to their nests and one, recently emerged, was found in the three-celled nest.

Antepipona de Saussure

Antepipona is found in the Afrotropical, Palaearctic and Oriental regions. Carpenter *et al.* (2009) recognise 76 species, 38 of which are represented in southern Africa.

The nesting knowledge for *Antepipona* is limited. For southern Africa, there appears to be only a published account for *A. scutellaris* G. Soika (Gess & Gess 1991) from the Grahamstown area in the Eastern Cape and some observations for *A. tropicalis* (de Saussure) (Robert Gess notes, photographs and voucher specimens 2009) from Bathurst in the Eastern Cape.

The only previously published accounts of the nesting of *Antepipona* in the Afrotropical Region appear to be those of Roubaud (in Bequaert 1918) and of Bonelli (1973a). Roubaud's study concerned the nesting of a species identified by him as *Odynerus tropicalis* (de Saussure) (= *Antepipona tropicalis* (de Saussure)) in Dahomey (Benin according to Giordani Soika (1985) and Carpenter *et al.* (2009)). Whereas Giordani Soika accepted Roubaud's species as belonging to *Antepipona*, he believed that it was not *A. tropicalis*. Carpenter *et al.* (2009), however, accept Roubaud's identification. Bonelli's studies concern the nesting in Ethiopia of *A. silaos silaos* (de Saussure) and of its subspecies, *A. silaos quartinae* (Gribodo) (as *A. asmarensis* (von Schulthess)—for synonymy see Giordani Soika 1985; Carpenter *et al.* 2009).

Antepipona silaos is a widespread species over the whole of central, eastern and southern Africa (Giordani Soika 1985) and is known also from the Grahamstown area where it is sympatric with *A. scutellaris* on the farm Hilton. From Bonelli's account, it would appear that the nesting of these two species is very similar.

Nest situation

Antepipona scutellaris on Hilton was nesting in aggregations in the floor of a sandpit on the flood plain of the Iron Put River. The substrate contained a sufficient clay factor to make it malleable when mixed with water. In addition, two nests were found on the bank of an irrigation furrow, the soil of which was non-friable clay.

Antepipona tropicalis by contrast was nesting in the clay wall of a rondavel (Figure II.2.40). It is significant that Roubaud's *A. tropicalis* was nesting similarly in a clay wall.

Nest structure

The nest of *Antepipona scutellaris* is typical for species of eumenines that nest in non-friable soil excavating a burrow and constructing a turret with the aid of water. It consists of a subterranean burrow surmounted by an erect mud-turret that is flared or funnel-shaped (Figures II.2.38 & 39). The burrow consists of a shaft of the same diameter as the base of the turret terminating in a single cell or branching to terminate in two cells. No nest was found with more than two cells. However, as none of the nests was sealed it is possible that further cells might have been constructed.

The nest of *Antepipona tropicalis* is similar but with the main shaft sub-horizontal rather than vertical.

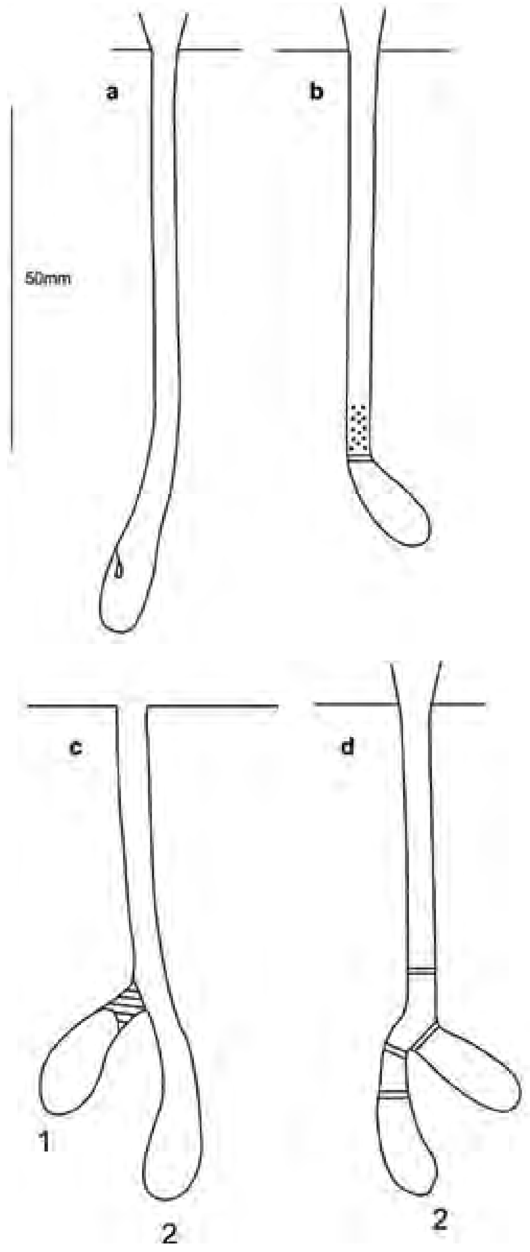


Figure II.2.39.—a.–d. *Antepipona scutellaris* Giordani Soika, diagrammatic vertical plans of four nests, a. showing placement of egg.

Method of nest construction

The mud pellets extracted at the start of burrow excavation are used for the construction of the entrance turret (Figure II.2.40). Further pellets extracted after the turret has been completed are discarded. *Antepipona scutellaris* establishes a distinct pellet dropping area 600–900 mm from the nest. *Antepipona tropicalis* simply drops the pellets so that they accumulate at the base of the wall.

At an average depth of 70 mm, the burrow of *A. scutellaris* curves slightly and the diameter is increased to create a somewhat oval cell.

The burrow of *A. tropicalis* is of similar design except that, instead of the main shaft being vertical, it slopes downwards making an acute angle with the face of the wall.

Figure II.2.40.—a.–d. *Antepipona tropicalis* (de Saussure): a. female beside nest entrance turret; b.–d. showing transport of prey caterpillars to nests.

Figure II.2.41.—*Delta hottentotum* de Saussure, female inserting prey caterpillar into nest cell.

The egg is laid hanging from a thread attached to the cell wall near its opening. After oviposition and provisioning have been completed, the cell is sealed with a mud plate, which may be followed by earth, and a second mud plate cutting it off from the shaft at the point where the burrow starts to curve.

A secondary shaft terminating in a second cell may then be excavated from immediately above the seal. In *A. scutellaris* the second cell is at a greater depth than the first.

Oviposition and provisioning

After a cell has been prepared, oviposition takes place. As the wasp is unable to turn around in the shaft, she enters backwards when preparing to oviposit. The egg is suspended from the ceiling of the cell on a short filament. Only after oviposition does cell provisioning take place. Pyralidid caterpillars are used for provisioning, the number supplied dependending on size. Up to thirteen prey caterpillars per cell have been recorded.

Robert Gess (pers. comm.) noted that *A. tropicalis* females make visits to more than one nest at a time. At the time he was unaware of the observations of Roubaud who had noted that *A. tropicalis* visits more than one nest at a time. Roubaud suggested that this species is a progressive provisioner and that it was providing for more than one larva at a time.

Sleeping and sheltering

Antepipona, typically for eumenines, shelter in their nests, head towards the entrance, during inclement weather and overnight.

After a period of rain *Antepipona scutellaris* females were found to have plugged their nests so that the cells were unharmed, with the wet soil accumulated above the wasps. This seems to be characteristic behaviour of ground nesting species of eumenids.

Associates

Two second instar (caraboid) meloid larvae (Coleoptera, Meloidae) were found in two nests of *A. scutellaris*.

Three of a sample of 17 nests of *A. scutellaris* were invaded and usurped by a megachilid bee, *Megachile* (*Eutricharaea*) *meadewaldoi* Brauns. These bees constructed their cells with pieces cut from the perianth of a violet flowered *Wahlenbergia* (Campanulaceae) growing in the vicinity of the nests.

Delta de Saussure

Delta (Figures II.2.41–44) is one of the most cosmopolitan eumenine genera having been recorded from all zoogeographical regions. Carpenter *et al*. (2010a) list 19 species, 12 of which have been recorded from southern Africa.

Little appears to have been published on the nesting of *Delta* in southern Africa, however, nests of *Delta* are a familiar sight. Alan Weaving (1995a) investigated nests of *D. hottentotum* de Saussure in eastern southern Africa (Figure II.2.41). Bonelli, working in Ethiopia, gave an account of the nests of *D. bonelli* Giordani Soika (Bonelli 1973c) and *D. emarginatum* (L.) (Figure II.2.42) (Bonelli 1973d)—species occurring in southern Africa. Ledger and Bannister (1979), in their popular book based on Skaife (1953), give an account of nesting by *D. caffrum* (L.) (Figure II.2.43.a) (correctly illustrated by Skaife 1953), but accompanied by new illustrations, three black and white photos (Figures 317–319, as *Delta* sp.) and one colour photo (Figure 122, as *D. caffrum*) all, however, not of *D. caffrum* but of *D. fenestrale* (de Saussure) (det. F.W. Gess).

Nest situation

In southern Africa *Delta* species, variously, construct their nests on vertical and horizontal surfaces of stones and rocks (Figure II.2.43.b & c). Examples include on vertical banks, including walls of man-made structures such as walls (Figure II.2.43.c) and gravestones, on the branches and trunks of trees and shrubs (Figure II.2.43.d), on the ribbed stems of *Euphorbia* species, on the stems of herbaceous plants and on leaves.

Nest structure

The nests of all *Delta* species are aerial, single pots or grouped cells with an outer envelope, and are constructed from mud. The number and robustness of the cells varies according to the species, as does the robustness of the outer envelope (Figures II.2.41, 42.c–f. and 43.b–d).

Oviposition and provisioning

The egg is laid before provisioning and is hung from the roof of the cell by a thread.

Geometrid caterpillars are favoured as prey (Figure II.2.41). These may be large in comparison to the wasp. A fully provisioned cell of *D. hottentotum* contained four geometrid caterpillars varying considerably in weight from little more than that of the wasp to four times its weight (Gess & Gess fieldnotes 1978).

Eumenes Latreille

Eumenes is one of the most cosmopolitan of the eumenines having been recorded from all zoogeographical regions. Carpenter *et al*. (2010a) list 12 species, six of which have been recorded from southern Africa.

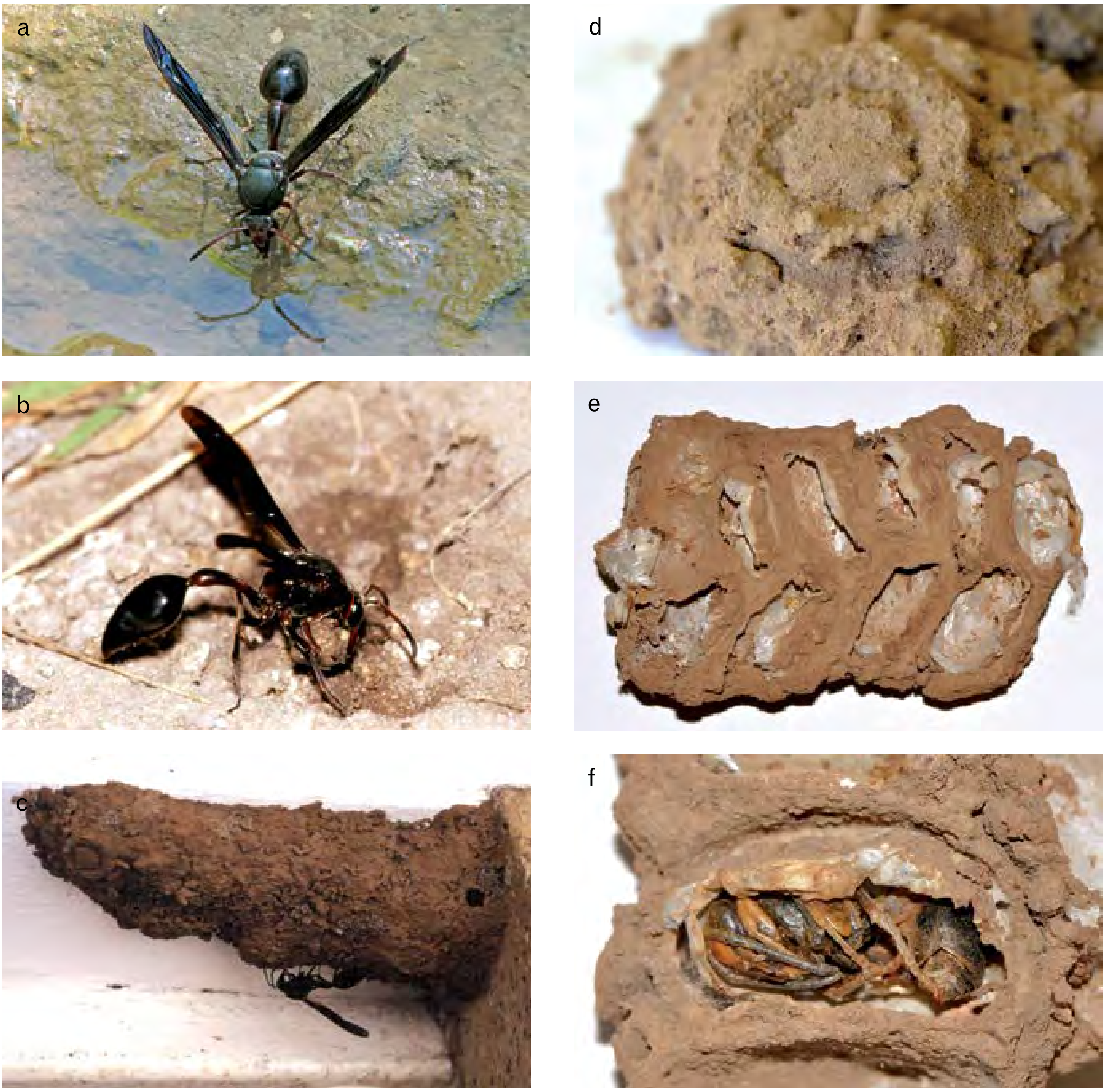


Figure II.2.42.—a.–f. *Delta emarginatum* (L.): a. female imbibing water; b. female collecting mud; c. mud nest; d. cell seal; e. nest removed from substrate showing arrangement of cells; f. pupa in cell.

Little has been published on the nesting of *Eumenes* in southern Africa, however, the small mud pot nests, easily confused with those of *Afreumenes*, are a familiar sight. *Eumenes lucasius* de Saussure builds its cells, either exposed or in sheltered places on banks or walls, or concealed, for example under loose bark or in pre-existing cavities (Figure II.2.45). We found nests of this species commonly on the neighbouring farms Hilton and Broadfields. Trap nests were accepted and 9–10 separate pots were constructed in a single row within.

Knemodynerus Blüthgen

Knemodynerus is known from the Afrotropical, Palaearctic and Oriental regions. Carpenter *et al*. (2010a) list ten species, five of which have been recorded from southern Africa.

Little seems to have been published on the nesting of *Knemodynerus.* The only account for southern Africa seems to be for *K. euryspilus* (Cameron) (as *Euodynerus euryspilus* (Cameron), Gess & Gess 1991, 1993).

Nest situation

The nests studied were in trap nests, three with borings of 6.4 mm and one with a boring of 9.5 mm, attached to branches of *Acacia karroo* growing along the banks of a water furrow on the farm Hilton. Natural nesting sites are almost certainly pre-existing cavities such as abandoned

Figure II.2.43.—a.–d. *Delta caffrum* (L.): a. female imbibing water; b. and c. nests on stones, b. three cells, two closed and one open, c. completed nest, cells covered by a mud envelope; d. nest on plant.

Figure II.2.44.—*Delta lepeletierii* (de Saussure), female imbibing water.

Figure II.2.45.—*Eumenes lucasius* de Saussure, mud pots in trap nest.

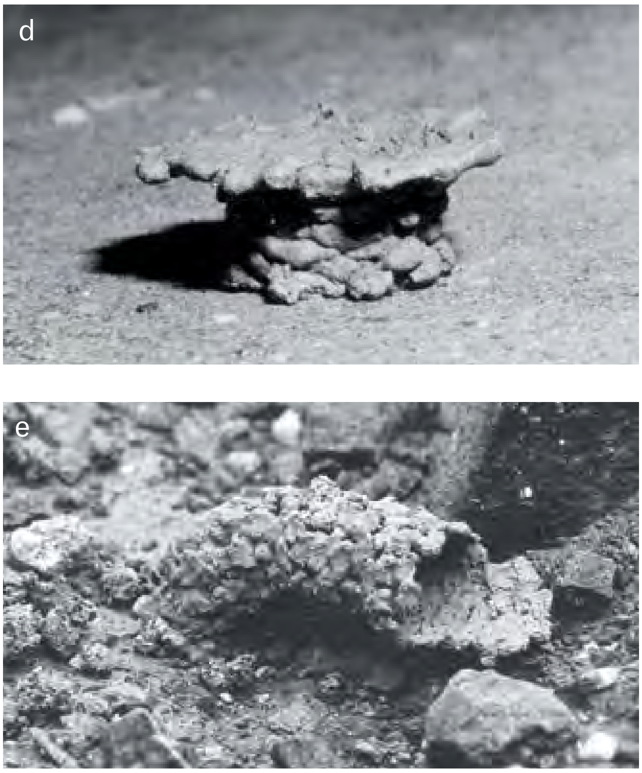


Figure II.2.46.—a.–e. *Paravespa* (*Gestrodynerus*) *mima* Giordani Soika: a. and b. female building nest entrance turret; c. and d. funnel-shaped nest entrance turret; e. curved nest entrance turret.

beetle borings in the branches of bushes and small trees along the banks of drainage channels and rivers.

Nest structure

The nests in the borings consist of a series of linearly arranged cells with unlined walls and mud closures 1–2 mm thick. In three of the four nests, there was a preliminary mud plug and in the only completed nest a vestibular cell and final closure constructed from mud. No intercalary cells such as are found in the nests of *Rynchium marginellum* were present.

Oviposition and provisioning

Oviposition is into the empty cell, the egg being attached from the roof at the inner end.

The cells of the nests examined were provisioned with pyralidid caterpillars, mostly and in two nests solely those of *Loxostege frustalis* Zeller, the karoo caterpillar, a serious pest of *Pentzia incana* (Thunb.) Kuntze (Asteraceae). Completed cells contained 7–13 caterpillars, depending upon the size of the caterpillars.

Sheltering

During inclement weather, females were found sheltering in their nests, facing outwards. Presumably, they also spend the night in their nests.

Associates

The nests of *K. euryspilus* are parasitised by *Chrysis hoplites* Mocsáry (Chrysididae) and *Toxophora australis* Hesse (Bombyliidae).

Paravespa Radoszkowski

Paravespa is known from the Afrotropical and Palaearctic regions. Carpenter *et al*. (2010a) list 13 species, of which six have been recorded from southern Africa. We investigated the nesting of *P.* (*Gestrodynerus*) *mima* Giordani Soika, known only from South Africa, on the farm Tierberg near Prince Albert in the southern Great Karoo and at Onverwacht near Oudtshoorn in the Little Karoo both at the interface between the Succulent and Nama-Karoo.

Nest situation

The nests were situated in bare areas in close proximity to water. The soil was somewhat non-friable to non-friable with a high enough clay element to make it malleable when mixed with water.

Nest structure

The nest is a multicellular subterranean burrow surmounted by a mud turret (Figures II.2.46 & 47). Funnel shaped turrets (Figure II.2.46.c & d) were present at both sites but, remarkably, additional turrets in the form of a curved tube (Figure II.2.46.e) were constructed at the Tierberg site. The subterranean burrow consists of a relatively long vertical main shaft terminating in a cell and several secondary shafts each of which, after leaving the main shaft at a gentle angle, curves down steeply to end in a vertical cell. All cells lie at the same depth. The cell diameter is equal to or only slightly in excess of that of the shaft. The sides of the cell are parallel and the end of the cell is truncate. There is no subdivision of the cell into compartments as is found in cells of *Aethiopicodynerus.*

Method of construction

Water required for nest excavation is transported in the crop. The turret is constructed early during nest excavation. Pellets are laid down around the shaft initial in such a way that the turret will have the same initial diameter as that of the shaft, that is, about 8 mm (average of 19 measured turrets). Initially pellets are laid down regularly so that the base of the turret is in the form of a vertical cylinder. As turret construction proceeds, the manner in which the pellets are laid down changes in one of two ways. Either the diameter is rapidly increased to form a stalked funnel with an almost horizontal rim with a diameter of around 23 mm (average of 9 measured), or the original diameter is maintained but the turret curves to one side and is continued sub-horizontally so that the lower lip (which is somewhat longer than the upper) extends around 35 mm from the shaft opening (average of 4 measured). The pellets used in the construction of funnel-shaped turrets are closely packed and no interstices are left open, whereas those used in the construction of curved turrets are closely packed only on the underside of the tube with a large number of interstices being left open on the upper side (Figure II.2.47).

After completion of turret construction, further pellets extracted from the excavation are discarded in a distinct pellet dropping area in close proximity to the nest or randomly at some distance from the nest. The shaft walls are smoothed with water so that they appear plastered. Cells varied in depth from 102–125 mm. After oviposition and provisioning, a cell is sealed with a thin mud plate

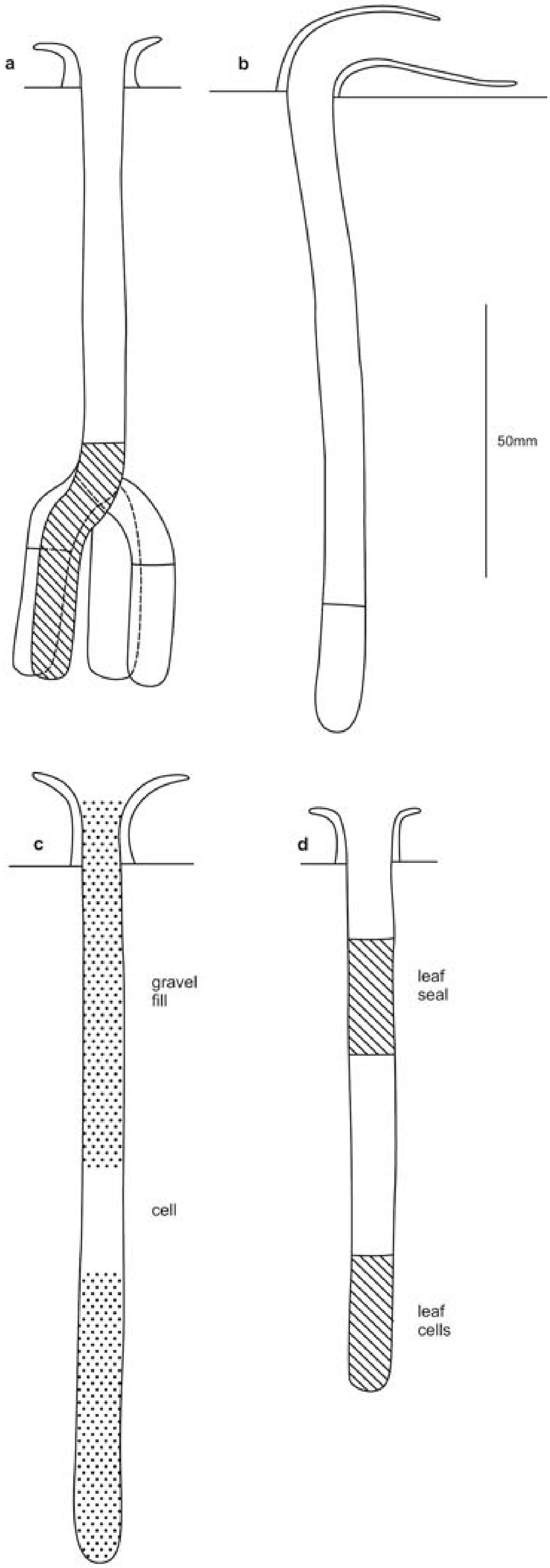


Figure II.2.47.—*Paravespa* (*Gestrodynerus*) *mima* Giordani Soika, diagrammatic vertical plans of four nests: a. and b. showing the two types of turret architecture; c. nest usurped by *Ammophila* sp. (Sphecidae); c. nest usurped by *Megachile stellarum* Cockerell (Megachilidae).

Figure II.2.48.—*Proepipona meadewaldoi meadewaldoi* Beaquaert, ribbed closures to cells in old nest of *Sceliphron spirifex* (L.).

and the portion of the shaft close to the cell is filled with earth. A second mud seal is then constructed between it and the rest of the shaft. Final sealing of the nests was not observed.

Oviposition and provisioning

In excess of 50 prey caterpillars were recovered. They were tentatively determined as Noctuidae of at least four species.

Life history

The fully grown larva spins a cocoon which is closely bonded to the cell walls and fills the cell entirely. The cocoon is capped with the head capsules of the prey caterpillars, which separate it from the mud plate closing the cell.

Associates

Megachilid bees, *Megachile stellarum* Cockerell and *Megachile aliceae* Cockerell, had usurped a high percentage of the nests on Tierberg. All but one had been usurped before provisioning by *P. mima.* The bees harass the rightful owners of the nests until they abandon them.

Proepipona Giordani Soika

Proepipona is known from the eastern and southern Afrotropical Region. The only nesting account for the genus is that of Weaving (1995) for *Proepipona meadewaldoi meadewaldoi* (Beaquaert) nesting in coastal bush on the north coast of KwaZulu-Natal.

Nest situation

The nests of *P. maedwoldoi maedwoldoi* were all constructed in pre-existing cavities, trap nests and old vacated cells in aerial mud nests of *Sceliphron spirifex* (L.) (Figure II.2.48) (Sceliphrinae), *Synagris analis* de Saussure, *Delta hottentotum* (de Saussure) and *Afreumenes* sp. (all Eumeninae).

Nest structure

Within a pre-existing nest *P. meadewaldoi meadewaldoi* constructs linearly arranged cells, the number depending on the length of cavity. Up to 13 cells were constructed in trap nests. The walls of the cavity form the cell walls. In some instances the first cell is preceded by a thin mud layer. Each cell is closed with a fragile mud plate with a maximum thickness of 1 mm. The final closure is more robust with a thickness of 2 mm and its outer surface is characteristically grooved (Figure II.2.48). In 74.5% of the nests the final closure was preceded by one or two vestibular cells.

Oviposition and provisioning

After oviposition, the egg being suspended from the roof of the cell, a cell is provisioned with small caterpillars, the maximum number recorded being 16. Evidence suggested that progressive provisioning may be practised.

Sleeping and sheltering

The nest entrance remains open during absences from the nest and at night. In inclement weather the females were in the nest facing outwards.

Associates

Nests were parasitised by a miltogrammine fly, *Amobia africa* Curran (11.9%), eulophid, *Melittobia* sp. (6%), a chrysidid, *Chrysis* sp. (5%), a mutillid, *Stenomutilla syrinx* (0.7%) and an ichneumonid, *Osprynchotus* sp. (1.4%).

Pseudonortonia Giordani Soika

Pseudonortonia is known from the Afrotropical and Palaearctic regions. Carpenter *et al*. (2010a) list 40 species, of which 16 have been recorded from southern Africa.

The only available observations on nesting by *Pseudonortonia* appear to be those for *P. soror* (Kohl) in Grahamstown and an unidentified species on the farm Broadfields neighbouring the farm Hilton (Gess & Gess fieldnotes 1977).

Nest situation

In Grahamstown, three nests of *P. soror* had been constructed seven feet above the ground on the smooth concavity between courses of bricks on an unplastered 12 foot high east facing wall (Figure II.2.49). This suggests that

Figure II.2.49.—*Pseudonortonia soror* (Kohl), pair of cells each with a curved entrance turret.

the nesting situation for this wasp is most probably on vertical rock faces. This theory is supported by the nests at Broadfields having been constructed on a shale krantz and a sandstone riverbank.

Nest structure

The nest consists of a mud cell, about 18 mm by 8 mm with, at the open end, a lacy mud entrance turret 7–9 mm in length and about 4 mm in outer diameter.

Oviposition and provisioning

Only one of the nests had been provisioned. This contained a large eumenine larva and five caterpillars, all Oecophoridae.

Raphiglossa Saunders

Raphiglossa is represented in the Palaearctic and Afrotropical regions. Four species are listed by Carpenter *et al*. (2010a) for the Afrotropical Region.

The only published account of nesting by *Raphiglossa* in the Afrotropical Region appears to be that of Hans Brauns (1910) for *R. natalensis* Smith (as *R. aphidogloss flavo-ornata* (Cameron)) in Meade-Waldo (1913). To this can be added our observations for the same species found nesting at Nieuwoudtville (Gess & Gess fieldnotes 1990).

Nest situation

Brauns recorded that *Raphiglossa natalensis* excavates its nests in dry pithy stems, chiefly 'Liliaceae'. We found two nests in dry *Berkheya* stems in karroid scrub.

Nest structure

Brauns recorded that within the burrow the cells are separated by simple partitions. The two nests investigated by us each consisted of a burrow 2 mm in diameter excavated in the pith of dry *Berkheya* stems (Figure II.2.50) the entrance having been made where the still erect stems had been broken off. Within the burrows were, respectively, one cell and three cells in linear series with the cell partitions constructed from sand. The three-celled nest had been completed and sealed at the entrance. The cells were 14–18 mm long and the cell partitions 3.4–5.8 mm thick.

Provisioning

Brauns recorded small larvae of Lepidoptera as the provision whereas in the cells in the two nests investigated by us, the prey were beetle larvae, all of the same species, 3 mm in length, with up to 21–29 individuals per cell. The beetle larvae were arranged transversely and were extremely tightly packed (Figure II.2.50).

Life history

Brauns recorded that the mature larvae may remain for two or three years without pupating and that the imagines do not leave the stem in the ordinary way, but each one perforates its cell sideways.

Rynchium Spinola

Rynchium is an Old World genus. For the Afrotropical Region Carpenter *et al*. (2010a) list three species, the only published accounts for nesting being for *R. marginellum sabulosum* (Saussure) in Ethiopia (Bonelli 1973b) and in the Eastern Cape (Gess & Gess 1991).

Rynchium marginellum sabulosum (de Saussure)

Nest situation

In the Eastern Cape, we found *R. marginellum sabulosum* nesting in cut culms of the reed, *Arundo donax* L. (Poaceae) used for the making of bean frames and varying in angle from 0–70° from the horizontal and in trapnests placed in the field in a crevice in a sandstone bank. Bonelli's observations for this wasp in Ethiopia were of nesting in abandoned *Xylocopa* burrows in dry wood and in hollow stems. It seems likely therefore that, like many nesters in pre-existing cavities above ground level, it will accept suitable pre-existing cavities in a variety of substrates.

Nest structure

The nest constructed within a pre-existing cavity consists of a linear series of cells separated by mud partitions and

Figure II.2.50.—*Raphiglossa natalensis* Smith, nest in dry *Berkheya* stem, provisioned with beetle larvae.

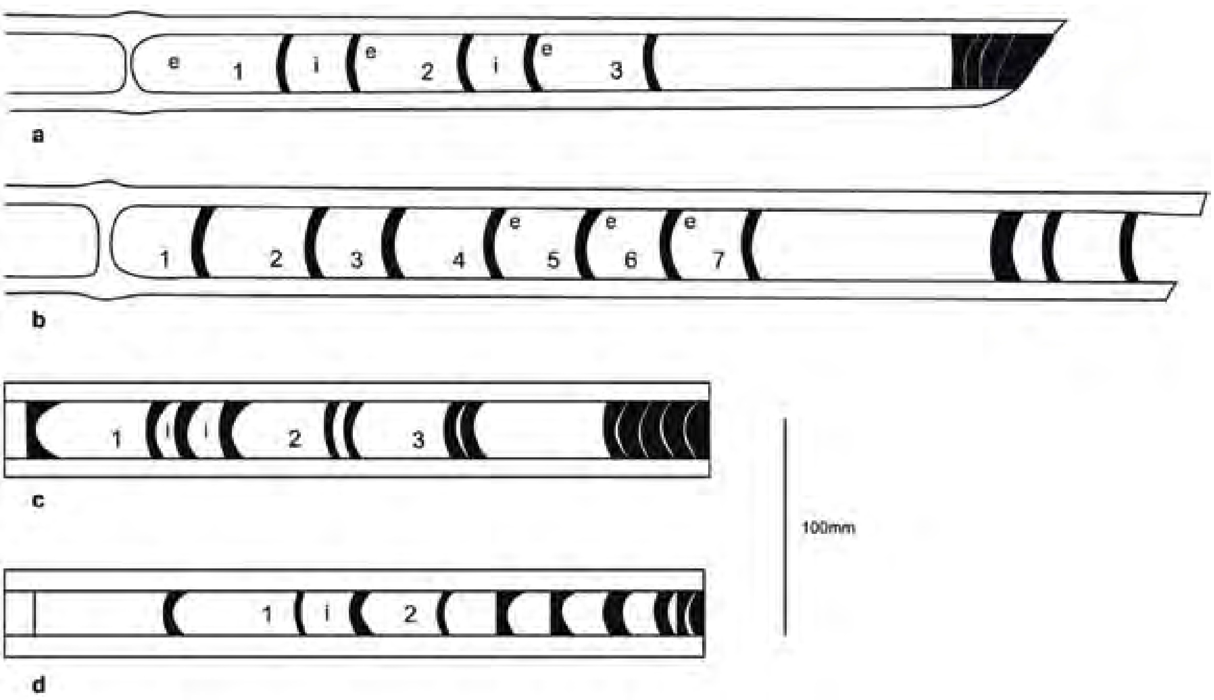


Figure II.2.51.—*Rynchium marginellum sabulosum* (de Saussure), diagrammatic plans of four nests in hollow culms of the reed *Arundo donax* L. (Poaceae), e indicates position of egg, i indicates intercalary cell.

in some nests one or more interstitial cells. One or more vestibular cells precede the final closure (Figure II.2.51).

Method of construction, oviposition and provisioning

Modifications to the pre-existing cavity—cell end walls and nest closures—are all constructed from mud. The mud is mixed at a fixed quarry site. Water for the purpose is fetched from a nearby source and is imbibed by the wasp whilst standing on the ground at the edge of the water.

Upon completion of the preliminary plug, when present, the wasp oviposits. The egg is yellow, gently curved and suspended from the roof or side of the cell so that it hangs down on a short filament. The egg in this species is always positioned towards the inner end of the cell. After oviposition, provisioning with pyralidid caterpillars is undertaken. Having captured a prey caterpillar and subdued it by stinging it several times, the wasp transports it to her nest in flight grasped beneath her body by her legs and held by her mandibles near its head end. Successive prey are added until the cell is fully provisioned. Within the cell the prey are not arranged in any set pattern. The cell is sealed with a mud plug thicker around the edges than at the centre. Before proceeding once again with oviposition and provisioning, the wasp may construct an empty intercalary cell. The number of cells constructed is dependent upon the length of the cavity and the availability of prey and water. After the full number of cells has been completed, the nest is sealed by the construction of a thick, layered mud plug, which is usually positioned at the entrance to the cavity leaving a vestibular cell that may be subdivided by partitions.

Life history

When the larva commences spinning, it lines the cell with a layer of cellophane-like material composed of 'varnished' spinnings. In nests of *Rynchium marginellum sabulosum*, this lining has a characteristic aromatic scent.

In nests from which both males and females are produced, the female producing cells are situated at the inner end of the cavity with the male producing cells situated at the outer end.

Sleeping and sheltering

During intervals in nest building resulting from inclement weather or at night the female is to be found in the nest facing outwards guarding an open cell containing an egg or an egg and prey.

Synagris Latreille

Synagris is represented in the Palaearctic and Afrotropical regions. Carpenter *et al*. (2010a) list 36 species for the Afrotropical Region.

As noted by Bequaert (1918) the provisioning behaviour is of particular interest. Some species, for example *S. calida* L. (Roubaud 1911), have been recorded to mass provision with caterpillars like most eumenines. However, other species practise progressive provisioning, for example *S. sicheliana* de Saussure (Roubaud 1911), *S. analis* de Saussure (Weaving 1995a). Some species feed their young with macerated caterpillars, for example *S. cornuta* L. chews up the prey and feeds the larva with the resulting semi-fluid mash (Roubaud 1911). *Synagris calida*, although a mass provisioner when prey are abundant, is reported to provision slowly during periods of prey scarcity, often bringing in the last prey when the larva is fairly large (Roubaud 1908 as *S. sicheliana* Saussure in Bequaert 1918).

Nests of *Synagris analis* Saussure were investigated by Alan Weaving in KwaZulu-Natal (Weaving 1995a).

Nest situation

The nests were attached to the branches of trees, roof beams and walls.

Nest structure

The nests were substantial, multi-celled mud nests (Figure II.2.52.a), some exceeding 0.5 kg in weight. Up to 17 cells per nest were recorded.

Method of construction

Mud cells (Figure II.2.52.b) were constructed progressively upwards. After each cell was constructed and before it was provisioned, it was daubed with mud such that the cells were imbedded in a matrix.

Provisioning

Provisioning was progressive and the cell was sealed once the larva was fully grown.

Sleeping and sheltering

Females, when at rest, were found inside cells facing outwards.

Associates

Nests were subject to parasitism by a cuckoo wasp, *Chrysis* sp., *wahlbergi* group (Chrysididae) and velvet ants, *Dolichomutilla sycorax* (Smith) and *Stenomutilla syrinx* (Péringuey) (Mutillidae).

Osprynchotus flavipes Brullé (Ichneumonidae) is cited as a parasite of several species of *Synagris* by Roubaud (1911) and suggests that it is probably a parasite of all species of *Synagris.*

Roubaud (1911) also records beetles of the family Rhipiphoridae in nests of *S. cornuta.* Two specimens of a rhipiphorid, *Macrosiagon* (*Emenadia*) *ferrugineum* (Fabricius) were reared from a cell of *S. calida* from mud nests collected by H. Lang at Stanleyville (Bequaert 1918).

Tricarinodynerus Giordani Soika

Tricarinodynerus is represented in the Palaearctic and Afrotropical regions. Carpenter *et al.* (2010a) list eight species for the Afrotropical Region with two of these occurring in southern Africa.

Nesting by *Tricarinodynerus guerinii* (de Saussure) has been studied on the farm Hilton, Eastern Cape (Gess 1981; Gess & Gess 1991) and False Bay Park, Mkuzi Game Reserve and Hluhlwe Game Reserve, KwaZulu-Natal (Weaving 1994b). The wasp is widespread in distribution in tropical and southern Africa and appears to be able to exist under a wide range of climatic conditions.

Nest situation

Tricarinodynerus guerinii (de Saussure) studied at Hilton was nesting in pre-existing cavities in protected situations in vertical banks, a west facing river cut bank of compacted very fine sand, a north facing river cut bank of partly silicified fine sand, referred to as a 'sandstone' bank (Gess 1981) and a southeast facing shale cliff. Nests were also found on Tierberg farm, Prince Albert, in the Karoo north of the Swartberg Mountain Range (Gess & Gess 1991) and in a river cut bank and under a bridge near Omaruru, Namibia (Gess & Gess fieldnotes 1998 and label data). The nests studied in KwaZulu-Natal were in trap nests constructed from reeds and in empty cells of aerial mudnesters. All nest sites were close to water.

Nest structure

The nest of *T. guerinii* is characterised by a down curved, ribbed mud entrance turret, usually slightly flared at the distal opening (Figure II.2.53.a & b). Within are several

Figure II.2.52.—a.–c. a and b. *Synagris analis* de Saussure: a., female on nest; b. female collecting mud; c. *Synagris* sp., larva and provision.

cells arranged, depending on the shape of the pre-existing cavity that forms the nesting gallery, in either single or multiple linear series (Figures II.2.53.c & 54).

The degree of modification of the cavity is determined by its suitability for nest construction. The cavities in the sand and 'sandstone' banks were circular in cross section as too were those in reeds. Those in trap nests used on Hilton were sub-circular, curved below and straight above. In all of these, very little mud is used for smoothing the walls, whereas in irregular shaped crevices between layers of shale, a greater amount of mud is required to round off any unevenness and to create cells and an entrance passage.

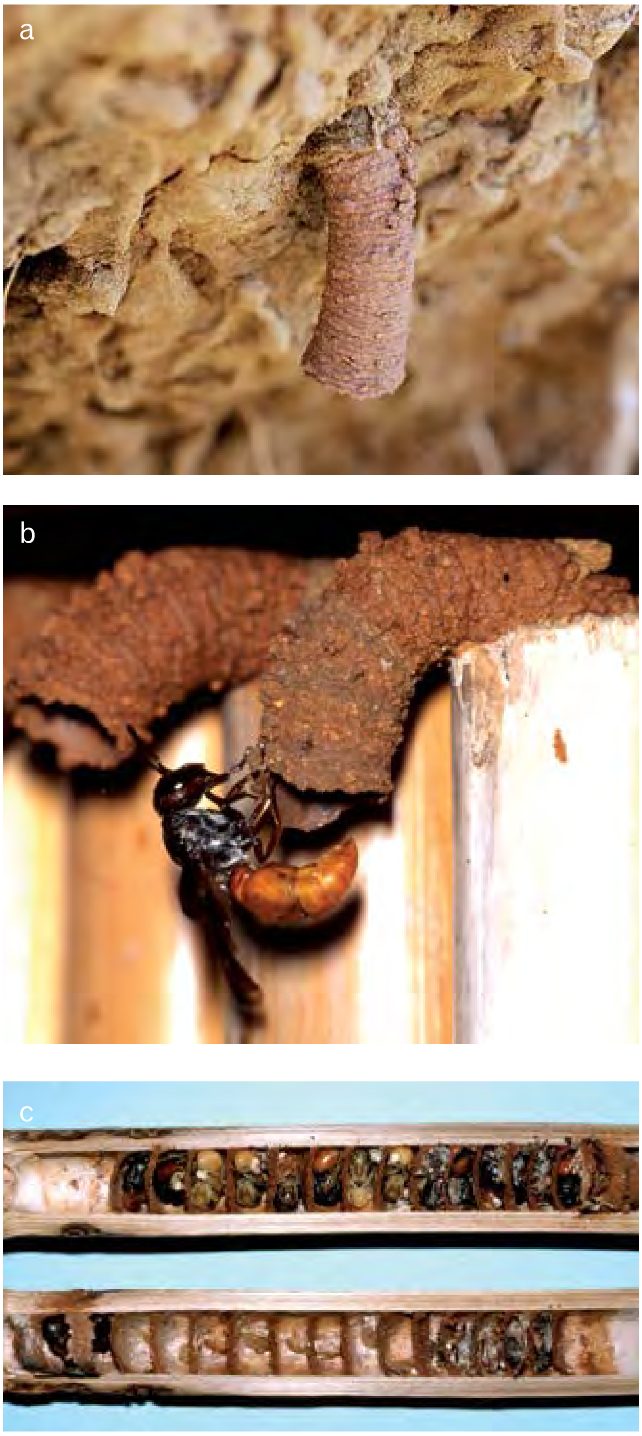


Figure II.2.53.—a.–c. *Tricarinodynerus guerinii* (de Saussure): a. entrance turret of nest in bank; b. female on entrance turret of nest in cut *Arundo donax* culm; c. two nests cut longitudinally to show cells.

The size of the nest is not necessarily determined by the available space as a preliminary plug may be constructed reducing the depth of a deep cavity. Each cell is sealed by a thin mud-plug and the last cell is separated from the closing plug by a vestibular cell. In addition to the plug, closing the gallery the entrance turret is sealed at its distal opening and may be divided along its length by additional mud partitions.

Method of nest construction

Nest construction is initiated with the construction of the mud turret at the cavity entrance. As turret construction advances, the wasp carefully smoothes the inner surface but leaves the external surface roughcast, giving the turret its characteristic ribbed and knobbly appearance. No interstices are left.

After completion of the turret, the cavity is prepared for construction of the first cell. After oviposition into and provisioning of the cell has been completed, the cell is sealed with a mud plug of even thickness, approximately 1 mm. Work then starts on the second cell. When the full number of cells has been completed, final closure takes place. The nest closures are somewhat thicker than the cell partitions.

Oviposition and provisioning

The egg is laid suspended on a thread at the inner end of the cell. Hunting then commences. The wasp captures a prey caterpillar, stings it and flies to her nest holding it with her mandibles, supported beneath by her legs and facing the direction of travel. On reaching the nest, she enters rapidly. The prey taken from the nests at Hilton were determined as probably Tortricidae and those from nests in KwaZulu-Natal as Tortricidae, Gelechiidae, Oecophoridae and Pyralididae, all likely to have been obtained from concealed situations.

Life history

Observations on a nest from Hilton yielded a time interval from egg hatch to full-grown larva of nine days.

When the larva has consumed all its provision, it lines its cell with a parchment like substance composed of 'varnished' spinnings so firmly attached to the cell walls and sealing plug that it cannot separate from them.

Associates

Four *Chrysis laminata* Mocsáry (as *Octochrysis laminata* in Gess 1981) (Chrysididae) and one male *Anthrax cf. teraspilus* (Hesse) (Bombyliidae) were reared from *T. guerinii* cells from the sandbank on Hilton. From nest cells from KwaZulu-Natal, *Chrysis* sp., *wahlbergi* group, was reared from almost a quarter of the investigated nests. Mutillidae, *Dolichomutilla heterodonta* Bischoff, *Dolichomutilla sycorax* (Smith) and *Stenomutilla syrinx* (Péringuey), Leucospidae, *Leucospis ornata* Westwood and *L. varicollis* Cameron and miltogrammine flies (Sarcophagidae; *Amobia africa* Curran) were reared from a comparatively small number of nests.

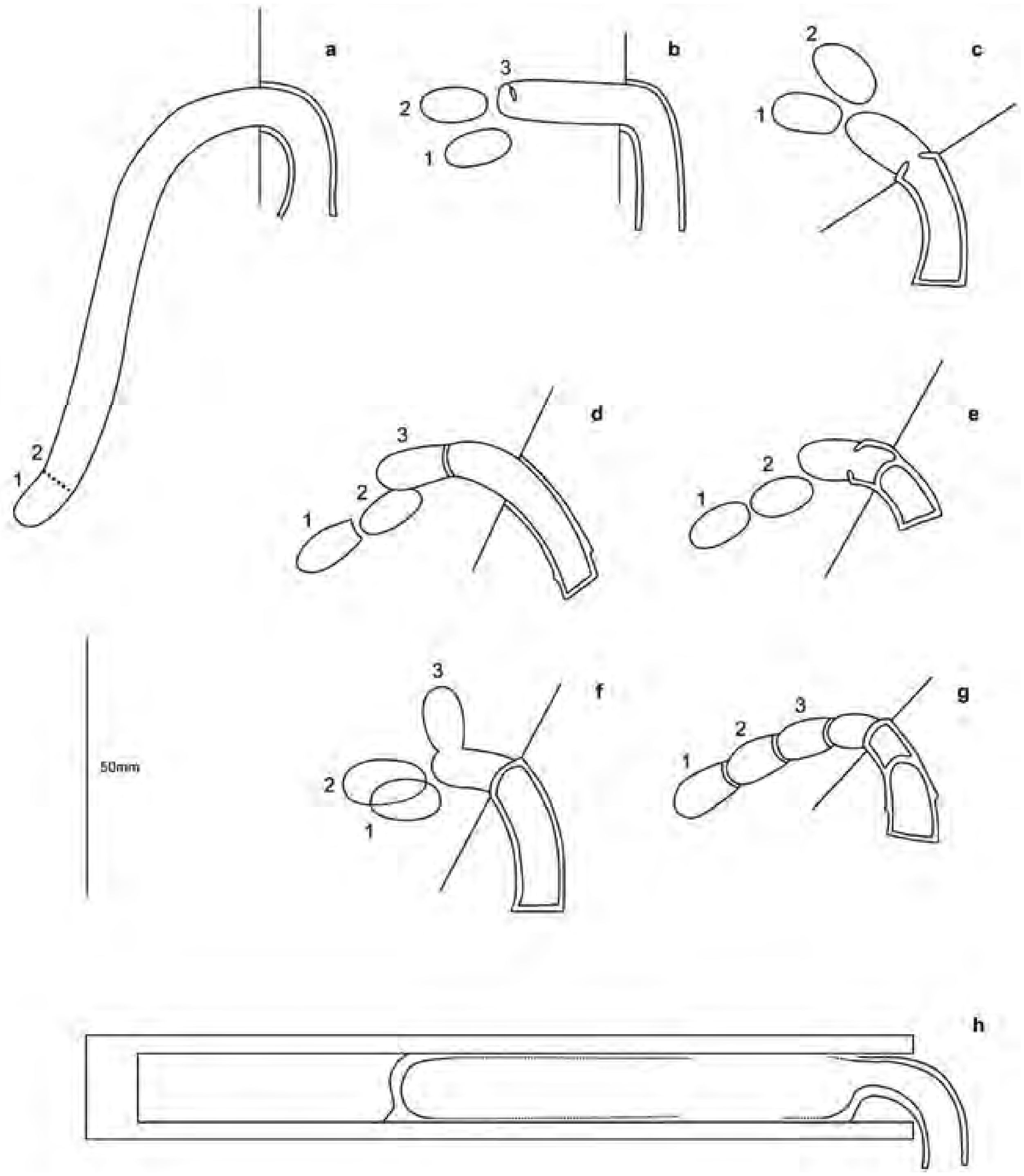
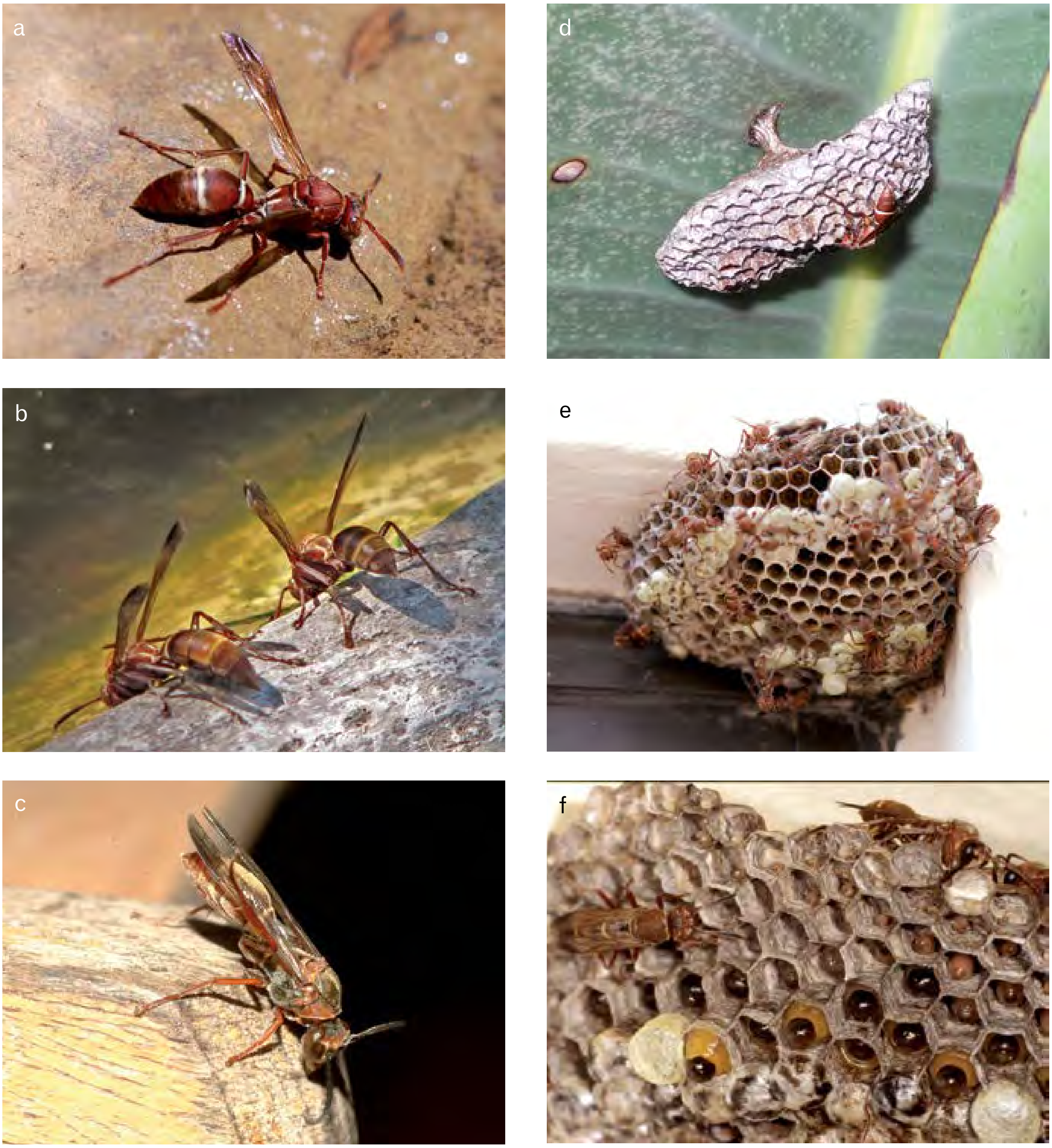


Figure II.2.54.—*Tricarinodynerus guerinii* (de Saussure), diagrammatic plans of eight nests: a–g. in bank, position of egg indicated in cell 3, nest b; h. in wooden trap nest.

Zethus Fabricius

Zethus is widespread being found in the Australian, Afrotropical, Nearctic, Neotropical and Oriental regions. Carpenter *et al*. (2010a) list 14 species represented in the Afrotropical Region, with eight having been recorded from southern Africa.

There seems to be no record of the nesting of *Zethus* species in southern Africa. However, records of the nesting of some species of this genus in the Americas indicate that it is of great phylogenetic interest (Bohart & Stange 1965). The species range from the more primitive solitary taxa nesting in abandoned borings of other insects, to sub-social species in which as many as 12 females co-operate in nest building. Some of the building materials are most unusual for wasps. Resin is commonly used for cementing together the building materials, which are generally of plant origin. Some species are even recorded to make cells from discs cut from leaves—behaviour generally associated with megachilid bees. Provisioning is progressive.



Subfamily Polistinae

Vespids, the social wasps, are relatively poorly represented in southern Africa. Of the three sub-families, Polistinae, Polybiinae and Vespinae, only the Polistinae—represented by *Polistes* Latreille (Figure II.2.55), *Ropalidia* Guérin (Figure II.2.56) and *Belonogaster* de Saussure (Figure II.2.57)—are indigenous to southern Africa. *Vespula germanica* (Fabricius), a European member of the Vespinae, has become established in the southwestern Cape, into which it was accidentally introduced (Whitehead & Prins 1975; Tribe & Richardson 1994). An additional recent accidental introduction, also in the southwestern Cape, is *Polistes dominulus* (Christ) (Eardley *et al.* 2009).

The Polistinae are commonly called paper wasps in reference to the material they use for building their nests. The wasps make this ‘paper’ by macerating dry plant tissue (Figure II.2.55.c) and mixing it with fluid from their mouths. A polistine nest consists of an aerially suspended single comb not enclosed in an envelope (Figures II.2.55.d–e, 56.a & b and 57). The combs are suspended by a pedicel from bushes, branches of trees, the undersides of rocks, the roofs of rock shelters or from man-made structures, particularly the eaves of houses. Depending on the species, the cells may be arranged in a single row, a cluster, a roughly circular disc or an inverted dome.

Figure II.2.55.—a.–g. *Polistes*: a. and b. females imbibing water; c. female collecting fibre for nest construction; d. and e. nests, e. showing capped cells containing pupae; f. larvae in cells; g. females feeding larvae.

The nest of *Vespula germanica* is constructed from wood pulp and consists of a series of combs, one below the other, surrounded by a multi-layered envelope. This is usually positioned in a hole, most commonly in the ground but sometimes in a tree or a man-made structure.

Polistinae show very little external differentiation between ‘queens’, that is fertilised egg-laying females, and ‘workers’, that is, unfertilised females which do not lay eggs.

Figure II.2.56.—a.–c. *Ropalidia*, females on nests.

Figure II.2.57.— *Belonogaster*: females on nest.

Females produced late in the nesting season and fertilised overwinter and establish new colonies in the spring. In some species there is only one egg-producing female in a colony whereas in other species there may be several. In *Vespula germanica*, each colony has a single queen, which is readily distinguishable from the workers. Though in its native northern temperate climate colonies are annual, there is some indication that in countries into which it has been introduced and in which the climate is mild, perennial nests may become established.

The young of all species are fed directly by regurgitation of nectar and macerated insects, particularly caterpillars, ingested by adult females (Figure II.2.55.g).

Flower visiting

Polistinae visit flowers of a wide range of plant families. They were not included in the flower visiting survey but were taken, notably, in samples of flower visitors from Fabaceae (Mimosoideae), Apiaceae and Asteraceae.

Family Pompilidae

Pompilidae, commonly called spider wasps, are well represented in southern Africa. They are relatively slender and long legged. Many species are black bodied, or black and orange with orange legs and antennae, and have metallic blue black or orange wings. Charcoal-coloured bodies with smoky barred wings are not uncommon. The wasp pattern of banded yellow and black abdomen occurs very rarely. Also rarely found are mimics, an example being a species that mimics a mutillid. Their movements are fussy and their antennae are in constant motion, particularly when active on the ground. Upon death, the female is readily distinguished from the male as her antennae become spirally curled.

Pompilids prey on spiders. A single spider is utilised for the rearing of one of these wasps and the spiders taken are therefore large compared to the size of the wasp. The spider prey of any one species may be taken from a range of families. The most important factors in the selection of the prey seem to be size and habitat, the wasps being better ecologists than systematists. Table 8 gives some known prey taken by pompilids in southern Africa.

The understanding of sub-familial groupings in the Pompilidae has varied considerably (Haupt 1930; Arnold 1932a, 1932b, 1932c; Banks 1934; Arnold 1935a, 1935b, 1936a, 1936b, 1937; Townes 1957; Shimizu 1994; Pitts *et al.* 2006). The classification of Shimizu (1994) is followed here.

Flower visiting

Flower visiting records are available for 50 species of Pompilidae (including Pepsinae and Pompilinae). The families of flowers visited with the percentage of species visiting each family were notably Apiaceae with a remarkable 67% and Fabaceae (Mimosoideae) 33%; Celastraceae 18%; Fabaceae (Papilionoideae) 16%; Euphorbiaceae, Apocynaceae (Asclepiadaceae) and Asteraceae 14% each. Other plant families included Asparagaceae 10%;

Table 8.—Some known prey taken by Pompilidae in southern Africa. Note that Araneidae was formerly known as Argiopidae

Identity of wasp	**Identity of prey**	**Locality**	**Reference**
Pompilinae			
Anoplius fuscous Arnold	LYCOSIDAE: *Lycosa bimaculata*	Eastern Cape, Grahamstown, Hilton	Weaving research notes and vouchers 1982
Argyroclitus fasciatipennis Arnold	SALTICIDAE	Eastern Cape, Alexandria Forest	Gess & Gess fieldnotes 1982 and vouchers
Batozonellus fuliginosus (Klug)	ARANEIDAE: *Araneus* sp. ♀	Eastern Cape, Grahamstown, Eastern Cape	F.W. Gess fieldnotes 1973 and vouchers
	ARANEIDAE: *Araneus* sp. ♀	Eastern Cape, Grahamstown	F.W. Gess fieldnotes 1975 and vouchers
	ARANEIDAE: *Caerostris corticosa* Pocock, ♀	Eastern Cape, Grahamstown, Hilton	C.F. Jacot Guillarmod vouchers 1976, two records
	ARANEIDAE: *Caerostris sexcuspidata* (Fabricius), ♀	Eastern Cape, Kenton-on-sea	R.A. Jubb vouchers 1969
	ARANEIDAE: *Caerostris sexcuspidata* (Fabricius), ♀	Eastern Cape, Grahamstown	F.W. Gess fieldnotes 1973 and vouchers
	ARANEIDAE: *Caerostris sexcuspidata* (Fabricius), ♀	Eastern Cape, Grahamstown	F.W. Gess fieldnotes 1974 and vouchers
	ARANEIDAE	Eastern Cape, Grahamstown, Hilton	Gess & Gess fieldnotes 1982 and vouchers
	ARANEIDAE: ♀	Eastern Cape, Grahamstown, Hilton	Gess & Gess fieldnotes 1982 and vouchers
	ARANEIDAE: probably *Caerostris* sp.	Eastern Cape, Grahamstown, Hilton	Gess & Gess fieldnotes 1982 and vouchers
	ARANEIDAE	Eastern Cape, Grahamstown, Hilton	Gess & Gess fieldnotes 1985 and vouchers
	ARANEIDAE: *Caerostris sexcuspidata* (Fabricius)	Eastern Cape, Grahamstown, Hilton	Weaving research notes and vouchers 1982
	ARANEIDAE: probably *Caerostris* sp.	Eastern Cape, Grahamstown, Hilton	Weaving research notes and vouchers 1982
	ARANEIDAE: *Araneus* sp.	Eastern Cape, Grahamstown, Hilton	Weaving research notes and vouchers 1982
	ARANEIDAE: *Cyrtophora citricola*	Eastern Cape, Grahamstown, Hilton	Weaving research notes and vouchers 1982
	ARANEIDAE: *Argiope nigrovittata*	Eastern Cape, Grahamstown, Hilton	Weaving research notes and vouchers 1982
Dicyrtomellus leptacanthius (Cameron)	SPARASSIDAE		Weaving photograph
	SPARASSIDAE: *Dicyrtomellus meruensis* Cameron	Eastern Cape, Grahamstown	R.W. Gess fieldnotes 1974 and vouchers
Dicyrtomellus Gussakovskij	SPARASSIDAE: *Dicyrtomellus meruensis* Cameron	Eastern Cape, Bathurst	R.W. Gess vouchers
	SPARASSIDAE	Eastern Cape, Grahamstown	Gess & Gess fieldnotes 1985 and vouchers
Elaphrosyron insidiosus (Smith)	THOMISIDAE	Eastern Cape, Grahamstown, Hilton	Gess & Gess fieldnotes 1978 and vouchers
	THOMISIDAE	Eastern Cape, Grahamstown, Hilton	Gess & Gess fieldnotes 1978 and vouchers
	THOMISIDAE	Eastern Cape, Grahamstown, Hilton	Gess & Gess fieldnotes 1982 and vouchers
	THOMISIDAE	Eastern Cape, Grahamstown, Hilton	Weaving research notes and vouchers 1982, two records
Episyron argillaceous Arnold	ARANEIDAE: *Araneus* sp.	Eastern Cape, Grahamstown, Hilton	Weaving research notes and voucher 1982

Identity of wasp	Identity of prey	Locality	Reference
Episyron braunsii Arnold	ARANEIDAE: *Araneus* sp.	Eastern Cape, Grahamstown, Hilton	Weaving research notes and voucher 1982
Episyron histrio (Lepeletier)	ARANEIDAE: *Araneus holzapfeli*	KwaZulu-Natal, Widenham	Weaving research notes and voucher 1982
	ARANEIDAE: *Araneus* sp.	KwaZulu-Natal, Widenham	Weaving research notes and voucher 1982
	ARANEIDAE	Eastern Cape, Bathurst	R.W. Gess vouchers and photograph
	ARANEIDAE	Eastern Cape, Bathurst	M.W. Gess vouchers and photograph
Episyron sp.	ARANEIDAE: *Nephila* sp.	Eastern Cape, Grahamstown, Hilton	Weaving research notes and voucher 1982
	ARANEIDAE: *Nephila* sp.	Eastern Cape, Grahamstown, Hilton	Gess & Gess fieldnotes 1982 and vouchers
Microphadnus bicolor Cameron	CLUBIONIDAE: *Clubiona* sp.	Eastern Cape, Grahamstown, Hilton	Weaving research notes and voucher 1982
Paracyphononyx africanus (Radoszkowski)	LYCOSIDAE: probably *Lycosa* sp.	Zambia, Ndola	Grout & Brothers 1982
Pompiloides braunsii Kohl	THOMISIDAE: *Xysticus* sp.	Eastern Cape, Grahamstown, Hilton	Weaving research notes and voucher 1983
Pompilus cinereus (Fabricius)	GNAPHOSIDAE	Angola, Porto Alexandre	Day 1981
	LYCOSIDAE: *Lycosa* sp.	Tanzania, Tanga	W.A. Lambourn in Day 1981
	LYCOSIDAE: probably *Lycosa* sp.	Eastern Cape, Port Elizabeth	E. McC. Callan in Day 1981
	LYCOSIDAE: probably *Lycosa* sp.	Eastern Cape, Port Elizabeth	Day 1981
	LYCOSIDAE	Botswana, Lake Ngami	Day 1981
	SALTICIDAE: *Phlegra* sp.	Botswana, Lake Ngami	Day 1981
Psammochares plumbeus (Fabricius)	LYCOSIDAE: *Pardosa manubriata*	Eastern Cape, Grahamstown, Hilton	Weaving research notes and voucher 1982
	LYCOSIDAE: *Pardosa manubriata*	Eastern Cape, Grahamstown, Hilton	Weaving research notes and voucher 1982
	LYCOSIDAE: *Pardosa* sp.	Eastern Cape, Grahamstown, Hilton	Weaving research notes and voucher 1982
Psammochares rutillus Klug	LYCOSIDAE: *Lycosa promontorii*	KwaZulu-Natal, Widenham	Weaving research notes and voucher 1982
Tachypompilus ignitus (Smith)	SPARASSIDAE: *Palystes superciliosus* L. Koch	Eastern Cape, Grahamstown	D. Brothers vouchers 1967
	SPARASSIDAE: *Palystes superciliosus* L. Koch, ♂	Eastern Cape, Grahamstown	A.S. Harper vouchers 1969
	SPARASSIDAE: *Palystes superciliosus* L. Koch, immature	Eastern Cape, Grahamstown	F.W. Gess fieldnotes 1974 and vouchers
	SPARASSIDAE: *Palystes superciliosus* L. Koch, ♀	Eastern Cape, Grahamstown	F.W. Gess fieldnotes 1974 and vouchers
	SPARASSIDAE: *Palystes superciliosus* L. Koch, immature ♂	Eastern Cape, Grahamstown	D.W. Gess fieldnotes 1974 and vouchers
	SPARASSIDAE: *Palystes superciliosus* L. Koch, immature	Eastern Cape, Grahamstown	F.W. Gess fieldnotes 1975 and vouchers
	SPARASSIDAE: *Palystes superciliosus* L. Koch, immature	Eastern Cape, Grahamstown	F.W. Gess fieldnotes 1976 and vouchers, two records

Identity of wasp	Identity of prey	Locality	Reference
	SPARASSIDAE: *Palystes superciliosus* L. Koch, immature	Eastern Cape, Grahamstown	R.W. Gess fieldnotes 1976 and vouchers
	SPARASSIDAE: *Palystes superciliosus* L. Koch, immature ♂	Eastern Cape, Grahamstown	F.W. Gess fieldnotes 1976 and vouchers
	SPARASSIDAE: *Palystes superciliosus* L. Koch, immature	Eastern Cape, Grahamstown	F.W. Gess fieldnotes 1977 and vouchers
	SPARASSIDAE: *Palystes superciliosus* L. Koch, immature ♀	Eastern Cape, Grahamstown	R.W. Gess fieldnotes 1978 and vouchers
	SPARASSIDAE: *Palystes superciliosus* L. Koch, ♀	Eastern Cape, Grahamstown	H.W. Gess & R.W. Gess fieldnotes 1978 and vouchers, two records
	SPARASSIDAE: *Palystes* sp., immature	Eastern Cape, Grahamstown	D.W. Gess fieldnotes 1978 and vouchers
	SPARASSIDAE: *Palystes superciliosus* L. Koch	Eastern Cape, Grahamstown	S.K. Gess fieldnotes 1978 and vouchers
	SPARASSIDAE: *Palystes superciliosus* L. Koch, immature ♂	Eastern Cape, Grahamstown	F.W. Gess fieldnotes 1978 and vouchers
	SPARASSIDAE: *Palystes superciliosus* L. Koch, immature ♀	Eastern Cape, Grahamstown	H.W. Gess & R.W. Gess fieldnotes 1978 and vouchers
	SPARASSIDAE: *Palystes superciliosus* L. Koch, immature ♀	Eastern Cape, Grahamstown	H.W. Gess fieldnotes 1978 and vouchers
	SPARASSIDAE: *Palystes superciliosus* L. Koch, ♀	Eastern Cape, Grahamstown	D.W. Gess fieldnotes 1979 and vouchers
	SPARASSIDAE: *Palystes superciliosus* L. Koch, ♀	Eastern Cape, Grahamstown	F.W. Gess fieldnotes 1979 and vouchers, two records
	SPARASSIDAE: *Palystes* sp.	KwaZulu-Natal, Margate	Weaving research notes and vouchers 1983
Telostegus capensis Arnold	SALTICIDAE	Eastern Cape, Hilton	R.W. Gess in Gess & Gess fieldnotes 1982 and vouchers
	SALTICIDAE	Eastern Cape, Hilton	Gess & Gess fieldnotes 1982 and vouchers, two records
	SALTICIDAE	Eastern Cape, Hilton	Gess & Gess fieldnotes and vouchers, three records
Pepsinae: Auplopodini			
Auplopus femoralis (Arnold)	SALTICIDAE	KwaZulu-Natal, north coast	Weaving 1994
Auplopus (Conagenia) mazoensis (Arnold)	THERIDIIDAE: *Theridion*, immatures	KwaZulu-Natal, Hilton	Taylor 1968
Auplopus personata ornaticollis (Cameron)	SALTICIDAE: immature	Zimbabwe (Rhodesia) Gwanda	R.H.R. Stevenson vouchers 1937
	SALTICIDAE: ♀	Eastern Cape, Grahamstown	H.W. Gess fieldnotes 1975 and vouchers
	CLUBIONIDAE: *Clubiona* sp., ♀; two records	Eastern Cape, Kenton-on-Sea	R.A. Jubb vouchers 1973
	SPARASSIDAE: *Olios* sp.	Eastern Cape, Grahamstown	H.W. Gess fieldnotes 1978 and vouchers
Auplopus personata (Gribodo)	SALTICIDAE	KwaZulu-Natal, Margate	Weaving research notes and vouchers 1983

Identity of wasp	Identity of prey	Locality	Reference
Auplopus rossi nigricornis (Arnold)	LYCOSIDAE	Eastern Cape, Hilton	Gess & Gess fieldnotes 1976 and vouchers
Cyemagenia rubrozonata (Cameron)	LYCOSIDAE	Eastern Cape, Hilton	Gess & Gess fieldnotes and vouchers
	LYCOSIDAE	Eastern Cape, Hilton	Gess & Gess fieldnotes and vouchers
	LYCOSIDAE	Grahamstown, Belmont Valley	Gess & Gess fieldnotes 1982 and vouchers
	LYCOSIDAE: *Pardosa* sp.	Eastern Cape, Hilton	Weaving research notes and voucher specimens 1982
Dichragenia pulchricoma (Arnold)	LYCOSIDAE: ♀	Eastern Cape, Grahamstown, Hilton	Gess and Gess 1974 and vouchers, 15 records
	LYCOSIDAE: immature ♀	Eastern Cape, Grahamstown, Hilton	Gess and Gess 1974 and vouchers
	LYCOSIDAE: ♂	Eastern Cape, Grahamstown, Hilton	Gess and Gess 1974 and vouchers, two records
	SPARASSIDAE: *Olios* sp.	Eastern Cape, Grahamstown, Hilton	Gess & Gess 1974 and vouchers, two records
	SPARASSIDAE: *Olios* sp. ♂	Eastern Cape, Grahamstown, Hilton	Gess & Gess 1974 and vouchers
	SPARASSIDAE: *Pseudomicrommata vittigerum* (Simon) ♀	Eastern Cape, Grahamstown, Hilton	Gess & Gess 1974 and vouchers, two records
	PISAURIDAE: *Euphrosthenops* sp. ♀	Eastern Cape, Grahamstown, Hilton	Gess & Gess 1974 and vouchers, two records
	SALTICIDAE: ♀	Eastern Cape, Grahamstown, Hilton	Gess & Gess 1974 and vouchers
	LYCOSIDAE: *Lycosa bimaculata*	Eastern Cape, Grahamstown, Hilton	Weaving research notes and vouchers 1982
Dichragenia neavei (Kohl)	LYCOSIDAE: immature ♂	Eastern Cape, Grahamstown, Hilton	Gess & Gess fieldnotes and vouchers, two records
	SPARASSIDAE: *Palystes* sp., 1 immature	Eastern Cape, Grahamstown, Hilton	Gess & Gess fieldnotes and vouchers
Dichragenia jacob (Arnold)	LYCOSIDAE: 2 ♀	Eastern Cape, Grahamstown, Hilton	Gess & Gess fieldnotes 1978
Pepsinae: Pepsini			
Cyphononyx decipiens (Smith)	SPARASSIDAE: *Palystes natalius* (Spar.)	Eastern Cape, Kudu Reserve	Weaving research notes 1982
	SPARASSIDAE: *Palystes* sp.	Eastern Cape, Grahamstown	Gess & Gess fieldnotes and vouchers
Cyphononyx flavicornis antennatus Smith	SPARASSIDAE: *Palystes peroratus* Pocock, ♀	Eastern Cape, Willowmore	C.F. Jacot Guillarmod vouchers 1976
	SPARASSIDAE: *Palystes* sp., not *P. superciliosus* L. Koch, ♀	Eastern Cape, Grahamstown, Hilton	H.W. Gess fieldnotes 1978 and vouchers
Cyphononyx optimus (Smith)	SPARASSIDAE: *Palystes* sp.	KwaZulu-Natal, Widenham	Weaving research notes and vouchers 1982
Hemipepsis vindex Smith	THERAPHOSIDAE	Little Karoo, Ladismith, Towerkop Nature Reserve	C.V. Deventer vouchers
Ctenocerinae (Claveliinae)			
Paraclavelia caffer Kohl	CTENIZIDAE: *Stasimopus robertsi* Hewitt	North West, Koedoespoort	Arnold 1932

Aizoaceae together with Molluginaceae 6%; Elatinaceae, Ebenaceae, Proteaceae and Scrophulariaceae (Selagineae) 4% each; and Tiliaceae, Euphorbiaceae (extrafloral nectaries) and Scrophulariaceae (excluding Selagineae) 2% each.

The flowers most commonly favoured are small, white to cream or yellow, and clustered in heads. Particularly favoured are *Deverra denudata* (Viv.) Pfisterer & Podlech and *Foeniculum vulgaris* Mill. (Apiaceae = Umbelliferae), *Acacia karroo* Hayne (Mimosaceae), *Gymnosporia linearis* (L.f.) Loes. (Celastraceae), *Asparagus* spp. (Asparagaceae) and *Gomphocarpus filiformis* (E.Mey.) D.Dietr. (= *Asclepias buchenaviana* Schinz) (Apocynaceae, including Asclepiadaceae). Notably attracted to *G. filiformis* from the southern karoo into southern Namibia is *Clavelia ramosa* Smith with *Euphorbia mauritanica* L. (Euphorbiaceae) often attracting *Hemipepsis vindex* Smith.

Subfamily Ceropalinae

Typically, pompilids are nest constructors. However, no Ceropalinae are known to construct nests. All those for which 'nesting' is known oviposit onto the spider prey of other pompilids. *Ceropales* inserts an egg into the book lungs of a spider already paralysed by some other pompilid but not yet placed in its nest cell. The interference is not detected and the rightful owner takes the spider into her own cell and there oviposits on it in the normal way. The egg of the *Ceropales* hatches before that of the host, which it kills before feeding upon the spider. *Ceropales* are known to be hosted by several genera of Pompilinae and Pepsinae in Britain (Richards & Hamm 1939) and North America (Evans & Yoshimoto 1962). However, as far as we have been able to ascertain, the only documented associations for southern Africa are those of *Ceropales punctulatus* Cameron with *Dichragenia pulchricoma* (Arnold) (Gess & Gess 1974a, 1974b) and *Auplopus vitripennis* Smith (both Pepsinae, Auplopodini) (Weaving 1995a).

Evans (1953) considered this behaviour to be derived from nesting, with the loss of the behavioural elements associated with nest construction. Shimizu (1994), in his consideration of the phylogeny of the Pompilidae, on the basis of the presumption that the Ceropalinae are the most primitive offshoot of the Pompilidae, concludes that nest construction has not been abandoned by these wasps. Rather, their behaviour is derived from that of parasitoids, which exhibit the most likely life pattern of a common ancestor of the Pompilidae.

Subfamily Pompilinae

Typically, Pompilinae are sand-rakers excavating simple single-celled nests. Examples of species studied in southern Africa are two relatively large species, *Tachypompilus ignitus* (Smith) and *Batozonellus fuliginosus sepulchralis* (Smith), and a smaller species, *Pompilus cinereus* (Fabricius). *Tachypompilus ignitus* (Smith) is black bodied with fiery orange wings and reddish brown antennae, legs and abdominal tip and occurs throughout the southeast (Gess & Gess 1980). *Batozonellus fuliginosus sepulchralis* (Smith) is altogether black with a purplish blue lustre to its wings and occurs from Sudan southwards (Gess & Gess 1980). The very tiny, smoky-grey species *Pompilus cinereus* (Fabricius) (Day 1981; Gess & Gess fieldnotes and voucher specimens 1973) occurs throughout the continental Old World and the associated islands on coastal dunes and sandy riverbeds. All three species hunt before excavating their nests. Exceptional are species which do not construct nests but oviposit onto an active prey individual that is not confined in any way. A putative example from Ndola, Zambia, is that of a wasp, probably *Paracyphononyx africanus* (Radoszkowski) (Pompilinae), which was observed to temporarily paralyse its spider host, probably *Lycosa* sp., deposit an egg and then abandon the spider which recovered after 20 minutes (Grout & Brothers 1982).

Argyroclitus Arnold

Argyroclitus fasciatipennis Arnold

Provisioning

Argyroclitus fasciatipennis was captured together with its prey spider, a bright green individual, a species of Salticidae in the Alexandria Forest, a coastal forest in the Eastern Cape. The weights of wasp and spider were, 11.5 mg and 50.8 mg respectively, i.e. the spider was 4.4 × the weight of the wasp.

Batozonellus Arnold

Batozonellus fuliginosus sepulchralis (Smith)

Nest situation

Batozonellus fuliginosus (Figure II.2.58) prefers moist soil in the open and may occasionally be observed nesting in dug over soil in town gardens.

Provisioning, construction of nest and oviposition

Batozonellus fuliginosus seems to be restricted to Araneidae (= Argiopidae) commonly called orb web spiders

Figure II.2.58.—*Batozonellus fuliginosus sepulchralis* (Smith).

Figure II.2.59.—a.–c. *Dicyrtomellus meruensis* Cameron: a. excavating nest; b. transporting prey (Sparassidae); c. opened nest, showing nest plan, prey orientation and egg.

which it hunts during the late afternoon. The wasp attacks the spider in the web and falls with it to the ground. The difference in size between wasp and spider is not as great as between some pompilids and their prey, ratios of as little as 1.3 and 1.6 having been obtained for some spiders to the wasp nesting on the farm Hilton (Gess & Gess fieldnotes and voucher specimens 1982).

Having paralysed the prey, *B. fuliginosus* drags it over the ground, the wasp walking backwards. This mode of transport is dictated by the weight of the prey relative to that of the wasp and by the spider's long legs which make straddling it a physical impossibility. *Batozonellus fuliginosus* holds her prey with one of the hind legs.

Whilst digging her nest the wasp commonly hides her prey on a small plant at a little distance. The burrow she excavates is shallowly sloping and widened at the inner end to form a cell. After excavation of the nest is completed, the wasp fetches her prey from its temporary hiding place and, walking backwards, drags it into the burrow. Once the paralysed spider is installed in the cell with its head facing the nest entrance and its legs directed forwards, the wasp oviposits onto it, the egg being cemented over its anterior third to the spider's abdomen, either on its dorsal surface or at its base laterally.

Batozonellus fuliginosus closes the burrow by filling the entire shaft leading to the cell with earth raked from the tumulus, which had formed during nest excavation. When the earth fill has almost reached the burrow entrance, the wasp begins tamping it down with the tip of her abdomen. During the tamping operation, which is clearly audible, the feet are kept firmly planted upon the ground, flexing of the legs takes place between the femur and tibia and the wasp's entire body and antennae vibrate up and down so rapidly that they appear blurred. Thereafter, additional earth for the burrow filling is quarried from a site next to the burrow opening. It is loosened with the aid of the jaws and is raked into the burrow. From time to time, any remaining excavated earth from the burrow is raked away and levelled so that, when closure is completed, the burrow closure is level with the surrounding ground. By contrast, the quarry site becomes a noticeable pit which may serve as a false burrow to confuse would-be nest robbers.

Dicyrtomellus Gussakovskij

Robert Gess observed the nesting of *Dicyrtomellus meruensis* Cameron at Bathurst, Eastern Cape.

Nest situation

The nest was excavated in friable soil (Figure II.2.59.a).

Nest structure

The nest consisted of a short sloping burrow ending in a single cell (Figure II.2.59.c).

Provisioning

The nest builder was observed dragging its prey, a sparassid spider, to the nest (Figure II.2.59.b) in which it was found to have positioned the spider facing the inner end of the cell and to have oviposited on it (Figure II.2.59.c).

Figure II.2.60.—*Dicyrtomellus leptacanthius* (Cameron) transporting prey (Sparassidae).

Robert Gess collected a second female *D. meruensis* with its prey, a sparassid spider, which it held by a leg and dragged backwards, on a verandah in Grahamstown. The weight of the wasp was 57 mg and that of the spider 437 mg, i.e. 7.67 × the weight of the wasp (voucher specimens).

A second species of *Dicyrtomellus*, *D. leptacanthius* Cameron, photographed by Alan Weaving (Figure II.2.60), was dragging a sparassid spider in the same manner as was *D. meruensis* photographed by Robert Gess in Bathurst, suggesting that this is characteristic for the genus.

Elaphrosyron Haupt

Provisioning

Elaphrosyron insidiosus (Smith), weight 27.0 mg, was captured transporting a crab spider (Thomisidae), weight 46.5 mg, on foot on the bank of a sandpit on the farm Hilton (Gess & Gess fieldnotes and voucher specimens 1982).

Episyron Schiödte

Provisioning

All the available records for *Episyron* suggest that the genus specialises in hunting spiders of the family Araneidae (Table 8) (Figure II.2.61).

Pompilus Fabricius

The genus *Pompilus* is illustrated here by *Pompilus irpex* Gerstaecker (Figure II.2.62), no photographs of living *Pompilus cinereus* (Fabricius) being available.

Pompilus cinereus (Fabricius)

Figure II.2.61.—*Episyron histrio* (Lepeletier) transporting prey (Araneidae).

Figure II.2.62.—*Pompilus irpex* Gerstaecker.

Although we have observed *Pompilus cinereus* (Fabricius) frequently on foredunes along the Eastern Cape coast, and have sometimes taken females with prey, we have never made a study of nesting by this wasp. The only published account for southern Africa seems to be that in Day (1981).

Provisioning and oviposition

Pompilus cinereus hunts free-running spiders of a wide range of families with Lycosidae, Gnaphosidae, Zoriidae, Clubionidae, Pisauridae, Thomisidae and Salticidae having been recorded from across its range (Day 1981). The spiders taken are approximately the same size as the wasp, making it possible for *P. cinereus*, when carrying prey, to progress forwards, running or even flying for short distances.

Before excavating her burrow, *P. cinereus* excavates a shallow depression in which she buries her spider. The nest burrow, which is dug in dry or moist sand, consists of a shaft and a single cell. Day (1981) records that the walls of the cell are stabilised with the spinnings of the spider prey.

The shaft is filled with sand and the completed closure is compacted by tamping with the tip of the abdomen. Day (1981) records that the thorax is held rigid on the legs whilst the abdomen itself moves forwards and backwards and from side to side beneath the thorax.

Tachypompilus Ashmead

Tachypompilus ignitus (Smith)

Nest situation

Tachypompilus ignitus nests in dry earth under cover and is, therefore, often seen entering air bricks giving access to dry ground under houses with sprung floors.

Provisioning and oviposition

Tachypompilus ignitus seems to be restricted to spiders of the genus *Palystes* (Sparassidae) taking such species as *P. superciliosus* L. Koch (= *P. natalius* Karsch), commonly called the hedge spider or rain spider. Hedge spiders are well known not only for their habit of coming into houses at night (being attracted by light), but also for their egg packets, the size of an orange, formed from dry leaves enveloped in silk and suspended within a bush. The wasp attacks the spider in vegetation, holds onto it stinging it repeatedly as the two fall to the ground together. The ratio of weight of wasp to weight of spider was found to vary considerably—in a sample of eleven wasps with prey collected by us in Grahamstown in only one instance was the ratio 1:1; in nine cases the range was from 1:2 to 1:9; and in one case an astonishing 1:29.6.

Having paralysed the prey, *T. ignitus* drags it over the ground, the wasp walking backwards (Figure II.2.63). This mode of transport is dictated by the weight of the prey relative to that of the wasp—up to eight times—and by the spider's long legs which make straddling it a physical impossibility. *Tachypompilus ignitus* holds the spider by one of the chelicerae or more rarely one of the pedipalps.

Telostegus A. Costa

Provisioning

Three females of *Telostegus capensis* Arnold were captured on the farm Hilton, Grahamstown, where each was transporting a salticid spider (Gess & Gess fieldnotes and voucher specimens 1982). The weights of two of the wasps were both 11.0 mg and those of the prey 27.5 mg and 35.5 mg respectively, i.e. the spider in one case was 2.8 × and in the other 3.5 × heavier than the wasp.

Subfamily Pepsinae

Two tribes are recognised in the Pepsinae, Pepsini and Auplopodini (= Ageniellini).

Tribe Pepsini

Although Pepsini includes many of the largest and most familiar southern African pompilids, little seems to have been recorded concerning the nesting of members of this tribe. The general picture for the tribe seems to be excavation of a burrow in friable ground but cavity nesters have also been recorded (Medler & Koerber 1957; Evans & Yoshimoto 1962; Fye 1965; Krombein 1967 for *Dipogon* spp.; Harris 1987 for *Spictostethus* spp.).

Iwata (1976) categorises *Cyphononyx* Dahlbom (Figure II.2.64) and *Hemipepsis* Dahlbom (Figure II.2.65) as hunting before excavating nests and it seems likely that the southern African species will be found to follow this pat-

Figure II.2.63.—*Tachypompilus ignitus* (Smith) transporting prey, *Palystes superciliosus* L. Koch (Sparassidae).

Figure II.2.64.—*Cyphononyx* sp.

Figure II.2.65.—*Hemipepsis vindex* Smith, imbibing water.

tern. Widespread in the Afrotropical Region and extremely familiar throughout the Karoo because of its loud rattling flight is *Hemipepsis vindex* Smith, a large black wasp with a dark greenish blue sheen. *Hemipepsis vindex* and *H. capensis* Fabricius (specimen with prey collected by C.V. Deventer in Towerkop Nature Reserve, Ladismith, Little Karoo; vouchers in Albany Museum) are known to hunt baboon spiders (Theraphosidae)—some of the largest spiders in southern Africa. *Cyphononyx decipiens* (Smith), like *Tachypompilus ignitus*, which also has fiery orange wings, is a hunter of hedge spiders, *Palystes* spp., and is a familiar garden insect through KwaZulu-Natal and the Eastern Cape.

Relative weights of wasp and prey were obtained for *Cyphononyx flavicornis antennatus* Smith with *Palystes* prey captured by Harold Gess on the farm Hilton and for *Dipogon dregei* (Arnold) captured by David Gess in a garden in Grahamstown. For *Cyphononyx flavicornis antennatus* the wasp weighed 450 mg and the spider 1101 mg, i.e. the prey was 2.5 × the weight of the wasp. For *Dipogon dregei* the wasp weighed 14 mg and the spider 55 mg, i.e 4 × the weight of the wasp—an interesting difference in relative sizes. It was noted that *D. dregei* was transporting the spider holding it by the spinneretes.

Tribe Ageniellini (= Auplopodini)

Nesting in Ageniellini has been reviewed by Evans & Shimizu (1996, 1998). Most species of Ageniellini, including many southern African species, carry water to make mud pellets from which ovoid nest cells are constructed. Usually such cells are sited in groups in a sheltered place, for example under loose bark, on the underside of stones or in pre-existing cavities, such as hollow stems or the abandoned nests of other wasps. Some species are known to nest communally, co-operating in nest defence and in cell building. Such behaviour has been recorded for two southern African species, *Auplopus femoralis* (Arnold) and *A. personata* (Gribodo) (Weaving 1994a) in coastal savanna and woodland on the KwaZulu-Natal north coast.

At least five species, three in Australia and two (probably three) in Africa, use water not for the construction of cells but for the excavation of multicellular nests in horizontally presented hard, clayey soil. Two of the Australian species, a species of *Auplopus* (Evans & Hook in Evans & Shimizu 1996) and a species of *Fabriogenia* (Gess & Gess in Evans & Shimizu 1998) make rudimentary nest entrance turrets. However, well developed entrance turrets are constructed by the African species, *Dichragenia pulchricoma* (Arnold) and *Dichragenia neavei* (Kohl) (Gess & Gess 1974a, 1974b, 1975).

Nests consisting of a linear series of cells in a tubular cavity, in which the cavity walls form the longitudinal walls of the cells and only the end walls and cavity closure are constructed, is unusual. Such nesting has only been recorded for two southern African species, *Auplopus vitripennis* Smith (Weaving 1994a) and *A. rubirostris* Arnold (Robert Gess fieldnotes and photographs 2009, 2011).

Taylor (1968) recorded that *Auplopus* (*Conagenia*) *mazoensis* (Arnold), provisioned nests in glass tubes in a wooden block at Hilton, KwaZulu-Natal with immatures of two species of *Theridion* but, unfortunately, did not indicate the nature of the nests.

All Ageniellini amputate the legs of the prey spider taking advantage of a natural point of weakness at their bases. The advantages of 'dressing' the prey in this manner are two-fold. Time and energy are saved both in transporting the prey and in constructing the cell, which can be considerably smaller than if the legs were left attached. In transporting the spider, the wasp straddles it with her legs and, grasping it in a way characteristic for each genus, picks it up off the ground, and walks forwards rapidly (Figures II.2.66.a & b). This is a markedly more efficient way of moving the spider than that employed by those spider wasps that do not amputate the legs of their prey, which they then have to drag over the ground, walking backwards.

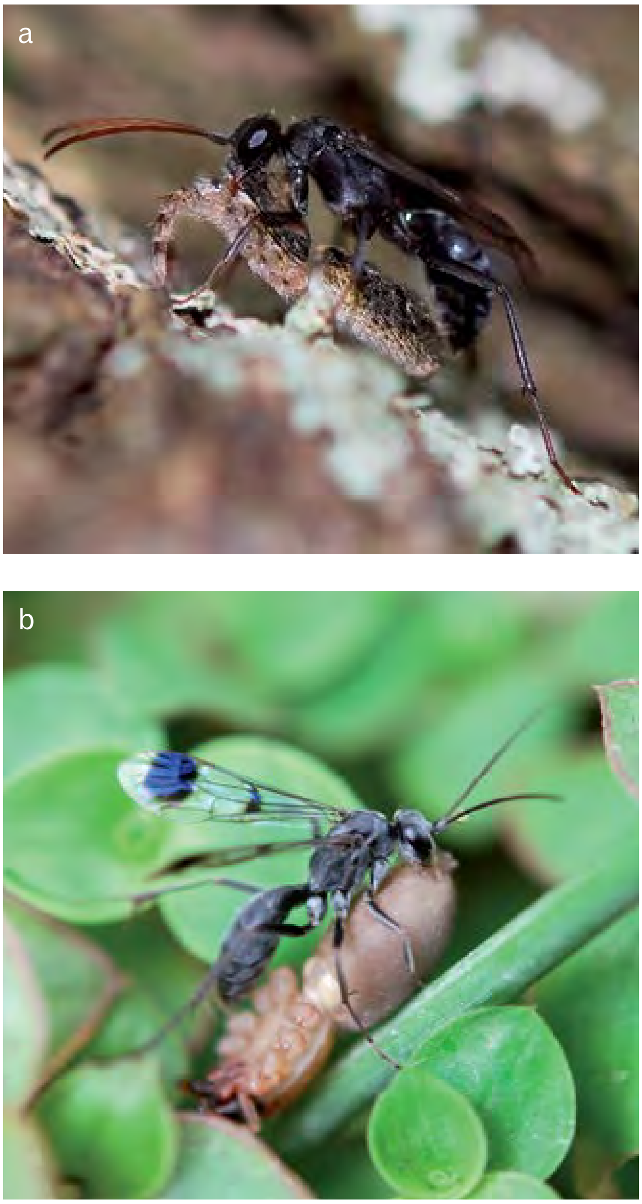


Figure II.2.66.—a and b. Auploplines showing two modes of prey transport: a. prey dorsum up facing the direction of travel (*Auplopus rubirostris* (Arnold)); b. venter up facing away from the direction of travel.

Auplopus Spinola

Nest situation

Auplopus species construct nests in concealed sites such as on the underside of stones, under bark and in cavities.

Nest structure

A nest of *Auplopus rossi nigricornis* (Arnold) attached to the underside of a large flat stone lying on the ground on the farm Hilton consisted of nine closely packed cells covered by a mud envelope (Gess & Gess fieldnotes and voucher specimens 1976).

The nests of *Auplopus rubirostris* were in pre-existing cavities, vacated nests of *Hylaeus* sp. (Colletidae) in the vertical mud wall of a shade house at Bathurst, Eastern Cape (Figure II.2.68). Nests of *Auplopus femoralis* and *Auplopus vitripennis* were in trap nests (Figure II.2.69) suspended in shrubs in coastal bush and Savanna on the north coast of KwaZulu-Natal (Weaving 1994a).

The nests were very different in structure. Those of *A. femoralis* consisted of groups of mud cells within the pre-existing cavity (Figure II.2.67) and those of *A. rubirostris* and *A. vitripennis* were remarkable for the genus in that the cells were not discrete mud cells but a linear series of cells with mud used only for the construction of partitions and closures. Completed nests of *A. vitripennis* had up to seven cells. Intercalary cells were present in only a small percentage of nests. Basal plugs were present in about 50% of nests. Basal plugs and cell partitions were constructed from sand bonded with liquid, probably water, regurgitated at the quarry site. The outer concave surfaces were normally coated with a resinous material resulting in a very hard finish. This material, which could not be identified, was transported as a globule held in the wasp's mouthparts. Closing plugs were usually flush with the cavity entrance. These were constituted of an inner layer of cemented sand and an outer layer of exuviae of hairy caterpillars and/or flakes of bark.

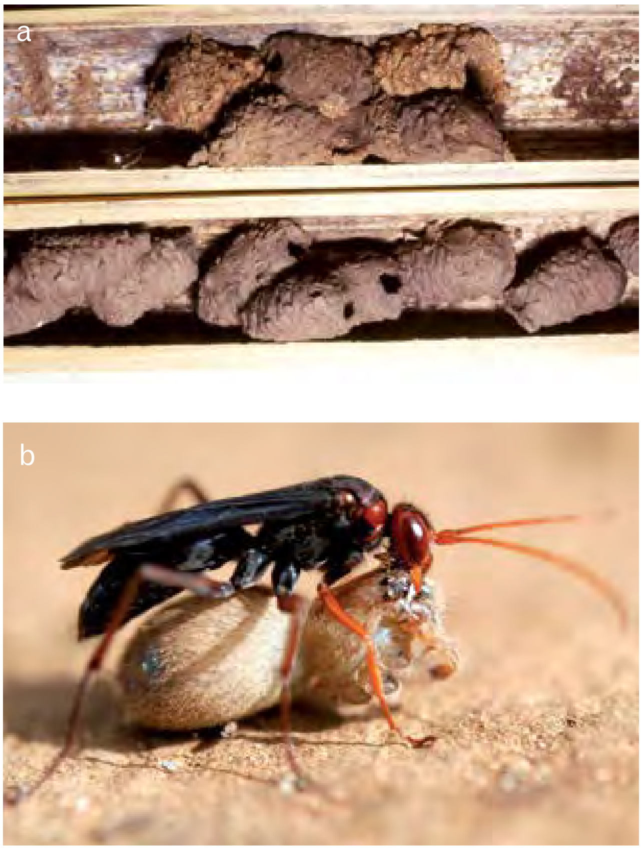


Figure II.2.67.—a and b. *Auplopus femoralis* (Arnold): a. mud cells constructed in pre-existing cavity, reed trap nest; b. female transporting prey to the nest, Bathurst, Eastern Cape.

Auplopus rubirostris sealed its nests with mud mixed at a quarry site, in the vicinity of *Hylaeus* nests and with web-like material pealed from the bee's cell closure. Mud was carried to the nest entrance as a pellet held between the mandibles and was added to the seal, the gaster curved under and supporting the surface under construction (Figure II.2.68. d & e).

Provisioning and oviposition

After a cell has been prepared, hunting takes place. The prey, like that of *Dichragenia*, are wandering ground-living spiders. Those of *A. rossi nigricornis* were Lycosidae and those of *A. femoralis* Salticidae.

The spider, having been captured, stung, subdued and had its legs amputated, is carried beneath the wasp. Most records for *Auplopus* suggest that this genus holds the spider by the spinneretes with the result that the prey faces away from the direction of travel. The prey is carried venter up. However, Robert Gess observed *A. rubirostris* carrying a spider dorsum up facing the direction of travel (Figure II.2.68.b) and a female holding a spider ventral side up by the spinneretes when taking it into her nest (Figure II.2.68.c). After oviposition has taken place, the cell is sealed.

Prey records are available for *Auplopus personata ornaticollis* (Cameron). All are errant spiders of three families, two of Clubionidae collected by Rex Jubb at Kenton-on-Sea, Eastern Cape, one of Salticidae collected by Roy Stevenson at Gwanda, Zimbabwe and three of Sparassidae collected by the authors in the Grahamstown area.

Nest sharing

Alan Weaving (1994a) reported nest sharing by *A. femoralis.* The impression obtained was that a single female initiates a nest and that at a later stage in nesting more than one female works within a cavity and that one of the females acts as a guard.

Associates

Of particular interest is the pompilid labour parasite, *Ceropales punctulatus* Cam., otherwise recorded from *Dichragenia pulchricoma* (Gess & Gess 1974a, 1974b). The parasite had been successful in inserting its eggs into 2.6% of the spider prey of *A. vitripennis.*

Velvet Ants (Mutillidae) were reared from cells of all three species. Three male *Antennotilla phoebe* Péringuey were

Figure II.2.68.—a.–e. *Auplopus rubirostris* (Arnold): a. at entrance to pre-existing burrow; b. transporting prey to burrow; c. taking prey into burrow; d. carrying mud for sealing nest entrance; e. supporting nest closure with tip of gaster whilst applying mud.

reared from three of the cells of *A. rossi nigricornis* (Gess 1981). Unidentified *Antennotilla* emerged from 3.7% of the cells of *A. vitripennis* and with *Dolichomutilla heterodonta* Bischoff from 4.5% of the cells of *A. femoralis.*

Cuckoo wasps were reared from cells of *A. vitripennis* and *A. femoralis*—a species from the *Chrysis wahlbergi* group from cells of both species and a species from the *Primeuchroeus ghilianii* group solely from *A. femoralis.*

Auplopus vitripennis was also subject to parasitism by a leucospid, *Leucospis varicollis* Cameron (Leucospidae). An ichneumonid *Stenarella* and a miltogrammine fly, *Amobia africa* Curran, had also been successful in parasitising *A. vitripennis*.

Figure II.2.69.—a.–c. *Auplopus vitripennis* Smith: a. at entrance to nest in reed trap nest; b. prey and small larva in nest in wooden trap nest; c. prey, large larva, and cell partitions in nest in wooden trap nest.

Cyemagenia Arnold

Arnold (1934) lists six species of *Cyemagenia*, all from southern Africa.

Provisioning

A female *Cyemagenia rubrozonata* (Cameron) with lycospid prey was captured on the floor of a sandpit on the farm Hilton. The difference in weight of the wasp and its prey spider was unusually small, the weights having been 17.5 mg and 20.0 mg respectively.

Deuteragenia Süstera

Robert Gess collected a female *Deuteragenia dregei* Arnold and its spider prey in a Grahamstown garden. The wasp was walking backwards carrying its spider prey, dorsal side up, held by the spinneretes. The weight of the wasp was 10 mg and that of the spider 75 mg, that is 7.5 × greater than that of the wasp (Gess & Gess fieldnotes and voucher specimens).

Dichragenia Haupt

Our studies of the *Dichragenia pulchricoma* and *D. neavei* (Gess & Gess 1974a, 1974b, 1976) were conducted in areas of karroid vegetation in the Eastern Cape. Nests of *D. pulchricoma* were noted, but not investigated, on the farm VanWyksfontein near Norvalspont. Previously, turrets of *D. pulchricoma* had been noted in Lesotho (Jacot Guillarmod 1945 as the 'Zimbabwe builder') and of *D. neavei* (as *Pseudagenia neavei* Kohl) (Chapman 1958) in Tanzania.

Nest situation

The nests are always sited in areas of bare clayey soil close to water.

Nest structure

The nests consist of a subvertical burrow surmounted by a mud entrance turret (Figure II.2.70.a–d).

The mud turrets of both species are constructed from large mud pellets, in shape like two-seeded peanuts.

They are readily distinguishable, however, as that of *D. pulchricoma* is retort-shaped with the diameter of the base greater than that of the shaft (Figures I.4.10 and II.2.70.a & b. and 71), whereas that of *D. neavei* is funnel-shaped with the diameter at the base equal to that of the shaft (Figure II.2.70.c).

The burrows are indistinguishable, with both consisting of a vertical shaft with near its base one or two whorls of cells radiating out from the shaft terminating short downwardly sloped secondary shafts (Figure II.2.71).

In the nests of *Dichragenia*, the advantages of 'dressing' the prey are not only that the cells can be relatively small but also that the required diameter of the shaft is considerably less than it would otherwise be.

Method of construction

Water used in nest excavation is collected by the wasps whilst standing on the mud at the shallow edge of a water source.

Provisioning and oviposition

Each cell, after excavation, is provisioned with a single spider positioned with its head facing the cell opening. The recorded spiders are all wandering, ground-living species of the families Lycosidae, Sparassidae, Pisauridae and Salticidae. The wasps stalk and run down their prey on foot.

The spider, having been captured, subdued and its legs amputated, is transported rapidly to the nest. However, in contrast to the mode of transport employed by most species of *Auplopus*, *Dichragenia* holds the prey by the chelicerae not by the spinneretes, resulting in the prey facing the direction of travel. Furthermore, whereas most *Auplopus* carry the prey venter up, *Dichragenia* carries it dorsum up. After oviposition has taken place, the cell is sealed.

A third species of *Dichragenia*, *D. jacob* (Arnold) was observed to fly from bush to bush carrying its prey (Gess & Gess fieldnotes and voucher specimens 1978).

After the spider has been positioned in the cell, oviposition takes place, the egg being attached antero-laterally to the spider's abdomen (Figure II.2.71.c.). The cell is then sealed off from the main shaft by the construction of a mud plug. Successive cells are excavated, provisioned, oviposited into and sealed. No attempt to fill or seal the main shaft has been observed and the turret is left intact, eventually crumbling away.

Associates

The only instance of parasitism of either species of *Dichragenia* was by the pomplilid labour parasite, *Ceropales punctulatus* Cameron, reared from two cells of *D. pulchricoma* from nests on the farm Hilton.

A greater problem to nesting *D. pulchricoma* on the farm Hilton was a cavity nesting megachilid bee, *Megachile* (*Eutricharaea*) *stellarum* Cockerell, which usurped nests under construction before the turret had curved over to conceal the shaft opening.

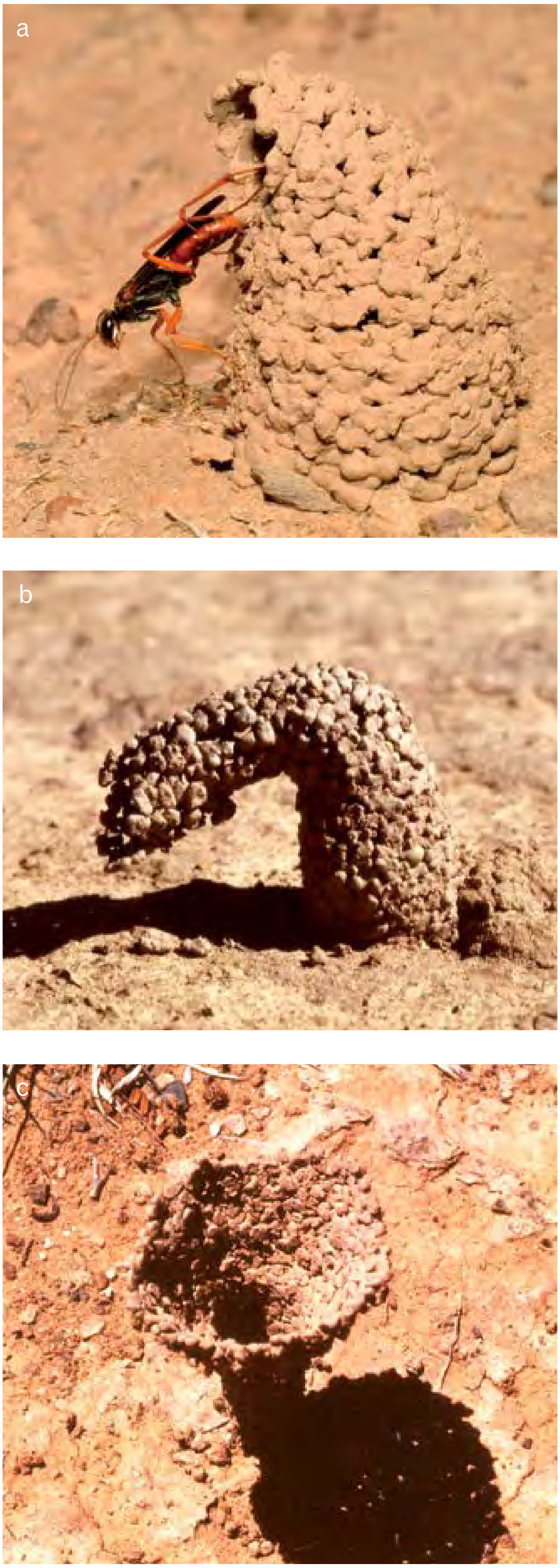


Figure II.2.70.—a.–c. *Dichragenia* spp.: a and b. *D. pulchricoma* (Arnold), a. female nest builder on partially constructed nest entrance turret, b. retort-shaped nest entrance turret; c. *D. neavei* (Kohl), funnel-shaped nest entrance turret.

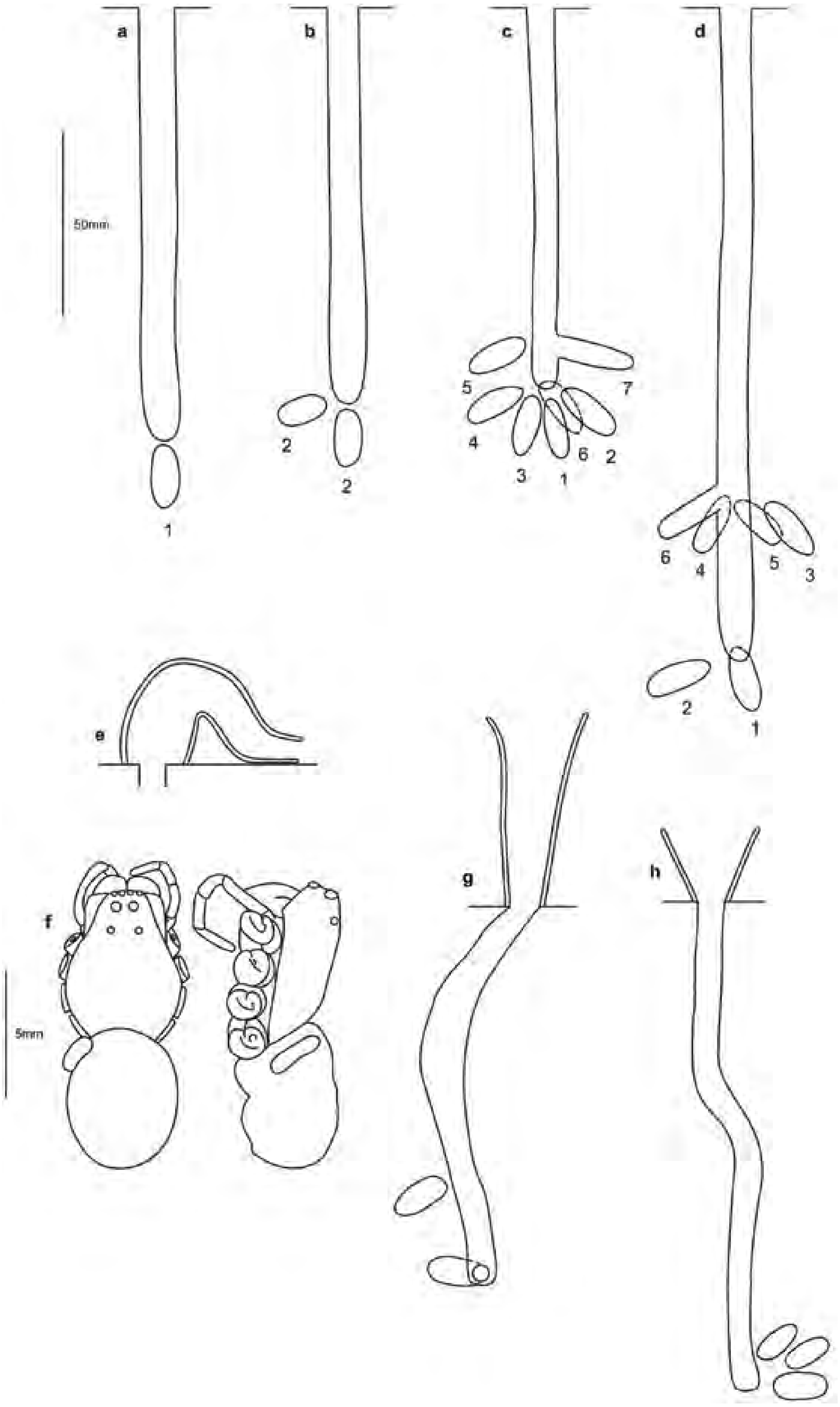


Figure II.2.71.—a.–h. *Dichragenia* spp.: a.–f. *D. pulchricoma* (Arnold), a.–d. diagrammatic vertical plans of four nests without turrets, e. an entrance turret and, f. placement of egg on prey (Lycosidae); g. and h. *D. neavei* (Kohl) diagrammatic vertical plans of two nests.

Subfamily Ctenocerinae (= Claveliinae)

The subfamily Ctenocerinae is best represented an Africa where 11 genera have been recognised. Characteristic is that the greater part of the clypeus is flattened with the basal portion depressed and that the antennae of the males are greatly modified. In some species this results in the flagellomeres being uni- or bi-flagellate, making the antennae appear 'feathered', a unique condition in the Pompilidae.

Nothing is known with certainty about the prey or nesting behaviour of these wasps in southern Africa, except that one species, *Paraclavelia caffer* Kohl, has been taken from the nest of a trap-door spider, *Stasimopus robertsi* Hewitt (Arnold 1932b). Arnold suggested that the unusually shaped clypeus may be useful in prising open the closely fitting doors of the prey.

Family Rhopalosomatidae

There are four genera of rhopalosomatids, two of which, *Paniscomima* Enderlein and *Oxilon* Cameron, are represented in southern Africa (Townes 1977). *Paniscomima* species range in length from 8–20 mm and *Olixon* species from 3–8 mm. They are not commonly known.

Paniscomima species are nocturnal or crepuscular and do not come to flowers. *Paniscomima erlangeriana* Enderlein is winged and pale fulvous.

Olixon species are diurnal, flightless and brown to black. *Olixon saltator* (Arnold) and *O. myrmosaeforme* (Arnold) have greatly reduced wings and *O. dentatum* (Cameron) is entirely wingless. Arnold (1935a) noted *O. saltator* (as *Psyllosphex*) at Beach Bush, Durban and observed that, "This insect was found running on sandy ground and when disturbed took short jumps like a flea, a mode of progression obviously facilitated by the development of the femora."

Nothing is known of the biology of the southern African species, however, some details are known of the biology of a Nearctic species, *Rhopalosoma nearcticum* Brues (Gurney 1953) and of the Australian *Olixon australiae* (Perkins) (Perkins 1908) (as *Harpagocryptus*). Both spend their larval stages feeding on crickets. The fullest account is that of Gurney (1953). An egg is laid onto a cricket, which is not paralysed nor confined in any way. The larva feeds on the cricket, being attached above the base of a hind femur, and ultimately causes the death of the cricket. The fully grown larva then burrows into the soil where it spins a cocoon in which it diapauses. Pupation is delayed, probably until near the emergence time of the adult.

Family Tiphiidae

The Tiphiidae are represented in southern Africa by four subfamilies, Anthoboscinae (Figures I.3.59.a & b.), Tiphiinae (Figure I.3.59.c), Myzininae and Methocinae. The first two subfamilies show very little sexual dimorphism. However, the Myzininae are markedly sexually dimorphic with stout females and slender, elongate males. Although most Tiphiids are winged, some species of Myzininae are wingless and female Methocinae are ant-like and wingless. Little work has been done on the taxonomy of the Tiphiidae in southern Africa, making an estimate of the number of species impossible.

Tiphiids do not construct nests. They prey on beetle larvae, which they find in the soil or in rotten wood. The female locates a beetle larva, stings it and oviposits upon it, leaving it *in situ*. Little is known of the biology of southern African species. *Tiphia transvaalensis* Cameron is known to prey on the larvae of the black maize beetle, *Heteronychus arator* Fabricius (Annecke & Moran 1982). It has been established elsewhere that most attack larvae of Scarabaeidae. One subfamily, the Methochinae, attacks larvae of tiger beetles (Cicindelidae). Williams (1919) give accounts for two species in the Phillipines. Gess (1981) in his community study on the farm Hilton, Eastern Cape, lists *Methoca mosutoana* Péringuey as almost certainly preying upon *Cicindela brevicollis* Wiedemann with which it is found in close association.

Flower visiting

Flower visiting records are available for 22 species of Tiphiidae in four genera, *Anthobosca* (Anthoboscinae), *Meria* and *Mesa* (Myzininae) and *Tiphia* (Tiphiinae). A wide range of plant families is represented—most frequently and most widespread, Apocynaceae (including Asclepiadaceae), Asteraceae, Scrophulariaceae (Selagineae), Apiaceae, Fabaceae (Mimosoideae); often in the west, Proteaceae; often in the east Asparagaceae; and variously but not commonly, Molluginaceae, Euphorbiaceae (extrafloral nectaries), Ebenaceae, Zygophyllaceae, Elatinaceae, Campanulaceae, Iridaceae, Aizoaceae (Mesembryanthema).

Family Mutillidae

Mutillids, commonly called velvet ants, are well represented in southern Africa, several hundred species in about 30 genera being known. Females are most usually red and black with bands or spots of silvery white and are invariably wingless, whereas the males which may be similarly coloured or may be predominantly black, are with few exceptions winged, the wings of most species being dark (Figures I.3.60.a–d and II.2.72 & 73). Night flying mutillids, such as species of *Tricholabiodes*, are pale ginger in colour (Figure II.2.74.a & b).

Mutillids are 'parasites'. They develop in the cocoons or puparia of other insects, most commonly wasps and bees, but also flies, beetles and moths. The egg is introduced into the cocoon or puparium where the mutillid larva feeds on the mature larva or pupa of the host. As the host is at that time in a non-active stage, it is not stung, the sting of mutillids being solely for self-defence. Some known host associations (rearing records) of mutillids occurring in southern Africa are listed in Table 9. Mutillidae do not appear to demonstrate any great degree of host specificity—rather, they appear to be associated with a particular ecological niche and to attack suitable host species found within that niche. Any species of mutillid is therefore not necessarily limited to a single species or genus of host. Conversely, a single host species may be attacked by more than one species of mutillid. For example, *Dasylabroides caffra* (Kohl) has been reared from cocoons of a masarid wasp, *Ceramius lichtensteinii* (Klug), (Gess & Gess l980c) and also from cocoons of two sphecid wasps, *Ammophila*

Figure II.2.72.—Mutillid opening a nest of *Hylaeus* (*Nothylaeus*) *heraldicus* (Smith).

Figure II.2.74.—a and b. *Tricholabiodes* sp. undescribed, female, reared from nest of *Quartinia* in *Trigonephrus* shell.

ferrugineipes Lepeletier and *A. insignis* Smith (A. Weaving pers. comm.). Conversely, a tsetse fly, *Glossina morsitans* Westwood, has been shown to host three species of mutillids, *Chrestomutilla auxiliaris* (Turner), *C. glossinae* (Turner) and *Smicromyrme benefactrix* (Turner) (Turner 1915, 1916,1920; Brothers 1971).

Flower visiting

We have rarely encountered mutillids visiting flowers: 13 male *Psammotherma flabellata* (Fabricius) from Apiaceae and one record for a male *Dasylabroides phylira* (Péringuey) from Celastraceae near Grahamstown in the southeast; and a small, unidentified female mutillid from *Zygophyllum simplex* L. (Zygophyllaceae) from Swakopmund on the Namib coast.

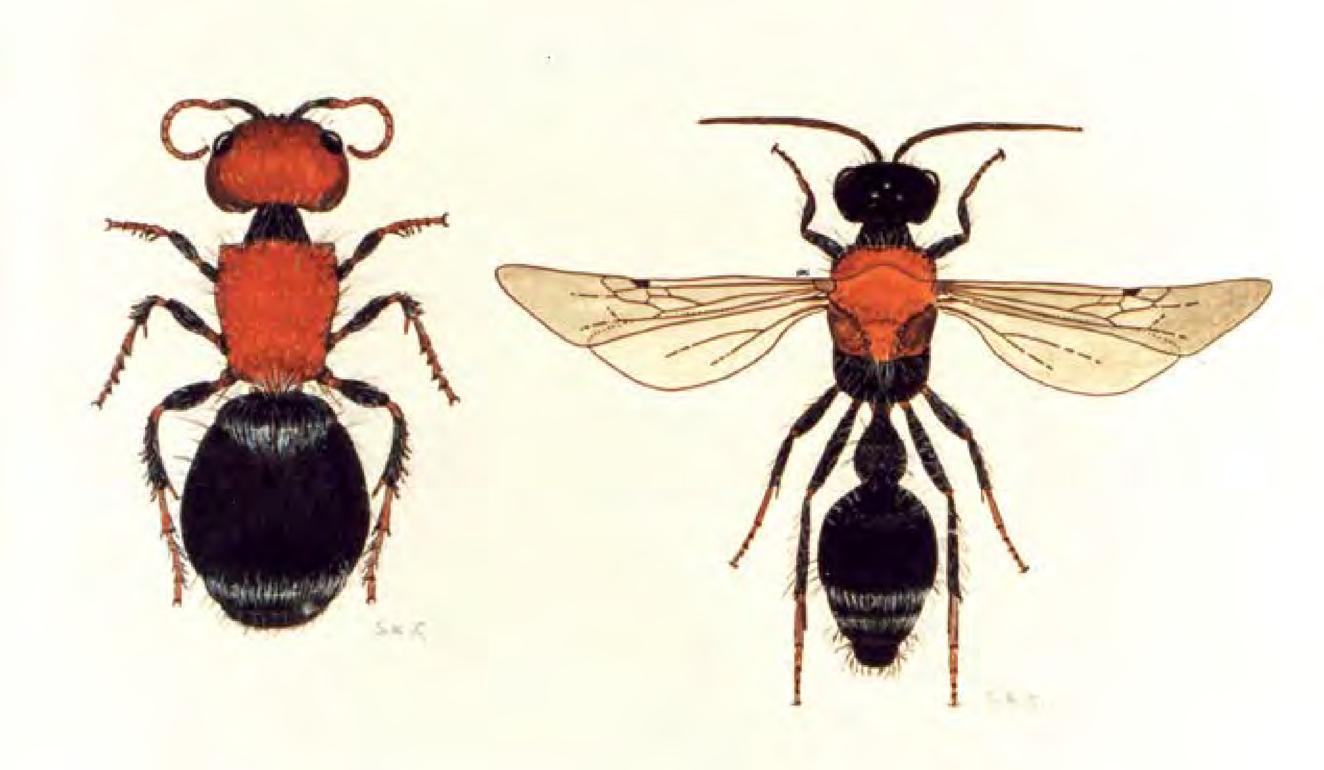


Figure II.2.73.—*Dasylabroides caffra* (Kohl), female on left, male on right (actual length 8 mm).

Table 9.—Some known host associations of Mutillidae in southern Africa

Mutillidae	**Host family**	**Host genus and species**	**Reference**
	HYMENOPTERA		
Antennotilla phoebe (Péringuey)	Pompilidae, Pepsinae	*Auplopus rossi nigricornis* (Arnold)	Gess 1981
Antennotilla sp.	Pompilidae, Pepsinae	*Auplopus femoralis* (Arnold) *Auplopus vitripennis* Smith	Weaving 1994a; 1995a
Antennotilla sp.	Sphecidae, Sphecinae	*Isodontia pelopoeiformis* (Dahlbom)	Weaving 1995a
Dasylabroides caffra (Kohl)	Vespidae, Masarinae	*Ceramius lichtensteinii* (Klug)	Gess & Gess 1980
Dasylabroides caffra (Kohl)	Sphecidae, Ammophilinae	*Ammophila ferrugineipes* Lepeletier *Ammophila insignis* Smith	Weaving label data
Dolichomutilla heterodonta Bischoff	Vespidae, Eumeninae	*Afreumenes aethiopicus* de Saussure *Tricarinodynerus guerinii* (de Saussure)	Weaving 1995a Weaving 1994b; 1995a
Dolichomutilla heterodonta Bischoff	Pompilidae, Pepsinae	*Auplopus femoralis* (Arnold)	Weaving 1995a
Dasylabroides merope (Smith)	Crabronidae, Bembicinae	*Stizus imperialis* Handlirsch	Brauns 1911 as *Mutilla merope* Sm.
Dolichomutilla minor minor Bischoff	Sphecidae, Sphecinae	*Sceliphron spirifex* (L.)	Krombein & Walkley 1962
Dolichomutilla sycorax (Smith)	Vespidae, Eumeninae	*Tricarinodynerus guerinii* (de Saussure) *Synagris analis* de Saussure	Weaving 1994b, 1995a Weaving 1995a
Dolichomutilla sycorax (Smith)	Sphecidae, Sphecinae Sphecidae, Sphecinae	*Sceliphron spirifex* (L.) *Sceliphron spirifex* (L.)	Péringuey 1898 as *Mutilla sycorax* (*M. cf. guineensis*) and *Pelopaeus spirifex* Weaving 1995a
Glossotilla speculatrix (Smith)	Crabronidae, Bembicinae	*Bembecinus* sp.	Gess 1981 circumstantial evidence
Mutilla aglae Péringuey	Apidae, Xylocopinae	*Ceratina* sp.	Péringuey 1898
Mutilla inconspicua	Megachilidae	*Heriades spiniscutis* (Cam.)	D.J. Brothers label data
Smicromyrme hecuba Péringuey	Crabronidae, Bembicinae	*Bembecinus* sp.	Gess 1981 circumstantial evidence
Stenomutilla baucis Péringuey	Megachilidae, Megachilinae	*Lithurgus spiniferus* Latreille	Eardley 1988 as *Lithurge spiniferus* Latreille
Stenomutilla syrinx (Péringuey)	Vespidae, Eumeninae	*Delta hottentotum* de Saussure *Proepipona meadewaldoi* (Bequaert) *Tricarinodynerus guerinii* (de Saussure) *Synagris analis* de Saussure	Weaving 1995a Weaving 1994b, 1995a Weaving 1994, 1995 Weaving 1995b
Stenomutilla syrinx (Péringuey)	Sphecidae, Sceliphrinae	*Chalybion* (*Chalybion*) *laevigatum* (Kohl) *Sceliphron spirifex* (L.)	Weaving 1994b, 1995a Weaving 1995a
Stenomutilla sp.	Vespidae, Eumeninae	*Pseudonortonia* sp.	Gess 1981 as Eumenid A
Stenomutilla sp.	Megachilidae, Megachilinae	*Hoplitis* sp.	D.J. Brothers label data
Tricholabiodes sp.	Vespidae, Masarinae	*Quartinia* sp.	Gess & Gess 1999, 2008
Undescribed genus near *Tricholabiodes* (*T. teste* D.J. Brothers)	Vespidae, Masarinae	*Quartinia* sp.	Gess & Gess 2008
	DIPTERA		
Chrestomutilla auxiliaris (Turner)	Glossinidae	*Glossina morsitans* Westward	Turner 1920 as *Mutilla auxiliaris* Turner
Chrestomutilla glossinae (Turner)	Glossinidae	*Glossina morsitans* Westward	Turner 1915 & 1916 as *Mutilla glossinae* Turner
Smicromyrme benefactrix (Turner)	Glossinidae	*Glossina morsitans* Westward	Turner 1916 as *Mutilla benefactrix* Turner
	COLEOPTERA		
Mutilla thyone Péringuey	Chrysomelidae, Clythrinae	Clithrid beetle in nest of ant *Crematogaster peringueyi* Emery	Brauns in Péringuey 1898

Family Bradynobaenidae

There are four subfamilies in the Bradynobaenidae. They are characterised by having the first and second metasomal segments abruptly constricted posteriorly. The females are wingless. Only one subfamily, Apterogyninae, represented by one genus, *Apterogyna*, with around 25 species (Brothers 1989), is found in southern Africa. The other three subfamilies are restricted to the New World.

Nothing is known of the biology of *Apterogyna*, however, it has been assumed that the larvae develop on the immatures of other insects. However, the larvae of *Typhoctes* of the New World subfamily Typhoctinae have been found on immature sun spiders, Solfugidae (Arachnida) Brothers & Finnamore (1993).

Flower visiting

Flower visiting records are available for three species of *Apterogyna*: *A. globularia* (Fabricius) visiting Apiaceae and Celastraceae near Grahamstown, eastern Nama-Karoo; *A. karroa* Péringuey visiting Apocynaceae (Asclepiadaceae) near Prince Albert, southern Nama-Karoo/Succulent Karoo interface; and *A. mnemosina* Péringuey visiting Apiaceae and Zygophyllaceae in southwestern and northwestern Namib fringe.

Family Scoliidae

Scoliidae are well represented in southern Africa. They are generally large, elongate, setose wasps with relatively short legs, which in the female are stout, spiny and suited to burrowing (Figure II.2.75). The wings, which may be clear, smoky, black, or black with striking metallic blue iridescence, are characteristically closely longitudinally corrugated apically. Sexual dimorphism is common, the males (besides being less robust than the females) frequently differ also in colouration: whereas females are generally predominantly black, males are often marked with yellow bands or spots. Flight is generally relatively slow, close to the ground and often follows a circular or figure of eight course.

Scoliidae typically prey upon the larvae of scarab beetles occurring in the ground, less commonly in decaying vegetable matter. At least one species, *Scolia ruficornis* Fabricius, preys upon the larvae of *Oryctes* species (large rhinoceros beetles) associated with decaying palm stems (Greathead 1971). It is of interest that amongst the few non-scarab beetle larvae known to be preyed upon by scoliids, are those of the weevil *Rhynchophorus* that are similarly associated with decaying palms. This seems to illustrate the common phenomenon that aculeate wasps are often better ecologists than systematists—the hunting wasp investigates a specific ecological niche and may accept prey of unrelated species found there, provided these satisfy certain requirements of size and other attributes.

To locate ground inhabiting scarab larvae, the female scoliid burrows into the ground where she may well follow the tunnels made by her prey. A larva, having been located, is stung by the wasp. Thereafter the prey may either be oviposited upon where it is within its burrow or cell, or may first be dragged to a greater depth where microclimatic conditions may be more favourable for the development of the wasp young.

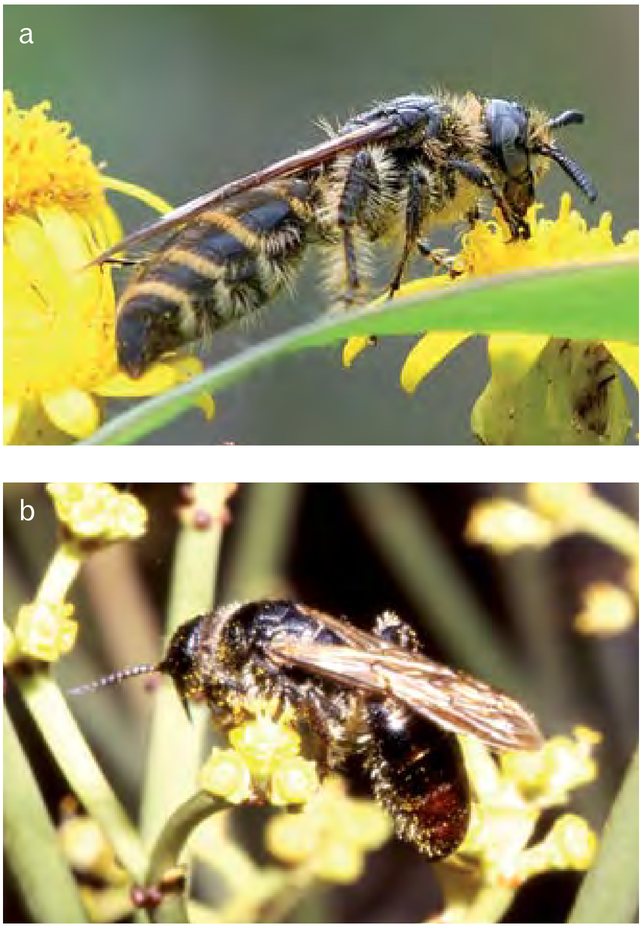


Figure II.2.75.—a and b. scoliids: a. *Cathimeris capensis* (de Saussure); b. species undetermined.

Some known prey associations for Scoliidae occurring in southern Africa are listed in Table 10. With the exception of *Scolia ruficornis*, all the species listed are associated with ground-inhabiting larvae causing damage to agricultural crops.

Observations by the authors provide circumstantial evidence for some additional associations in the Eastern Cape Province. At the coast, *Cathimeris capensis* (Saussure) and *Charimeris soni* Betrem have commonly been found on the vegetated foredunes where females have occasionally been seen digging into the loose sand in which the only scarab larvae are those of *Anoplochilus variabilis* (Gory & Percheron) and *A. germari* (Wiedemann) (subfamily Cetoniinae). These two *Anoplochilus* species feed on the roots of pioneer plants such as *Arctotheca populifolia* (P.J.Bergius) Norl. (Asteraceae). Whereas *C. capensis* is a widespread species, which extends down to the beaches, *C. soni*, the two beetles and the plant appear to be restricted to the supra-littoral zone. Similarly, in a Grahamstown garden both sexes of a large black *Scolia* sp. were commonly observed in late summer patrolling an area of cut turf into which the females were occasionally seen to penetrate. As this turf was known to be heavily infested with the larvae of *Asthenopholis subfasciata* (Blanch.) (subfamily Melolonthinae), as evidenced by the large number of adult chafers which emerged nightly during summer and were attracted to lights, it was presumed that this species constituted the prey for which the female wasps were hunting.

Table 10.—Some known prey taken by Scoliidae in southern Africa

Identity of wasp	**Identity of prey**	**Reference**
Aureimeris africana Saussure	Scarabaeidae, Melolonthinae *Schizonycha* sp.	Jepson (1939) as reported by Pope (1960) as *Campsomeris felinas* Saussure
Aureimeris mansueta (Gerstaecker)	Scarabaeidae, Melolonthinae *Cochliotis melolonthoides* Gerstaecker	Harris 1944 as *Campsomeris mansueta* (Gerstaecker)
Campsomeriella caelebs (Sichel)	Scarabaeidae, Melolonthinae *Eulepida mashona* Arrow	Jack 1935 as *Campsomeris coelebs* Sichel
Campsomeriella caelebs (Sichel)	Scarabaeidae, Rutelinae *Adoretus* sp. Scarabaeidae, Dynastinae *Heteronychus* sp.	Greathead 1971 as *Campsomeris coelebs* Sichel
Campsomeriella caelebs (Sichel)	Scarabaeidae 'white grubs'	Betrem 1972
Campsomeriella madonensis (Buysson)	Scarabaeidae, Melolonthinae *Schizonycha* sp.	Jepson (1939) as reported by Pope (1960) as *Campsomeris madonensis* du Buysson
Cathimeris capensis (Saussure)	Scarabaeidae, Dynastinae *Heteronychus arator* Fabricius	Annecke & Moran 1982
Cathimeris hymenea (Gerstaecker)		Jepson (1939) as reported by Pope (1960) as *Campsomeris aureoloides* Bradley
Micromeriella atropos Saussure	Scarabaeidae, Dynastinae *Heteronychus arator* Fabricius	Annecke & Moran 1982
Scolia chrysotricha Burmeister	Scarabaeidae, Dynastinae *Heteronychus arator* Fabricius	Annecke & Moran 1982
Scolia ruficornis Fabricius	Scarabaeidae, Dynastinae	Greathead 1971

Flower visiting

Flower visiting records are available for 22 species of scoliids in seven genera, *Aureimeris* Betrem, *Campsomeriella* Betrem, *Campsoscolia* Betrem, *Cathimeris* Betrem, *Guigliana* Betrem, *Micromeriella* Betrem and *Trielis* Saussure, representing the Campsomerinae, and *Scolia* Fabricius representing the Scoliinae. A wide range of families is represented—frequently and widespread Apiaceae, Fabaceae (Mimosoideae) and Asteraceae; often Aizoaceae (Mesembryanthema) and Apocynaceae (Asclepiadaceae); and variously Molluginaceae, Aizoaceae (non-Mesembryanthema), Scrophulariaceae, Asparagaceae (in the east), Zygophyllaceae, Sapotaceae, Boraginaceae, Fabaceae (Papilionoideae), Amaranthaceae, Capparaceae, Solanaceae, Campanulaceae, Ebenaceae, Sterculiaceae (*Hermannia*), Lamiaceae (northwestern Namib fringe) and Proteaceae (in the west).

Family Sapygidae

The Sapygidae is a widespread family that is absent from the Australasian Region and contains about 80 species in two subfamilies (Brothers & Finnamore 1993). They are relatively small, less than a centimetre in length and are mainly black with some pale markings.

Sapygids are nest parasites of other aculeate Hymenoptera, mainly bees of the families Megachilidae and Apidae but also wasps of the vespid subfamily Eumeninae. The egg is laid loose in the cell of the host. The larva feeds upon the host's egg and provision or upon the fully grown larva.

One subfamily, Sapyginae, is represented in southern Africa. Little is known of the biology of southern African species. *Sapyga simillima* Arnold has been reared from a nest of *Heriades* sp. (Megachilidae) (Gess 1981) and an undetermined species of *Sapyga* was reared from nests of *Othinosmia* (*Megaloheriades*) *globicola* (Stadelmann) (Megachilinae, Osmiini) collected 11 km west of Clanwilliam, Western Cape, and in the Goegap Nature Reserve, Namaqualand (Gess & Gess and voucher specimens 1987, 1990, 1992). There appear to be no flower visiting records for Sapygidae.

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Apoidea: Spheciformes

Family Ampulicidae

Ampulicids, commonly called cockroach wasps, occur principally in the tropics of both the Old and the New Worlds. Wojciech Pulawski (2010) lists six genera of which the two largest, *Ampulex* Jurine with 130 species and *Dolichurus* Latreille with 49 species, are represented in the Afrotropical Region. They are small to medium-sized, generally black, metallic blue or metallic green. Two species of *Ampulex* are mutillid mimics, with the head and anterior part of the thorax reddish. Ampulicids are rare in collections probably because they fly little and are generally found walking on the bark of the trees in which they nest or, as with the mutillid mimics, on the ground in which they probably nest.

That the majority of species of *Ampulex* lead an arboreal life is clear from the structure of their 'feet'. The penultimate or fourth tarsomere is equipped with a ventral 'hair mat' but lacks apical setae and the last tarsomere is inserted dorsally near the base of the fourth. Occasionally several are found together on a plant producing a sticky exudate on which the adults feed, for example, males and females of two species were observed under drought conditions feeding at petiolar glands on a castor oil plant, *Ricinus communis* L.

Flower visiting

Very few records are available for flower visitation by *Ampulex*. *Ampulex bantuae* Gess usually drinks nectar from the extrafloral nectaries of *Acacia karroo* Hayne (Fabaceae, Mimosoideae), however, the flowers may also be visited. Other male and female *Ampulex* species have been collected from flowers of *A. karroo* on Hilton and near Colesberg. A single male *A. bantuae* was collected from flowers of *Lasiospermum bipinnatum* (Thunb.) Druce (Asteraceae) on the farm Hilton. Charles Jacot Guillarmod collected a single female *Ampulex* sp. from *Calpurnia glabrata* Brummitt (Fabaceae, Papilionoideae) at Mamathes, Lesotho.

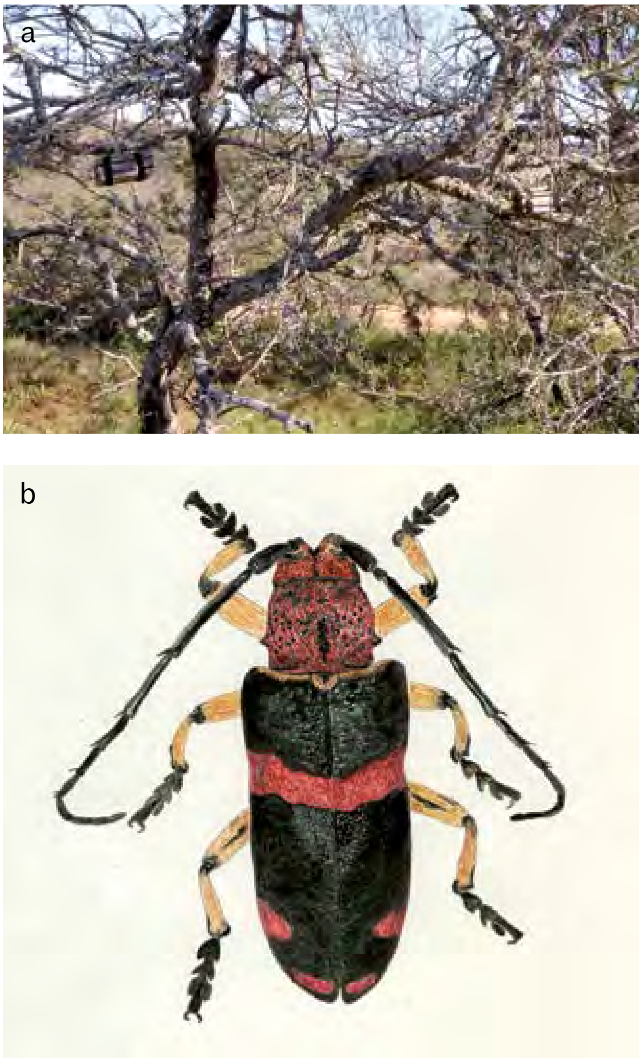
Nesting

Nesting by these wasps is known for relatively few species worldwide. However, from these records it seems that there is a marked interspecific uniformity. Nesting is in pre-existing cavities not modified prior to hunting. Each nest is single-celled and each cell is supplied with a single prey, which is then walled in with debris. The prey, as indicated by the common name and as far as is known, is exclusively cockroaches.

The fullest account of the nesting of a southern African species is that for *Ampulex bantuae* Gess (Gess & Gess 1982b; Gess 1984).

Nest situation

Ampulex bantuae nests in branches of *Acacia karroo* (Figure II.3.1.a) in abandoned borings of the larvae of a longicorn beetle, *Ceroplesis hottentota* (Fabricius) (Figure II.3.1.b). That it is restricted to *Acacia karroo* is suggested by it being found to nest in trap nests suspended in these shrubs but never in trap nests suspended in neighbouring shrubs of other species.



The circumstancial evidence linking *Ampulex mutilloides* Kohl, a mutillid mimic, to a cockroach, *Pilema* sp., which lives in burrows in clayey soil, suggests not all southern African species nest in pre-existing cavities above ground level (Gess 1981).

Nest structure

The nest of *A. bantuae* is single-celled (Figure II.3.1.c). The only building material added to the pre-existing cavity is debris used for constructing the cell closure. No preliminary plug and no closure to the gallery opening are constructed. Occasionally two cells are found in series. However, as no preparation precedes hunting, these represent two separate 'nests' which may have been provisioned by different females.

As a pre-existing cavity is used and as no preliminary plug is constructed, nest construction is confined to nest sealing. After provisioning and oviposition, collection of detritus for the sealing of the nest is undertaken. Each piece of detritus is held with the mandibles and is carried to the nest on foot. Any available detritus is utilised. As it is gathered on and beneath the shrub in which the nest is

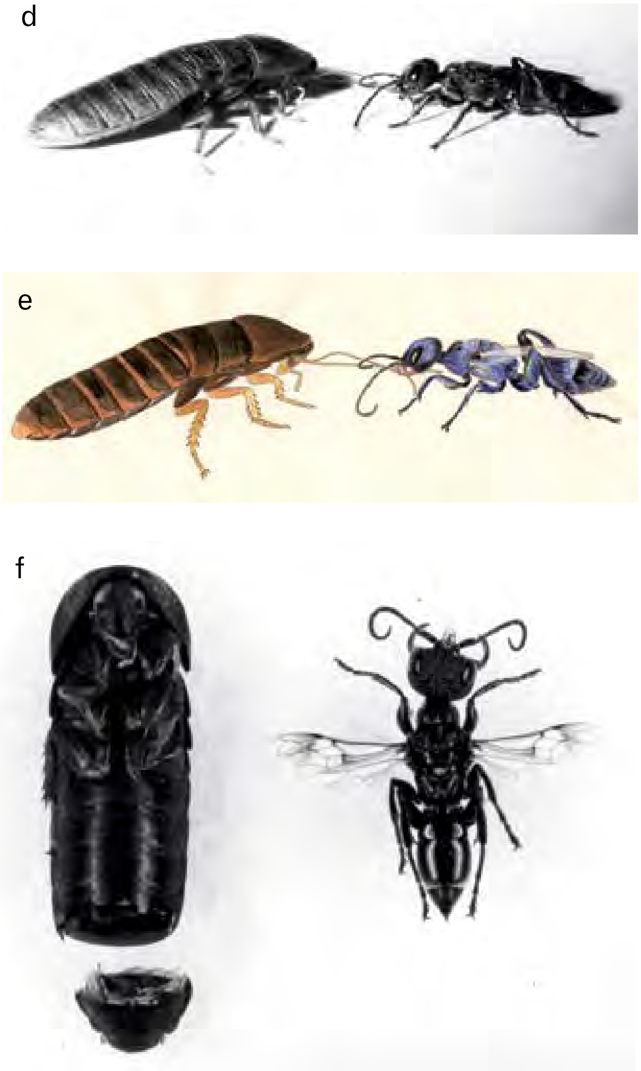


Figure II.3.1.—a.–e. *Ampulex bantuae* Gess: a. nesting site *Acacia karroo* (note bundles of trap nests suspended from branches; b. *Ceroplesis hottentota* (Fabricius) (Cerambycidae); c. provisioned nest in trap nest; d. and e. showing mode of transport of prey cockroach, *Bantua dispar* (Burmeister); f. *B. dispar* after emergence of *A. bantuae* adult.

situated, small pieces of bark, lichen, dry leaflets, seeds, flowers, pieces of exoskeletons of insects, and insect and rodent droppings are included.

Provisioning and oviposition

The cockroach prey, *Bantua dispar* (Burmeister) (Figures II.3.1.f), is restricted to *Acacia karroo.* Other cockroaches collected on *Acacia karroo* offered to captive nesting *A. bantuae* were rejected. *Bantua dispar* feeds exclusively on the gum that exudes from damaged stems of *A. karroo*, the most notable damage being that caused by *C. hottentota*, and shelters under loose bark on dead branches, the cause of death of which is largely attributable to the activities of the beetle. Like most cockroaches *B. dispar* feeds at night.

The wasp hunts on foot, moving hurriedly by fits and starts, twitching her wings, which are held folded over her back. Very noticeable are the antennae, which are held out in front of the head curving out to the sides and are kept in constant motion. A suitable cockroach having been located and, if attempting to escape, pursued, the wasp advances upon it with widely separated mandibles. She lunges forwards and seizes it by the anterior, antero-lateral or lateral margin of the pronotal shield, one mandible positioned above and one below the shield, with the wasp's head held sideways. The wasp then flexes her abdomen forwards to reach the underside of the prey. One or more stings are given. The cockroach, having been stung, immediately stops struggling and lies still. The wasp relinquishes her hold and withdraws to a short distance where she grooms herself. The cockroach recovers somewhat and stands up. The wasp then reaches with her head and mandibles beneath the pronotal shield covering the cockroach's head, takes hold of, and draws out forwards one of the antennae. Taking hold of this antenna near its base, the wasp proceeds to walk backwards leading the cockroach towards the nesting cavity (Figure II.3.1.d & e). The cockroach at the end of its antennal leash walks forwards following the wasp and makes no attempt to resist or escape, even when the wasp occasionally releases her hold in order to run off to inspect the nesting cavity or the way leading to it.

Occasionally a wasp does not lead away her prey immediately upon grasping the antenna, but rather passes the antenna through between her jaws until a point near the end is reached, when the jaws tighten their grip and the wasp proceeds to pull and tug vigorously. The tugging is accompanied by wing buzzing and finally a short length of antenna is severed and discarded. The wasp then imbibes blood from the now slackly held antenna. It should be noted that whereas the cockroach walks forwards when grasped near the base of an antenna, it stands firm when grasped near the tip of the antenna.

On arriving at the nesting cavity, the wasp enters it backwards and continues backing until she reaches the inner

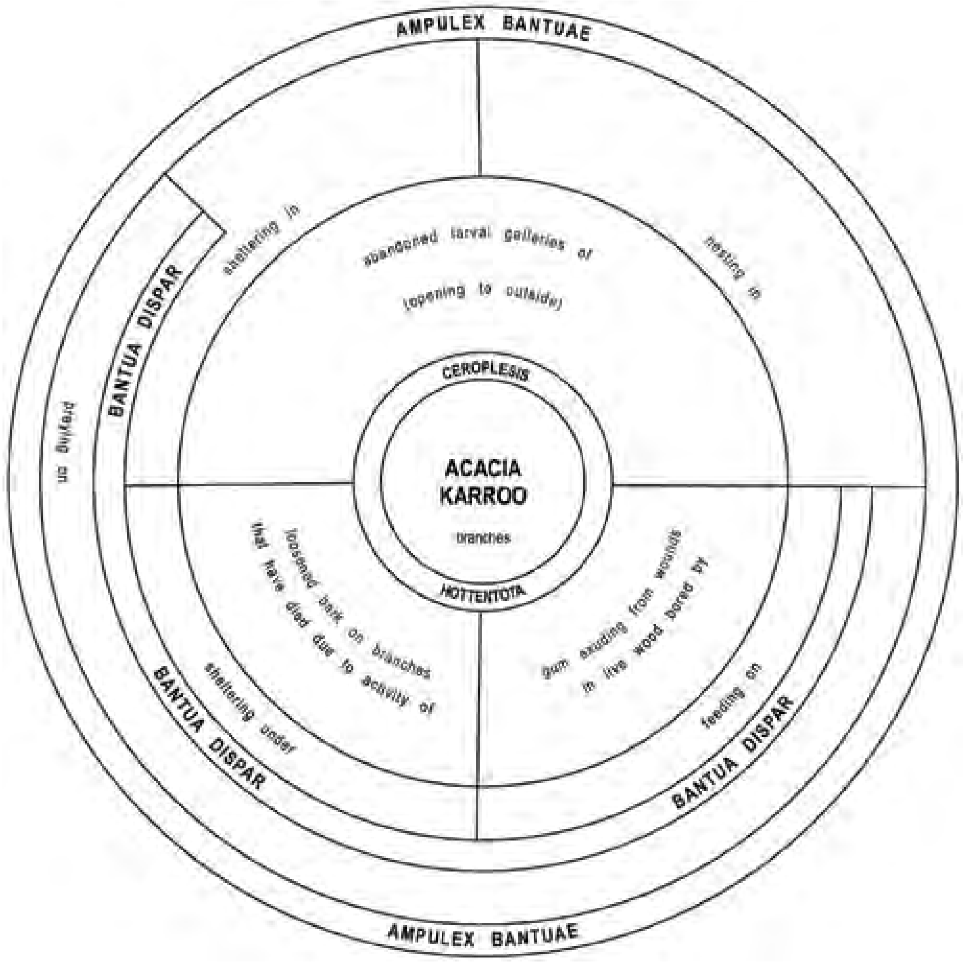


Figure II.3.2.—Diagram showing the structure of the complex of three insect species, *Ceroplesis hottentota* (Fabricius) (Cerambycidae), *Bantua dispar* (Burmeister) (Blattidae) and *Ampulex bantuae* Gess (Ampulicidae) associated with and restricted to the shrub or small tree *Acacia karroo* (Fabaceae, Mimosoideae).

end, all the while drawing the cockroach in after her so that it comes to face the blind end of the cavity. Oviposition upon the prey then takes place. The wasp's abdomen is flexed downwards and forwards and extended under the left side of the cockroach so that the tip is near the base of a metathoracic leg where the egg is attached. Whether a cockroach is positioned on its right or left side is random, however, the egg is more than twice as likely to be laid on the side of the cockroach on which it is lying.

Oviposition completed, the wasp squeezes past the cockroach and emerges from the nest.

Life history

The time from oviposition to egg hatch is three to nine days. Larval feeding commences very close to the position of the anterior end of the egg. When the larva is about 4.5 mm long, it migrates from the exterior feeding position through the hole created by it during feeding and continues its development within the cockroach. The cockroach dies two to six days after the wasp larva entered it. The presence of the *Ampulex bantuae* larva within the cockroach causes its body to be slightly arched, its sterna to be noticeably curved and its legs frequently to be somewhat held away from the body. After the death of the cockroach its exoskeleton dries in this configuration so that in the field dead cockroaches containing *A. bantuae* are easy to recognise.

The mature wasp larva, having eaten out all the soft tissue within the cockroach, spins its cocoon and pupates within the cockroach. The adult *A. bantuae* emerges by cutting off first the end of its cocoon and then the end of the cockroach's abdomen (Figure II.3.1.f).

Ampulex bantuae is bivoltine. The wasps of the non-diapausing generation take a fixed number of days to develop from egg to adult. Those of the diapausing generation, irrespective of how early or how late the eggs are laid, pause in their development at the prepupal stage. Further development takes place in the following summer.

A chain of dependence

The dependence of *A. bantuae* on the plant, *Acacia karroo*, the beetle, *Ceroplesis hottentota*, and the cockroach, *Bantua dispar*, is summarised in Figure II.3.2.

Prey subdual and transport by other Ampulicidae

Not all Ampulicidae subdue and transport their prey in the same manner as *A. bantuae.* This is demonstrated in the

Figure II.3.3.—a and b. *Dolichurus* sp. showing mode of transport of prey cockroach.

photographs (Figure II.3.3.a & b) which show a species of *Dolichurus* dragging a heavily paralysed cockroach positioned on its side (a) and ventral side up (b).

Family Sphecidae

Sphecids are widely distributed throughout the world. Of the nineteen genera recognised (Pulawski 2010) nine—*Ammophila* W. Kirby, *Parapsammophila* Taschenberg and *Podalonia* Fernald (Ammophilinae); *Chlorion* Latreille (Chloriontinae); *Chalybion* Dahlbom and *Sceliphron* Klug (Sceliphrinae); and *Sphex* L., *Isodontia* Patton and *Prionyx* Vander Linden (Sphecinae)—are represented in southern Africa. The mud-dauber, *Sceliphron spirifex* (L.), and the cutworm predator, *Podalonia canescens* (Dahlbom), are probably the most familiar, being very widespread and noticeable around human dwelling places. All have well developed 'wasp waists' and as a result they are sometimes known collectively as thread waisted wasps.

Flower visiting

Flower visiting records are available for 30 species of sphecids representing the nine genera occurring in southern Africa. The flowers visited represented 22 plant families. Although all of the sphecids are polyphagous, the flowers of some plant families attract visits from a higher number of species than others. Plant families and percentage of sphecid species visiting them are as follows: Fabaceae (Mimosoideae), 47%; Apiaceae and Asteraceae, 40% each; Aizoaceae (Mesembryanthema) (never more than occasional except for male *Podalonia canescens* (Dahlbom)), Amaranthaceae and Zygophyllaceae 30% each; Scrophulariaceae (non-gullet flowers) 23%; Acanthaceae, Aizoaceae (non-Mesembryanthema), Asparagaceae, Boraginaceae, Campanulaceae, Celastraceae, Elatinaceae, Euphorbiaceae (extrafloral nectaries), Fabaceae (Papilionoideae), Lamiaceae, Malvaceae, Molluginaceae, Plumbaginaceae (*Limonium*), Proteaceae, Rhamnaceae, Solanaceae, each less than 2%.

Podalonia canescens is highly polyphagous and was recorded from 14 plant families. We have found that males are sometimes present in large numbers indiscriminately visiting whatever nectar source is available. While studying the pollination of *Disa* (Orchidaceae) in the fynbos, southwestern Western Cape, Steiner *et al*. (1994) found *P. canescens* pollinating the non-nectar producing flowers of *Disa atricapilla* (Lindl.). They recorded the wasps exhibiting mate seeking behaviour, suggesting that pollination of these orchids is through sexual deception.

Nesting

Nesting behaviour within the family is wide ranging: no nest construction by *Chlorion*; typically excavation in usually horizontally presented friable soil by *Ammophila*, *Podalonia*, *Prionyx* and *Sphex*; excavation in vertically presented non-friable soil with the aid of water by *Chalybion* (*Hemichalybion*); construction of aerial mud nests by *Sceliphron*; and use of pre- existing cavities by *Chalybion* (*Chalybion*) and *Isodontia*. The nesting of *Parapsammophila* is still unknown, however, its possession of sand rakes suggests that it excavates in friable soil.

A wide range of prey is taken by the family as a whole but within each genus the choice is more limited—crickets by *Chlorion*, short-horned grasshoppers by *Prionyx*, long-horned grasshoppers by *Sphex* and *Isodontia*, caterpillars by *Podalonia* and *Ammophila*, and spiders by *Chalybion* and *Sceliphron*.

Subfamily Ammophilinae

Podalonia Fernald

The genus *Podalonia* is represented in all the major temperate and tropical areas of the world. Of the 66 species recognised (Pulawski 2010), the majority occur in the Mediterranean area and southwestern Asia with only a few species in southern Africa.

Podalonia provision with a single prey, which is hunted before nest excavation, however, the prey is carried away from the site of capture and a burrow terminating in a cell is excavated for its reception. The nesting biology of *P.*

canescens (Dahlbom), the only species of *Podalonia* occurring in semi-arid to arid areas of southern Africa, is typical of that of the genus as a whole. The preferred prey is a caterpillar of the moth family Noctuidae, particularly those caterpillars commonly known as cutworms, which burrow in the ground in the daytime and emerge to feed at night.

Nest situation

Podalonia canescens is an extremely widespread species, which nests in friable soil in a wide variety of situations and vegetation types. In the semi-arid areas it is found in both karroid and fynbos vegetation and amongst coastal dunes. It is also a common insect in gardens.

Nest structure

A simple shallow burrow excavated in friable soil consisting of a sub-vertical to sloping shaft, which, at its lower end, curves sharply to become an almost horizontal cell (Figure II.3.5.a). The shaft above the cell is filled with soil raked into the burrow and compacted by the wasp with, at intervals, the addition of small pebbles.

Figure II.3.4.a and b. *Podalonia canescens* (Dahlbom) with prey caterpillars (Noctuidae).

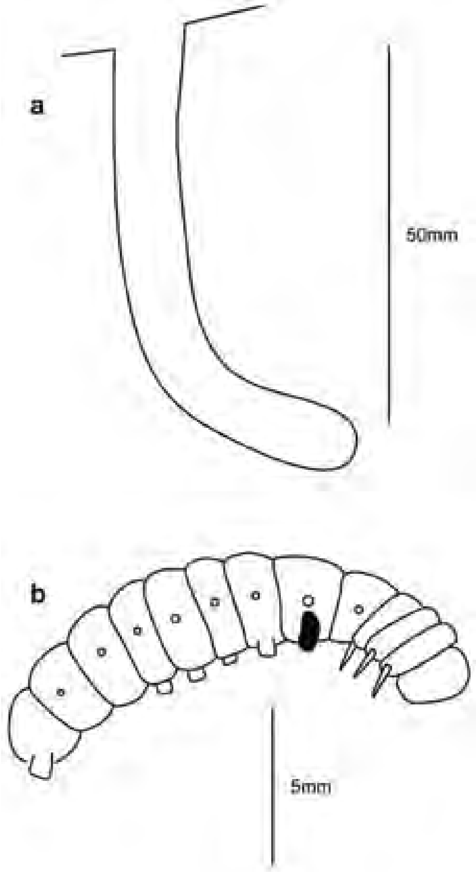


Figure II.3.5.—a and b. *Podalonia canescens* (Dahlbom): a. Diagramatic vertical plan of nest; b. prey caterpillar showing placement of egg.

Provisioning and oviposition

As *P. canescens* hunts in the daytime she must locate her cutworm prey in the ground, to which end she may be seen walking over the ground surface with her antennae in constant motion. After locating a caterpillar, she digs down and pulls it out. The caterpillar is stung several times on the ventral surface, the first sting being in the neck region. The caterpillar is transported to a hiding place, carried beneath the wasp, ventral side up, and facing the direction of travel (Figure II.3.4.a–c).

After the burrow has been excavated the caterpillar is fetched from its hiding place and deposited a short way from the nest, which is inspected before the wasp finally takes the caterpillar into it. The wasp brings the prey to the nest entrance, puts it down, enters the nest, turns around within and, returning to the entrance, draws the caterpillar in, head foremost. Oviposition then takes place. The egg is attached laterally on the first or second abdominal segment (Figure II.3.5.b). The shaft is then filled.

Ammophila W. Kirby

The genus *Ammophila* is widespread throughout the world. Wojciech Pulawski (2010) lists 201 species of which

Figure II.3.6.—a.–c. *Ammophila* spp., showing prey transport: a. *A. beniniensis* (Palisot de Beauvois) with prey (Arctiidae); b. *A. insignis* F. Smith with prey (Noctuidae); c. *A.* sp. with prey, *Achaea lienardi* Boisduval (Noctuidae).

around 18 species have been recorded from southern Africa.

Ammophila species typically nest in friable soil in which is excavated a short shaft ending in a single cell, two-celled nests being exceptional. The prey, which are located above ground in vegetation, are typically caterpillars, however, saw fly larvae and weevil larvae have been recorded. Mass provisioning is most common though 'delayed' mass provisioning has been recorded but is not necessarily constant within a species.

For southern Africa some aspects of the nesting of two species, *A. beniniensis* (Palisot de Beauvois) and *A. ferrugineipes* Lepeletier, are given in Gess (1981). Later we discovered and described the nesting of *A. braunsi* (Turner) in pre-existing cavities (Gess & Gess, field notes and voucher specimens 1983). With the addition of Alan Weaving to the team, further observations were made of these three species and an additional five species: *A. conifera* (Arnold), *A. dolichocephala* Cameron, *A. dolichodera* Kohl, *A. insignis* F.Smith and *A. vulcania* du Buysson (Weaving l984, 1988, 1989a & 1989b) in an intensive comparative study.

Nest situation

Excavation of nests in friable soil is, as for the genus, typical for the southern African species. *Ammophila braunsi* is exceptional in its use of pre-existing cavities in non-friable soil. Most species nest in the open in horizontal ground although some, such as *A. beniniensis*, show a preference for more protected situations amongst vegetation or beneath the canopy of trees, and vertical ground is preferred by *A. insignis*.

Nest structure

The form of the nest is a short vertical to sub-vertical main shaft terminated by a laterally extended cell of greater diameter than that of the shaft (Figure II.3.8.a), the exception, of course, being *A. braunsi* the burrow of which has the form of that of the original excavator.

Method of construction

The spoils of excavation are either removed on foot or flown a short distance from the nest according to species. Those species, which excavate their nests before hunting, construct a temporary seal. Final sealing of the nest is undertaken after oviposition by species, which provision with one prey and after the completion of provisioning by those species provisioning with more than one prey. Typically, a relatively large object such as a pebble, earth clod or item of organic debris is inserted above the provisioned cell. A mixture of earth and clods or other relatively large objects follows this and from time to time the material is compacted, the wasp's buzzing being audible. Earth used for sealing (Figure II.3.10) is gathered from one or more quarry sites. Soil is loosened with the aid of the mandibles and, using widely spread mandibles and front legs, is gathered together and drawn up until it is supported from below by the legs and above by the mandibles and setae on the underside of the head. The shaft opening is generally sealed with a few relatively large items and soil is then added to conceal the opening. The Peckhams (1898) were the first to record some species tamping the soil with a pebble held in the mandibles but this has not been observed for southern African species. Some species has been observed holding a pebble at the nest entrance and vibrating it to compact the fill. In one instance of nest sealing by *A. braunsi*, 175 loads of fill were brought in during the course of completing the final seal—an arduous task! After nest sealing is completed, the wasp takes a break, grooming, resting and feeding at flowers before embarking on the preparation of a new nest.

Provisioning and oviposition

Provisioning generally follows nest excavation and the nest is typically sealed temporarily before the wasp leaves to go hunting. Three species, however, are known to hunt

Figure II.3.7.—a.–c. *Ammophila* spp., showing insertion of prey into burrow: a. *A. insignis* F. Smith with prey (Geometridae); b and c. *A.* sp. with prey *Achaea lienardi* Boisduval (Noctuidae).

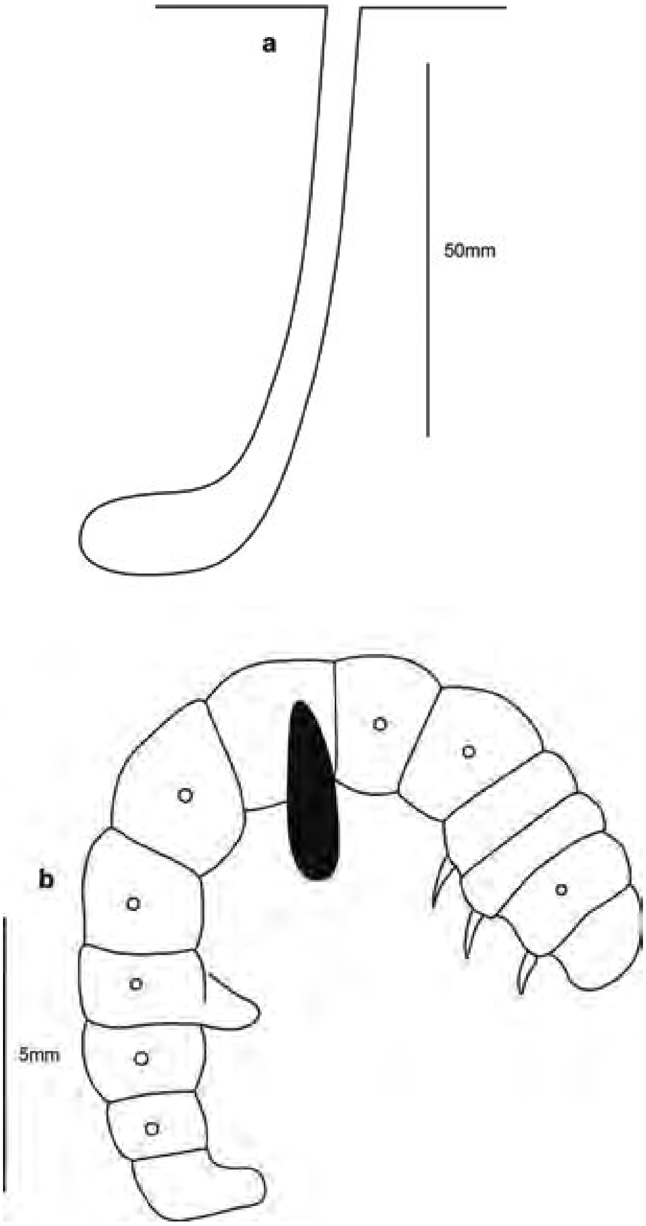


Figure II.3.8.—a. and b. *Ammophila ferrugineipes* Lepeletier: a. Diagrammatic vertical plan of nest; b. prey caterpillar showing placement of egg.

before nest excavation, one of these being a southern African species, *A. dolichodera*. Mass provisioning with a single prey, *A. braunsi*, *A. beniniensis*, *A. dolichodera*, *A. vulcania*, or with more than one prey, *A. insignis* and *A. ferrugineipes*, is most common. 'Delayed' provisioning in which mass provisioning is completed only after the egg has hatched may be practised by *A. ferrugineipes* and this species may also maintain more than one nest at a time. Progressive provisioning has been recorded exceptionally elsewhere in the world and may yet be found to be practised by some southern African species.

Noctuid caterpillars have been recorded as taken by all the southern African species investigated except *A. conifera*, which takes pyralidid and lycaenid caterpillars, the latter also being taken by *A. ferrugineipes*. However, *A. ferrugineipes* and *A. dolichocephala* show a preference for geometrid caterpillars which are also taken by *A. insignis*. Furthermore, *A. dolichocephala* takes mainly 'hairy' arctiid and lasiocampid caterpillars which it 'shaves'. The differences in prey selection have been shown by Alan Weaving to result from an interaction between hunting habitat, the size and the provisioning strategy of the wasp, the abundance of and, apparently, stage of development of the prey. Of interest, with respect to the location of the prey, is the response by hunting *Ammophila* to the presence of caterpillar frass.

Figure II.3.9.—Prey caterpillar (Noctuidae) of *Ammophila braunsi* (Turner) showing placement of egg (extracted from nest).

Figure II.3.10.—*Ammophila ferrugineipes* Lepeletier carrying earth for sealing nest.

We were able to observe clearly the capture, subdual and transport of a caterpillar by *A. braunsi* nesting in an area of sparse dwarf karroid vegetation. At first contact, the caterpillar lashed out at the wasp with the 'front' of its body. The wasp initially withdrew and then, taking her chance, advanced upon the caterpillar causing it to fall to the ground, the caterpillar defecating at the same time. The wasp then grasped the caterpillar with her mandibles firmly clamped in the neck region dorsally and bending her abdomen around to beneath the caterpillar, whilst straddling it, stung it in the neck region. She relinquished the caterpillar and then taking hold of it again and straddling it, stung it repeatedly working from head end to tail end, holding the caterpillar with her mandibles and her front pair of legs and standing on her middle and hind legs. With each sting or group of stings, she shifted her grip to a position between the segments forward of the sting point. When the last sting had been applied, the wasp moved to the anterior end, chewed the caterpillar and began malaxating, her abdomen pointing straight up into the air.

In transporting the caterpillar, the wasp straddled it and held it with her mandibles clasped just behind the last pair of legs, the caterpillar being now venter up and facing the direction of travel. The caterpillar was taken to a temporary hiding place in a low bush where it was left whilst the wasp removed the temporary seal from the nest entrance. She then fetched the caterpillar and transported it to the nest entrance where she put it down with its head facing the nest entrance, entered the nest, came out, backed in and drew the caterpillar in after her. The caterpillar was positioned head downwards.

The mode of holding the caterpillar for transport seems to be typical for the genus (Figure II.3.6.). Progression is on foot when the prey taken is large, however, small prey taken by species provisioning with several prey are frequently transported in flight. When arriving at the opened nest not all species enter the nest first and then draw in the caterpillar. Some species enter still holding the prey (Figure II.3.7).

During oviposition the egg is most usually positioned laterally on one of the anterior abdominal segments (Figure II.3.8b & 9). When the provision consists of more than one prey, oviposition is onto the first prey.

Figure II.3.11.—*Parapsammophila consobrina* (Arnold) visiting flowers of *Petalidium lanatum* (Engl) C.B.Clarke (Acanthaceae).

Associates

Dasylabroides caffra (Kohl) (Mutillidae) was reared by Weaving from nests of *A. ferrugineipes* and *A. insignis.*

Parapsammophila Taschenberg

As noted above, the nesting of *Parapsammophila* (Figure II.3.11) is still unknown, however, its possession of sand rakes suggests that it excavates in friable soil.

Subfamily Chloriontinae

Chlorion Latreille

Of the genus *Chlorion*, for which 20 species are recognised (Pulawski 2010), only one species, *C. maxillosum* (Poiret) (Figure II.3.12), is known to occur in southern Africa, where it is recorded from the Northern Cape north into Namibia and from north of the Vaal River and down the east coast of Zululand.

Figure II.3.12.—*Chlorion maxillosum* (Poiret).

The nesting biology of very few species of *Chlorion* is known. A New World species, *C. aerarium* Patton, excavates nests and provisions its cells with a number of prey (Peckham & Peckham 1900). However, the Old World species, of which the biology is known and of which *C. maxillosum* (Poiret) is an example, exhibit behaviour similar to that of the scoliids. A single prey is used for provisioning a larva and this prey is not transported to a nesting cavity or a nest excavated by the wasp, development of the wasp taking place in the prey's own burrow. Its prey is large crickets of the genus *Brachytrypes—B. megacephalus* Lefebre in North Africa and *B. membranaceus* Drury in eastern and southern Africa.

The prey crickets live in burrows in the soil. They emerge at night, when they cut off plants and drag them down into their burrows. In the daytime, the occupied burrows are indicated by small mounds of loose earth under which the burrow entrances are found. These crickets may become very numerous and a serious pest of crop plants. In 1933 a local outbreak of *B. membranaceus* in tobacco seed beds in Zimbabwe (then Southern Rhodesia) was controlled by *C. maxillosum* (Jack 1936), which would indicate that this wasp may also become relatively numerous.

The most complete account of its nesting behaviour was given by Valdeyron-Fabre (1955, as quoted by Bohart & Menke 1976) who observed its nesting in Tunisia.

Provisioning and oviposition

Valdeyron-Fabre (1955) noted that the wasp usually dug a tunnel which intersected that of the cricket so that its attack on the crickets could be made from the rear. In some cases, the cricket escaped or was chased out of the burrow. Stinging and egg laying then took place above ground. The wasp grasped the cricket's thorax from behind holding it with its remarkably long mandibles and stung the cricket on the venter near the hind legs, immobilising it. A second sting was administered under the neck and a third on the body, the position being variable. An egg was attached to the pleural region of the first abdominal segment. In a few minutes, the cricket revived and dug a fresh burrow.

Life history

The cricket dies during the course of the wasp's larval development but is not completely consumed. Pupation takes place within the cricket's burrow.

Subfamily Sphecinae

Prionyx Vander Linden

Prionyx is widespread throughout the world. Of the 59 species recognised (Pulawski 2010) around seven occur in the Afrotropical Region. At least one of these, *P. kirbii* (Vander Linden) has a remarkably wide distribution having been recorded from South Africa to Spain and eastwards to China.

The prey of *Prionyx* seems to be exclusively grasshoppers (Acrididae). The majority of species for which nesting is known consistently provision a cell with one grasshopper; others, however, provision with one or more grasshoppers depending upon size. The burrow is either excavated before or after hunting according to species. Some of those species that hunt after nest excavation make multicellular nests but the number of cells per nest is always small. A South American species, *P. spinolae* (F. Smith), is remarkable in that the cells are constructed serially.

Three species of *Prionyx* have been recorded as preying upon and following locust swarms in Africa. In December 1896, during a locust outbreak, Hans Brauns noted that *Prionyx inda* (L.) (as *Sphex englebergi* Brauns) appeared together with locust swarms at Zwartkops, near Port Elizabeth, Eastern Cape (Brauns 1899). Within a few hours, the ground was covered 'sieve-like' with the nest entrances of the wasps. In 1924, George Arnold reported that the same species (as *Chlorion* (*Harpactopus*) *tyrannum* Smith) appeared at Sawmills in Zimbabwe together with swarms of migratory locusts on which it preyed (Arnold 1928).

Following this, *Prionyx crudelis* (F. Smith) (as *Sphex aegyptius* Lepeletier) was observed preying upon swarms of desert locusts, *Schistocera gregaria* Forskål, in East Africa (Williams 1933; Haskell 1955). Then in November 1986, Dick Brown discovered *Prionyx subfuscatus* (Dahlbom) associated with swarms of the brown locust, *Locustana pardalina* (Walker), in the Karoo in the Hopetown, Douglas and Colesberg areas, Northern Cape. The hoppers were being captured not uncommonly by the wasp (pers. comm., voucher specimens of the wasp, submitted by Dick Brown for determination, and its prey in the Albany Museum). Previously *P. subfuscatus* had not been recorded from as far south.

It seems that the only detailed published account of the nesting of *Prionyx* in southern Africa is that for *P. kirbii* (Vander Linden) (Gess 1981; Gess & Gess fieldnotes and voucher specimens 1971). The nesting of this species was previously studied in southern Europe (Ferton 1902; Guido Grandi 1961) and in North Africa (Roth 1925).

Prionyx kirbii (Vander Linden)

Nest situation

In the Eastern Cape Province, we observed *P. kirbii* in association with a sandpit in which it may well have been nesting in the manner described by Charles Ferton (1902), Guido Grandi (1961) and Roth (1925). However, we found it more commonly in association with non-friable soil where it was nesting in pre-existing cavities, as many as nine or more of these wasps being seen actively nesting in close proximity on any one day (Gess & Gess fieldnotes and voucher specimens 1977). The pre-existing cavities were the abandoned burrows of *Aethiopicodynerus insignis* (de Saussure). This species thus exhibits considerable plasticity in its behaviour with respect to the choice of a nesting site and the manner in which a nest is prepared for the reception of the prey.

Nest structure

Generally, nests are one-celled, however, Charles Ferton (1902) recorded one two-celled nest.

Method of construction

A female nesting in a pre-existing burrow, having selected a burrow, proceeds to clear it out, entering head forwards and backing out carrying earth particles or old pellets in her mandibles. She drops them at a distance of 30–45 mm from the nest opening. The direction of emergence varies with each load so that a ring of earth and debris with an inner diameter of about 60 mm and an outer diameter of about 90 mm develops around the opening. The direction of emergence is, however, purely random with no indication of a rotational pattern. This ring is very noticeable on the hard clayey soil making it possible to spot and identify a nest of this wasp without difficulty (Figure II.3.13). The manner in which the spoils of cavity cleaning are removed is comparable with the manner in which excavation by this species in friable soil is performed. Cavity cleaning therefore represents token nest excavation.

The burrow, having been cleaned out, a temporary closure is made. The wasp searches for a piece of debris, for example a stone, clod of earth, sheep dropping or stick, which is large enough not to fall down the hole when placed over it or wedged just inside the opening. In the former case, additional pieces are added to partially close and at least break the outline of the hole and in the latter, some of the excavated earth is raked into the opening until it is no longer visible.

After the completion of provisioning and oviposition, the nest is sealed. The wasp rakes all the loose earth previously extracted from the burrow back into it. Whilst doing so, she faces away from the nest entrance and sweeps the sand towards it with rapid backward movements of the tarsal rakes. She also collects mud pellets, earth clods and debris from further afield and packs them into the shaft 'buzzing' to consolidate the fill.

Provisioning and oviposition

The acridids recorded as prey in the Eastern Cape were species of *Acrotylus*, *Aiolopus*, *Anaeolopus* and *Calliptamulus* (example Figure I.3.40.c). Capture and subduing of the prey was not observed. However, a grasshopper procured is straddled by the wasp, which holds it near the base of an antenna facing forwards and dorsum up, and proceeds forwards with a hopping motion. Having come to the ring of earth, the wasp leaves the prey and flies up and to the nest opening which she inspects and from which she removes the temporary closure. She then fetches the prey and brings it to the burrow entrance putting it down facing the opening. She enters backwards and, taking the grasshopper by an antenna, draws it into the burrow.

Figure II.3.13.—*Prionyx kirbii* (Vander Linden), nest entrance with circle of discarded earth and debris.

The grasshopper is positioned at the bottom of the burrow, head down or slightly obliquely, venter up, one or two prey being provided per cell. When two grasshoppers are supplied they may either be positioned side by side or one above the other, presumably depending upon size. Oviposition takes place onto a grasshopper, the egg being attached to the membrane just dorsal to the coxa of a metathoracic leg.

Sphex L.

Sphex is a large cosmopolitan genus with 118 species (Pulawski 2010), around 28 of which occur in the Afrotropical Region. They are relatively large wasps mostly with black bodies and with fuscous or golden wings.

The nesting biology of those species studied shows considerable uniformity. Burrows, usually multicellular, are excavated in friable soil. The prey is long-horned grasshoppers. Nesting is gregarious, typically in open areas, less typically under shelter.

Nesting accounts are available for two Afrotropical species, *Sphex decipiens* Kohl (Gess & Gess fieldnotes and voucher specimens 1985/1986 and 1986/1987) and *Sphex tomentosus* Fabricius (Weaving 1990).

Nesting situation

The nesting sites of *S. decipiens*, which were on the farm Clifton to the northwest of Grahamstown, were on the flat top of an almost bare earthen bank, the de-structured clay of which was friable (Figure II.3.14). Those of *S. tomentosus*, which were at Fanies Island on the shores of Lake St Lucia, were in bare patches of deep, loosely compacted sand in the camping ground and hutted camp grounds shaded by trees or buildings.

Though the use of abandoned burrows of other wasps and the practice of nest sharing has not been observed for *S. decipiens* or *S. tomentosus*, both behaviours are known for *S. ichneumoneus* (L.) in North America (Brockmann *et al.* 1979; Brockmann & Dawkins 1979). These observations are of interest when considered in conjunction with the nesting of *Prionyx kirbii* in abandoned *Aethiopicodynerus insignis* burrows and of *Bembix bubalus* Handlirsch practising nest sharing.

Nest structure

The nest is a multicellular burrow in friable soil, the main shaft gently sloping for a short distance before descending sub-vertically with few to many lateral shafts each ending in a cell (Figure II.3.15). Nests of *S. tomentosus* were associated with one or two accessory burrows. Such accessory burrows have been recorded for *S. argentatus* Fabricius (Tsuneki 1963).

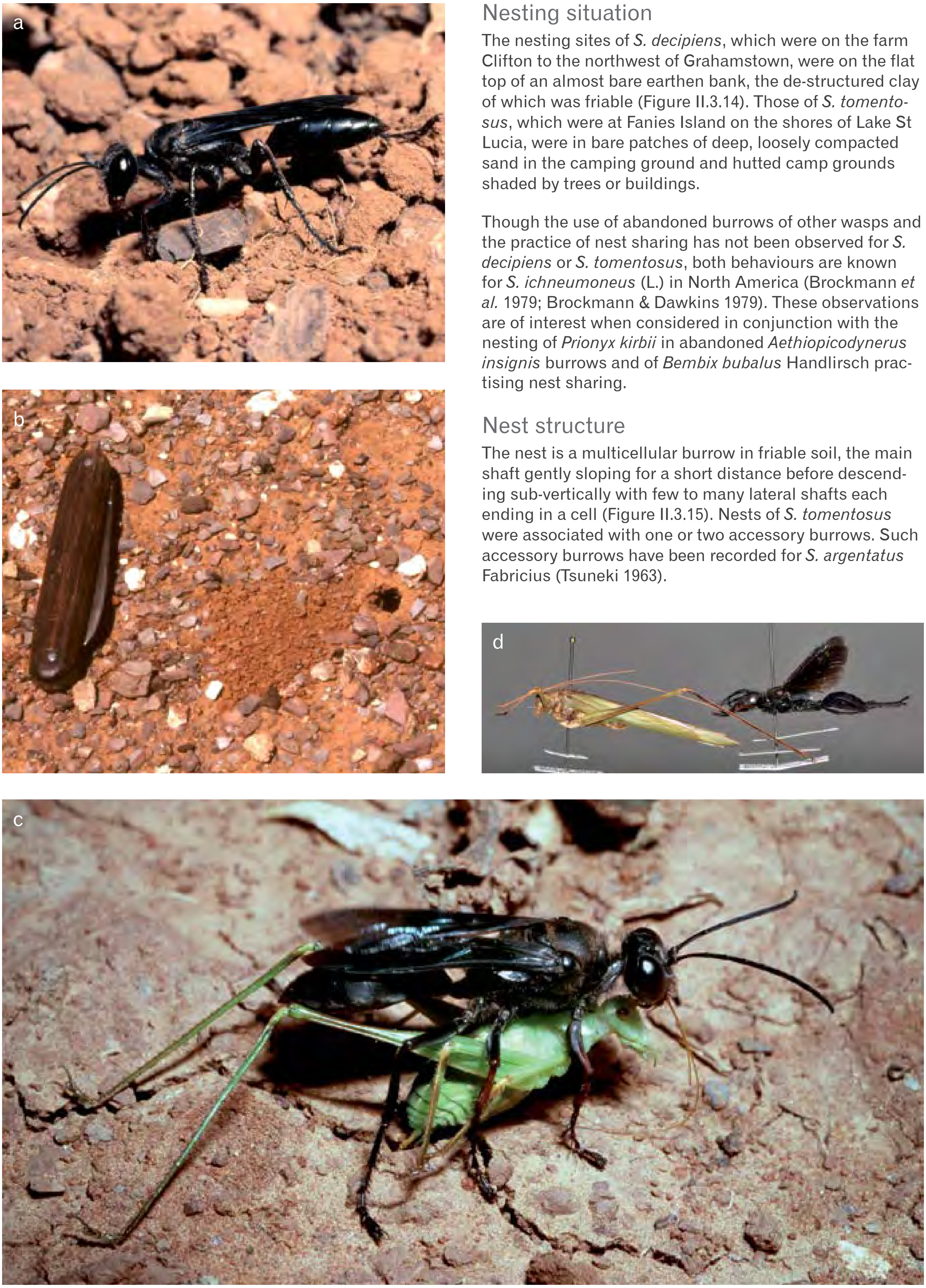


Figure II.3.14.—a.–d. *Sphex decipiens* Kohl: a. female at nest entrance; b. nest entrance; c. transporting prey (Tettigoniidae); d. with prey *Phaneroptera* sp. (actual length of wasp 27.5 mm).

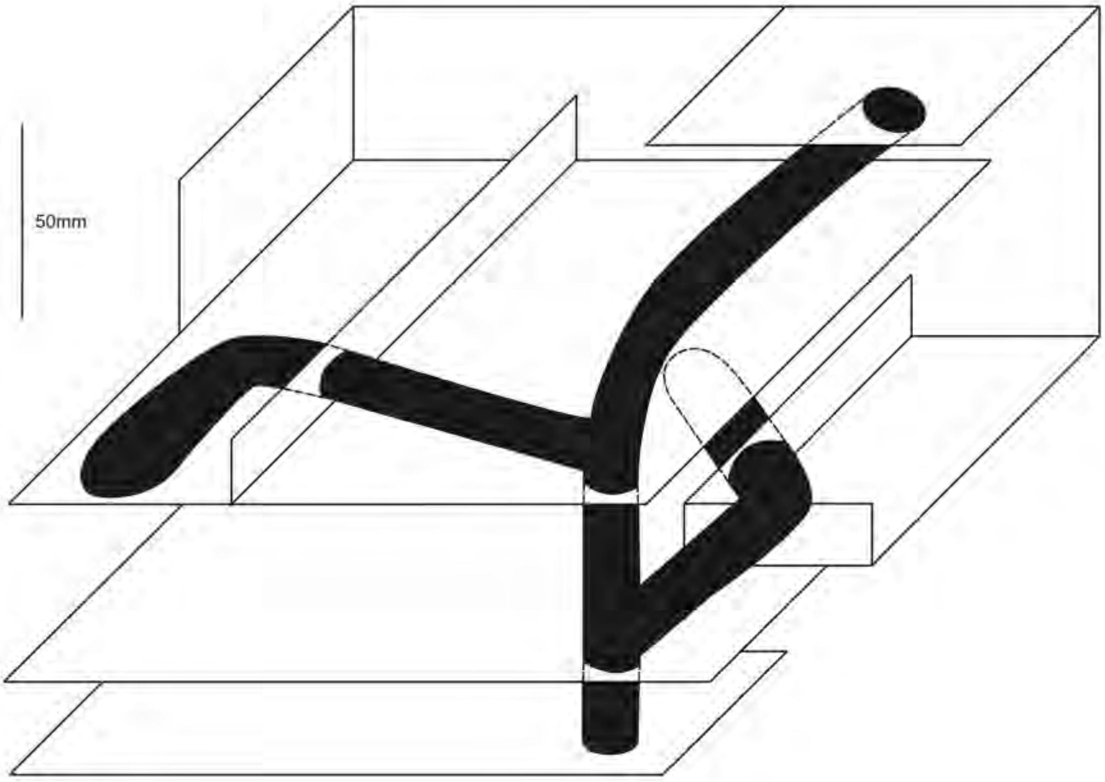


Figure II.3.15.—*Sphex decipiens* Kohl, diagrammatic vertical plan of nest.

Method of excavation

When excavating a nest, *S. decipiens* loosened the earth by buzzing. The spoils of excavation, loose earth and earth clods, were carried out clamped between the femora and tibiae of the forelegs below the mandibles and underside of the head above. A wasp, walking backwards, regularly deposited her load 70–100 mm from the nest in a fixed direction so that a tumulus developed to one side of the entrance (Figure II.3.14.a and 16.a & b). After the excavation of a cell 100–300 mm below the ground surface, the wasp left the nest to go hunting. No temporary closure was made. At the end of each working day a temporary closure was made. This is at variance with the behaviour of *S. tomentosus*, which always made a temporary closure before an absence from the nest. Such behavioural variation between species is not unusual for *Sphex* (Bohart & Menke 1976).

Several cells may be excavated per nest by both species. After completion of a nest, the shafts were filled with the soil extracted from the burrow during excavation. At intervals, *S. decipiens* was heard buzzing, whilst it compacted the soil. When the nest entrance was reached, it could be seen that whilst she was buzzing she was holding a pebble on the ground surface with her mandibles so that her vibrations pass through it to the soil beneath. The remainder of the soil was raked into a loose pile over the nest entrance so that sealed nests were recognisable by the pile of soil covering them.

Provisioning and oviposition

The prey of both species is long-horned grasshoppers, katydids (Tettigoniidae). Species of *Odontura* and *Phaneroptera* (Figure I.3.45.d) were recorded as prey of *S. decipiens*, and *Terpnistria zebrata* (Serville), *Eurycorypha* sp. and *Phaneroptera* sp. of *S. tomentosus*. After capture and subduing a grasshopper, it is carried to the nesting area in flight or on foot, depending on its size (Figures II.3.14.c. and II.3.16.c). On the ground both species were observed to hold the prey in similar fashion, dorsum up, facing the direction of travel with the mandibles gripping the antennae near the bases. In flight *S. decipiens* was seen to be holding her prey in a similar fashion except that, whereas on the ground *S. tomentosus* was seen to hold the prey with her front legs around the neck, in flight *S. decipiens* was seen to support it with her front legs around the thorax. When flying with prey, *S. decipiens* either flew straight to the nest entrance and entered rapidly without hesitation or alighted on the ground near the nest and carried the prey to the nest on foot. Sometimes the prey was deposited next to the nest entrance, the wasp entering first, turning around and drawing the prey in after her or else first bringing out earth that had fallen into the nest before drawing in the prey. Depending upon the size of the prey, the number per cell varied, up to six per cell was recorded for *S. decipiens* and three to eight for *S. tomentosus*.
The prey of *S. decipiens* were generally positioned head inwards but exceptionally facing outwards. The position of the prey of *S. tomentosus* was not recorded.

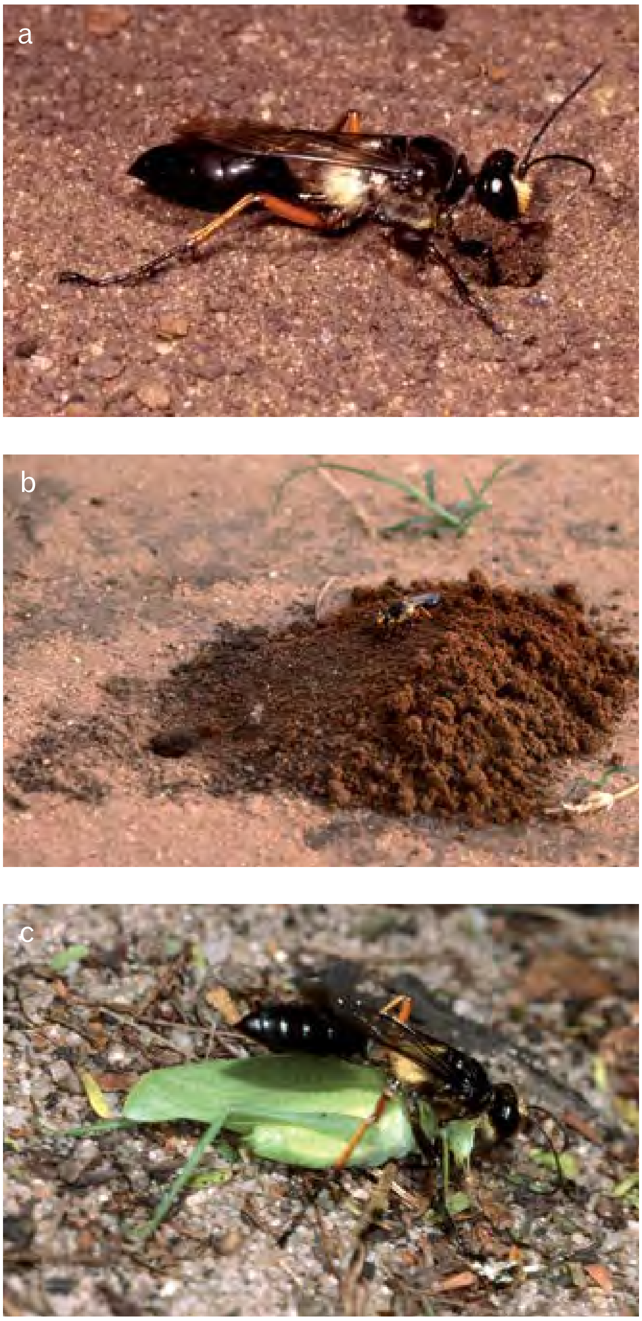


Figure II.3.16.—a.–c. *Sphex tomentosus* Fabricius: a. female at nest entrance; b. on nest entrance tumulus; c. transporting prey (Tettigoniidae).

The cells were mass provisioned. Oviposition was onto the first prey to be introduced into a cell. The egg is positioned ventrally between the fore and mid pairs of coxae.

Isodontia Patton

Of the 61 described species of *Isodontia* (Pulawski 2010), nesting has been described for around 14 species including the three southern African species, *I. pelopoeiformis* (Dahlbom), *I. stanleyi* (Kohl) and *I. simoni* (du Buysson). Our account of the nesting of these three species (Gess & Gess 1982a) is the most comprehensive. However, it is predated by an account of the nesting of *I. pelopoeiformis* (Smithers 1958 as *Sphex* (*Isodontia*) *pelopoeiformis* (Dahlbom)).

Nest situation

The nesting sites chosen by *I. pelopoeiformis* and *I. stanleyi* like those of all of the other species, other than *I. simoni*, for which nesting has been recorded are situated above ground. Insect borings such as those of carpenter bees and beetle larvae are selected, however, trap nests suspended in shrubs and trees and even such unlikely cavities such as metal pipes are readily accepted. As far as we know, *I. simoni* is the only species known to nest in cavities in horizontal ground. The burrows selected in the Eastern Cape where this species was studied all appear to be those of a cockroach *Pilema thoracica* (Walker).

Nest structure

The nests consist of a number of serially arranged cells each sealed with a plug, the series frequently being preceded by a preliminary plug and always being succeeded by a closing plug, which completely fills the space between the last cell and the nest entrance (Figure II.3.17–19). The materials from which the plugs are constructed are in each species of two types. In nests of *I. simoni* and *I. pelopoeiformis* the materials are:

a. Clods of earth with, in the case of *I. pelopoeiformis*, the addition of debris collected off the ground including pieces of stick, bark, vetch burs, insect remains and small mammal droppings.

b. Plant 'fluff'.

The preliminary plug in nests of *I. simoni* is a thin layer of material 'b' and, where present, in the nests of *I. pelopoeiformis* is of either or both materials in distinct layers. The cell partitions in nests of *I. simoni* are constructed of materials 'a' with an admixture of a little of material 'b'. However, those of *I. pelopoeiformis* are constructed almost exclusively from material 'b'. Plant 'fluff' used by *P. pelopoeiformis* on the farm Hilton, Grahamstown was derived from fruiting inflorescences of various Asteraceae. The closing plug in the single completed nest of *I. simoni* found consisted of material 'b' sealed at the ground surface with a thin layer of wet dung. The closing plugs of nests of *I. pelopoeiformis* are constructed in two distinct layers, the first of 'a' and the second of 'b'. Exceptionally, when material 'b' is in short supply, lengths of very soft grass leaf blades or dry *Acacia* flowers are used as a substitute by *I. pelopoeiformis* in the construction of cell partitions. It may, however, be omitted from the nest closure.

The materials from which the plugs in nests of *I. stanleyi* are constructed are:

a. Short lengths of grass blades (Figure II.3.18.f).

b. Longer lengths cut from grass inflorescences including lengths of unbranched culm and the branched portions including the flower heads (Figure II.3.18.e).

The cell partitions are constructed from material 'a' transversely arranged. The preliminary plug and the inner part of the closing plug are constructed from material 'b' transversely coiled and the outer part of the closing plug from material 'b' arranged longitudinally, the stems lying parallel, and projecting from the nest entrance. Grasses used on Hilton were *Karroochloa curva* (Nees) Conert & Türpe (as *Danthonia curva*), *Leptochloa fusca* (L.) Knuth (as *Diplachne fusca*), *Eragrostis* sp, *Melica racemosa* Thunb. and *Sporobolus* sp.

Method of construction

The female collects material for the construction of plugs with her mandibles. She holds them in her mandibles as she flies to her nest. In all three species, whilst the nesting female is compacting the materials, buzzing sounds can be heard within the nest.

When a cell has been prepared for the reception of prey, a temporary closure is constructed from loosely packed material, fluff in the case of *I. simoni* and *I. pelopoeiformis* and grass in the case of *I. stanleyi*, through which the wasp will pass on entering and leaving the cell during provisioning. Hunting is then commenced.

After the full provision for a cell has been supplied the cell is closed. *I. simoni* seals the cell with compacted clods of earth mixed with a little fluff, leaving the temporary closure intact. However, *I. pelopoeiformis* and *I. stanleyi* close their cells by compacting the material, which formed the temporary closure, and adding to this further material of the same nature. In these two species, if a further cell is to be provisioned, a new temporary closure is constructed.

Provisioning and oviposition

A prey katydid is captured, subdued by stinging and its antennae are pruned. The wasp then holds it with her mandibles and legs, and flies with it held beneath her, head forwards and dorsum uppermost. Having arrived at the nest entrance, *I. pelopoeiformis* puts down the prey within the entrance, enters, turns around and pulls the prey in towards her. *Isodontia pelopoeiformis* and *I. stanleyi* position prey in the cell so that they face the inner end and lie on their backs or on one side. Oviposition is usually on the first prey but may be on the second. *I. simoni* takes very small prey in relation to the diameter of a cell and positions them so that they lie across the cell.

The number of prey per cell varies according to the size of the prey.

In a sample of 111 cells of *I. pelopoeiformis* the range was 1–10, 5 being most frequent. Prey identity appears to be affected by the wasps hunting whatever species of katydids

Figure II.3.17.—a and b. *Isodontia pelopoeiformis* (Dahlbom): a. female at entrance to nest in reed trap nest; b. four nests in wooden trap nests.

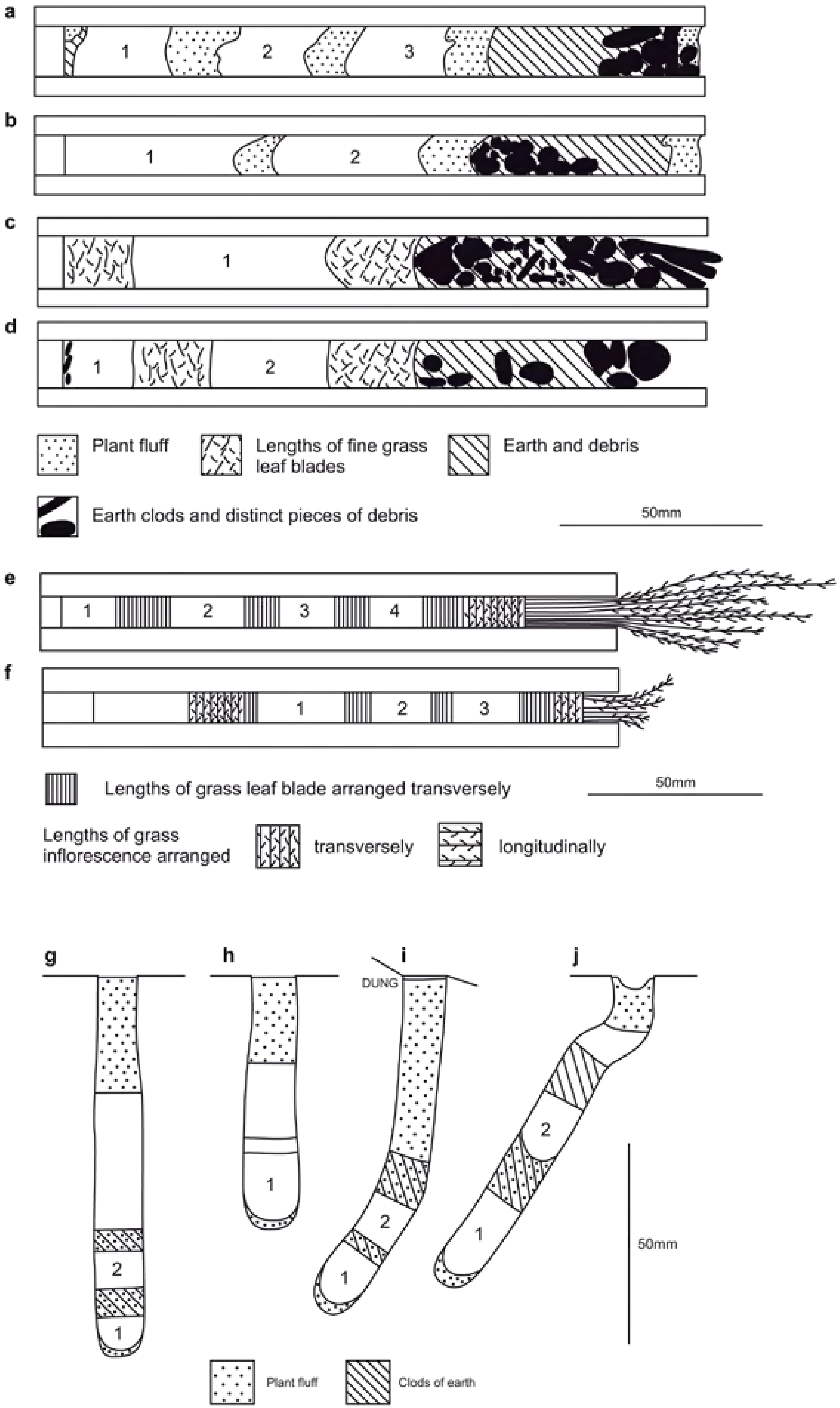


Figure II.3.18.—a.–j. *Isodontia*, diagrammatic plans of nests: a.–d. *I. pelopoeiformis* (Dahlbom); e. and f. *I. stanleyi* (Kohl); g.–j. *I. simoni* (du Buysson).

are common in the immediate vicinity of the nest. Thus 372 of a total of 377 prey katydids in 83 cells constructed by *I. pelopoeiformis* in trapnests suspended from *Acacia karroo* Hayne in thorn scrub, were nymphs of *Terpnistria zebrata* (Serville) (Figure I.3.45.c), whereas only two of a total of 179 katydids in 37 cells constructed in trap nests suspended from *Gymnosporia linearis* (L.f.) (as *Maytenus linearis*) and *Rhus lancea* L.f. in the riverine bush were of this species. In the riverine bush *Eurycorypha prasinata* Stal (Figure I.3.45.a) (all nymphs with one exception) and *Phaneroptera* species (Figure I.3.45.b) (nymphs and adults) constituted the prey commonly used for provisioning.

Sheltering

During the period of nest construction, when nesting activities ceased for the day and during unfavourable weather, females of *I. stanleyi* shelter in the nest. However, despite the large number of *I. pelopoeiformis* nests examined, females of this species were never found sheltering in their nests.

Associates

One species of cuckoo wasp, *Chrysis* sp. *succincta* group, was reared from nests of *I. pelopoeiformis* and *I. stanleyi* (Weaving 1995).

One species of velvet ant, Mutillidae, *Antennotilla* species was reared from a nest of *I. pelopoeiformis* (Weaving 1995).

Alan Weaving reared a single female leucospid, *Leucospis fuelleborniana* Enderlein, from a nest in a trap nest and collected four females in association with nests in trap nests at Lake Sibaya, KwaZulu-Natal (voucher specimens 1991 in the Albany Museum).

Subfamily Sceliphrinae

Chalybion Dahlbom

Wojciech Pulawski (2010) lists 45 species of *Chalybion*, most of which are Old World species. Two sub-genera are recognised, *Chalybion* and *Hemichalybion*.

The nesting of three species has been studied in the Afrotropical Region, *Chalybion* (*Chalybion*) *tibiale* (Fabricius) (Gess & Gess 1980b), *Chalybion* (*Chalybion*) *laevigatum* (Kohl) and *Chalybion* (*Hemichalybion*) *spinolae* (Lepeletier) (Gess 1981; Gess *et al.* I982). The two species of *C.* (*Chalybion*) nest in pre-existing cavities and the species of *C.* (*Hemichalybion*) in self-excavated burrows in vertical banks. All three are mud users, *C.* (*C.*) *tibiale* and *C.* (*H.*) *spinolae*, and therefore most probably *C.* (*C.*) *laevigatum*, are water carriers and mix mud at a quarry site. The mud is used for lining or modifying the inner end of the cavity and for cell sealing. All provision with spiders. The two species of *C.* (*Chalybion*), as is characteristic for the subgenus, apply a layer of lime or uric acid from animal faeces to the outer surface of their mud seals.

Chalybion (*Chalybion*) *tibiale* (Fabricius)

Nest situation

Pre-existing cavities used by *C.* (*C.*) *tibiale* include galleries in woody stems of shrubs and trees and in wooden structures, crevices in vertical earthen banks and masonry walls and abandoned nests of other wasps (Figure II.3.20.a). The present account is based on nests in trapnests (Figure II.3.21). Those used by *C.* (*C.*) *tibiale* had been tied horizontally at heights of 100–1 300 mm above

Figure II.3.19.—a. and b. *Isodontia stanleyi* (Kohl): a. nest in abandoned burrow of *Xylocopa sicheli* Vachal (Apidae, Xylocopinae). b. nest in wooden trap nest.

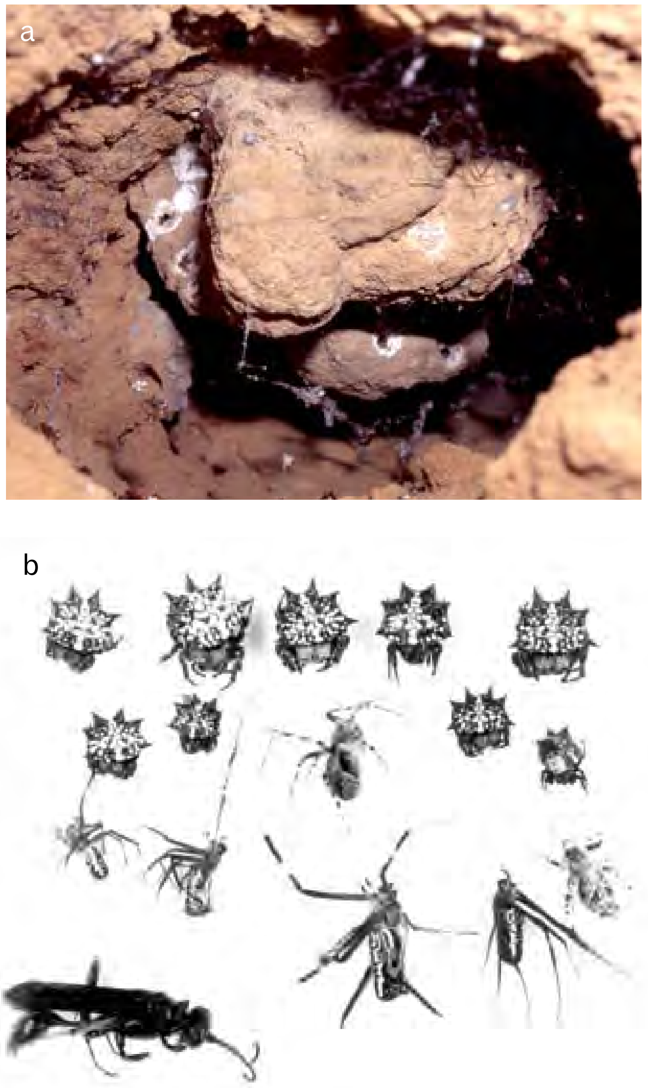


Figure II.3.20.—a. and b. *Chalybion* (*Chalybion*) *tibiale* (Fabricius): a. showing 'whitewashed' closure of cell in abandoned nest of *Sceliphron spirifex* (L.); b. female with prey extracted from nest cell.

ground to a dead tree stump in thick riverine bush in a karroid area to the northwest of Grahamstown and those used by *C.* (*C.*) *laevigatum* in bushes and trees up to 1.8 m above the ground in coastal forest on the KwaZulu-Natal north coast.

Nest structure and method of construction

Nesting is initiated by the introduction into a selected cavity of mud with which the wasp constructs a preliminary plug. This may be applied to the blind inner end of the cavity or may take the form of a 2 mm thick partition constructed some distance from it. In either case, the preliminary plug forms the smooth inner end wall of what will be the first of a number of cells arranged in linear series along the length of the cavity. The preliminary plug, like all subsequently constructed cell partitions, is dished (i.e. the inner surface towards the blind inner end of the cavity is concave). This dishing of the cell partitions, the result of their being constructed from their outer side, is common to many tube nesting wasps.

Construction of the preliminary plug is followed by hunting for prey.

After completion of the provisioning of a cell it is sealed with a mud plug and the outer concave surface is whitewashed with a substance believed to be composed of uric acid obtained by the wasp from bird droppings. Provisioning of a second cell then commences and the sequence is repeated until the cavity is filled or nearly filled with cells after which a final closure is constructed (Figure II.3.20.a).

Provisioning and oviposition

The prey was immature and adult spiders of both sexes, predominantly orb web spiders, Araneidae (= Argiopidae) (*Araneus*, *Argiope*, *Caerostris*, *Cyclosa*, *Isoxya* and *Nephila*), though Theridiidae and Zodariidae were also taken (Figure II.3.20.b).

The number of spiders constituting the provision of a single cell varied from 14–34. Female producing eggs were supplied with a greater mass of provision than were male producing eggs. The egg was attached to the base of the abdomen of a spider, in all instances a species of *Araneus*. This was remarkable as in three of the cells this spider was the only one of this genus present and in the fourth cell, it was one of only two. It would appear that in provisioning the wasp made a special effort to obtain an individual of *Araneus* sp. on which to oviposit and, having done so in an early stage of cell provisioning, continued to provision with a variety of other species. Possibly *Araneus* was preferred for oviposition due to its having a thin soft abdominal integument easy for a newly hatched larva to puncture and penetrate at the commencement of feeding. *Isoxya circtatricosa*, the most common prey species, by contrast, has a very hard exoskeleton.

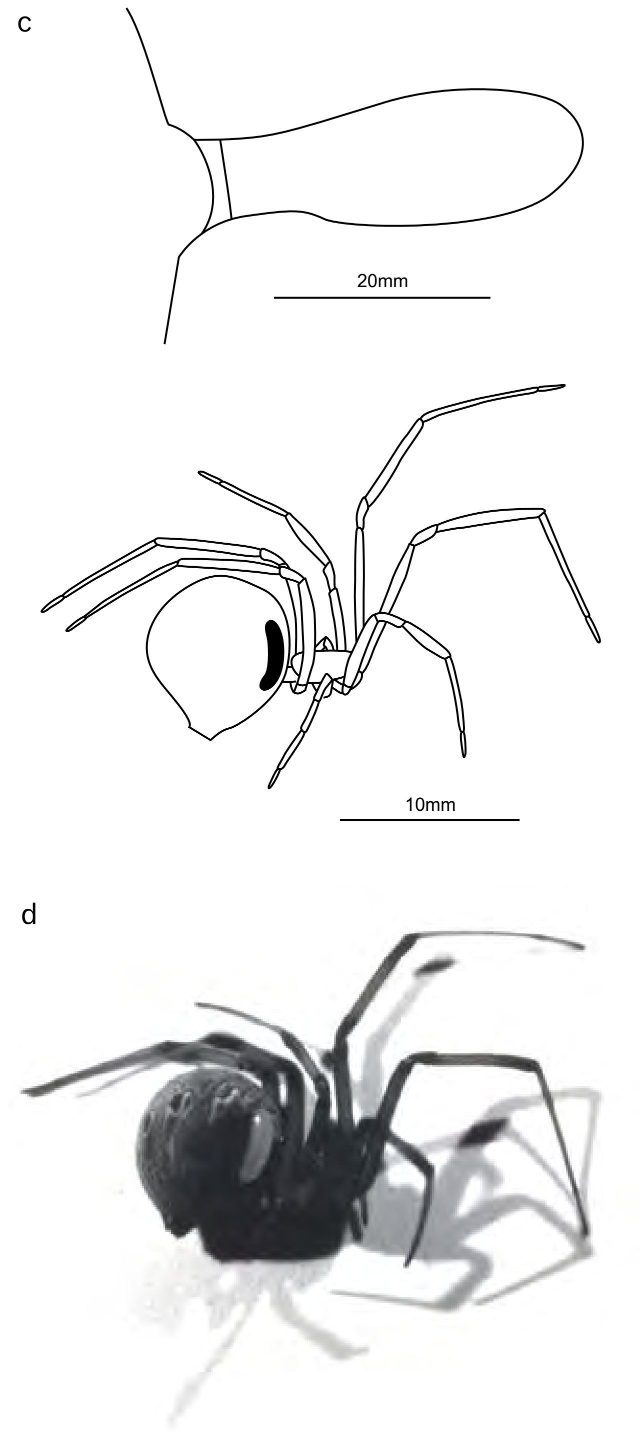


Figure II.3.21.—a.–d. *Chalybion* (*Hemichalybion*) *spinolae* (Lepeletier): a. imbibing water; b. opened nest showing cell and provision; c. diagrammatic vertical plan of nest; d. prey spider *Latrodectus geometricus* (Theriidae) with egg of wasp.

Associates

One species of cuckoo wasp, Chrysididae, *Chrysis* sp. *wahlbergi* group has been reared from nests of *C.* (*C.*) *laevigatum* (Weaving 1994; 1995).

One species of velvet ant, Mutillidae, *Stenomutilla syrinx* (Péringuey) has been reared from nests of *C.* (*C.*) *laevigatum* (Weaving 1994, 1995).

Chalybion (*Hemichalybion*) *spinolae* (Lepeletier)

Apparently unusual for sphecids is excavation of nests in non-friable soil with the aid of water. *Chalybion* (*Hemichalybion*) *spinolae* (Lepeletier) nests in such a manner in vertical banks. It is in appearance very much like the large showy slender waisted yellow and black mud-dauber *Sceliphron spirifex* (L.) so familiar around human dwellings. It can be best distinguished in flight by its bluish lustre and the dark tips to its wings, the dark portions of *S. spirifex* being pure black and the tips of the wings clear. The similarity in its appearance to that of *S. spirifex* led to its being erroneously reported to construct aerial mud nests (Arnold 1928; Van der Vecht 1961) and to the suggestion that it may use empty *S. spirifex* nests (Bohart & Menke 1976).

Nest situation

Nesting was studied on the farm Hilton and the neighbouring farm Broadfields northwest of Grahamstown in the Eastern Cape Province. Nesting sites were in vertical banks of compacted to silicified alluvial sand, both cut in the excavation of building sand and naturally cut by river action. Nests form groups, a single female excavating several nests in close proximity.

Nest structure

The burrow consists of a short, slightly upwardly inclined burrow terminating in a single ovoid cell (Figure II.3.21.b & c).

Method of construction

Water is used in nest excavation and is fetched by the wasp and carried in her crop. After the completion of burrow excavation, the cell is lined with mud mixed at a quarry site close to the burrow entrance. Application of mud to the surface of the excavated cell is aided by vibrations produced by the manipulation of the flight mechanisms and transmitted through the mandibles and is accompanied by a buzzing sound.

After provisioning the cell, the wasp flies off to collect water for sealing the nest. Mud for this purpose is mixed in a new quarry, which like the first, formed by extraction of material for lining the cell, is close to the nest entrance. The cell itself is not sealed nor the entrance passage filled, However, the entrance to the nest is sealed with a mud plug. Pellets for the construction of this seal are laid down spirally. After closing the nest entrance, more pellets are added to thicken the plug which, however, when complete is somewhat concave.

Once a nest has been completed, the wasp begins another that may be closely associated with the first, for example within the second quarry. In such a case, the distance between the two nests may be less than 10 mm.

Provisioning and oviposition

After completing the cell lining, the wasp flies off in search of her prey leaving the nest open. The prey recorded are all button spiders, *Latrodectus indistinctus* O.P. Cambridge (as *mactans* (Fabricius)) and *Latrodectus* *geometricus* C.L. Koch. A spider, having been captured and stung, is carried to the nest in flight held beneath the wasp, orientated dorsum up and facing the direction of travel. The mandibles grip the spider at the anterior end and the front legs support it from below. Within the cell, the spiders are positioned on their backs or sides, facing the inner end of the cell. Oviposition must take place on one of the spiders during its positioning within the cell because, during provisioning, the wasp enters the nest only when carrying prey. The spider chosen for oviposition is always a relatively large one though not necessarily the largest. The egg is attached medially on one side of the anterior part of the spider's abdomen (Figure II.3.21.d). Either side may be chosen.

Sceliphron Klug

The genus *Sceliphron* is found in all of the temperate and tropical continental areas of the world and on many islands. Thirty-five species are recognised (Pulawski 2010) of which around four species occur in southern Africa. Of the species occurring in southern Africa, the most common and widespread is *Sceliphron spirifex* (L.), which is also found in southern Europe, southwest Asia, throughout Africa and on the Canary and Cape Verde Islands.

Sceliphron are characterised by a long petiole, black body and the legs of most species are banded with yellow. All build aerial nests constructed from moist mud or, less commonly, dung and all mass provision with small spiders.

Nest situation

The nests of *Sceliphron spirifex* (L.) are the best known as this species builds its nests in sheltered situations, which include human habitations (Figure II.3.22). The nests of *S. quartinae* (Gribodo) and *S. fossuliferum* (Gribodo) are more cryptic, as they are built on plant stems.

Nest structure

The nests of *S. spirifex* are robust and consist of several relatively thick-walled mud cells, elongate and contiguous, covered with a substantial mud envelope.

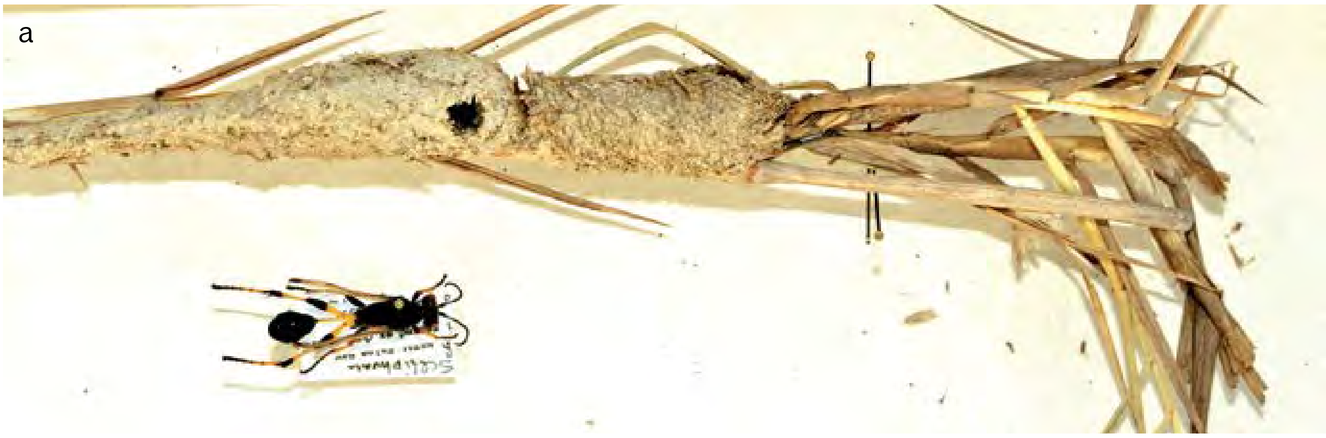
Those of *S. quartinae* and *S. fossuliferum* are relatively delicate, the cells, which are constructed respectively from mud and dung, are arranged end to end attached to a plant stem.

Method of nest construction

Sceliphron spirifex is commonly seen collecting mud near the edge of water. The mud is laid down in such a way that the cells, rounded at the inner end, are characteristically ribbed, the ribs being at an acute angle to the longitudinal axis of the cell (Figure II.3.22). A cell, having been completed, is provisioned and after oviposition sealed with a transverse mud plug with a flat inner and outer surface that extends to just within the lip of the cell. Successive cells are constructed parallel to each other, usually in two to three layers. On average, around 12 cells are constructed per nest. In some large nests, additional cells are sometimes constructed at right angles to the original group so that their openings are at 90° to each other. On completion of cell construction, a mud envelope is added.

Figure II.3.22.—a.–c. *Sceliphron spirifex* (L.): a. female on nest, holding mud pellet; b. female using mud for nest construction; c. spider prey from nest cell.

The mud loads used by *S. quartinae* are laid down in a similar fashion to that employed by *S. spirifex* such that the cell is clearly ribbed, however, the walls are relatively thin. The cells of *S. fossuliferum* are constructed from dung containing plant fibres and consequently are not smooth, nor are the walls ribbed in appearance. Both species con-



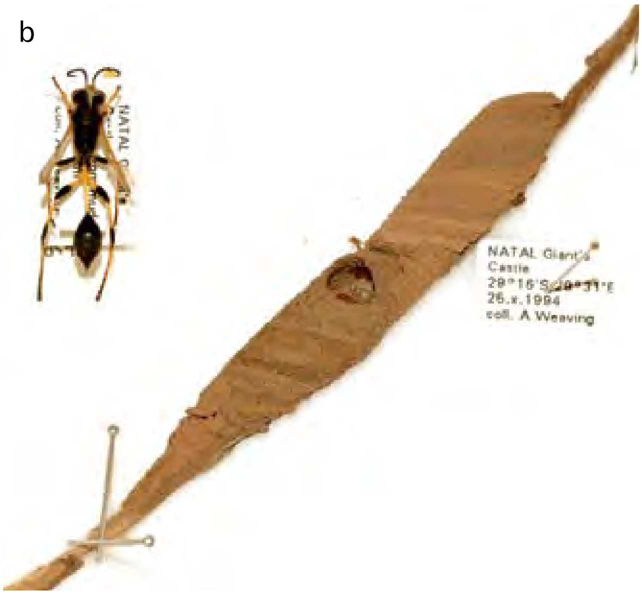


Figure II.3.23.—a. *Sceliphron fossuliferum* (Gribodo) with nest; b. *Sceliphron quartinae* (Gribodo) with nest.

struct their cells in a single vertical row end to end and do not cover them with an envelope (Figure II.3.23).

Provisioning and oviposition

Sceliphron hunt small spiders, which they transport to the nest in flight. A large number of individuals are therefore required to fully provision each cell (Figure II.3.22.c). Oviposition is onto one of the last spiders added to the provision.

Associates

Two cuckoo wasps, Chrysididae, *Chrysis lincea* Fabricius and *Chrysis* sp. *wahlbergi* group, were reared from the nests of *S. spirifex* (Weaving 1995).

Three velvet ants, Mutillidae, have been reared from nests of *S. spirifex*. These are *Dolichomutilla minor* Bischoff (Krombein & Walkley 1962), *Dolichomutilla sycorax* (Smith) (Péringuey 1898 as *Mutilla sycorax* (? *guineensis*) and *Pelopaeus spirifex*) and *Stenomutilla syrinx* (Péringuey) (Weaving 1995).

A frequent parasite of *Sceliphron spirifex* in the Eastern Cape is its mimic *Osprynchotus violator* (Thunberg) (Ichneumonidae) (Figure II.3.24).

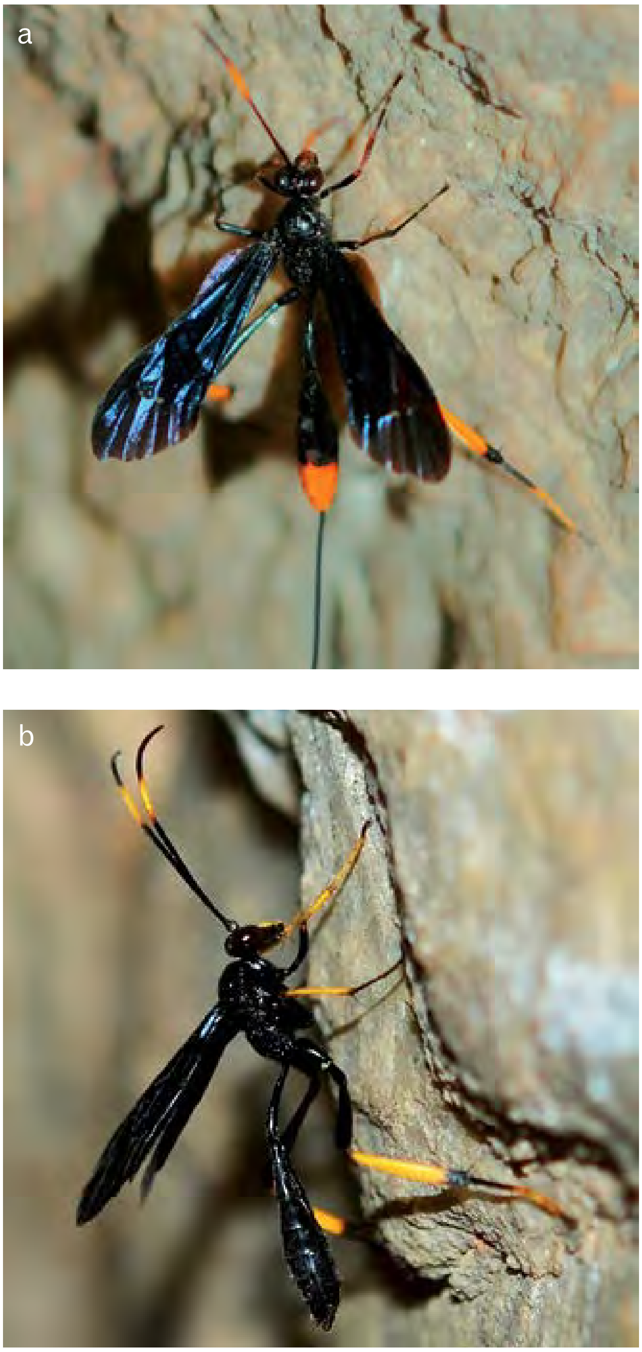


Figure II.3.24.—a. and b. *Osprynchotus violator* (Thunberg): a. female; b. male.

Family Crabronidae

The family Crabronidae is by far the most diverse of the spheciform families with 8 724 species in 240 genera recognised (Pulawski 2010).

Due to the diversity, prey, flowers visited and nesting are here addressed under the subfamily headings.

Subfamily Astatinae

Four genera of Astatinae, including 153 species, are recognised (Pulawski 2010). Three genera, *Astata* Latreille represented by about five species, and *Diploplectron* W. Fox and *Dryudella* Spinola, apparently each represented by a single species, occur in southern Africa. All those species for which nesting has been recorded excavate nests in sandy soil and provision with bugs (Hemiptera) of various families. It was observed that *Astata fuscistigma* Cameron nest in compact sand at the base of a bank on the farm Hilton near Grahamstown in the Eastern Cape and it was noted that *Dryudella flavoundata* (Arnold) was present in a sandpit (Gess 1981).

Flower visiting

On Hilton, we on no occasion encountered any Astatinae visiting flowers. However, in southern Namibia we found *Astata fuscistigma* visiting Aizoaceae (non-Mesembryanthema) in the east and Apiaceae in the west. A range of typical 'wasp flowers' can be expected based on flower visiting records for *Astata* assembled by Wojciech Pulawski (2010) which include: Apiaceae for Hungary; Euphorbiaceae, Zygophyllaceae and Brassicaceae (formerly Capparaceae) for North America; Euphorbiaceae, Polygonaceae and Tamaricaceae for Kazakhstan; and Asteraceae for Italy.

Subfamily Bembicinae

The subfamily Bembicinae, commonly known as sand wasps, is currently (Pulawski 2010) constituted of 79 genera divided between three tribes, Alyssontini, Bembicini and Nyssonini. Of these genera, 18 are represented in the Afrotropical Region. The knowledge of the behaviour of the sand wasps was recently reviewed by Evans & O'Neill (2007).

Flower visiting

For southern Africa, we have assembled flower visiting records for 46 species in nine genera, *Bembix* Fabricius (13), *Afrogorytes* Menke (1), *Ammatomus* A. Costa (2), *Hoplisoides* Gribodo (1), *Handlirschia* Kohl (1), *Kohlia* Handlirsch (1), *Bembecinus* A. Costa (18), *Stizus* Latreille (6) and *Stizoides* Guérin-Méneville (3), visiting 17 families of plants. The flowers most favoured based on the percentage of species visiting them are Apiaceae and Asteraceae (each 39%), Amaranthaceae (37%), Zygophyllaceae (26%) and Aizoaceae (Mesembryanthema and non-Mesembryanthema) (24%). Also visited, each by fewer than 2% of the species, are Molluginaceae, Nyctaginaceae, Celastraceae, Fabaceae (Papilionoideae), Fabaceae (Mimosoideae), Euphorbiaceae (extrafloral nectaries), Rhamnaceae, Boraginaceae, Vahliaceae, Apocynaceae (Asclepiadaceae), Acanthaceae and Scrophulariaceae (small non-gullet flowers). Amongst the families visited by a small number of species are those which are visited abundantly by some genera of sand wasps, for example, Apocynaceae (Asclepiadaceae) was on occasion receiving many visits from species of *Bembix* and *Stizus*, which carry pollinia after visiting these flowers (Figure II.3.33).

Tribe Alyssontini

Alyssontini are rarely collected and poorly known. Apparently, only one of the three genera, *Didineis* Wesmael, is represented in the Afrotropical Region where it has been recorded from Kenya but none appears to have been recorded from southern Africa.

Nesting by all genera seems to be in self-excavated, multicellular burrows in friable soil with the prey taken being Homoptera.

Tribe Bembicini

The tribe Bembicini *sensu* Pulawski (2010), is constituted of 62 genera divided into six subtribes Bembicina, Exeirina, Gorytina, Handlirschiina, Heliocausina and Stizina, all but two (Exeirina and Heliocausina) being represented in the Afrotropical Region.

Subtribe Bembicina

Of the 17 genera listed for Bembicina, all but *Bembix* are strictly New World genera. *Bembix* is, by contrast, cosmopolitan and is well represented in the Afrotropical Region including southern Africa.

Bembix Fabricius

Bembix, with 346 species recognised (Pulawski 2010), is by far the most species rich of the Bembicinae. It is most diverse in the Afrotropical and Australian Regions, however, only about 43 species have been recorded from southern Africa.

All species of *Bembix* for which nesting has been described excavate multicellular sloping burrows in friable soil. *Bembix* typically prey on flies (Diptera) of various families. Unusual for the Afrotropical Region is *Bembix regnata* Parker which was found by Benson (1934) provisioning with butterflies (Lepidoptera) of three families in East Africa. That it cannot be assumed that the prey are necessarily flies, is supported by the findings of Evans & Mathews (1973, 1975) that there is considerable radiation with respect to prey taken by Australian *Bembix*. Of the 22 species studied, 14 took only flies, however, one took damselflies (Odonata) in addition to flies, one bees and wasps in addition to flies, three only bees, principally stingless bees of the genus *Trigona* (Apidae), one only tiphiid wasps, one only damselflies and yet another only antlions (Neuroptera). Species hunting flies seem to show little selection with respect to fly family, the qualifying criteria being apparently size and habitat.

The knowledge of the nesting of *Bembix* in southern Africa is based on investigations of the nests of five species. Four species, *B. albofasciata* Smith, *B. cameronis* Handlirsch, *B. melanopa* Handlirsch, *B. sibilans* Handlirsch were ob-

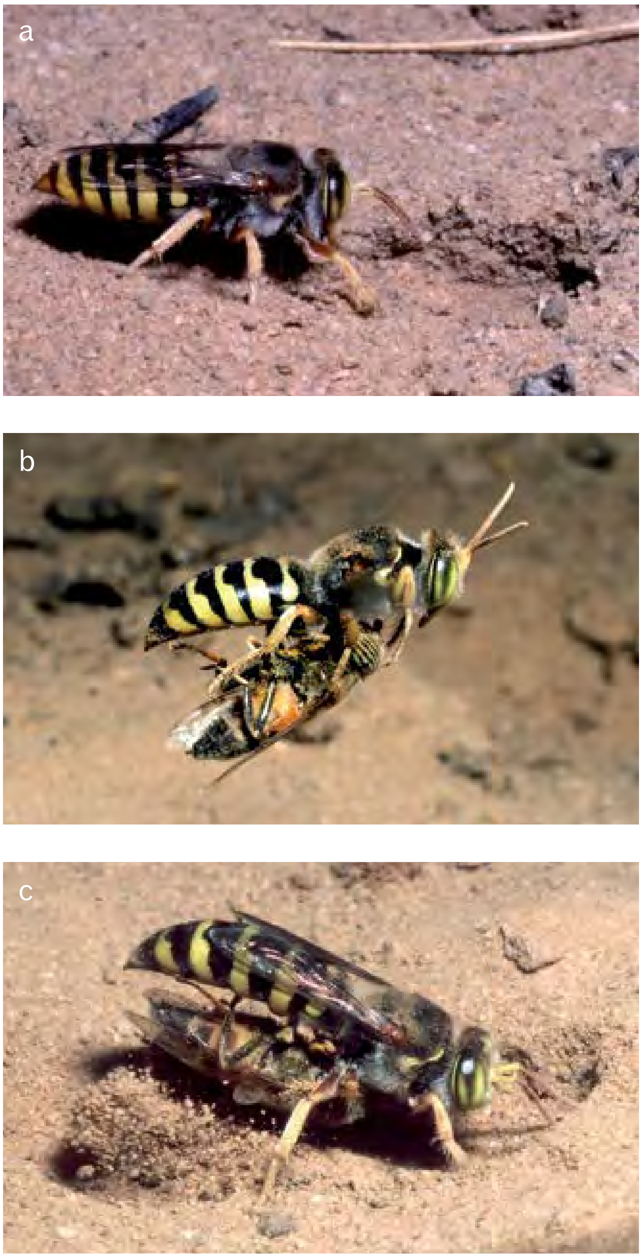


Figure II.3.25.—a.–e. *Bembix bubalus* Handlirsch: a. at nest entrance; b. carrying prey in flight (Syrphidae); c. opening nest whilst holding prey (Syrphidae); d. opening nest whilst holding prey (Bombyliidae); e. at opened nest about to enter with prey (Bombyliidae).

served in karroid areas in the vicinity of Grahamstown on the farms Hilton and Slaaikraal (Gess 1986). Observations of *B. bubalus* Handlirsch in the Little Karoo in the vicinity of Oudtshoorn were also made (Gess & Gess 1989).

Nest situation

All nests excavated were excavated in friable soil. In addition to the five species listed above, which are associated principally with alluvial sand flanking watercourses, either horizontal or sloping, *B. arnoldi* Arnold and *B. fraudulenta* Arnold were collected on coastal foredunes in the Eastern Cape, where the former was observed excavating into the side of a dune.

Nest structure

The nests, typical for the genus, are single to multicellular burrows with a short entrance burrow dipping down to end in a spur and giving rise, just above the spur, to a secondary shaft ending in a large ovoid cell. Succeeding lateral burrows lead off from the shaft, each slightly above the one preceding it (Figure II.3.26). No spur was found in the nests of *B. sibilans.*

Method of construction of nest

Nests of all but *B. bubalus* were found singly or in small groups. Those of *B. bubalus* were in an aggregation of a thousand or more.

The nests were excavated in the usual *Bembix* manner. That is, the two forelegs, equipped with sand rakes, are repeatedly swept back in unison whilst the abdomen is synchronously raised and lowered allowing the soil to be shot out behind the wasp. The spoils of excavation are drawn back some little distance from the nest entrance where they accumulate to form a tumulus. The nest is temporarily sealed with sand when the builder is away or within the nest but not actively working.

Provisioning and oviposition

Bembix hunt their prey on the wing. They tend to find a good source of flies, often decaying organic matter such as faeces and corpses, in the case of *B. arnoldi* ocean wrack, but also flowers. Having found a good source of flies they return to it repeatedly. Fly prey has been recorded for 18 species of Afrotropical *Bembix* namely, *B. albofasciata* Smith, *B. arnoldi* Arnold, *B. bequaerti dira* Arnold, *B. braunsii* Handlirsch, *B. bubalus* Handlirsch, *B.*

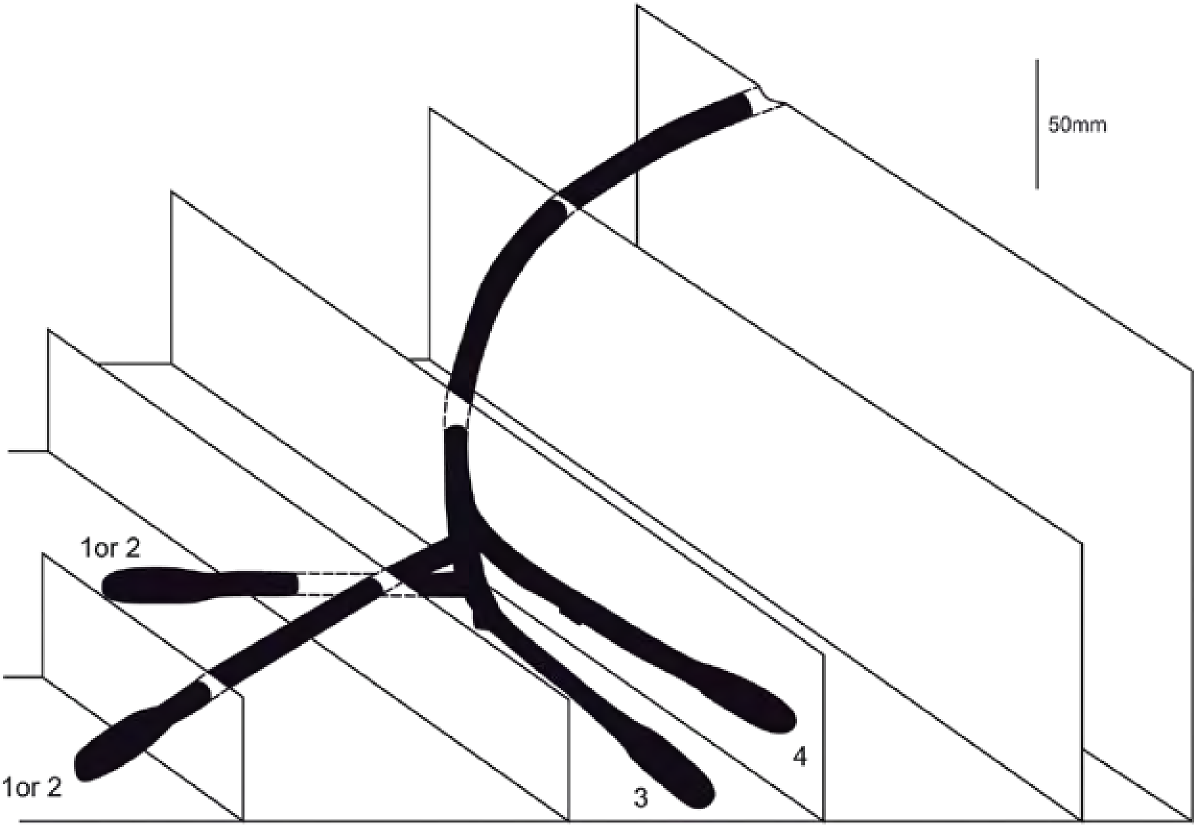


Figure II.3.26.—Diagrammatic vertical plan of nest of *Bembix bubalus* Handlirsch.

cameronis Handlirsch, *B. capensis* Lepeletier, *B. capicola* Handlirsch, *B. flavocincta* Turner, *B. forcipata* Handlirsch, *B. fraudulenta* Arnold, *B. fuscipennis* Lepeletier, *B. massaica* Cameron, *B. moebii* Handlirsch, *B. olivata* Dahlbom, *B. sibilans* Handlirsch, *B. ugandensis* Turner and *B. zinni* Gess (Gess 1986; Gess & Gess 1989; Gess & Gess field-notes and voucher specimens 2000). Thirteen fly families have been recorded namely, Stratiomyidae (Figure I.3.68.b), Tabanidae (Figure I.3.69), Mydidae, Asilidae (Figure I.3.70), Bombyliidae (Figures I.3.70.c–e, II.3.25.c & d), Syrphidae (Figures I.3.72.b & II.3.26.a & b), Conopidae, Muscidae (Figure I.3.76), Calliphoridae (Figure I.3.77), Sarcophagidae, Tachinidae (Figure I.3.78), Glossinidae and Nemestrinidae. The number of families represented in the prey of a single species ranging up to 11.

David Gess observed *B. arnoldi* seize prey in flight and, whilst hovering, reach underneath the fly with its gaster, and sting it from below. Prey carriage was most clearly observed for *B. bubalus.* The prey is held ventral side up, close beneath the wasp by the middle pair of legs when she is in flight (Figure II.3.25.b). On nearing the nest, the wasp moves the fly back so that her approach to the nest is very 'tail heavy'. She alights at the concealed nest entrance and immediately clears the sand with her forelegs whilst standing on her hind legs and continuing to hold the prey with her middle legs (Figure II.3.25.c–e). Opening of the nest and entry into it are rapid so that little opportunity is given to the satellite flies for larviposition.

Most *Bembix* lay the egg on one of the prey, usually the first prey to be placed in the cell, however, oviposition before the start of provisioning has been recorded for some extra-territorial species.

Furthermore, most species of *Bembix* are progressive provisioners, that is, the larva is provided with fresh prey throughout its development.

Nest sharing

Typically there is only one female per nest, however, *B. bubalus* was found to practise nest sharing. In a four-celled nest in which three females were present, only two cells were being provisioned, both cells were being guarded and the third female was bringing in prey, suggesting possible division of labour.

Subtribe Gorytina

Thirty genera are recognised in Gorytina (Pulawski 2010), of these *Afrogorytes* Menke, *Dienoplus* W. Fox, *Gorytes* Latreille (including *Pseudoplesis* Ashmead), *Harpactus* Schuckard (including *Dienoplus* W. Fox), *Hoplisoides* Gribodo, *Lestiophorus* Lepeletier and *Oryttus* Spinola occur in the Afrotropical Region.

Worldwide all species for which the biology is known nest in the ground and provision their nests with nymphs or adults of homopterous bugs of the families Cicadellidae, Membracidae, Psyllidae, Fulgoridae or Cercopidae. However, nothing is known of the nesting of *Afrogorytes.*

The only southern African species for which nesting has been observed appear to be two species of *Gorytes*, *G.*

natalensis (Smith) and *G. effugiens* (Brauns), and *Hoplisoides aglaia* (Handlirsch) (Gess & Gess, field notes and voucher specimens).

Gorytes Latreille (including *Pseudoplesis* Ashmead)

Gorytes are widely distributed in the Nearctic, Palaearctic and Afrotropical Regions but are absent from the Australasian and Neotropical Regions. A total of 75 species are recognised (Pulawski 2010), with around four species from southern Africa. Little seems to have been published on the nesting of *Gorytes*. All accounts suggest that nesting in friable soil in relatively shallow burrows and provisioning with Homoptera is likely to be the norm.

Little seems to have been published concerning the biology of *Gorytes* in southern Africa. There are no records of nesting by *G. natalensis* and *G. effugiens* in natural habitats, however, from time to time we receive enquiries from homeowners in the Eastern Cape concerning them due to the fact that they apparently have a predilection for nesting in flower pots on verandahs. The account that follows is for their nesting in flower boxes and pots on a west facing verandah, three storeys up on a block of flats in Grahamstown, Eastern Cape (Gess 1988).

Nest structure

A multicellular burrow in friable soil.

Method of construction

The earth was friable and easily excavated. The spoils of excavation were thrown out beneath the wasps and were allowed to accumulate in a low mound. Where there was sufficient space in the container, the sand was raked back to form a mound at a short distance from the nest entrance, a noticeable path developing between the two. The nest entrance was always left open when the wasp was away hunting.

After provisioning and oviposition have been completed, it is sealed with earth and a secondary shaft terminating in a cell is excavated.

At the end of each working day, the nest entrance is concealed with raked earth.

Provisioning and oviposition

The prey taken by both species were cercopoids, however, their choice of cercopoids was distinct. Over a period of several years *G. natalensis* provisioned with *Ptyelus grossus* Fabricius (Figure I.3.49), whereas *G. effugiens* provisioned with *Poophilus terrenus* Walker. The nests were multicellular and several bugs were provided for each cell. The choice of *P. grossus* by *G. natalensis* seems to be widespread having been recorded by Arnold (1929) from 'Natal; Vumbu Mts and Sanyati River, S.R'.

The prey, held beneath the wasp, is transported in flight. Each cell is supplied with about six bugs to one of which the egg is affixed.

Hoplisoides Gribodo

Seventy-nine species of *Hoplisoides* are recognised (Pulawski 2010), about 11 from southern Africa and the rest distributed over all continents except Australia. Richard Bohart and Arnold Menke (1976) gave biological notes for a range of species. Nesting in a sloping burrow in sandy soil, carrying the prey in flight and specialising in a single family of Homoptera is apparently typical for the genus. The only study of nesting in southern Africa seems to be that for *Hoplisoides aglaia* (Handlirsch) nesting on the farm Hilton (Gess & Gess fieldnotes and voucher specimens 1982).

Nest situation

On the farm Hilton, *H. aglaia* was nesting in a sand pit near the base and the top of a bank.

Nest structure

The three nests investigated were single-celled shallow sloping burrows 100–250 mm long.

Provisioning

The prey obtained from nests and those being transported by females were in all cases Membracidae. Nymphs and adults were taken. Of 12 prey, seven were *Beaufortiana cornuta* Distant (Figure I.3.51). The other five prey, all from one cell, were nymphs of an unidentified membracid (but not of *B. cornuta*). Brauns (in Capener 1952) recorded the prey of *H. aglaia* (as *Gorytes aglaia*) from Willowmore in the Eastern Cape (voucher specimens, that of the bug being the holotype of the species).

Lycium species (Solanaceae) have been recorded as the hosts of *B. cornuta* (Capener 1952 as *Centrotobelus braunsi*; Capener 1968). *Lycium* plants on Hilton were beaten and yielded *B. cornuta* adults and a nymph, which indicated that *H. aglaia* hunts on these plants.

Subtribe Handlirschiina

Six genera are listed for the subtribe Handlirschiina, of which *Ammatomus* A. Costa, *Handlirschia* Kohl, *Kohlia* Handlirsch and *Sphecius* Dahlbom, are represented in the Afrotropical Region; *Handlirschia* only from southern Africa.

Some aspects of nesting have been recorded for three New World species (Evans & O'Neill 2007), one Australasian species (Evans & O'Neill 2007) and one African species, *Sphecius milleri* Turner (Arnold 1929). All excavate nests in friable soil. For three species, the nest is known to be multicellular. Prey has been recorded for ten species. This was without exception cicadas (Homoptera, Cicadidae). The best known is the spectacular American 'cicada killer' *Sphecius speciosus* (Drury).

Nothing is known of the nesting of *Ammatomus*, *Kohlia* and *Handlirschia.*

Sphecius milleri Turner

Sphecius milleri is known from Eritrea, Zimbabwe and Zambia (Pulawski 2010).

Nest situation

In Zimbabwe *Sphecius milleri* was found nesting in Mopane Savanna, often in the loose sandy walls of burrows which had been dug by aardvarks.

Provisioning

Cicadas recorded as taken are *Munza furva* Distant, *Platypleura quadraticollis* Butler, *Platypleura lindiana* Distant and *Platypleura marshalli* Distant, all of which are found on Mopane trees, *Colophospermum mopane* (J.Kirk ex Benth.) J.Kirk ex J. Léonard (as *Copaifera mopani* J.Kirk ex Benth.) (Fabaceae, Caesalpinioideae).

George Arnold (1929) noted that, when hunting, a wasp circles around the trees, and makes a sudden swoop at its prey, bearing it to the ground, where it stings it. He made the interesting observation that, when one of these wasps comes close to the trees, the noise made by the cicadas stops quite suddenly.

Subtribe Stizina

The subtribe Stizina includes three genera *Bembecinus* A. Costa, *Stizus* Latreille, and *Stizoides* Guérin-Méneville all of which are represented in the Afrotropical Region and within it in southern Africa.

Bembecinus A. Costa

Bembecinus, with 186 species recognised (Pulawski 2010), is the third most species diverse of the spheciform genera, distributed throughout the warmer parts of the world, and is known from all the continents and many of the island groups.

Typically *Bembecinus* species possess 'sand rakes' and nest in aggregations in friable soil, excavating a one- or two-celled sloping burrow (Figure II.3.28), ovipositing into an unprovisioned cell, and provisioning progressively with small homopterans such as leafhoppers.

Figure II.3.27.—a. and b. *Bembecinus* spp. examples of nesters in friable soil, females at their nest entrances: a. *B. haemorrhoidalis* (Handlirsch); b. *B. rhopalocerus* (Handlirsch).

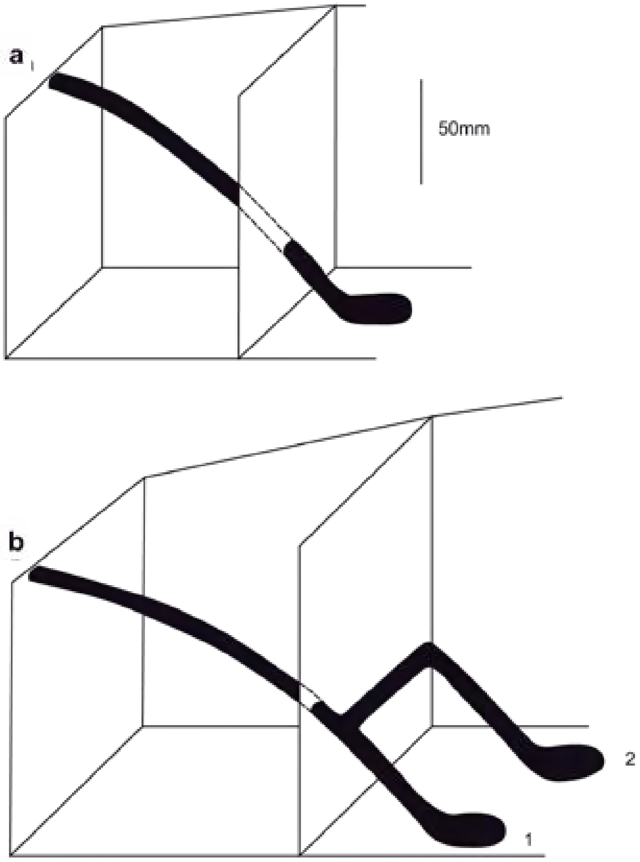


Figure II.3.28.—a. and b. *Bembecinus haemorrhoidalis* (Handlirsch), diagrammatic vertical plans of two nests.

The majority of species of *Bembecinus* in the Afrotropical Region are typical for the genus, having sand rakes. Examples of nesting studies of such species are for *B. argentifrons* (F. Smith) (as *B. braunsi* (Handlirsch) in Gess 1981) and *B. haemorrhoidalis* (Handlirsch) (Figure II.3.27.a) on the farm Hilton (Gess 1981), *B. rhopalocerus* (Handlirsch) (Figure II.3.27.b) at Onverwacht near Oudtshoorn (Gess & Gess fieldnotes and voucher specimens 1986) and *B. packhuisae* Bohart in the Goegap Nature Reserve near Springbok (Gess & Gess fieldnotes and voucher specimens 1987).

Two species, *B. cinguliger* (Smith) and *B. oxydorcus* (Handlirsch), apparently restricted to southern Africa lack the tarsal comb or sand rake usually associated with the forelegs of these wasps and used by them in burrow excavation. Their nesting has been investigated (Gess & Gess 1975). They nest in non-friable clayey soil in which they excavate a burrow with the use of water and surmount the burrow entrance with a mud turret (Figures II.3.29–31). This type of nesting, though common in the Eumeninae and Masarinae, is as exceptional in the spheciform wasps as it is in the Pompiloidea.

Nest situation

In areas of otherwise non-friable soil, the sand-rakers are found nesting in alluvial sand, which either is naturally

Figure II.3.29.—a.–d. *Bembecinus cinguliger* (Smith): a. nest aggregation showing nest entrance turrets and discarded mud pellets; b. and c. females constructing nest entrance turrets; d. completed nest entrance turret.

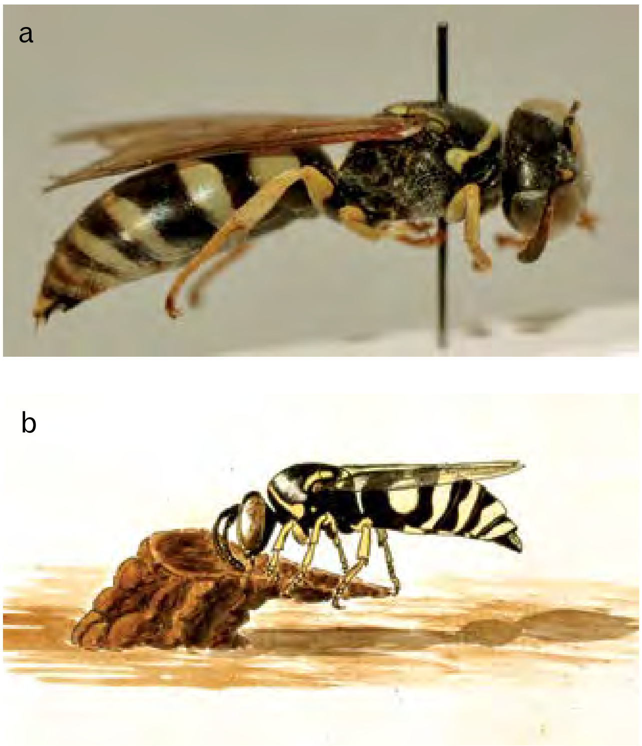


Figure II.3.30.—a. and b. *Bembecinus oxydorcus* (Handlirsch): a. female; b. female on closed nest entrance turret.

without vegetation or sparsely vegetated, or has been exposed in sand pits created by builders collecting sand. Sand is more extensively available along the coast and in the Western Cape in the Sandveld than inland where it is most often in the form of alluvial deposits associated with watercourses.

The nesting of *B. cinguliger* and of *B. oxydorcus* was investigated on the farm Hilton, Grahamstown, where they were nesting in aggregations in bare areas of hard clayey soil in close proximity to water sources in the form of rainwater pools and pools in a contour water furrow leading to an earthen dam. Nesting aggregations of both species have also been recorded by us in bare clayey areas near a water source at other sites to the north of Grahamstown. *Bembecinus cinguliger* was always more abundant and was amongst the first insects to emerge in spring whereas *B. oxydorcus* was less common and emerged later in the summer. *Bembecinus cinguliger* was also found nesting in extensive aggregations similarly situated to the west of Grahamstown on Tierberg farm near Prince Albert in the southern Great Karoo, and near Oudtshoorn in the Little Karoo (Gess and Gess unpublished fieldnotes).

Nest structure

The burrow of all species investigated was typical for the genus in that it consisted of a shaft terminating in a single cell with, in some instances, an additional secondary shaft also terminating in a single cell. However, whereas the typical burrows for species nesting in friable soil were gently sloping (Figure II.3.28) those of the nesters in non-friable soil were sub-vertical (Figure II.3.32).

The turrets of *B. cinguliger* and *B. oxydorcus* are readily distinguishable. In both there is an extended lip to one

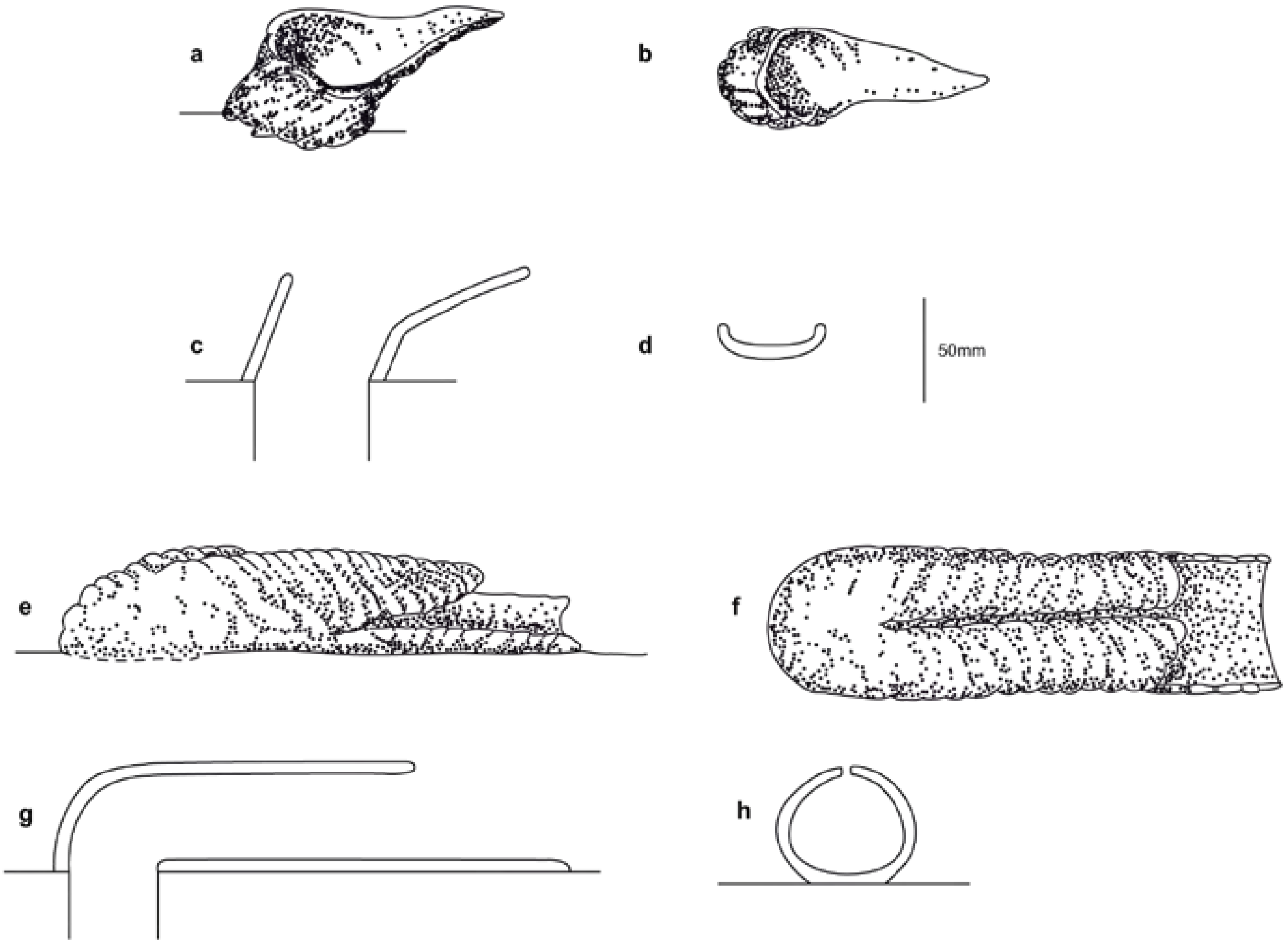


Figure II.3.31.—a.–h. Comparison between the nest entrance turrets of *Bembecinus cinguliger* (Smith) (a–d) and *B. oxydorcus* (Handlirsch) (e–h).

side of the structure. However, the lip of the turret of *B. oxydorcus* is raised above the ground and extends from the edge of the shaft opening at an acute angle with the ground surface. The lip of the turret of *B. cinguliger* is most commonly in contact with the surface of the ground 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 of *B. oxydorcus* is visible from above whereas in *B. cinguliger* the hood obscures it. 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 high whereas in *B. cinguliger* it forms arched sides that 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.

Method of nest construction

Typically, *B. cinguliger* and *B. oxydorcus*, when filling their crops with water for use in nest excavation, stand on the mud at the water's edge. Less commonly, *B. cinguliger* alights on the water surface or on a floating object.

At the nest site, the water is regurgitated and, using the mandibles, the nest builder works it into the soil to form mud that is extracted in the form of pellets, which are, as shaft sinking progresses, used for turret construction. When the turret is completed, the shaft is not yet at its full depth. Additional mud pellets extracted are discarded in a pellet dropping area 3–4 m from the nest, the wasp flying a regular elliptical flight path.

In the case of *B. cinguliger* it was found that a crop full of water was sufficient for the extraction of 13–20 pellets.

In two-celled nests, the portion of the original burrow below the opening to the second shaft is filled with pellets. As pellets are not carried into the nest it is thought that the pellets extracted from the secondary shaft are probably dropped into the main shaft and not carried out of the nest.

Bembecinus cinguliger and *B. oxydorcus* both seal their nests at the end of each working day. The temporary seals consist of thin mud plates, one immediately above the cell that is still being provisioned and a second at a depth varying from 3–19 mm below the ground surface. *Bembecinus oxydorcus* in addition seals the mouth of the turret. This seal is made by moistening the rim of the turret at a point furthest from the lip and by drawing the resultant mud towards herself. Mud is consistently taken alternately from the right and left sides. When the end of the lip is reached, the wasp steps off, buzzing her wings to support herself whilst she completes the sealing at the tip.

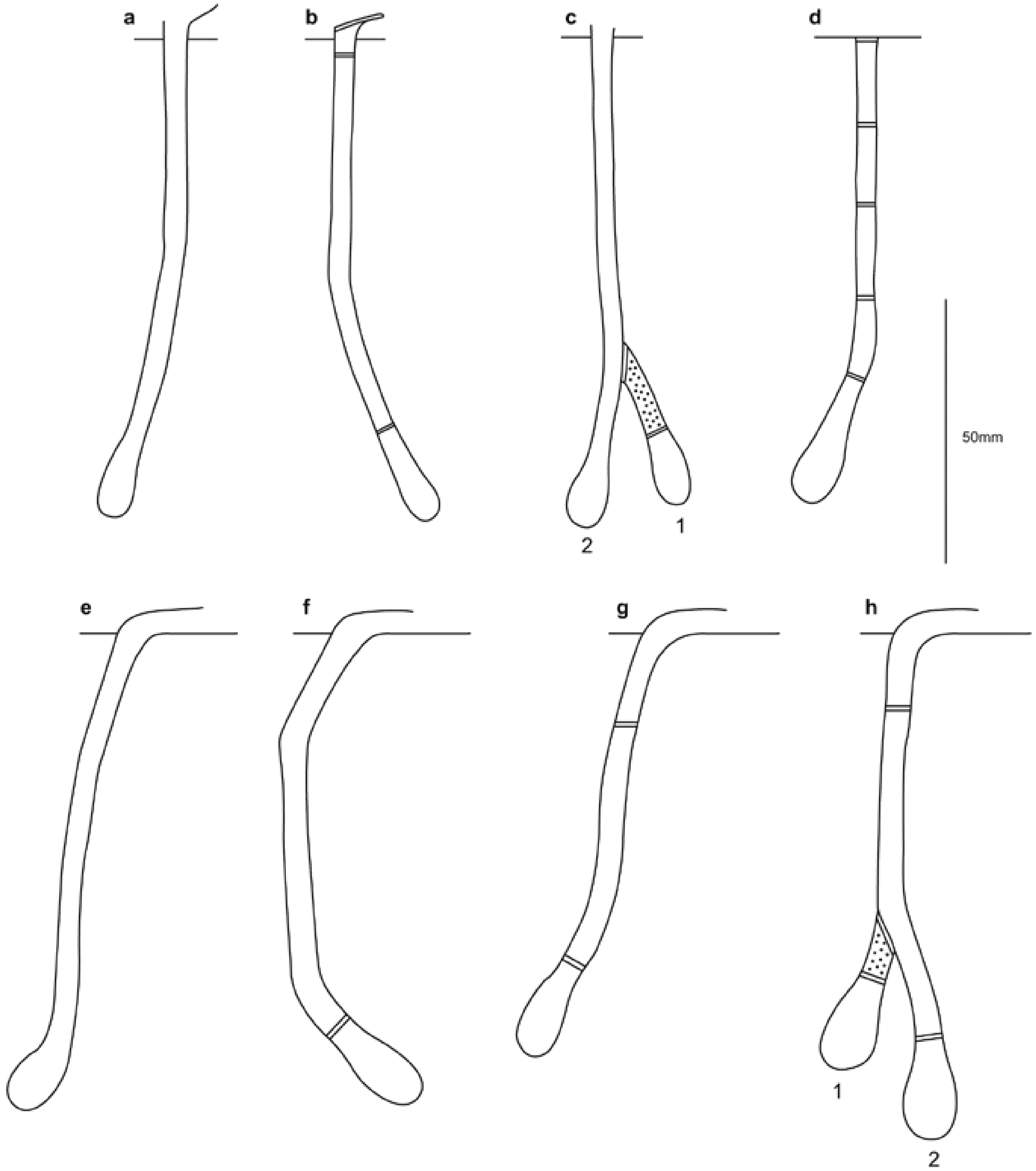


Figure II.3.32.—a.–h. *Bembecinus*, diagrammatic vertical plans of nests: a.–d. *B. oxydorcus* (Handlirsch); e.–f. *B. cinguliger* (Smith).

Finally, she returns with an additional water load, which she uses to smooth off the seal. When opening the nest, the wasp alights on the lip and moves forward to a point furthest from the lip, forms a pellet, flies off and drops it. She repeats this process until the lid is removed and then removes the upper and lower inner seals in a similar way.

Both *B. cinguliger* and *B. oxydorcus*, in nests with two cells, seal off the original shaft bearing the first cell from the secondary shaft. After the cell or cells are finally completely sealed, the wasp makes two or three further seals at intervals in the shaft. The spaces between these seals are not filled with earth.

Provisioning and oviposition

Prey from nests of *B. haemorrhoidalis* investigated on the farm Hilton included *Coloborrhis corticina* Germar, *Exitianus nanus* (Distant), *Macropsis octopunctata* China, *Macropsis chinai* Metcalf, *Macropsis* sp. nov., *Idioscopus* sp. and *Batracomorphus subolivaceus* (Stal) (all Cicadellidae) (Figure I.3.50) with, in exceptional cases, an additional one or two Fulgoroidea (Figure I.3.52) or Membracidae (Gess 1981).

Prey taken from nests of *Bembecinus rhopalocerus* (Handlirsch) at Onverwacht were fulgoroids, *Telmosias cf. crito* Fennah (Nogodinidae) and *Sajuba reversa* (Melichar) (Flatidae).

The prey by far the most commonly used for provisioning by *B. cinguliger* nesting on the farm Hilton judged from an analysis of 223 prey individuals from 31 cells were species of Cicadellidae (179 individuals). Also represented were two species of Fulgoroidae (30) and two species of Tephritidae (14). Adult females, adult males, nymphal females, and nymphal males were represented in that order.

Although the sample of prey for *B. oxydorcus* was smaller being derived from only nine cells, the preference was also clearly for Cicadellidae. Several Tephritidae were present but no Fulgoroidae.

Though no conclusive observations were made on hunting by *B. cinguliger* and *B. oxydorcus* and thus on the source of prey brought to the nests, circumstantial evidence is very strong that the cicadellid prey were obtained from the low-growing *Pentzia* bushes which surround the nesting sites. It is more than likely that the Tephritidae were also obtained from 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.

The eggs of *B. cinguliger* and *B. oxydorcus* are pearly white and almost straight. In both species, the egg was found on the floor of the cell, in *B. cinguliger* at the top of a small cone of earth and in *B. oxydorcus* on loose earth. 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 only after the larva had hatched. Provisioning thereafter appeared to be rapid, prey being brought in at a rate faster than it was consumed. Various cells occupied by small larvae were found to contain as many as thirty identifiable prey in addition to fragments of consumed prey.

Sleeping aggregations

At the end of the working day *Bembecinus* seal their nests and aggregate in sleeping clusters. Brauns (1911) recorded clusters of several thousand individuals, mostly females, at Willowmore, Jacot Guillarmod (pers. comm. in Gess & Gess 1975) observed prior to our nesting study a cluster on Hilton. At the time of our study, we found a cluster in a grass tussock, on Hilton, and another in the foliage of a low branch on Tierberg, both at considerable distances from the nesting aggregation. We observed the sleeping cluster of *B. cinguliger* on Hilton for a period of 46 days. Thousands of individuals clustered in the centre of the grass tussock in inclement weather and at night. Samples taken during this period suggested that at the beginning of the season males and females sleep together. Later in the season, as the flight periods of females and males change, only females are present. When disturbed, they showed no aggression.

Stizus Latreille

Stizus (examples *Stizus dewitzii* Handlirsch, Figure II.3.33 and *S. imperialis* Handlirsch Figure II.3.34) is the third most species diverse genus in the Bembicinae with 120 species recognised (Pulawski 2010). It is widespread in temperate and tropical regions but has not been recorded from South America, Australia and Southeast Asia. About 22 species are known from southern Africa. *Stizus* are mostly medium sized to large, stoutly built wasps. Many are boldly coloured in black and yellow with some red markings.

Apparently, typically multicellular nests are excavated in friable soil and each cell is provisioned with grasshoppers, katydids, or mantids. Tsuneki (1965) recorded communal nesting by *Stizus pulcherrimus* (F. Smith).

For the Afrotropical Region nesting accounts are available for *Stizus chrysorrhoeus* Handlirsch (Whitehead 1980), *Stizus imperialis* Handlirsch (Brauns 1911; Weaving 1989c), *Stizus fuscipennis* (F. Smith) (Weaving 1989c) and some observations are available for *Stizus atrox* (Brauns 1911 as *S. pentheres* Handlirsch; Patrick Hulley voucher specimens; Gess & Gess fieldnotes and voucher specimens 1994).

Nest situation

Stizus imperialis nests in sandy soil in vertical banks. Hans Brauns recorded it as nesting in the vertical banks of watercourses in the ‘Karoo’ and Alan Weaving in the bank of a sandpit on the farm Hilton, Grahamstown, Eastern Cape. Nesting by this species in the banks of sandpits in this situation on Hilton is a regular event and has been observed by ourselves in subsequent years, most recently in 2005. The sandpits, resulting from sand removal for building purposes, are situated on the flood plain of the Iron Put River, a small usually dry watercourse lined with riverine bush. As new pits are dug, *S. imperialis* extends its nesting into these.

The nests of *Stizus fuscipennis* investigated by Alan Weaving were located in bare, horizontal to gently sloping sand at the top of a consolidated coastal dune flanked by thick coastal bush in Widenham in KwaZulu-Natal. The climate and vegetation of the Eastern Cape and KwaZulu-Natal sites contrasts strongly. The former is arid with an annual rainfall of about 356 mm and sparse low-growing vegetation, except along the watercourses, which are lined with tall shrubs and small trees, while the latter is in a densely vegetated coastal area with an annual rainfall of nearly 1000 mm.

Both *S. chrysorrhoeus* and *S. atrox* appear to favour waterlogged saline soil.

Stizus chrysorrhoeus was found by Vincent Whitehead nesting in a saltpan, sometimes covered with salt water, near Hermanus, and Hans Brauns noted that it favours situations of a similar nature.

Stizus atrox was found by Hans Brauns nesting in level saline ground close to the coast at Port Elizabeth. Fur-

Figure II.3.33.—*Stizus dewitzii* Handlirsch, showing pollen carriage.

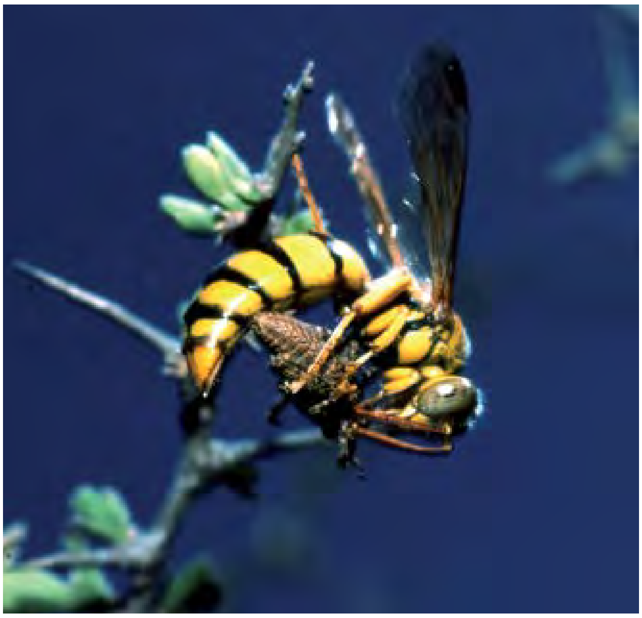


Figure II.3.34.—*Stizus imperialis* Handlirsch with prey grasshopper.

thermore, it was found nesting in bare patches of white, muddy, sandy soil in a salt marsh someway upstream on the east bank of the Kowie River by Patrick Hulley. Apart from these Eastern Cape sites, it was also found nesting in saline, saturated, muddy sand on the flood plain of the Spoegrivier near Wallekraal, inland from Hondeklip Bay on the west coast by ourselves.

Nest structure

The nest of *S. imperialis* and *S. chrysorrhoeus* Handlirsch are typical for the genus, consisting of a main shaft and lateral shafts each ending in a cell. There were up to four secondary shafts and each shaft terminated in a cell. Secondary shafts leading to fully provisioned cells were filled with sand.

The structure of only one nest of *S. fuscipennis* was established. It was unusual in that it lacked a main shaft, consisting of two gently sloping shafts with a common entrance and with each shaft terminating in a single cell.

The nests of *S. chrysorrhoeus* investigated by Vincent Whitehead consisted of an initial burrow that initially sloped downward at an angle of about 35° to a depth of 100 mm after which it levelled off and extended for up to 300 mm, ending in an unlined cell. Up to eight more secondary burrows were present.

Method of construction

Alan Weaving recorded that when excavating a nest, *S. fuscipennis* allows the extracted sand to accumulate in a crescent-shaped tumulus near the entrance. Sand from this tumulus is scraped back into the nest to be used for filling shafts to fully provisioned cells. Vibration is used for the compaction of the fill.

Similarly, Vincent Whitehead recorded that *S. chrysorrhoeus* deposits the excavated sand in a mound and that, when the female leaves, she rakes sand from this mound into the nest entrance.

As the nests of *S. imperialis* were excavated in a bank there was no accumulation of sand to form a tumulus, however, after a cell had been provisioned the lateral shaft leading to it was filled with sand.

Provisioning and oviposition

Alan Weaving recorded that *S. fuscipennis*, studied by him, provisioned exclusively with mantid nymphs of a single species, five to 13 individuals being provided per cell whereas *S. imperialis* provisioned exclusively with grasshopper nymphs of six species. The majority (79%) were Pamphagidae (Figure I.3.42) and Pyrgomorphidae (Figure I.3.43), the remaining 21% being Lentulidae (Figure I.3.41) and Acrididae. Prey were positioned with their heads facing the end of the cell. The orthopteran prey recorded by Hans Brauns for *S. imperialis*, though mostly nymphs, were occasionally adults. Grasshoppers, most usually nymphs, have been recorded as prey of *Stizus atrox* F. Smith (Brauns 1911; Patrick Hulley, female and four prey from nest in Hymenoptera collection, Albany Museum), *S. chrysorrhoeus* (Brauns 1911, Whitehead in Weaving 1989c) and *S. dewitzii* Handlirsch (Brauns 1911).

Stizus imperialis and *S. chrysorrhoeus* were found to carry the prey in flight, facing forwards, the former holding the prey by the middle and hind legs and the latter solely by the middle legs. Apparently, *S. imperialis* females landed on vegetation (Figure II.3.34) where they manipulated the prey before proceeding with it to the nest where they hovered briefly before entering directly whilst still holding the prey. *Stizus chrysorrhoeus* landed at the burrow entrance, opened it with the front legs and entered without changing the position of the prey.

During provisioning, there was evidence that *S. imperialis*, like *Cerceris* species, accumulates prey in a cache in the main burrow before a cell is provisioned. Mass provisioning is practised.

Both *S. fuscipennis* and *S. imperialis* were found to attach the egg to the first prey. The positioning of the egg appears from the available accounts to be variable.

Life history

The fully fed larva constructs a firm, oval parchment cocoon.

For *S. imperialis* Brauns recorded 2–3 generations, of which the last overwinters, and in addition that the pupae can remain 2–3 years without emerging.

For *S. chrysorrhoeus* Whitehead recorded two generations per year, the second resulting from about 20% of the first generation which did not diapause. The diapausing mature larvae remain in the soil until the following summer, sometimes submerged under 100 mm of salt water for three months.

Sleeping

Hans Brauns (1911) recorded that the males of *S. imperialis* are often found together in numbers towards evening, overnighting amongst the twigs of herbaceous plants; more rarely the females, these presumably before they have been fertilised and are busy with the business of nesting. When they are busy with the latter, they withdraw at night to their burrows and overnight therein.

Associated organisms

Hans Brauns (1911) reared both sexes of *Dasylabroides merope* (Smith) (as *Mutilla merope* Sm.) (Mutillidae) from cocoons, some even after three years, and also recorded a rhipiphorid (Rhipiphoridae) as a parasite of this wasp.

Vincent Whitehead (1980) recorded two miltogrammine flies and a meloid beetle as cleptoparasites of *S. chrysorrhoeus*.

Stizoides Guérin-Méneville

Wojciech Pulawski (2010) lists 29 species, predominantly from the Old World, with about six from the Afrotropical Region. Typically they have blackish wings (example *Stizoides funebris* (Handlirsch); Figure II.3.35). Little is known of the nesting of these wasps, however, Evans & O'Neill (2007) state that all information available to them indicated that all are brood parasites of digger wasps. The wasp apparently digs into the host's nest, destroys the host's egg, lays its own, and then re-seals the nest.

There appear to be no host records for the Afrotropical Region.

Tribe Nyssonini

The tribe Nyssonini currently includes 226 species in 17 genera (Pulawski 2010). Only two genera, *Brachystegus* A. Costa and *Nysson* Latreille (which includes *Synnevrus* A. Costa) have been recorded from the Afrotropical Region. *Brachystegus* is principally Palaearctic and Afrotropical in distribution with around five species in southern Africa, whereas *Nysson*, with around 101 species, has a worldwide distribution and is represented in southern Africa by around four species (Pulawski 2010). Evans & O'Neill (2007) state, on the basis of both behavioural and morphological evidence, that it is generally agreed that Nyssonini are all brood parasites of other spheciform wasps. However, definite or presumptive proof of parasite-host relationships has been obtained for a relatively small percentage of species, none in the Afrotropical Region. For the genus *Brachystegus*, Evans & O'Neill (2007) list only *B. scalaris* (Illiger) with *Tachytes europaeus* Kohl, however, they list 11 species of *Nysson* associated with six genera, all Gorytina. Confirmation of parasitism by these species has been proven for five species.

Figure II.3.35.—*Stizoides funebris* (Handlirsch).

Most species have a heavily reinforced integument, presumably as a protection against the stings or bites of their hosts.

Subfamily Crabroninae

The subfamily Crabroninae includes a wide range of forms. As delimited by Wojciech Pulawski (2010) it consists of 104 genera that include 4 635 species, more than half of the species of Crabronidae. Of the seven tribes recognised, six (Crabronini, Oxybelini, Larrini, Miscophini, Palarini and Trypoxylini) are represented in the Afrotropical Region. However, fewer than half of the genera are represented in this region.

Flower visiting

For southern Africa we have assembled flower visiting records for 73 species in 14 genera, representing all six tribes. The flowers most favoured, based on the percentage of species visiting them, are Apiaceae (37%, comparable with 39% for Bembicinae), Asteraceae (25%, somewhat below the 39% scored for Bembicinae), Zygophyllaceae (21%, comparable with 26% for Bembicinae) and Aizoaceae (Mesembryanthema and non-Mesembryanthema combined) (19%, comparable with 24% for Bembicinae). The most marked difference is the score of one species only for Amaranthaceae compared with 37% for Bembicinae. On the other hand, Molluginaceae is visited by 14% of the species (principally species of *Tachysphex*) as compared with fewer than 2% of Bembicinae. Also visited, each by fewer than 2% of the species are Celastraceae, Fabaceae (Papilionoideae), Fabaceae (Mimosoideae), Rhamnaceae, Apocynaceae (Asclepiadaceae), Scrophulariaceae (Selagineae), Ebenaceae, Campanulaceae, Elatinaceae, Rutaceae and Proteaceae.

Tribe Crabronini

The tribe Crabronini includes 49 genera, only eight of which occur in the Afrotropical Region. These wasps are characterised by having a large cuboidal head, relatively stout thorax and stout legs.

The habits of less than half the total number of genera are known. Included are excavators in the ground, excavators in plant tissue, users of pre-existing cavities, and a few genera, for example *Dasyproctus* Lepeletier & Brullé, exclusively nesters in plant tissue in burrows excavated by themselves. Pre-social behaviour is known to occur in five genera including *Dasyproctus*.

Encopognathus Kohl

Encopognathus includes 38 species (Pulawski 2010) of which about five occur in the Afrotropical Region. Those species for which nesting is known excavate burrows in sandy soil (Bohart & Menke 1976). The only prey records seem to be those of R.H.R. Stevenson (Arnold 1932) who took a female in the act of attacking an ant, *Tetramorium setuliferum* Emery, and also dug out the contents of several galleries, consisting entirely of ants, but not all of the same species.

Entomognathus Dahlbom

Entomognathus includes 63 species (Pulawski 2010), about 11 of which occur in the Afrotropical Region. Those species for which records of nesting biology are available, nest in soil and provision with chrysomelid beetles (Bohart & Menke 1976). Some species construct a chimney of soil 10–25 mm high, *E. brevis* (Vander Linden) (Grandi 1961), but this does not seem to be a general characteristic of the genus. The only Afrotropical species for which anything has been recorded seems to be *E. patricius* (Arnold) which R.H.R. Stevenson (Arnold 1932) found nesting in clayey banks of a stream. The prey was a small beetle of the family Chrysomelidae.

Rhopalum Stephens

Rhopalum is a cosmopolitan genus including 279 species (Pulawski 2010), four of which occur in the Afrotropical Region, one in South Africa and four in Zimbabwe. Nothing is known of the biology of these four species. Most extralimital species, that have a narrow pygidial plate and for which nesting data are available, nest in twigs or reeds. The provision is commonly small flies of a great variety but especially Chironomidae. Psocoptera and Aphididae (winged and wingless) are also frequently used and, in exceptional cases, winged ants, psyllids and Microlepidoptera. It is expected that the species that have a relatively wide pygidial plate nest in the ground. Evans & Mathews (1971) observed *Rhopalum variitarse* Turner, in Canberra, Australia, nesting in sandy loam in the sloping side of a furrow. The nest consisted of a short straight shaft which sloped obliquely for 100 mm and then gave rise to two short closed off galleries ending in spherical cells. Each was packed tightly with five small flies belonging to the families Stratiomyidae, Dolichopodidae, Lauxaniidae and Tachinidae.

Nothing seems to be known of the biology of any of the Afrotropical species.

Crossocerus Lepeletier & Brullé

Crossocerus includes 245 species (Pulawski 2010), around 24 of which occur in the Afrotropical Region. They fall into two groups, those species with a wide pygidial plate, which excavate nests in friable sandy or clayey soil, and those species with a somewhat narrowed pygidial plate, which excavate burrows or utilise pre-existing cavities in woody plant tissue. Diptera are the most commonly taken prey, however, Homoptera, Trichoptera, Microlepidoptera, Hemiptera, Psocoptera and Ephemeroptera are taken by some species.

Nothing seems to be known of the biology of any of the Afrotropical species.

Arnoldita Pate

Arnoldita appears to be a small genus, there being only four described species (Pulawski 2010), one from Zaire and Nigeria, one from Somalia and two from Zimbabwe. The pygidial plate is narrow. The only indication of the probable nesting behaviour of the genus is the record of Arnold (1926) of a male *A. senex* (Arnold) having been reared from a burrow of a bostrychid beetle in a wooden post in Zimbabwe.

Dasyproctus Lepeletier & Brullé

Dasyproctus includes 73 species (Pulawski 2010), the region with the highest species representation, just over half, being the Afrotropical Region. The rest are known from the Oriental and Australian Regions. Published biological accounts varying from fragmentary to fairly extensive, pertain to seven species, the fullest account being that for *D. westermanni* (Dahlbom) (Gess 1980b). All nest up off the ground in galleries, which they 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.

Nest situation

Dasyproctus utilises stems of both dicotyledonous and monocotyledonous plants, however, each species seems to be restricted to either one or the other although the choice of plant does not seem to be specific.

Nesting in dicotyledonous stems has been recorded for four species, *D. barkeri* Arnold, *D. kibonotensis* Cameron, *D. ruficaudis* Arnold and *D. stevensoni* Arnold.

Dasyproctus barkeri, described from Durban, Umgeni and Malvern in KwaZulu-Natal, was recorded by Arnold (1927) as “nesting in dry stems of the Kaffir-boom [sic]” (*Erythrina* sp.) (Fabaceae).

Dasyproctus kibonotensis was found by Bowden (1964) to be restricted to the stems of *Rubus* sp. (Rosaceae) for the excavation of its nests.

Dasyproctus ruficaudis was found nesting in a dry branch of a jacaranda tree in Grahamstown, Eastern Cape (Gess fieldnotes and voucher specimens). A single entrance leads into a burrow with seven secondary shafts within which are numerous cells in linear series, each cell provisioned with four to five calliphorid flies (Figure II.3.36).

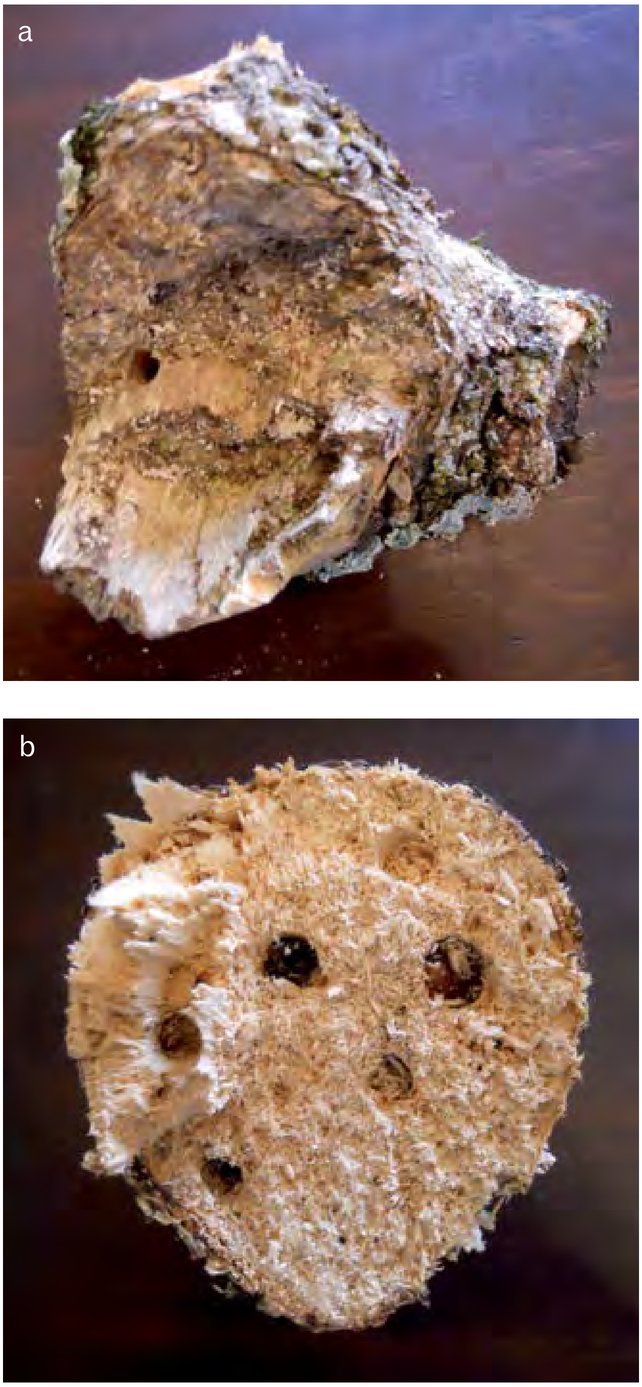


Figure II.3.36.—a. and b. *Dasyproctus ruficaudis* Arnold, nest in dead broken branch of a jacaranda tree: a. entrance to burrow; b. showing three provisioned cells and two cells closed with 'jaw dust'.

Dasyproctus stevensoni in West Cameroon was found nesting in a stem of *Conyza bonariensis* (L.) Cronquist (Asteraceae) (Michener 1971).

Additionally, an unidentified *Dasyproctus* sp. was found nesting in stems of *Berkheya decurrens* Willd. (also Asteraceae) on the farm Hilton, Grahamstown, Eastern Cape (Gess 1980b).

Figure II.3.37.—*Dasyproctus bipunctatus* Lepeletier and Brullé.

Dasyproctus bipunctatus Lepeletier & Brullé (including its colour forms *simillimus* (Smith) and *lichtenbergensis* (Arnold)) (Figure II.3.37) has been found by several observers to be restricted to nesting in inflorescence stems of the monocotyledonous families Amaryllidaceae, Iridaceae and Asphodelaceae. The most comprehensive account of the nesting of this species (*D. bipunctatus sensu stricto*) is that of Bowden (1964) who found it nesting near Kampala (Uganda) in the flowering stems of *Kniphofia* and *Aloe* species (Asphodelaceae), *Gladiolus* sp. (Iridaceae) and *Hippeastrum* (an American genus; Amaryllidaceae). Cuthbertson (1937) also found *Dasyproctus bipunctatus* nesting in *Gladiolus* stems near Salisbury (today Harare), Zimbabwe. *Dasyproctus bipunctatus simillimus*, in the Western Cape Province at least, appears to nest by preference in the green flowering stems of *Watsonia* species (Iridaceae). We found it commonly in such stems at Kirstenbosch, Cape Peninsula, as did Albert Hesse (unpublished notes) from an unnamed locality. It seems that the 'watsonia wasp' described by Sydney ('Stacey') Skaife (1953) is referable to *D. bipunctatus simillimus* and that the name *Dasyproctus capensis* Skaife, given it in the above publication may be considered to be a synonym (Gess 1980b). On Hilton, on several occasions, we found *D. bipunctatus* nesting in *Gasteria* (Asphodelaceae) stems.

The nesting of *D. westermanni* was investigated on Hilton (Gess 1980b) where it was found to be excavating galleries in the green sub-vertical pithy inflorescence stems of *Drimia altissima* (L.f.) Ker Gawl. (Hyacinthaceae) (as *Urginea altissima* (L.) Baker (Liliaceae)) (Figure II.3.38). The *Drimia altissima* plants were growing on rising clayey ground immediately to the east of the New Year's River in dwarf karroid scrub characterised by *Pentzia incana* (Thunb.) Kuntze (Asteraceae). Twenty-two nests in 17 inflorescence stems were investigated.

Nest structure

Of the twenty-two nests, 17 of the utilised stems contained a single nest each, one stem contained two nests and another contained three nests. The entrance hole to the

Figure II.3.38.—*Drimia altissima* (L.f.) Ker Gawl., the green inflorescence stems of which are used for burrow excavation by *Dasyproctus westermanni* (Dahlbom).

nest was situated from 500–1 070 mm above the ground. In all but one instance the entrance hole was sited below the level of the lowermost elements of the cylindrical raceme which occupies the terminal two fifths of the inflorescence stem (Figure II.3.39.a).

A completed nest consists of a circular entrance hole, 4 mm in diameter, bitten through the side of the stem giving rise to an ascending and a descending gallery hollowed out of the pithy centre of the stem (Figure II.3.39.b. & 40). 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 completed is a start made with hollowing out a descending gallery. Both galleries are divided serially into a number of cells, each sealed with a plug constructed from pith obtained in the process of hollowing out the gallery. The number of cells in fully utilised ascending galleries ranged from five to eight and the only fully utilised descending gallery found contained seven cells. The maximum number of cells found in any one nest was 14. 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.

Provisioning and oviposition

The prey of *Dasyproctus kibonotensis* were of the families Lonchaeidae, Muscidae, Platystomatidae, Tachinidae and Tephritidae (= Trypetidae). Most prey were *Trirhithrum coffeae* Bezzi (Tephritidae), a dominant member of the dipterous fauna of robusta coffee.

Those of *Dasyproctus stevensoni* in West Cameroon were Milichiidae (Michener 1971).

Six families of Diptera, Chloropidae, Lonchaeidae, Muscidae, Simuliidae, Sphaeroceridae and Tephritidae, were represented among the prey of *Dasyproctus bipunctatus* from near Kampala. Most were *Atherigona* species (Muscidae, Coenosiinae). However, the prey of *Dasyproctus bipunctatus* investigated near Salisbury (today Harare) were of the families Anthomyiidae, Sarcophagidae, Sapromyzidae, Syrphidae and Tachinidae and Albert Hesse

Figure II.3.39.—a. and b. *Dasyproctus westermanni* (Dahlbom): a. burrow entrance in inflorescence stem of *Drimia altissima* (L.f.) Ker Gawl.; b. inflorescence stem cut longitudinally to show nest plan and contents.

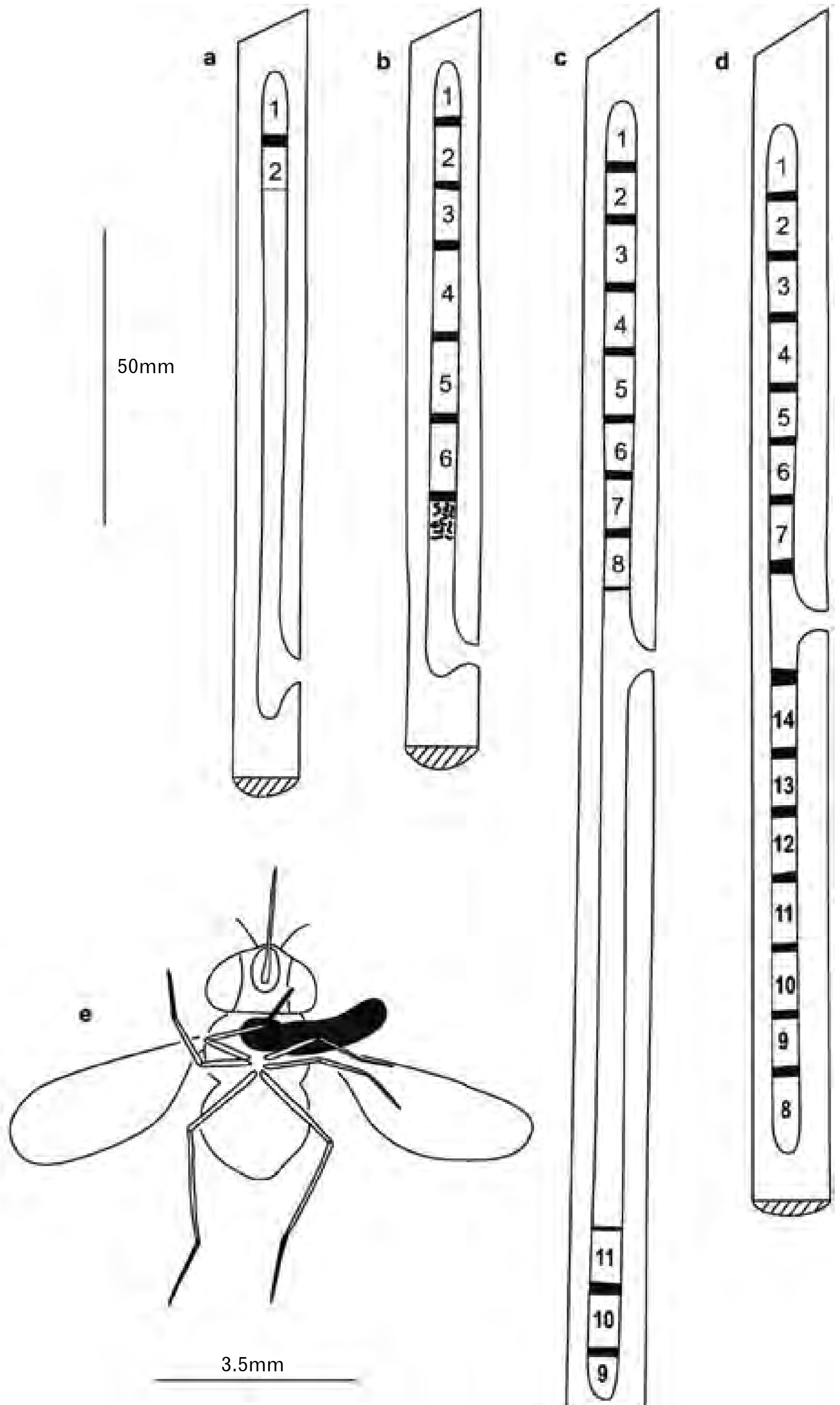


Figure II.3.40.—a.–e. *Dasyproctus westermanni* (Dahlbom): a.–d. diagrammatic plans of four nests; e. newly hatched larva feeding on bombyliid fly.

(unpublished notes) recorded its prey found in *Watsonia* stems as Otitidae.

D. bipunctatus lichtenburgensis at Tanga on the East African coast was found to provision its cells in stems (unspecified) almost entirely with Ototidae (= Ortalidae) (Carpenter 1942).

Prey of *D. westermanni* taken from the nests investigated on Hilton (Gess 1980b) were from eight dipterous families, Simuliidae (Figure I.3.67), Stratiomyidae (Figure I.3.68.), Bombyliidae (Figure I.3.71.a & b), Empididae, Syrphidae, Phoridae (Figure I.3.72), Otitidae (Figure I.3.74) and Chamaemyiidae (Figure I.3.75). All cells 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 might, upon finding a ready supply of that species, have concentrated upon it or its source. Each cell is provisioned with a relatively large number of prey which are closely packed and are orientated to face the inner end of the cell. The prey is alive but partially paralysed. Two fully provisioned and sealed cells, none of the contents of which had been consumed, contained 14 and 26 flies respectively.

In the same investigation, it was noted that oviposition was onto one of the flies but apparently not the first. The egg is glued to the ventral surface of the prothorax anterior to the legs.

During a subsequent investigation of nests of *D. westermanni* on Hilton in 2005, we found that, in addition to Diptera, Miridae (Hemiptera) had occasionally been taken as prey.

Life history

The development of *D. westermanni* from egg to adult was very rapid in the generation reared in *Drimia* stems, probably owing to the short time during which these stems are suitable for nesting. It is probable that there is at least one other generation per year but its nesting site has not been identified.

The silken cocoons are brown and papery. Their orientation and that of the pupae within them is unusual and of interest in that it appears to be governed by gravity rather than by the position of the nest opening. Thus, in all cells, whether constructed in the ascending or descending galleries, the anterior end of the cocoon is orientated upwards, that is, facing away from the ground.

Associated organisms

D. westermanni nesting on Hilton was subject to parasitism by *Perilampus* sp. (Chalcidoidea, Perilampidae) and Phoridae (Diptera).

Neodasyproctus Arnold

Neodasyproctus is morphologically very similar to *Dasyproctus*. It may, however, be distinguished by its shining integument, that of *Dasyproctus* being dull. Of the 12 described species (Pulawski 2010), seven occur in Madagascar, one in Zaire, one in Liberia, one in Zimbabwe and KwaZulu-Natal, one in Willowmore, Eastern Cape and, surprisingly, one in Fiji.

The only indication of its nesting biology is the observation by Hans Brauns recorded by George Arnold (1926) that *N. kohli* (Arnold) was found nesting in hollow stems at Willowmore, Eastern Cape Province.

Tribe Oxybelini

The Oxybelini are rather bee-like wasps, quick moving and fast flying. Nesting in all species seems to be fossorial. The prey of all species is flies, including some injurious forms such as black flies, testse flies, and houseflies (Bohart & Schlinger 1956). Out of the 13 genera, ten, *Belokohlus* Antropov, *Belomicrinus* Antropov, *Belomicroides* Kohl, *Brimocelus* Arnold, *Gessus* Antropov, *Minimicroides* Antropov, *Nototis* Arnold, *Oxybelus* Latreille, *Oxybelomorpha* Brauns and *Wojus* Antropov, are represented in the Afrotropical Region (Pulawski 2010).

Southern African species formerly included in *Belomicrus* A. Costa have been transferred to three other genera. *Belomicrus bicornutus* Arnold has been transferred to *Nototis*, previously treated as a subgenus of *Belomicrus* with an additional species *falcidens* described by Antropov (2007). *Belomicrus crassus* Arnold has been transferred to the monotypic genus *Belarnoldus*. *Belomicrus ferrieri* Kohl has been transferred to the monotypic genus *Belokohlus*. *Belomicrus braunsi* Kohl, *B. funestus* Arnold, *B. minutissimus* Arnold, *B. rufiventris* Arnold, *B. rhodesianus* Arnold, *B. sordidus* Arnold and *B. turneri* Arnold has been transferred to the Old World genus *Oxybelomorpha* Brauns, treated as a synonym of *Belomicrus* by Kohl (1923), with an additional six southern African species described by Antropov (2005).

Belokohlus Antropov

Belokohlus is a monotypic genus. The single species *B. ferrieri* (Kohl) was described by Kohl in 1924 in the genus *Belomicrus* from the Sundays River, Eastern Cape. In 1989, we collected two females and a male from flowers of *Euclea* sp. (Ebenaceae) at Karoopoort, east-northeast of Ceres, Western Cape. Nothing appears to be known about its biology.

Brimocelus Arnold

Brimocelus seems to be endemic to southern Africa. Only three species have been described, *B. radiatus* (Arnold) from Ceres in the Western Cape, *B. roosvelti* Antropov from 16 km south of Vioolsdrif, western Northern Cape, and *B. schwartzi* Antropov from Karibib, northwestern Namibia. Nothing seems to be known of its nesting.

Belomicroides Kohl

Belomicroides appears to be restricted to the Afrotropical and Palaearctic Regions. Only three species have been described from southern Africa. Its biology seems to be completely unknown.

Gessus Antropov

Gessus is a monotypic genus Antropov (2001). The single species *G. capensis* Antropov was collected by David Gess at Anenous, Namaqualand western Northern Cape from flowers of *Wahlenbergia* sp. (Campanulaceae) in an area with sandy soil.

Nototis Arnold

Nototis, described by Arnold (1927) as a subgenus of *Belomicrus* was elevated to generic status by Antropov (2007) with two species, *N. bicornutus* (Arnold) and *N. falcidens* Antropov.

Nothing appears to be known of the biology of these species.

Oxybelus Lateille

Oxybelus is the largest genus in the subfamily and has an almost worldwide distribution being absent only from the Australian area. Of the 262 species recognised (Pulawski 2010) only about 33 occur in the Afrotropical Region.

Nesting is in friable soils, most usually sandy soil along banks of water courses, lake margins, or in protected areas behind an ocean beach. Nests are unicellular or multicellular and there is a tendency towards the formation of aggregations. There seems to be no consistency in whether the nest is left open or closed during provisioning.

Diptera are the prey of all species. Some preference is shown for Muscoidea, however, these wasps are essentially opportunists and take whatever flies are abundant and locally available. Depending on the species, the prey fly is carried in flight either impaled on the sting or held beneath the body with the middle legs.

Published accounts of the nesting biology of this genus are reviewed by Richard Bohart and Arnold Menke (1976). These accounts all concern European and North American species.

The only Afrotropical species for which data concerning nesting biology seems to be available is *Oxybelus lingula* Gerstaecker (Gess 1980; Gess & Gess fieldnotes and voucher specimens 1982).

Nest situation

Oxybelus lingula nests on the farm Hilton, near Grahamstown in a sand pit dug in friable alluvial sand on the flood plain of a usually almost dry watercourse. This wasp, though the most common of five species of *Oxybelus* collected in the sand pit, was only rarely found nesting. Five nests were excavated.

On the farm Van Wyksfontein, near Colesberg, a nesting aggregation of this species was found in a bare area of friable, gritty soil flanking an earthen dam (Gess & Gess fieldnotes and voucher specimens 1988).

Nest structure

The burrow initially descended vertically to sub-vertically and then curved to one side to end in an ovoid cell. The sides of the shaft over the first 10 mm were ‘cemented’ in such a way that when the loose surface sand was brushed away, this ‘collar’ remained intact.

A cell having been provisioned and oviposition having taken place the shaft leading to it is firmly filled with sand to the point at which the burrow starts to curve strongly away from the vertical. A secondary curved shaft ending in a cell is then excavated and the process of provisioning, oviposition and shaft filling repeated. The largest number of cells prepared in this way in the nests investigated was four, however, as the nest was not yet complete it is not known what the maximum number of cells per nest may be. The cells were all sloping and varied in depth from 50–105 mm.

Provisioning and oviposition

The prey were Muscidae and Calliphoridae. Of particular interest was the use of *Stomorhina lunata* (Fabricius) (Calliphoridae), a species known as a predator in the egg pods of grasshoppers, including locusts (Acridoidea) (Greathead 1962).

After completing a cell, the shaft entrance is temporarily closed with loose sand. Hunting then takes place. The prey fly is carried to the nest impaled on the wasp’s sting. Having arrived at the nest the wasp clears the entrance and enters the nest without putting down the prey. Cells were provisioned with 1–7 prey (sample of 10). The flies appeared to have been positioned in the cells with their heads pointing inwards. We noted that in some instances in a single nest the identity of the prey differed between cells but that all the prey in a single cell were conspecific. This suggests that the wasp either hunted in different places or hunted at a different time of day.

Oviposition takes place onto one of these flies. The egg is affixed with the anterior end cemented to the underside of the head or, possibly in the neck region.

Oxybelomorpha Brauns

Oxybelomorpha Brauns was treated as a synonym of *Belomicrus* A. Costa by Kohl (1923) and subsequent authors but was restored to full generic status by Antropov (2005). Wojciech Pulawski (2010) lists 24 species, all from the Old World, 16 from southern Africa. Unlike *Belomicrus* it has no New World representatives.

Little appears to be known of the biology of this genus. The only records seem to be those of ourselves for *Oxybelomorpha kohlii* Brauns nesting in sandy soil 11 km west of Clanwilliam, Western Cape and at Rooikloof, Sutherland, southwestern Northern Cape. At the Clanwilliam site, a female was seen entering a burrow excavated into the side of a solidified dune mole rat mound. Upon investigation, the burrow, 4 mm in diameter, was found to slope gently and then turn downwards sub-vertically to end in a single cell. Eight prey individuals were obtained from the cell. All are *Bibio turneri* Edwards (Diptera, Bibionidae).

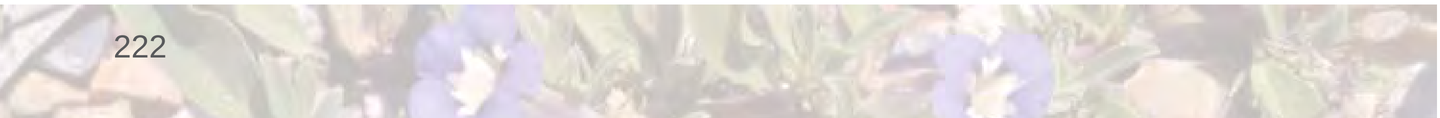
Wojus Antropov

Wojus is a monotypic genus (Antropov 1999). The single species, *W. inopinatus* Antropov was collected by Wojciech Pulawski at Swartrivier, 7 km northwest of Prince Albert in the southern Karoo.

Tribe Larrini

Larrini is constituted of 1 313 species in 14 genera. Two subtribes are recognised, Gastrosericina and Larrina. The genera of Gastrosericina represented in southern Africa are *Gastrosericus* Spinola, *Holotachysphex* de Beaumont, *Kohliella* Brauns, *Larropsis* (including *Ancistrosoma* W. Fox), *Parapiagetia* Kohl, *Prosopigastra* A. Costa, *Tachysphex* Kohl, *Tachytella* Brauns and *Tachytes* Panzer. Those of Larrina are *Dicranorhina* Shuckard, *Larra* Fabricius and *Liris* Fabricius.

The prey of most species is Orthoptera. Hemiptera are, however, taken by *Prosopigastra* and, although Orthoptera are taken by the majority of species of *Tachytes*, lepidopteran larvae have been recorded for the *ambides* group



of this genus in Asia. Nesting behaviour ranges from pseudo-parasitoid (*Larra*), through the excavation of unicellular or multicellular nests in friable soil (the majority of species), to the use of pre-existing cavities, either facultatively by some nest excavating species or obligatorily in pre-existing cavities in plant tissue (*Holotachysphex*). No species of Larrini use water in the excavation of nests nor mud for the construction of cell and nest closures as is practised in the Trypoxylini.

Subtribe Gastrosericina

Gastrosericus Spinola

Gastrosericus is an Old World genus with 61 species recognised (Pulawski 2010). In his revision of the genus, Wojciech Pulawski (1995) gives the distribution of the genus as throughout Africa, in the Arabian Peninsula north to southern Turkey, from Armenia to India and Sri Lanka, east to Vietnam and north to Kazakhstan and Mongolia with the highest numbers of species in West and southern Africa. He postulated that all species nest in the ground based on known nesting for some species and that all have a foretarsal rake and a pygidial plate. Disposal of excavated material is either by scattering or by the creation of a tumulus, crescent shaped, rounded or surrounding the entrance, according to species. The nests are multicellular with the main shaft perpendicular or inclined. During absences from the nest some species leave the nest entrance open whereas others close it. On returning to the nest with prey, the female either enters directly or drops the prey and, after entering the nest, draws it in after her. Recorded prey are acridid grasshopper nymphs, nymphal and adult tridactylid crickets, adult cicadellids and adult asilid flies. Wojciech Pulawski and others have recorded mixed prey being taken by a single species. The prey is carried either on foot or in flight. Notes on nesting by southern African species are given for *G. capensis* (Brauns), *G. chalcithorax* Arnold and *G. karooensis* (Brauns) by Hans Brauns (1911) and *G. braunsi* Arnold and *G. lamellatus* Turner by George Arnold (1922).

Holotachysphex de Beaumont

Holotachysphex is a small genus (only six species have been described) closely related to *Tachysphex*. Nesting have been recorded for only one species, *H. turneri* (Arnold), the only species occurring in southern Africa.

Nest situation

George Arnold (1926), reporting on the observations of Hans Brauns, stated that *H. turneri* nests in hollow stems of *Aloe* and *Datura* and that the cells are separated by partitions of earth and pebbles. No information was given on prey. Fred and Sarah Gess (field notes and voucher specimens) have found nests of this wasp in *Phragmites australis* (Cav.) Steud. which had been bored by a carpenter bee, *Xylocopa scioensis* Gribodo, and Fred Gess (1978) described nests from five trapnests suspended from the branches of trees at heights of one or two metres above the ground.

Nest structure

The five nests of *H. turneri* described by Fred Gess were one- to three-celled. In all the nests, a preliminary plug of earth or earth debris had been constructed at the inner end of the boring. Each cell had been sealed with a plug consisting of two parts, an inner part composed of detritus (small bits of bark, short lengths of twig, seeds and leaflets) and the outer part of clods of earth. After the last cell had been sealed, the remaining space between the cell and the boring entrance had been filled with detritus (Figure II.3.41).

Method of construction

The wasp was observed to carry building materials to the nest in flight.

Provisioning and oviposition

In all five nests, the prey were nymphs of a single species of short-horned grasshoppers of the family Pyrgomorphidae (Acridoidea) (Figure I.3.43.b & c). The number of prey stored in each cell was dependent on size and varied from 4–32 individuals! All the prey grasshoppers had been positioned facing the blind end of the trapnest, i.e. the inner end of the cell. All were deeply paralysed. A grasshopper bearing an egg or larva was positioned on its back, all the others were positioned on their venters or sides. It appears that oviposition is onto the first prey to be introduced into a cell.

Kohliella Brauns

Pulawski (2010) lists three species of *Kohliella*, two southern African endemics and one Sri Lankan endemic. Of the nesting of the *Kohliella* species, only that of *Kohliella alaris* Brauns has been described (Gess & Gess 1980a). This species excavates shallow nests in friable soil, each with one to a few cells. All prey obtained were nymphs of the tree cricket *Oecanthus capensis* de Saussure (Gryllidae, Oecanthinae).

Kohliella alaris is unusual in its pattern of daily activity, as it never appears before noon and is most active during the hottest time of day when most wasps show a fall off in activity. Interestingly Arnold (1922), with respect to *Gastrosericus* species, observed that they are only to be seen flying about in the hottest sunshine.

Nest situation

Nesting aggregations of *K. alaris* have been located by the Gess family on the farm Hilton, near Grahamstown in a sand pit dug in friable alluvial sand on the flood plain of a usually almost dry watercourse and on the farm Tierberg, Prince Albert, in a sandbank in a riverbed.

Nest structure

The nest consists of a short trench leading to a sub-circular entrance hole, slightly wider than high from which a shallow entrance passage extends for 20–35 mm to reach a depth of about 13 mm. From this shallow burrow, one to several secondary branches of a steeper gradient led off, some of which end in a more or less horizontal single cell at a depth of 16–70 mm (Figure II.3.42). Some passages appear to remain unused and are free from sand whereas those passages that end in a cell are, after a cell has been provisioned and oviposition has taken place, filled with

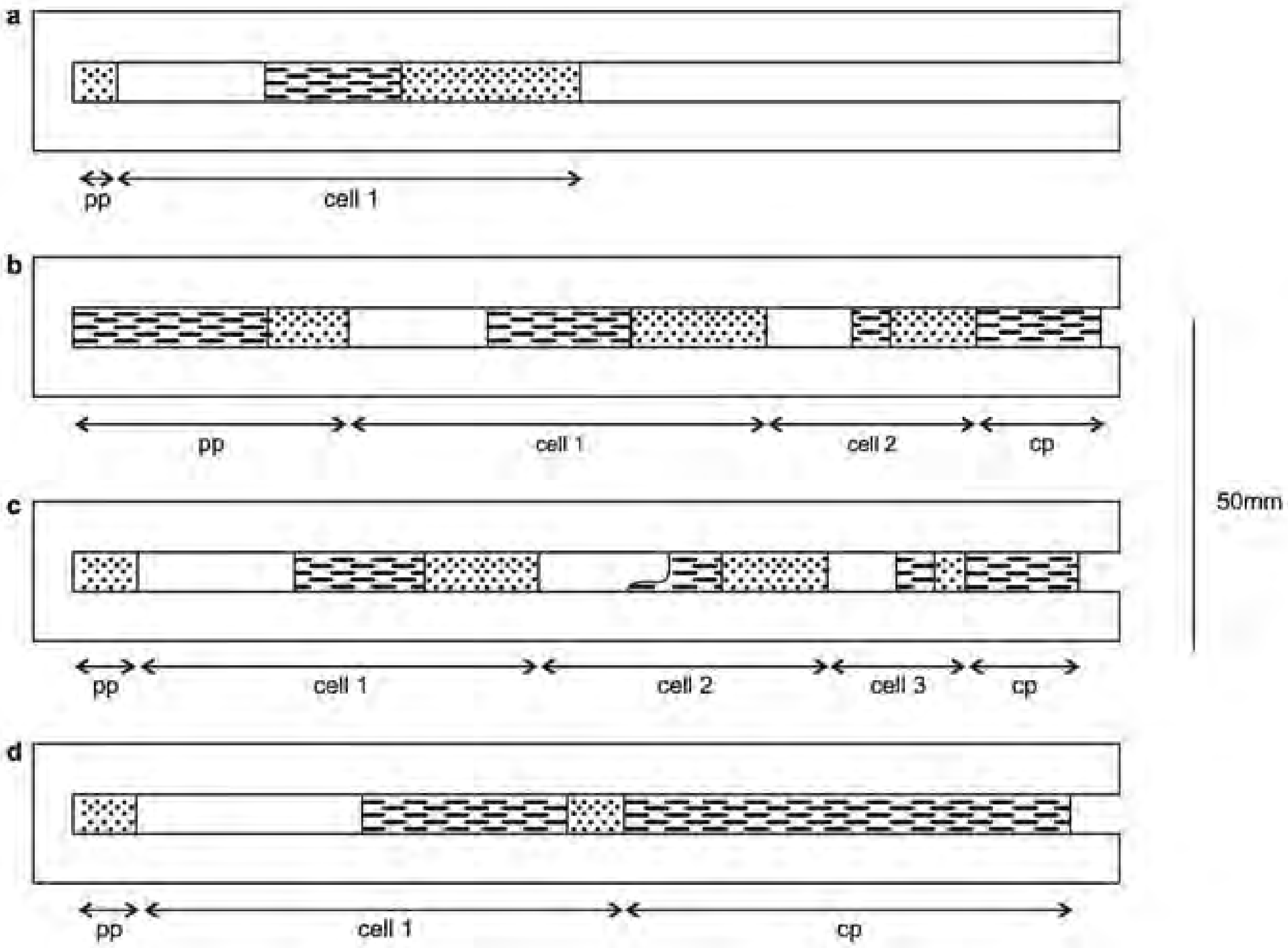


Figure II.3.41.—*Holotachysphex turneri* (Arnold), diagrammatic plans of four nests in wooden trap nests showing preliminary plugs (pp), cells, and closing plugs (cp) as well as nature of nesting materials, clods of earth (stippled) and course detritus (dashed).

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.

Method of construction of nest

Kohliella 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 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 that are too big to be extracted from the excavation by raking are carried out by the wasp in her mandibles.

Provisioning and oviposition

Hunting takes place after a cell has been excavated and the nest temporarily sealed with sand. A prey tree cricket (Figure I.3.44.a) having been located, captured, stung and mutilated by cutting the antennae short, is held beneath the wasp with its head facing the direction of travel as she flies with it to the nest. She alights close to the nest entrance, puts down the prey, rakes the sand of the temporary closure out of the nest entrance, enters, turns around within, and draws the prey in headfirst.

In a cell several prey are positioned venter up and 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.

In each cell, an egg is attached by its anterior end to the underside of the prothorax of one of the prey, posterior to either the right or left coxa and extending transversely across the venter of the prey.

Larropsis Patton (including *Ancistrosoma* W. Fox)

Larropsis as listed by Wojciech Pulawski (2010), includes 40 species, most of which occur in North America. One species, *L. obliqua* (F. Smith) (as *Larrada obliqua*), was described from southern Africa. Over the years, it has been variously placed in the genera *Larra*, *Tachytes* and *Ancistrosoma*. Nothing seems to have been recorded on the biology of this species, however, crickets seem to be the favoured prey of the genus.

Parapiagetia Kohl

Parapiagetia is a comparatively small genus with 26 species recognised (Pulawski 2010). It is primarily repre-

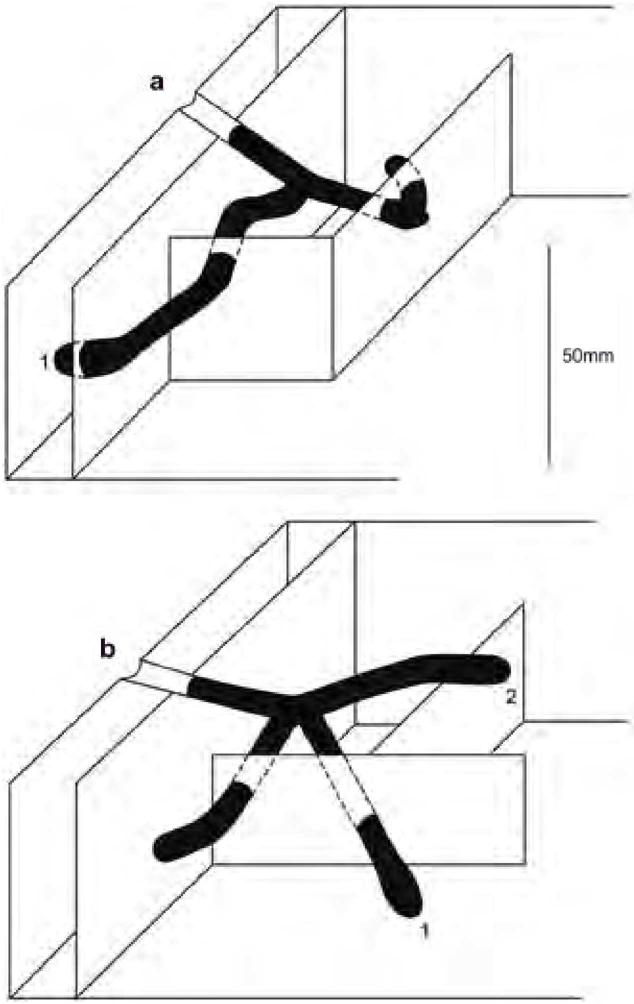


Figure II.3.42.—a. and b. *Kohliella alaris* Brauns, diagrammatic vertical plans of two nests.

sented in the Old World, with around three species having been recorded from southern Africa. One species has also been described from Argentina.

Little is known concerning the biology of *Parapiagetia.* Hans Brauns (1911) stated that *P. capensis* Brauns and *P. vernalis* Brauns nests in clay banks near Willowmore. Arnold (1922), however, recorded*. P. capensis* as nesting in loose sandy soil in Zimbabwe and Gess (1981) stated that the presence in the female of *P. vernalis* of a foretarsal rake and a pygidial plate was indicative of sand nesting. Arnold (1945) recorded immature Tetrigidae (as Acrydiidae) (pigmy grasshoppers) as the prey of *P. longicornis* Arnold, a Madagascan species.

Prosopigastra A. Costa

Prosopigastra is a comparatively small genus with 35 species recognised (Pulawski 2010). All except one are Old World species. Only two species have been recorded from southern Africa.

Little is known of the nesting and prey choice. Available records suggest that bugs (Hemiptera) are favoured by some species at least. For southern Africa, Arnold (1922) reported that *Prosopigastra creon* (Nurse) (as *Prosopigastra neavei* Turner) excavates shallow three- to six-celled nests in clayey soil and provisions with an average of six pentatomid bugs per cell. Charles Ferton (1912a, b) recorded the nesting of this species in Algeria where it was nesting in sand in pre-existing burrows of other Hymenoptera and cicindelid beetles and provisioning with lygaeid bugs. At the same site he found *P. orientalis* de Beaumont (as *Prosopigastra creon* ssp. *punctatissima*) nesting in a similar fashion and provisioning with fulgorid and lygaeid bugs, 13–19 per cell.

Tachysphex Kohl

With respect to species numbers, *Tachysphex* is the largest genus in the Larrini. Wojciech Pulawski (2010) lists 446, half of which occur in Africa. Although there are published accounts of nesting by this genus in other regions, there seem to be no published accounts of nesting in southern Africa. Some aspects of the nesting of two widespread species, *T. albocinctus* (Lucas) and *T. panzeri* Lind, which occur in this region have been described—*T. albocinctus* by Ferton (1912) and Grandi (1961) in Europe; by Bristowe (1925, in Pulawski 1971) in Somaliland, and *T. panzeri* by Fabre (1886) and Grandi (1961) in Europe. We investigated the nesting of *T. albocinctus*, *T. fugax* (Radoszkowski), *T. panzeri pentheri* (Cameron) (= *T. calban* Arnold) and *T. waltoni* Arnold (as near *T. modestus* in Gess 1981) near Grahamstown, Eastern Cape Province (Gess & Gess field notes and voucher specimens 1977/78, 1982/83). The prey of *T. albocinctus* is always mantids, nearly always nymphs (Figure I.3.47), (as also are those of a further species, *T. schoenlandi* Cameron, also caught with prey in the same area). Those of the other three species are always grasshoppers, those of *T. fugax* and of *T. waltoni* Lentulidae and those of *T. panzeri pentheri* Acrididae (Figure 1.3.40.d), also taken by *Tachysphex vanrhynsi* Arnold (Figure I.3.40.a). *Tachysphex turneri* (Arnold) has been observed with a Pyrgomorphidae (Figure I.3.43.c). A nest of *T. hermia* Arnold was discovered in a sand-filled shell of a desert snail, *Trigonephrus* sp. in the Sperrgebiet, Namibia (Gess & Gess 2008).

Nest situation

Most species of *Tachysphex* nest in horizontal to sloping friable soil, in areas clear of vegetation (Figure II.3.43). *T. waltoni* Arnold is exceptional, having been found to be nesting in old or abandoned burrows of *Aethiopicodynerus insignis* de Saussure (Vespidae, Eumeninae) excavated in non-friable soil. The use of a sand-filled snail shell by *T. hermia* was recorded once only and may be exceptional, however, seven species of *Quartinia* (Vespidae, Masarinae) nest in this situation. It is considered that in windswept desertic areas sand trapped in snail shells offers a more stable nesting site than do open sandy areas.

Nest structure

The nests of *T. albocinctus* (Figure II.3.44), *T. fugax*, *T. panzeri pentheri* are typical for the genus. They consist of a short sloping entrance burrow giving rise to one to three lateral shafts each terminating in a cell.

That of *T. waltoni* nesting in a pre-existing burrow is limited by the nature of the burrow.

Figure II.3.43.—*Tachysphex* sp. excavating burrow.

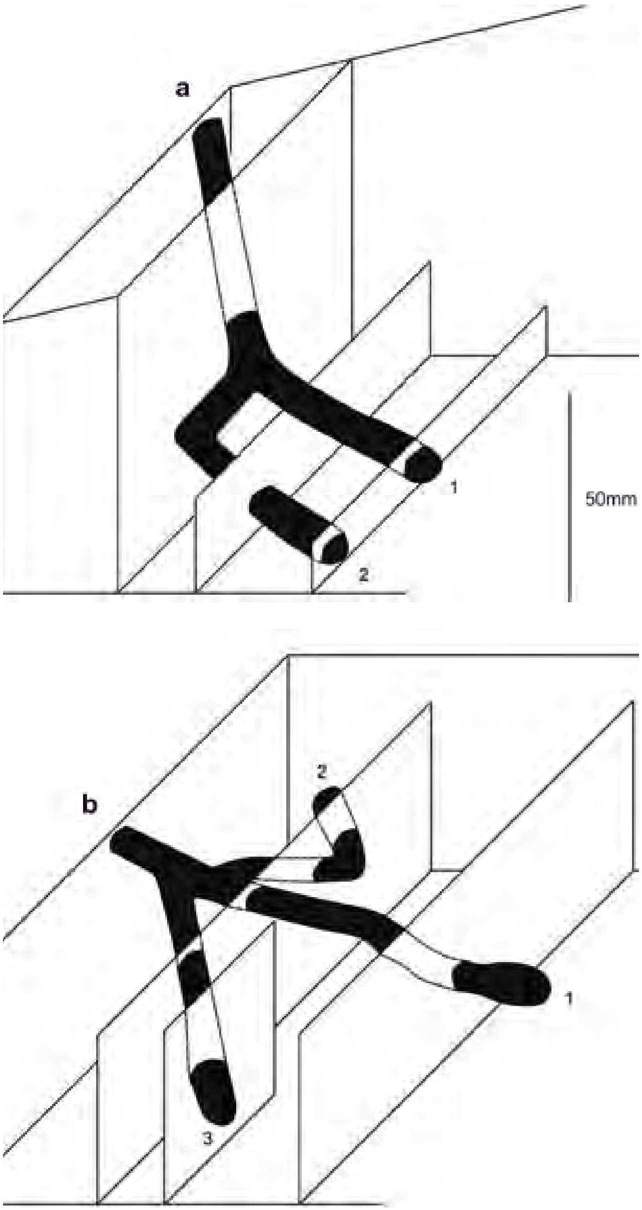


Figure II.3.44.—a. and b. *Tachysphex albocinctus* (Lucas), diagrammatic vertical plans of two nests.

Method of construction

Most *Tachysphex* are typical sand nesters, raking the sand out of the nest to a short distance from the nest entrance where it acculumulates to form a low tumulus. After excavating the main shaft, first lateral shaft and cell, hunting takes place. Before leaving the nest, *T. albocinctus* rakes sand into the entrance, creating a temporary seal, whereas the other species leave the nest entrance open.

After a cell has been supplied with provision and an egg, the lateral shaft is filled with sand and, usually, a second lateral shaft is initiated. No nests were found with more than three cells.

T. waltoni, when nesting in burrows of *Aethiopicodynerus insignis*, clears out and sometimes deepens the burrow. The debris removed in the process is deposited in a pile to one side of the nest entrance. Some earth is placed in the bottom of the burrow and compacted. Hunting then takes place. After provisioning the cell and oviposition, the cell is sealed with compacted earth.

Provisioning and oviposition

After locating a prey insect, it is stung. The effect of the venom is to deeply and permanently paralyse the prey, very different from that of *Larra* and *Liris*. The prey is carried to the nest held beneath the wasp, dorsum up and facing the direction of travel, progression being by walking, short hopping flights or full flight apparently depending upon the weight of the prey (Figure II.3.45). *Tachysphex albocinctus*, on reaching the nest, retains her hold on the prey whilst swiftly clearing the sand of the temporary closure and enters the nest rapidly. The other two species, which do not make a temporary closure, deposit the prey next to the nest entrance, enter the nest, possibly to check that no foreign insect has entered nor debris fallen in, turn around and pull the prey in head first. Cells are provisioned with one to several prey depending upon their weight. Oviposition is usually onto the heaviest prey although this is not always the case. There seems to be no correlation between order of placement of prey and upon which prey the egg will be deposited.

Tachysphex waltoni, when nesting in burrows of *Aethiopicodynerus insignis*, positions the prey grasshoppers in the

Figure II.3.45.—*Tachysphex aethiopicus* Arnold transporting prey grasshopper.

burrow head downwards, that is, with their heads towards the inner end of the cell.

Associates

A sarcophagid fly was seen following nesting *T. albocinctus* that was carrying its mantid prey and entering the nest. The three mantids removed from the nest during excavation were found, the next day, to have been completely hollowed out by 12 dipterous maggots (Gess & Gess, fieldnotes 1978).

Tachytella Brauns

Tachytella is a southern African endemic genus with only three described species (Pulawski 2010). These are *T. aureopilosa* Brauns from the southeastern Nama-Karoo, *T. heliophylla* Pulawski from the desert, Nama-Karoo, Savanna interface in northwestern Namibia and *T. nama* Pulawski from the Namaqualand Klipkoppe. Nothing appears to be known of the nesting biology of *Tachytella*, however, the presence in the female of a foretarsal rake and of a pygidial plate is indicative of sand nesting. *Tachytella aureospila* Brauns on the farm Hilton, Grahamstown, is believed to be nest in alluvial sand (Gess 1981).

Tachytes Panzer

Tachytes (example *Tachytes observabilis* Kohl Figure II.3.46) is a worldwide genus, found throughout the temperate and tropical areas. It is very similar in appearance to *Tachysphex* and consequently these two genera may easily be confused. Wojciech Pulawski (2010) lists 296 species of which around 38 species have been recorded from southern Africa. There seem to be no records of *Tachytes* nesting in southern Africa, however, it seems from accounts of the nesting of this genus elsewhere in the world that its nesting behaviour is similar to that of *Tachysphex* and that the use of pre-existing cavities as a starting point for nest excavation is not uncommon. Recorded prey are mostly grasshoppers, although two species are known to take pygmy crickets and rather surprisingly a species in Asia takes lepidopterous larvae (Gusskovskij 1952). This aberrant behaviour was confirmed based on observations by Pulawski given in a letter from him to Menke (cited in Bohart & Menke 1976).

Figure II.3.46.—*Tachytes observabilis* Kohl.

Subtribe Larrina

Dicranorhina Shuckard

Dicranorhina is a relatively small Old World genus. Of the 15 species recognised (Pulawski 2010) apparently only two occur in Africa, only one of which is known from southern Africa. The nesting biology of *Dicranorhina*, a genus closely related to *Liris* is reviewed by Bohart & Menke (1976). Nothing seems to have been recorded concerning the two African species. From accounts of nesting elsewhere it seems that nests are multicellular, excavated in protected situations and the prey are crickets. Of particular interest is the suggestion by Dupont & Fransen (1937) that offspring from a nest may continue to use and enlarge the maternal nest.

Larra Fabricius

Wojciech Pulawski (2010) lists 63 species of *Larra*, of which around ten species have been recorded from southern Africa. Little information is available on the ethology of *Larra* in Africa although wasps of this genus may commonly be seen sunning themselves and apparently hunting in sandy places. What is known for the genus from elsewhere in the world is reviewed by Richard Bohart & Arnold Menke (1976).

Larra preys upon mole crickets (Gryllotalpidae). A nest is not constructed. The wasp searches the soil surface for mole cricket burrows. After locating one, she either enters using the entrance or digs down to one of the passageways. The cricket usually leaves the burrow and is pursued by the wasp. The cricket, having been captured, is stung into temporary paralysis. The wasp egg is small, reminiscent of those of parasitoids. It is laid on the thorax, usually on the venter and between the legs. Paralysis of the cricket lasts only a few minutes after which it burrows into the ground. Pupation occurs in the host's burrow. The behaviour of *Larra* is very similar to that of *Chlorion*, the only other pseudo-parasitoid known in the spheciform Apoidea.

Liris Fabricius

Compared with *Larra*, *Liris* is a relatively large genus with 314 species recognised (Pulawski 2010), with ca. 30 species being recorded from southern Africa.

Liris species, like *Larra,* are commonly seen sunning themselves or hunting, particularly in sandy places inland and on beach dunes. The Gess family has collected a number of species carrying prey. In all instances, the prey were crickets of the family Gryllidae (examples Figure I.3.44.b & c). Richard Bohart & Arnold Menke (1976) suggest that crickets of the family Gryllidae may be the exclusive prey of this genus. Arnold (1945), however, stated that in

Madagascar camel crickets, Gryllacridae, are used by *L. brunnipennis* and that a mole cricket, Gryllotalpidae, was associated with one specimen of *L. incerta* although this seems to have been exceptional as he further stated that gryllids were the common prey of this species. It seems that as a rule *Liris* species prefer to use pre-existing burrows or galleries in the soil for nesting purposes but that, if no suitable cavities are available, they will excavate their own burrows. However, Williams (1928) records the excavation of extremely deep branched multicellular nests by *Liris haemorrhoidalis* Fabr. in Queensland, Australia. This is a widespread species occurring in the Mediterranean Region, Africa, Middle East, West India, Sri Lanka and Australia. It has been collected with prey, *Gryllus bimaculatus* De Geer, near buildings in the Kimberley district, Northern Cape Province by David Gess (voucher specimens in collection of Albany Museum), making Williams' account of interest in the context of this book. The burrows of *L. haemorrhoidalis* investigated by him were 5.5 and 6.5 feet long and reached a depth of 4.5 feet—remarkable feats of excavation both by the wasp and by the investigator! In the most extensive burrow excavated by Williams, one side branch terminated apparently in two cells and a second branch gave forth eight or nine cells. The cells had been provisioned with one or more crickets each. The egg had been affixed on the ventral surface between the first two pairs of legs. The crickets were found to be fairly active and alert, the effects of the stings having to a large degree worn off.

The relative size of wasp and prey was indicated by the weights of *Liris* (*Leptolarra*) *solstitialis* (Smith) and its wingless cricket prey captured by Harold Gess on the farm Hilton. The wasp weighed 156 mg and the cricket 326 mg, twice the weight of the wasp.

Tribe Miscophini

Wojciech Pulawski (2010) lists 16 genera in the Miscophini. Of these only two genera, *Lyroda* and *Nitela*, are cosmopolitan. There is a high degree of endemism. Of the ten genera occurring in southern Africa, five are widely distributed, *Lyroda* Say, *Miscophus* Jurine, *Nitela* Latreille, *Paranysson* Guerin-Meneville and *Solierilla* Spinola, and five are endemic, *Miscophoides* Brauns, *Miscophoidellus* Menke, *Namiscophus* Lomholdt, *Saliostethus* Brauns and *Saliosethoides* Arnold. Some species, for example *Saliosethoides saltator* Arnold which is 2–4 mm long, are among the smallest spheciform wasps known. None is more than medium sized.

On the whole the biology of this tribe is not well known and of the species occurring in southern Africa, nesting has apparently been recorded for only two species, *Nitela merceti* Brauns (Brauns 1911) and *Nitela cf. braunsi* Arnold (Gess & Gess fieldnotes and voucher specimens 1987). Bohart and Menke (1976) reviewed known aspects of their biology. Prey taken by the tribe as a whole are diverse, namely Hemiptera, Homoptera, Psocoptera, Diptera and Lepidoptera (larvae), although at the taxonomic rank of genus they show considerable selectivity.

Orthoptera of the families Gryllidae and Tetrigidae are taken by *Lyroda*; Hemiptera and nymphal pentatomids are taken by *Paranysson* and spiders are taken by *Miscophus*. These three genera nest in the ground in multicellular nests excavated by themselves or in pre-existing cavities. Each cell is provisioned with several prey. Even when not carrying prey, they are readily distinguished as they differ considerably in appearance. *Lyroda* are elongate wasps with slender legs and unspecialised wing venation. *Paranysson* are compact and rather bee like and have a distinctive colour pattern, head and thorax black, gaster and legs reddish brown and wings infuscate. *Miscophus* are sombre wasps with short wings, usually infuscate apically, and a tendency to reduction or loss of some veins. In keeping with their short wings, they seem to spend most of their time walking and are often seen in company of ants to which they show a superficial resemblance.

Psocoptera seem to be the predominant prey of *Nitela* although *N. spinolae* is known to use Aphididae and Psyllidae. Hemiptera of various families seem to be the more usual prey of *Solierilla* although some species take grasshoppers and one species takes Psocoptera. These two genera nest in pre-existing cavities, mostly above ground in plant tissue, though some species of *Solierilla* use abandoned burrows in the ground. *Nitela* species are readily separated from those of all the other miscophine genera by their reduced wing venation. They are largely black, unlike the *Solierilla* species, which like the closely allied *Paranysson* species, are colourful, the gaster and the last pair of legs often being partly or all red with yellow markings on the thorax and legs being common.

Nitela Latreille

Nest situation

The single nest of *N. cf. braunsii* Arnold was constructed in a trapnest with an aperture laterally at mid-length. It had been positioned vertically amongst the dry inflorescences of *Berkheya* sp. growing in the bed of a stream in the hills in Goegap Nature Reserve, Springbok. It is likely that the natural nesting cavities were in the *Berkheya* inflorescence stems, which were being used for nesting by *Xylocopa sicheli* Vachal (Anthophoridae).

Nest structure

The nest consisted of two linearly arranged cells, the walls of which were the walls of the trapnest. The cells were both sealed with loose plugs constructed from short lengths of dry twig, bark and seed heads. As the nest builder was present in the nest, it had clearly not been completed. Hans Brauns (1911) recorded clay as the material used by *N. merceti* Brauns for closing its nest.

Provision

The provision of both *N. cf. braunsi* (Figure I.3.48) and *N. merceti* consisted of a number of Psocoptera.

Miscophus Jurine

Our only record for the prey of *Miscophus* is for *M. ichneumenoides* Arnold which we captured carrying a salticid spider over salty sand in the bed of the Swakop River, a short distance inland from Swakopmund (Gess & Gess and voucher specimens 1998).

Tribe Palarini

The Palarini, constituted of two genera *Palarus* Latreille with 34 species and *Mesopalarus* Brauns with a single species, *M. mayri* Brauns, occur only in the Old World (Pulawski 2010).

Palarus species mass provision with Hymenoptera of many families, Ichneumonidae, Leucospidae, Tiphiidae, Scoliidae, Mutillidae, Formicidae (alates), Pompilidae, Vespidae (Eumeninae, Masarinae and Polistinae), Sphecidae, Crabronidae, Colletidae, Andrenidae, Halictidae, Megachilidae and Apidae. In exceptional cases, they also provision with Diptera, Stratiomyidae, Bombyliidae and Syrphidae (Pulawski & Prentice 2008).

There are very few prey records for *Palarus* species in southern Africa. *Palarus oneili* Brauns has been recorded as having taken a female *Meria* sp. (cited as *Myzine*) (Tiphiidae) and small bees by Hans Brauns (1911). Recently two females were taken with two species of *Bembecinus*, *B. haemorrhoidalis* (Handl.) (Figure I.3.63) (Gess & Gess fieldnotes and voucher specimens) and *B. cinguliger* (Smith) (Weaving, voucher specimens in Albany Museum). *Palarus latifrons* Kohl (Figure I.3.66.c) was recorded by Hans Brauns (1911) to be preying in their hundreds on honeybees at hives. This behaviour has resulted in their being commonly known to beekeepers as the 'banded bee pirate'. Hans Brauns states that other Hymenoptera are taken only exceptionally, a single male *Elis* (a campsomerine scoliid), a female pollen wasp, *Ceramius capicola* Brauns, and small bees having been recorded by him. It was therefore not surprising to us that, when investigating the nesting of this species, the prey which we took from these wasps were all *Apis mellifera* L.

Most recorded observations on nesting behaviour have been for *P. variegatus* (Fabricius), a species occurring in Europe, western Asia and China. The present is for *P. oneili* Brauns of the *variegatus* group (Gess & Gess fieldnotes and voucher specimens 1982/83) and *P. latifrons* Kohl of the *latifrons* group (Gess & Gess fieldnotes and voucher specimens 1977/78, 1982/83). Both species were investigated on the farm Hilton, near Grahamstown, where they occur in small numbers only.

Nesting situation

At Hilton, *P. oneili* and *P. latifrons* were nesting in a sand pit dug in friable alluvial sand on the flood plain of a usually almost dry watercourse.

Nest structure

Only one burrow of *P. oneili* was found. Like that described for *P. variegatus*, it followed a somewhat serpentine path to a single cell. The burrow entrance was in the centre of a tumulus of excavated soil. It sloped downwards to a depth of only 50 mm before turning up, down, up again to within 4 mm of the soil surface and finally down to end in a cell 30 mm deep and 200 mm from the entrance.

Four nests of *P. latifrons* were investigated. The burrow pattern of this species was found to be somewhat different. In all of the nests the burrow was found to slope steadily downwards for about half its length and then to turn abruptly through 45–90 degrees and then to continue steadily downwards to end in a cell at a depth of 13–70 mm (Figure II.3.47). In one of the nests, there were two cells. The first cell was sealed and the shaft filled with sand up to the angle from which a secondary shaft led to the second cell.

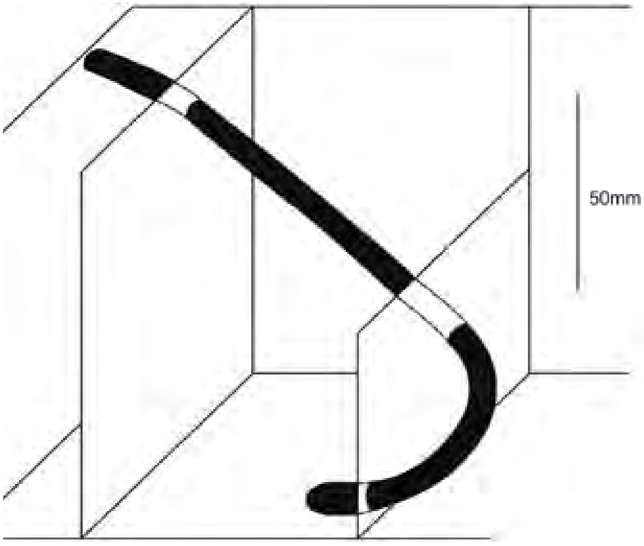


Figure II.3.47.—*Palarus latifrons* Kohl, diagrammatic vertical plan of nest.

Provisioning

Prey was carried to the nests in flight by *P. latifrons*. A wasp arriving at a nest entrance put down her prey, entered the nest, turned around and, reappearing, pulled the prey in headfirst.

Only two of the cells of *P. latifrons* were sealed and so only these could be considered to be fully provisioned. One of these cells contained two prey and an egg, and the other one prey and an egg. The egg was attached just behind a prothoracic coxa, in one instance the right and the other the left.

Mesopalarus Brauns

Nothing is known of the nesting or prey of the sole species of the genus, *M. mayri* Brauns, known from southwestern South Africa and from southwestern Namibia (Gess 1996; Pulawski & Prentice 2008). The latter authors speculate that it may excavate burrows in hard soils or may use abandoned nests of other aculeates. In December 1987 and November 1994, we found this species visiting flowers of *Gomphocarpus filiformis* (E.Mey.) D.Dietr. (= *Asclepias buchenaviana* Schinz) (Apocynaceae, formerly Asclepiadaceae) growing in a dry, sandy drainage channel on the farm Tierberg, near Prince Albert in the southern Great Karoo (Figure I.3.20.a). Despite careful search we were, unfortunately, unsuccessful in finding its nests. As we collected ten males and only one female during the first visit and two males and only one female on the second visit, we may have been there too early in the season on both occasions.

Tribe Trypoxylini

The tribe Trypoxylini consists of six genera of which two, *Trypoxylon* Latreille and *Pison* Jurine, occur in Africa. Both

Figure II.3.48.—*Pison* sp. nest in wooden trap nest, showing pupal cocoons.

are cosmopolitan genera, of the 631 species of *Trypoxylon* recognised (Pulawski 2010) around 75 occur in the Afrotropical Region, the largest number for any region in the Old World. Australia has the fewest, only one or two. On the other hand, of the 196 species of *Pison* recognised, about a third are found in Australia and only around 14 in the Afrotropical Region.

The prey of both genera seems to be, without exception, spiders. Both genera work all with mud. A South American species of *Pison* was observed (Janvier 1976 in Bohart & Menke 1976) nesting in burrows excavated by itself in a river bank (interestingly the cells were in linear series) and species of both *Trypoxylon* and *Pison* outside the Afrotropical Region have been observed building free mud nests, however, the majority of species nest in pre-existing cavities. *Trypoxylon* is a familiar wasp around human habitations and due to the frequent use of keyholes for nesting by some species they are commonly known as 'keyhole wasps'.

Very little seems to have been published on the nesting of *Trypoxylon* and *Pison* in the Afrotropical Region (Taylor 1968; Gess & Gess 1975; Gess 1981).

Nest situation

On the farm Hilton, Grahamstown, *Pison allonymum* Schultz females was observed inspecting various holes in the ground, including old *Aethiopicodynerus insignis* burrows, an old *A. insignis* burrow being used for nesting by *Tachysphex waltoni*, a turreted *Bembecinus cinguliger* burrow and several *Bembecinus oxydorcus* burrows. A female carrying an immature spider (Salticidae) held beneath her was observed flying low over the *B. oxydorcus* nesting area apparently trying to locate its nest but probably unable to do so as a result of the activities of the observers.

Using trapnests, tied at heights of 0.5–1.0 m above ground to horizontal branches of shrubs, we obtained 26 nests of a species of *Trypoxylon* and eight of *Pison montanum* Cameron. It is therefore to be expected that the natural nests of these species are to be found in pre-existing cavities in plants.

Taylor (1968) made some observations on the nesting of *P. transvaalensis* Cameron in trapnests in the form of glass tubes inserted into blocks of wood in Hilton, KwaZulu-Natal and we found nests of this species in cells of old *Polistes* nests attached to a building in Grahamstown (Gess 1990).

Nest structure

The nesting of *P. montanum* and of *Trypoxylon* sp. in trapnests on the farm Hilton, Eastern Cape, is presented in the form of a comparative account. A preliminary plug had been constructed in all of the *P. montanum* nests and in just over half of the *Trypoxylon* sp. nests. This plug consisted of a thin layer of mud filling in the corners and rounding off the end to form a smooth concave surface. In no instance was an empty space left between the end of the boring and the preliminary plug. Intercalary cells and vestibular cells were common but not always present in nests of *Trypoxylon* sp. and absent from all those of *P. montanum*. Cells of the somewhat longer and slender *Trypoxylon* sp. tended to be longer than those of the shorter and broader *P. montanum* in 6.4 mm trapnests. The average length of the cells of the former was 17.6 mm (average of 28) and of the latter was 12 mm (sample of 32). The cell closures and final closures were all constructed from mud and ranged between 2–5 mm in thickness. All were concave on their outer faces and convex on their inner faces (Figures II.3.48 & 49.c).

The nests of *P. transvaalense* in glass tubes were a linear series of cells with mud partitions and a mud plug. Clearly, the number of cells is dependent on the length of the cavity. The *Polistes* cells utilised by these wasps constituted a single cell each, capped with mud.

Provisioning and oviposition

Cells are provisioned with a variable number of small spiders (Figure II.3.49.b).

The cells of *Trypoxylon* on the farm Hilton were provisioned with 5–11 small spiders of various species of Lycosidae, including *Hippasa* sp., Pisauridae, *Euphrosthenops* sp. and Araneidae (= Argiopidae), including *Araneus* spp. and *Larinia* sp.

The cells of *P. montanum* contained 7–47 small spiders, various species of Araneidae (= Argiopidae) and those of *P. transvaalense* in glass tubes up to 17 immatures of a species of *Theridion* (Theridiidae).

The egg of both species of wasp is attached to the abdomen of one of the prey spiders with the anterior end of the egg facing towards the spider's posterior end.

Life history

The cocoons of *Trypoxylon* sp. and *P. montanum* are readily distinguished, those of the former are longer, narrower and of more even breadth than those of the latter which are relatively shorter and somewhat bulbous at the anterior end (Figure II.3.48 & 49.c). The cocoons of *P. transvaalense* in the *Polistes* cells were brown, very fragile, brittle and had the end towards the cell opening expanded and flattened.

Both *Trypoxylon* sp. and *P. montanum* are at least bivoltine as adults emerged from some of the nests during the same summer that the eggs were laid and adults are only present during the summer months.

Sheltering

Nesting females of *P. montanum* were found sheltering in incomplete nests during inclement weather and would therefore undoubtedly shelter in their nests at night.

Subfamily Pemphredoninae

The pemphredonids are small to minute wasps which, because of their diminutive size, are generally overlooked in the field and are consequently poorly represented in most collections.

Of the 38 genera, grouped in four tribes, recognised (Pulawski 2010) around ten are represented in Africa. These include *Odontosphex* Arnold, the single genus in the Odontosphecini; *Ammoplanus* Giraud (=*Ammoplanellus* Gussokovskij), *Carinostigmus* Tsuneki, *Diodontus* Curtis, *Polemistus* de Saussure, *Spilomena* Shuckard and *Xysma* of the 25 genera grouped in Pemphredonini; and *Mimesa* Shuckard, *Psen* Latreille and *Psenulus* Kohl of the 11 genera grouped in the Psenini. In southern Africa, *Psenulus* is the best represented with around 12 species, the other genera being represented by one to six species. With time and careful collecting, further African species will undoubtedly be discovered.

The single southern African species of *Odontosphex*, *O. damara* Pulawski, was described from two females and a male from 38 km west of Khorixas in northwestern Namibia where it was collected by Wojciech Pulawski and Maximilian Schwarz (Pulawski 1991). Since then we have collected this species at three sites, one 24 km west of Palmwag and one near Uis, both in northwestern Namibia, and at Nomitsas in southwestern Namibia (Gess & Gess fieldnotes and voucher specimens 1997, 1998 and 1999).

Flower visiting

Our specimens of *O. damara* were collected from the flowers of *Euphorbia glanduligera* Pax (Euphorbiaceae) where they were undoubtedly imbibing nectar from the extrafloral nectaries.

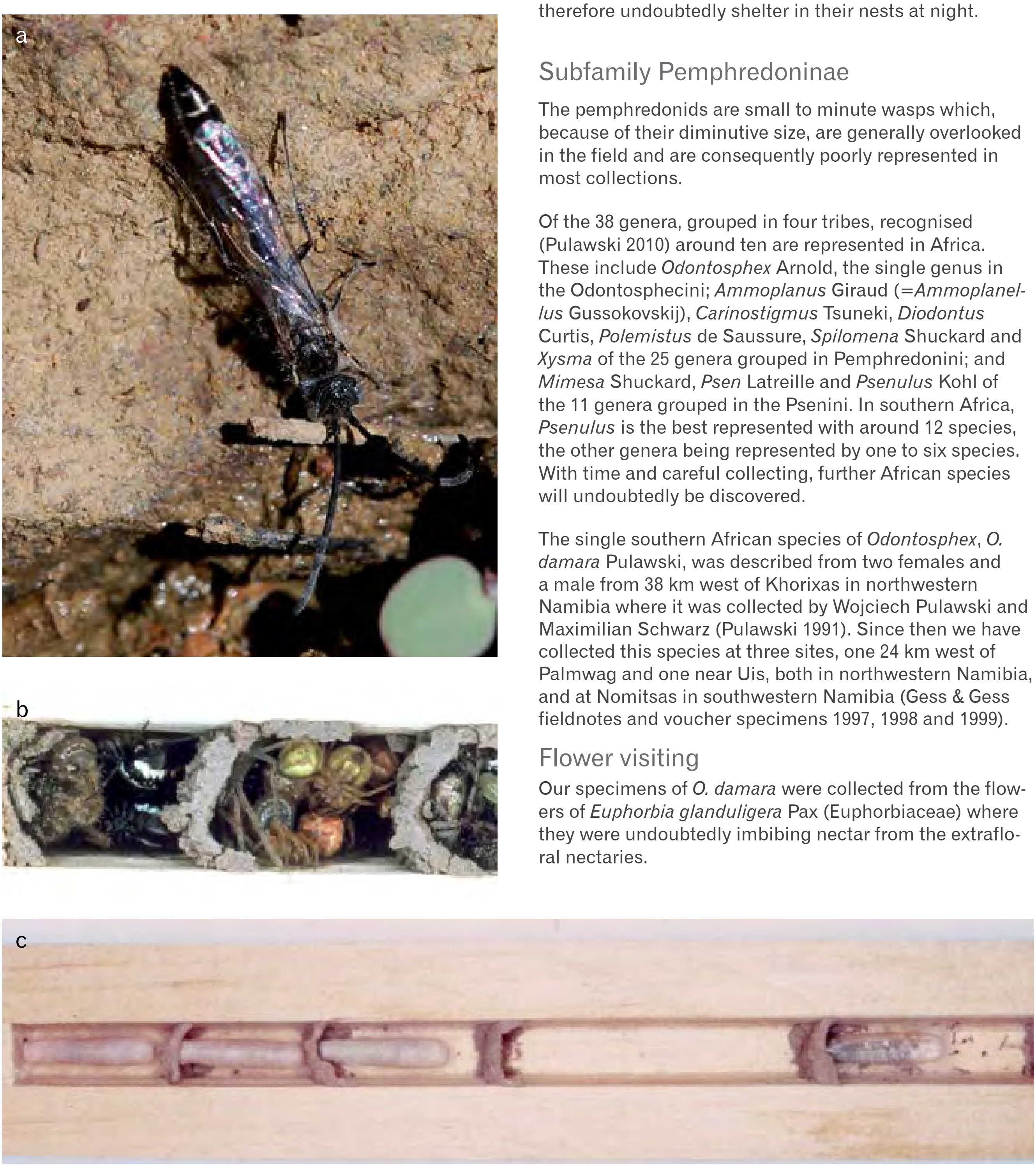


Figure II.3.49.—a.–c. *Trypoxylon* spp. a. imbibing water; b. three cells of a nest in a wooden trap nest, showing spider provision and larvae; c. nest in wooden trap nest, showing pupal cocoons.

Other Pephredoniae collected by us from flowers are: one female and one male *Psenulus* (Gess sp. A) from flowers of *Deverra denudata* (Viv.) Pfisterer & Podlech (Apiaceae) near Helmeringhausen in southwestern Namibia; one female and two male *Ammoplanus consobrinus* Arnold from *Galenia papulosa* (Eckl. & Zeyh.) Sond. (Aizoaceae, non-Mesembryanthema) at Swakopmund on the northwestern coast; one female *Diodontus atreatulus* Taschenberg from *Cotula* (Asteraceae) in the Richtersveld; and four male *Diodontus saegeri* Leclercq, two from *Psilocaulon salicornioides* (Pax) Schwantes (Aizoaceae, Mesembryanthema) at Swakopmund and two from *Deverra denudata* from Helmeringhausen.

Nesting

With regard to the African species, published observations appear to be limited. Hans Brauns recorded *Psenulus capensis* Brauns nesting in the culms of *Phragmites* reeds near Port Elizabeth (Brauns 1899). George Arnold recorded *Carinostigmus gueinzius* (Turner) (as *Stigmus rugosifrons* Arnold) and *Spilomena stevensoni* Arnold nesting in the straws of thatch and *Ammoplanus rhodesianus* Arnold nesting in a sandy bank and in cracks in an old mud wall in Zimbabwe (Arnold 1924).

The synopsis given below for the genera occurring in Africa is therefore mostly in the form of generalisations compiled from often rather fragmentary accounts concerning species from elsewhere in the world (see Bohart & Menke 1976).

Depending upon the genus, nesting may take place either in burrows excavated by the wasps themselves or in pre-existing cavities. Burrow excavation in soil and occasionally in rotten wood in stumps has been recorded for species of the genera *Mimesa*, *Psen* and *Diodontus* which characteristically have the female foretarsus furnished with a rake. Use of pre-existing cavities in the form of hollow stems (including thatch), the abandoned borings of various beetles in decayed wood, wooden posts, structural timber and even furniture, and also occasionally in the form of holes in earthy banks is recorded for species of *Psenulus*, *Polemistus*, *Carinostigmus*, *Spilomena* and *Ammoplanus*. These genera, in contrast to the above listed group of three genera, characteristically lack a rake on the female foretarsus. Species of *Ammoplanus*, which are as little as 2 mm in length and are the smallest spheciforms in southern Africa, similarly lack a foretarsal rake and most likely also nest in pre-existing cavities. A species of *Xysma* has been recorded entering beetle borings in which it has been suggested that it excavated galleries in the beetle frass contained within them. This would explain the apparent inconsistency of a wasp bearing a foretarsal rake nesting in a pre-existing cavity.

The nests of all the listed genera appear to be multicellular and each cell is provisioned with numerous small prey which are transported in flight, held in the mandibles. The prey taken is drawn from two insect orders, the Homoptera and Thysanoptera. Thus small plant sucking bugs are taken by *Mimesa*, *Psen*, *Psenulus*, *Diodontus*, *Polemistus* and *Carinostigmus*, the first three choosing leafhoppers amongst others, the last three specialising on aphids. Spilomena takes both plant sucking bugs and thrips, whereas *Xysma* and *Ammoplanus* take only thrips.

Subfamily Philanthinae

Of the four tribes of Philanthinae, the two largest, Cercerini and Philanthini, are represented in southern Africa by *Cerceris* Latreille and *Philanthus* Fabricius respectively. The remaining six genera are known only from the northern hemisphere.

Flower visiting

For southern Africa, flower visiting records were assembled for 25 species of *Cerceris* visiting 13 families of plants and eight species of *Philanthus* visiting 16 families of plants. This suggests that *Philanthus* is more polyphagous than *Cerceris* (Gess & Gess 2003).

Based on the percentage of species visiting them, the plant families most favoured by *Cerceris* are Fabaceae (Mimosoideae) 56%, Apiaceae 44% and Celastraceae 28%. Also visited are Fabaceae (Papilionoideae) and Asteraceae, each 16%; Zygophyllaceae and Apocynaceae (Asclepiadaceae), each 12%; and Amaranthaceae, Aizoaceae (Mesembryanthema), Aizoaceae (non-Mesembryanthema), Lamiaceae, Molluginaceae, Ebenaceae, Campanulaceae and Scrophulariaceae (Selagineae), each fewer than 10%.

Based on the percentage of species visiting them, the plant families most favoured by *Philanthus* are Asteraceae 63%, Apiaceae 50%, Fabaceae (Papilionoideae) and Molluginaeae and Aizoaceae (Mesembryanthema), each three species 38%. Also visited are Zygophyllaceae, Apocynaceae (Asclepiadaceae), Amaranthaceae, Aizoaceae (non-Mesembryanthema), Lamiaceae, Ebenaceae, Celastraceae, Scrophulariaceae (Selagineae), Boraginaceae (Hydrophyllaceae), Brassicaceae (Capparaceae), Euphorbiaceae, Malvaceae (Sterculiaceae) and Proteaceae, each one or two species.

Cerceris Latreille

The genus *Cerceris* (example Figure II.3.50) is cosmopolitan in its distribution and with 870 species, more than 80 from southern Africa, recognised (Pulawski 2010) is the largest genus of the spheciform wasps. Nesting has been studied in North America, South America, Asia, Australia and Europe. All species studied are ground nesting and provision their young with insect prey—Coleoptera or Hymenoptera being favoured according to species. The nest consists of a multicellular burrow with a vertical shaft, giving rise to secondary shafts each of which terminates in a cell. The nest entrance is characteristically surmounted by a tumulus of 'sand sausages', the products of nest excavation. *Cerceris* is exceptional in that several prey are accumulated in a cache positioned within the shaft before being moved to a cell.

The nesting of *Cerceris* in the Afrotropical Region follows the general pattern for the genus (Gess 1980a & 1981). On the farm Hilton, west-northwest of Grahamstown, the authors investigated nineteen sympatric species in relation to frequency of occurrence, nature of nesting sites and prey. The results of this investigation together with a discussion have been presented (Gess 1981).

Nest situation

The characteristic tumulus of 'sand sausages' is a familiar sight in bare areas of friable soil on roadsides, in dry wa-

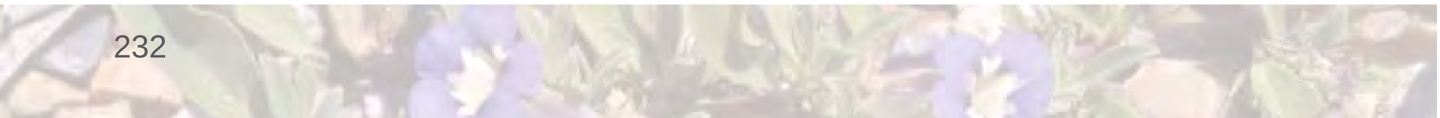


Figure II.3.50.—*Cerceris* sp. visiting flowers of Asteraceae.

tercourses, on floodplains and relatively stable vegetated coastal dunes. On the farm Hilton, nests of ten species were located. 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, although in sandy situations a layer of loose material sometimes overlay the firm underlying sand. Six species were found to nest in sandy alluvial soil and four other species in disturbed clayey soil. The nests in sand ranged markedly in depth between species so that for the deeper (in excess of 500 mm) nesting species the depth of sand would be a limiting factor.

Nest structure

The nest consists of a multicellular burrow with a vertical shaft, giving rise to secondary shafts each of which terminates in a cell. The nest entrance is characteristically surmounted by a tumulus of 'sand sausages', the products of nest excavation.

Method of excavation

Cerceris is unusual amongst the nesters in friable soil in that the main shaft is excavated vertically rather than sloping. The products of excavation are pushed up and out of the burrow by the wasp's reversing up the burrow, using her pygidium to push the soil out behind her in such a way that it collects over the entrance to form a tumulus of 'sand sausages'.

Provisioning

The available records of prey, Coleoptera and Hymenoptera, taken by *Cerceris* in southern Africa are presented in tabular form (Table 11) (examples of Coleoptera, Figures I.3.53–56 and of Hymenoptera, Figures I.3.58–62, 64 & 65). As a general rule *Cerceris* species are highly prey-specific though there are exceptions, for example, *C. holconota* Cameron, the recorded prey of which is derived from six families of Hymenoptera.

The prey is not immediately taken to a cell but is accumulated in a cache some distance below the ground surface before being moved into cells. It is of interest that a mixture of prey genera was on occasion present at one time, e.g. a cache of *C. holconota holconota* contained a single specimen each of three genera of tiphiids, *Anthobosca*, *Braunsomeria* and *Meria* (Gess & Gess fieldnotes and voucher specimens 1982).

Associates

Satellite flies were frequently observed following prey bearing *Cerceris* spp.

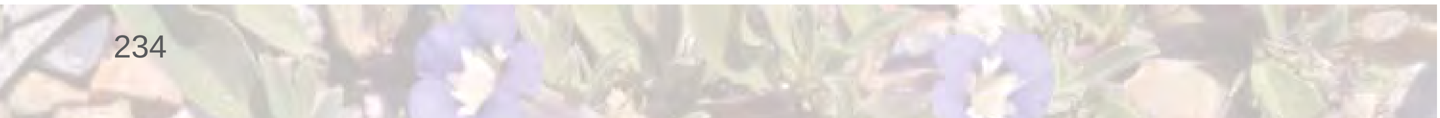
Philanthus Fabricius

Philanthus is well represented in the Afrotropical, Palaearctic, and Nearctic Regions. It is known from a small number of species from the Oriental Region, in the Neotropical Region only from Cuba and Central America, and is unknown from Australia. Of the 137 species recognised (Pulawski 2010) around 14 are known from southern Africa. They prey on bees or other Hymenoptera. The best-known and probably most studied species is *P. triangulum* (Fabricius) (Figure II.3.51). It is widespread in Europe and Africa, including southern Africa and notorious as a predator of honeybees. This behaviour has earned it the name beewolf and has resulted in all species of *Philanthus* being known as beewolves. In some areas of Europe and

Figure II.3.51.—a. and b. *Philanthus triangulum* (Fabricius): a. female; b. female at burrow entrance.

Table 11.—Some known prey taken by *Cerceris* species in southern Africa

***Cerceris* species**	**Prey species**	**Locality**	**Reference**
HYMENOPTERA wasps, bees, ants			
C. albifrons F. Smith	TIPHIIDAE: *Anthobosca* sp., 2♀; MUTILLIDAE: *Mimecomutilla renominanda* Bischoff, 1♂	Eastern Cape, Grahamstown, Hilton Farm	Gess & Gess field notes 1982 and vouchers
C. holconota holconota Cameron	BRACONIDAE: 1♀ BETHYLIDAE: 1♀ TIPHIIDAE: *Anthobosca* sp., 1♂; *Braunsomeria* sp., 5♂; *Mesa incisa* (Cameron), 2♀ MUTILLIDAE: *Dasylabris eunyce* (Péringuey) 1♂ FORMICIDAE: *cf. Camponotus* sp., 1♂ HALICTIDAE: *Lasioglossum* sp., 1♀	Eastern Cape, Grahamstown, Hilton Farm	Gess 1980a; Gess & Gess fieldnotes 1974/1975, 1975/1976, 1977 and vouchers
C. holconota holconota Cameron	TIPHIIDAE: *Anthobosca* sp., 3♀, 1♂; *Braunsomeria* sp., 3♂; *Meria* sp., 4♀; *Tiphia* sp., 1♀	Eastern Cape, Grahamstown, Hilton Farm	Gess & Gess fieldnotes 1982 and vouchers
C. lunigera Dahlbom	HALICTIDAE: *Halictus* sp., 1♀; *Lasioglossum* sp., 1♀	Eastern Cape, Grahamstown, Hilton Farm	Gess 1980a; Gess & Gess fieldnotes 1974 and vouchers
C. rufocincta polychroma Gribodo	TIPHIIDAE: *Anthobosca rufithorax* (Cameron), 1♀; *Tiphia* sp., 2♂ MUTILLIDAE: *Crestomutilla* sp., 1♂; *Dasylabroides caffra* (Kohl), 1♀, 3♂; *Psammotherma flabellata* (Fabricius), 2♂	Eastern Cape, Grahamstown, Hilton Farm	Gess 1980a; Gess & Gess fieldnotes, 1974, 1977/1978 and vouchers
C. rufocincta polychroma Gribodo	TIPHIIDAE: *Anthobosca* sp., 6♀, 4♂; *Meria* sp., ♂1; *Mesa incisa* (Cameron), 2♀; *Tiphia* sp., 2♀, 2♂ MUTILLIDAE: *Dasylabris eunyce* (Péringuey), 1♂; *Dasylabroides caffra* (Kohl), 1♂; *Psammotherma flabellata* (Fabricius), 1♂ BETHYLIDAE: 1♀ CRABRONIDAE: *Liris* sp., 1♂	Eastern Cape, Grahamstown, Hilton Farm	Gess & Gess field notes 1982 and vouchers
C. spinicaudata spinicaudata Cameron	COLLETIDAE: *Hylaeus* sp., 1♂	Eastern Cape, Kenton-on-Sea	Gess & Gess fieldnotes 1981/1982 and vouchers
C. spinicaudata spinicaudata Cameron	HALICTIDAE: 3 *Lasioglossum* spp., 5 ♀; *Nomioides* sp. (probably *N. halictoides* Blüthgen), 4♀	Eastern Cape, Grahamstown, Hilton Farm	Gess 1980a; Gess & Gess from nests of 3 ♀, fieldnotes 1974/1975 and vouchers
C. spinicaudata spinicaudata Cameron	HALICTIDAE: *Lasioglossum* sp., ♀	Eastern Cape, Grahamstown, Strowan Farm	Gess 1980a; C.F. Jacot Guillarmod 1972 vouchers
C. spinicaudata spinicaudata Cameron	HALICTIDAE: *Lasioglossum* sp., ♀	Lesotho, Mamathes	Gess 1980a; C.F. Jacot Guillarmod vouchers
C. spinicaudata spinicaudata Cameron	HALICTIDAE: '*Halictus*'		H. Brauns 1926
COLEOPTERA beetles			
C. bothavillensis Brauns	CURCULIONIDAE: *Leurops sublineata* Marshall	Lesotho, Mamathes	C.F. Jacot Guillarmod vouchers
C. chirindensis Arnold	CURCULIONIDAE	Zimbabwe	Arnold 1932
C. curvitarsis Schletterer	TENEBRIONIDAE: *Zophosis* sp.	Western Cape (Little Karoo), Oudtshoorn, Onverwacht Farm	H.W. Gess; Gess & Gess fieldnotes 1986 and vouchers
C. erythrosoma Schletterer	CURCULIONIDAE: *Tanymecus* sp.		Brauns 1911 also quoted in Gess 1980



***Cerceris* species**	**Prey species**	**Locality**	**Reference**
C. erythrosoma Schletterer	CURCULIONIDAE: *Tanymecus makkaliensis* Fahraeus 1; *Protostrophus* sp. (*cf. P. sceleratus* H. v. S.)	Lesotho, Mamathes	C.F. Jacot Guillarmod vouchers; Gess 1980a
C. erythrosoma Schletterer	CURCULIONIDAE: *Tanymecus trivialis* Fahraeus	Eastern Cape, Grahamstown, Hilton Farm	Gess & Gess fieldnotes 1982 and vouchers
C. languida languida Cameron	PHALACRIDAE: 34 *Olibrus* spp.	Eastern Cape, Grahamstown, Hilton Farm	Gess 1980a; Gess& Gess fieldnotes 1977/1978 and vouchers
C. latifrons latifrons Bingham	SCARABAEIDAE: Hopliini (Melolonthinae)	Zimbabwe	Arnold 1940 in Gess 1980
C. latifrons latifrons Bingham	SCARABAEIDAE: 11 Hopliini (Melolonthinae) from 3 nests	Eastern Cape, Grahamstown, Hilton Farm	Gess 1980a; Gess & Gess fieldnotes 1973, 1974/1975, 1977/1978 and vouchers
C. latifrons latifrons Bingham	SCARABAEIDAE: 3 Hopliini (Melolonthinae)	Eastern Cape, Grahamstown, Hilton Farm	Gess & Gess field notes 1982 and vouchers
C. multipicta F. Smith	CURCULIONIDAE: *Polyclaeis castaneipennis* Hust.	Limpopo, 30 km southeast of Hoedspruit	D.J. Brothers & C.F. Jacot Guillarmod 1978, vouchers
C. obscura Schletterer	SCARABAEIDAE: Melolonthinae	Eastern Cape, Grahamstown	E. McC. Callan pers. comm. in Gess 1980
C. obscura Schletterer	SCARABAEIDAE: 8 *Aldabera splendida* (Fabricius) (Melolonthinae)	Eastern Cape, Grahamstown, Hilton Farm	Gess & Gess fieldnotes 1982 and vouchers
C. tricolorata nigrifrons F. Smith	BUPRESTIDAE: *Sphenoptera* sp.	Zimbabwe	H. Brauns 1926 in Gess 1980a as *C. nigrifrons nigrifrons* Smith
C. tricolorata nigrifrons F. Smith	BUPRESTIDAE: 2 *Anthaxia splendida* Chev.; 11 *Anthaxia sexualis* Obern.; 1 *Chrysobothris dorsata* F.	Eastern Cape, Alexandria Forest	Gess & Gess fieldnotes 1981 and vouchers
C. oraniensis Brauns	CURCULIONIDAE: 5 *Protostrophus* sp. from 5 wasps	Eastern Cape, Grahamstown, Hilton Farm	Gess 1980a and Gess & Gess fieldnotes 1978 and vouchers
C. pearstonensis pearstonensis Cameron	CURCULIONIDAE: 1 *Protostrophus* sp.; 1 Curculionidae	Lesotho, Mamathes	C.F. Jacot Guillarmod vouchers, in Gess 1980
C. pearstonensis pearstonensis Cameron	CURCULIONIDAE:1 *Protostrophus* sp.	Eastern Cape, Grahamstown, Strowan Farm	Gess 1980a and Gess & Gess fieldnotes 1970 and vouchers
C. ruficauda ruficauda Cameron	CHRYSOMELIDAE: 26 Criocerinae	Eastern Cape, Grahamstown, Hilton Farm	Gess 1980a and Gess & Gess fieldnotes 1974 and vouchers

Egypt, populations of *P. triangulum* are known to become so numerous that they become a serious hindrance to beekeeping. Populations of 3 000 nesting *Philanthus* wasps are capable, in a single day, of capturing 30 000 honeybees.

Recent studies of the structure and functioning of the cephalic glands of *P. triangulum* and other Philanthinae have yielded some interesting results.

Kaltenpoth *et al.* (2006) recorded the presence of streptomycetes in the specialised antennal glands of 27 *Philanthus* species but the absence of endosymbionts in other genera of Philanthinae (including *Cerceris*). The bacteria appear to protect the beewolf larvae against infection by pathogens (Kaltenpoth *et al.* 2005). The streptomycetes are secreted in the subterranean brood cells and protect the larvae against mould fungi (Göttler *et al.* 2007).

Both females and males, at least of *P. triangulum*, have been shown to possess a postpharyngeal gland, for long assumed to be restricted to ants and to be associated with the maintenance of social integrity. Females of *P. triangulum* have been shown to use the hydrocarbons produced by the postpharyngeal gland to 'embalm' their honeybee prey to delay fungal infection and males to use the gland as a reservoir for the pheromone produced by the mandibular glands, used to scent-mark their territories (Göttler & Strohm 2008; Strohm *et al.* 2008). The male territory of *P. triangulum* has been found to be separate from and not to include the nesting area or resources used by the females. The pheromone is also considered a female attractant (Kroiss *et al.* 2010).

There seem to be few published records of the prey taken by *Philanthus* in southern Africa. Specimens in the Albany Museum with associated prey collected variously by Fred, Sarah, David, Harold and Robert Gess; Charles Jacot Guillarmod & Alan Weaving are as follows:

- *Philanthus capensis* Dahlbom with a honeybee from west of Clanwilliam.

- *P. histrio* Fabricius with a halictid bee, a species of *Halictus*, from Hilton (Figure I.3.65.a).
- *P. impatiens* Kohl and *P. promontorii* Arnold with honeybees from Mamathes, Lesotho.
- *P. loefflingi* Dahlbom with a honeybee (Figure I.3.66.a).
- *P. rugosus* Kohl with halictid bees of the genera *Thrinchostoma* and *Nomia* from Boknes, Eastern Cape.
- *P. triangulum* with honeybees from various localities (Figure I.3.66.b).

The considerable knowledge of the biology of the genus was briefly reviewed by Richard Bohart & Arnold Menke (1976) and updated in detail by Howard Evans & Kevin O'Neill (1988).

There appear to be no detailed studies of the behaviour of *Philanthus* in southern Africa, however, generalisations based on extraterritorial studies can be expected to apply.

Nest situation

All species for which nesting is known nest in small to large aggregations in friable soil, horizontal to vertical ground. Nests of *P. triangulum* on the farm Hilton were in friable clayey soil.

Nest structure

The nests consist of a sloping main shaft and several to many lateral shafts, each terminating in a cell. Some species excavate additional blind 'accessory burrows' which Evans & O'Neill (1988) suggest are primarily constructed to mislead hole seeking parasites.

Method of construction

The soil is loosened with the mandibles and swept out of the burrow by synchronous strokes of the front legs. The extracted soil accumulates in a mound, which may or may not be levelled from time to time during burrow excavation. Temporary closure of the nest prior to absences from the nest is practised by some but not all species. After a cell has been fully provisioned and the egg laid, the cell is closed and the secondary shaft leading to it is packed with soil. When the last cell has been provisioned and provided with an egg, both the secondary shaft leading to it and the main shaft are packed with soil. Some species level the remains of the tumulus and others leave it standing.

Provisioning and oviposition

Most species of *Philanthus* capture their prey on flowers but some species, including *P. triangulum*, also take honeybees at the entrance to the hive. On Hilton, *P. triangulum* was capturing its honeybee prey on flowers. The prey, if solitary bees or wasps, may be either male or female but only the workers of social bees, such as honeybees, are taken. The wasp's middle legs hold the prey during flight. On reaching the nest, the prey may be taken in directly (when the burrow is closed the soil being removed by the actions of the front legs) or deposited on the ground near the nest entrance and drawn in from inside the burrow.

Prey is not usually taken directly to a cell but is allowed to accumulate in the burrow at various points.

The prey are positioned in the cell, venter up. The egg is laid on the uppermost prey.

Life history

The egg hatches in about two days and larval development is completed within a week.

Male behaviour

Male *Philanthus* are known to excavate sleeping burrows. Territoriality is not uncommon. Territorial species have scent-producing mandibular glands. The scent is applied to plant stems in the territory. Territorial males will chase and fight with other males that enter their territories.

Associated organisms

Bee flies (Bombyliidae) have occasionally been reported.

Velvet ants (Mutillidae) and cuckoo wasps (Chrysididae) have often been sighted in nesting aggregations but there seem to be few records of confirmed associations.

Satellite flies (Sarcophagidae, Miltogramminae), depending on genus, follow females to their nests, wait at the nest entrances where they larviposit on the prey when *Philanthus* pause at the nest entrance or penetrate the nest closure.

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Apoidea: Apiformes

Family Colletidae

Colletids are morphologically diverse and worldwide in distribution. They are most diverse and abundant in temperate Australia and South America. Two of the four subfamilies, Colletinae and Hylaeinae, are represented in Africa south of the Sahara. Colletinae is represented by a southern African endemic genus, *Scrapter* Lepeletier & Serville with 43 species, and *Colletes* Latreille, a genus found in all temperate and tropical regions with the exception of the Indo-Australian Region, with 64 sub-Saharan species, around 54 represented in southern Africa. Hylaeinae is represented by the monospecific genus, *Calloprosopis* Snelling, and *Hylaeus* Fabricius, worldwide in distribution with 87 sub-Saharan species, around 54 species represented in southern Africa (Eardley *et al.* 2010; Eardley & Urban 2010).

Pollen carriage by Colletinae is in a well-developed scopa on the modified trochanter and femur of the hindlegs. That of the Hylaeinae, like that of the Masarinae, is internally in the crop.

Flower visiting

Our flower visiting records (Gess & Gess 2003) for the subfamily Colletinae show variation from possible oligophagy to broad polyphagy (Gess & Gess 2004). Records for 19 species of *Colletes* and 22 species of *Scrapter* are included.

Colletes rufotibialis (Friese) appears to show a strong preference for Papilionoideae having been obtained from these flowers from five sites from Wallekraal in Namaqualand to Oranjemund on the coast in the southern Namib Desert. However, two females and two males were collected from *Zygophyllum stapffii* Schinz (Zygophyllaceae) at one site at Swakopmund in the northern Namib Desert. *Colletes capensis* Cameron, a widespread species, is polyphagous, having been obtained from flowers of nine plant families. It was recorded from flowers at nine of the sampling sites, from Grahamstown in the extreme southeast, through the southern Karoo to the Olifants River Valley in the west and north to the Richtersveld. At each of two of the sites, one in the Richtersveld and the other in the southwest, it was collected from three plant families.

In our study, five of the 17 species of *Colletes* were recorded from Mesembryanthema (Aizoaceae), but never abundantly. However, at his study site in the Goegap Nature Reserve, Namaqualand, Michael Struck (1994) observed that *Colletes* were mostly encountered on Mesembryanthema.

Several examples suggest possible preferences by *Scrapter* species. *Scrapter bicolor* Lepeletier & Serville was collected solely from large, afternoon flowering Mesembryanthema at nine sites in the Sandveld, Olifants River Valley and Namaqualand. *Scrapter chloris* Eardley was collected solely from *Grielum* (Neuradaceae) at six sites in the Sandveld and Namaqualand (also on *Grielum* at three sites by Vincent Whitehead, who also collected one female on *Ruschia* (Mesembryanthema) and unspecified numbers of specimens on *Hemimeris* (Scrophulariaceae) (in Eardley 1996)). *Scrapter niger* Lepeletier & Serville and *Scrapter ruficornis* (Cockerell) were collected solely on Asteraceae, the former at three sites in the Olifants River Valley and Namaqualand and the latter at eight sites from Grahamstown in the extreme southeast of the study area through the Little Karoo, Olifants River Valley and north to Springbok in Namaqualand. Other species showing possible preferences are *Scrapter albifumus* Eardley and *Scrapter tomentum* Eardley, which were visiting solely *Zygophyllum* spp. (Zygophyllaceae) at two and three sites respectively, all, however, in the northern Richtersveld.

Too few flower visiting records were obtained for the subfamily Hylaeinae to make generalisations possible. The five species of *Hylaeus* collected visited nine plant families overall. For three species, there are fewer than five records. For the other two species sampled in western Namibia in the desert and associated savanna, there are nine and 16 records respectively. Both species visited Aizoaceae and Apiaceae. One was additionally collected on Zygophyllaceae and the other on Euphorbiaceae and Scrophulariaceae. It would seem that these two species are probably opportunistically polyphagous.

Nesting

Nesting is solitary in nests excavated in the ground, in banks or in pre-existing cavities. Nests may be in aggregations. In all species, the cell lining is cellophane-like, setting the Colletidae apart from all other bee families. No cocoon is constructed.

Subfamily Colletinae

In the subfamily Colletinae, *Colletes* is represented in southern Africa by around 54 species of which around 50 are known only from this region and *Scrapter* by all 43 species (Eardley & Urban 2010).

There appear to be no published accounts of the nesting of *Colletes* in southern Africa, however, some *Colletes* are known to excavate burrows and others to nest in pre-existing cavities. The burrow architecture is variable, that of some species with lateral shafts ending in a single cell and others with cells in series (Michener 2007).

Hans Brauns (1903) found two species of *Epeolus*, *E. caffer* Lepeletier (as *E. militaris* Gerstaecker) at Port Elizabeth and *E. friesei* Brauns at Willowmore, both in association with species of *Colletes* (Colletidae) which he believed to be their hosts. These appear to be the only observations for southern Africa, however, his perception is supported by the fact that, as far as is known, all *Epeolus* are nest parasites of *Colletes* species (Michener 2007). No comments were included on the situation or nature of the *Colletes* nests.

The most comprehensive accounts for *Scrapter* in southern Africa are those of Jerome Rozen & Charles Michener (1968) for *Scrapter striatus* Smith (as *S. alfkeni* (Friese)), *Scrapter erubescens* (Friese) (as *S. crassula* Cockerell) and *Scrapter niger* Lepeletier & Serville (as *S. longula* (Friese)) nesting near Kommetjie on the Cape Peninsula.

Scrapter Lepeletier & Serville

Nest situation

The nests were excavated in level to gently sloping ground in firm, moist sand. In all instances the burrow entrances of *S. niger* were obscured by vegetation or other objects.

Nest structure

The nests of all three species consisted of a subvertical main shaft and lateral secondary shafts all of which ended, without enlargement, in a sloping cell. The entrances of active burrows of *S. niger* and *S. erubescens* were usually surrounded by a symmetrical or nearly symmetrical tumulus 50–70 mm in diameter and 10–20 mm high in nests of *S. niger* and somewhat larger in nests of *S. erubescens*. The entrance of the single nest of *S. striatus* investigated was surrounded by an irregular scanty tumulus. Most nests of *S. niger* apparently had one or two cells but one nest with five cells was recorded, those of *S. erubescens* were clearly multicellular but the number of cells was not recorded, and that of *S. striatus* was single celled.

All secondary shafts, except the last excavated, were filled with sand. In nests of *S. niger*, at least, each successive secondary shaft was deeper than the one preceding it.

The cells were circular in cross section and of the same diameter as the shafts leading to them. They were lined with a nearly clear, colourless, tough, single layered, cellophane-like membrane similar to that of other colletids.

Provisioning and oviposition

The provisions of *S. niger* and *S. striatus* were bright yellow-orange and were dry on the inside but moist on all surfaces. That of *S. erubescens* was duller, darker and liquid throughout.

The pollen used by *S. niger* and *S. striatus* was from yellow-flowered composites (Asteraceae) growing at distances of about 12 metres and one metre from the nests respectively.

The preference of *S. niger* for Asteraceae as the pollen source is supported by our having collected females solely from this family. They were collected from *Arctotheca calendula* (L.) Levyns, *Helichrysum* and *Senecio* in the Olifants River Valley (six, one and seven specimens respectively), and from *Gymnodiscus linearifolia* DC. in the Kamiesberg (three specimens).

Our flower visiting records for *S. erubescens* give an indication of the possible provenance of the pollen used. We collected females of this species solely from Proteaceae. To the west of the Olifants River Valley, 13 specimens were collected from *Leucadendron* and four specimens from a small, unidentified proteaceous plant. Near Nieuwoudtville, we collected one specimen from *Paranomus bracteolaris* Salisb. ex Knight.

Possible provenance of pollen used for provisioning by other species may be indicated where a reasonable number of flower visiting records are available. Oligolecty appears to be usual.

We collected females of around 17 species of *Scrapter* from flowers. Those for which the records may give some indication of the pollen plants are listed below:

- *Scrapter albifumus* Eardley solely from Zygophyllaceae; *Zygophyllum prismatocarpum* E.Mey. ex Sond. in the Richtersveld (seven specimens).
- *Scrapter algoensis* (Friese) principally from Mesembryanthema in the Olifants River Valley (15 specimens).
- *Scrapter bicolor* Lepeletier & Serville solely from Mesembryanthema in the Olifants River Valley, to the west of this valley, and five sites in Namaqualand (66 specimens).
- *Scrapter chloris* Eardley solely from Neuradaceae, *Grielum* species, three sites to the west of the Olifants River Valley and three sites in Namaqualand (six and 39 specimens respectively).
- *Scrapter nitidus* (Friese) principally from Asteraceae, *Chrysocoma*, *Dimorphotheca*, *Euryops* and *Senecio* species, from two sites in Namaqualand, in the Springbok and Nieuwoudtville areas (17 specimens).
- *Scrapter ruficornis* (Cockerell) solely from Asteraceae, *Athanasia*, *Helichrysum*, *Lasioglossum*, *Othonna*, *Pentzia* and *Senecio* species, from eight sites from Grahamstown in the Eastern Cape to Kuboes in the Richtersveld (19 specimens).
- *Scrapter tomentum* (Eardley) solely from Zygophyllaceae, *Zygophyllum* species in the Richtersveld (six specimens).

Associates

Two species of ammobatine cuckoo bees, *Sphecodopsis* (*Pseudodichroa*) *capensis* (Friese) and *S.* (*P.*) *fumipennis* (Bischoff) were encountered by Jerome Rozen & Charles Michener (1968) at the nesting sites of *S. niger* and *S. erubescens.* They found *S.* (*P.*) *capensis* eggs and larvae present in the nests of *S. niger* and those of *S.* (*P.*) *fumipennis* in the nests of *S. erubescens*. The egg is inserted into the cell wall of the host.

Circumstantial evidence suggests that *Sphecodopsis vespericena* Eardley may be parasitic in the nests of *Scrapter bicolor* Lepeletier & Serville (Eardley & Brothers 1997).

Hylaeinae

Hylaeus Fabricius is represented in southern Africa by around 54 species of which 44 are known solely from southern Africa (Eardley & Urban 2010). In addition, an exotic species, *H. perhumilis* (Cockerell) has been introduced from Australia.

Hylaeus nests in pre-existing cavities (Michener 2007). The most detailed notes on the nesting of *Hylaeus* in southern Africa are for *Hylaeus* (*Nothylaeus*) *heraldicus* (Smith) (Skaife 1950; Taylor 1962b, both as *Nothylaeus heraldicus* (Smith); Robert Gess 2009 (unpublished & voucher specimens in Albany Museum)).

Nest situation

Hylaeus (*N.*) *heraldicus* nests in any suitable cavity such as hollow stems, holes in walls and the burrows of wood

Figure II.4.1.—a.–f. *Hylaeus* (*Nothylaeus*) *heraldicus* (Smith): a. and b. females at entrances to pre-existing burrows in clay wall of shade house (Bathurst, Eastern Cape); c. female cleaning out burrow in preparation for nesting; d. and e. lining burrow with cellophane-like material, e. also showing sealed burrow; f. early stage of nest sealing.

boring insects. The observations of John Taylor (1962b) and Sydney Skaife (1950) are for this bee nesting in glass tubes in Port Elizabeth and Hout Bay respectively. Robert Gess observed the bee nesting in old burrows of *Antepipona tropicalis* (de Saussure) (Eumeninae) in a vertical mud wall of a shadehouse in his garden at Bathurst, Eastern Cape, and in wooden Krombein-type trapnests placed on a windowsill in the wall (Figure II.4.1.a–f).

Nest structure

The burrow is lined with cellophane-like material. Sometimes before and sometimes after the construction of the first cell, a transverse barrier of the same material is formed at a short distance within the entrance to the nest. This barrier has a small round hole in the centre through which the bee passes to and from the nest. When the nest is complete, it is sealed off at or just inside the entrance.

Method of construction

The cellophane-like lining of the cell is constructed from a 'gummy' salivary secretion, which is smoothed with the 'tongue'. The antennae and front legs also appear to play a part. The secretion dries to form a thin transparent pellicle.

Provisioning

The pollen and nectar provision is semi-liquid, when regurgitated into the cell, where it is smoothed with the 'tongue', the tip of the abdomen also playing a part. Foraging trips take 10 or more minutes and deposition of the load a minute or two.

There appear to be too few flower visiting records for female *Hylaeus* for an indication of the possible origin of pollen for provisioning.

The sugars in the nectar are concentrated by evaporation, droplets being regurgitated and held at the mouth opening (Figure II.4.2).

Figure II.4.2.—*Hylaeus* sp., concentrating sugars in a regurgitated droplet of nectar by evaporation.

Life history

Sydney Skaife (1950) and Robert Gess reported more than one generation per summer season.

Associates

John Taylor (1962b), Sydney Skaife (1950) and Robert Gess all reared *Gasteruption caffrarium* Schletterer (Gasteruptiidae) from nests of *H.* (*N.*) *heraldicus.* Females attack cells in which the egg has not yet hatched. The ovipositor penetrates the cell closure. The egg is deposited on the side of the cell away from the sticky provision.

On hatching, the larva makes its way to the bee's larva which it eats. It then consumes all the provision in the cell and after a 24-hour rest, breaks through the partition into the next of the bee cells and eats the provision from below and then kills and eats the bee larva. The full grown larva rests for 14–18 days, pupates and after another 27–35 days becomes an adult or, if the larva reaches maturity at the end of the summer, remains in the larval state until the following summer.

Robert Gess observed females inspecting nest entrances with their antennae (Figure II.4.3.a) and ovipositing, in the case of nests in the wall, by inserting the ovipositor into the nest entrance whilst standing outside the nest. In the case of the deeper burrows in trap nests, females entered the nest backwards and, thus positioned, inserted the ovipositor through the bee's cell wall (Figure II.4.3.b–e).

John Taylor noted that a nest, whilst still being constructed, was usurped by *Heriades freygessneri* Schletterer (Megachilidae, Megachilinae).

Family Andrenidae

Andrenidae occur on all continents except Australia, however, they are most diverse in the temperate and xeric parts of North and South America. They are represented in Africa south of the Sahara by both subfamilies, Andreninae and Panurginae. Of the ten sub-Saharan species of *Andrena* Fabricius (Andreninae), two species occur in southern Africa (Eardley *et al.* 2010; Eardley & Urban 2010). The Panurginae are represented in Africa south of the Sahara by 18 species in four genera, of which 14 species in three genera are represented in southern Africa (Eardley *et al.* 2010; Eardley & Urban 2010). These are three species of *Melitturga* Latreille, eight species of *Meliturgula* Friese and the single species of the Namibian endemic genus *Mermiglossa* Friese (Eardley & Urban 2010).

Flower visiting

Flower visiting records of Vincent Whitehead and Kim Steiner, derived from label data of specimens in the South African Museum, have been given by Eardley (2006) for *Andrena notophila* Cockerell*.* They are Asteraceae (not specified), Fabaceae (Papilionoideae of the genera *Aspalathus* and *Lotononis*, the latter as *Buchenroedera*), Geraniaceae (*Erodium* sp.), Iridaceae (*Geissorhiza* sp., *Geissorhiza aspera* Goldblatt, and *Moraea cf. gawleri* Spreng.) and Zygophyllaceae (*Zygophyllum* sp.). This species would therefore appear to be a polyphagous opportunist.

Figure II.4.3.—a.–e. *Gasteruption caffrarium* Schletterer (Gasteruptiidae): a. female inspecting nest entrance of *Hylaeus* (*Nothylaeus*) *heraldicus* (Smith); b. inserting antennae into nest entrance; c. ovipositor inserted into burrow, ovipositor sheath with white tip; d. withdrawing ovipositor from burrow; e. inserting ovipositor into cell of *H*. (*N*.) *heraldicus* in trap nest, ovipositor sheath folded back over body.

Our observations on flower visiting by Andrenidae are based on records for Panurginae only (Gess & Gess 2003, 2004). No records of flower visiting were obtained for Andreninae. Nine of the 14 described southern African species of panurgines (all Melitturgini), three *Melitturga* and six *Meliturgula*, are included in the catalogue (Gess & Gess 2003, those of ours for the six species of *Meliturgula* representing most of the flowers listed without citation by Eardley 2009). No flower visiting seems to be known for the additional three species of *Meliturgula.* We obtained flower visiting records for *Mermiglossa rufa* Friese in March 2004.

A relatively high percentage of species visit Fabaceae, the three *Melitturga* species and three of the six *Meliturgula* species. There are too few records for *Melitturga* to judge whether this genus shows a preference for Fabaceae. However, all species visited *Indigofera* (Fabaceae, Papilionoideae). The records for *Melitturga penrithorum* Eardley are from five widely separated sites in Namibia (the Kalahari Desert fringe in the southeast, to east of the

Grootberg in the northwest). Furthermore, it has also been collected from *Indigofera* by Jerome Rozen (Eardley 1991).

Of the *Meliturgula* species, only one, *Meliturgula scriptifrons* (Walker) (= *minima* Friese), was collected repeatedly from *Indigofera* from which it was previously collected by Jerome Rozen (Eardley 1991). Although the largest samples were from *Indigofera* it is polyphagous having also been recorded from Zygophyllaceae at three sites (females and males), Molluginaceae at two sites (a female and a male), Lamiaceae (a female) and Boraginaceae (a female), and by Jerome Rozen (1968) from Mesembryanthema (Aizoaceae). *Meliturgula flavida* (Friese), apart from a visit by a female to *Tephrosia* (Fabaceae, Papilionoideae) and by five females to non-Mesembryanthema (Aizoaceae) at one of the sites, was visiting Molluginaceae at all eight sites, suggesting a possible preference for Molluginaceae. *Meliturgula haematospila* Cockerell, a common and relatively widespread species, was recorded from flowers at 23 sites from Kakamas on the Orange River through southern and western Namibia to east of the Skeleton Coast Park in the northwest. In addition to Fabaceae, females were recorded from Aizoaceae, Asteraceae, Boraginaceae, Malvaceae, Molluginaceae and Scrophulariaceae. This species would therefore appear to be a polyphagous opportunist.

Mermiglossa rufa was found in large numbers in mixed flower patches in arid savanna at two sites in northwestern Namibia where it was only visiting the flowers of two species of Convolvulaceae, *Merremia palmata* Hallier f. and *Ipomoea obscura* (L.) Ker Gawl. These constitute the first and only records of flower visiting by this bee. In the choice of flowers, it differs from *Melitturga* and *Meliturgula*.

Nesting

An overview of nesting by Andrenidae is given in Michener (2007). All species of Andrenidae for which nesting is known excavate burrows in soil. The lateral branches of the burrow end in one or a short series of cells. Except in some Panurgines, the cells of most are lined with a shiny secretion. The pollen and nectar provision of most species is firm and in shape a sphere or flattened sphere. However, the provision of the endemic American subfamily Oxaeinae is viscous. No andrenid spins a cocoon.

The only published accounts of nesting by Andrenidae in sub-Saharan Africa appear to be those of Hans Brauns (1913) and Jerome Rozen (1968) for a panurgine, *Meliturgula braunsi* Friese, in the Eastern Cape.

Meliturgula Friese

In his account of the nesting of *Meliturgula braunsi*, Jerome Rozen (1968) stated that in most respects the biology is typical of the Pangurinae. However, he concluded that in this species a number of females may share a nest. This is of particular interest as only a few other genera have species in which females share a common nest. There was no indication of division of labour among the females.

Nest situation

The nests of *M. braunsi* are grouped together to form aggregations (Brauns 1913; Rozen 1968). The entrances are not hidden near objects on the ground.

Nest structure

Unlike the nests of most panurgines, the burrow entrance is not marked by a tumulus.

The main shaft meandered downward. In the largest nest, the main shaft branched at a number of places and each branch descended in a winding fashion. Secondary shafts terminating in sealed cells had been filled. Cells seemed to be found both singly and clustered by twos and threes, at the end of laterals.

Rozen (1968) noted that no other panurgine nesting in horizontal ground has such a deep nest.

Method of construction

A temporary nest closure is made at the end of the working day.

Provisioning and oviposition

Rozen (1968) recorded that the pollen source was *Ruschia uncinata* (L.) Schwantes (Aizoaceae, Mesembryanthema), which was abundant in the area. The completed pollen and nectar provisions in cells were dull orange, homogeneously moist, and moderately hard. The provisions varied from being almost spherical to being flattened. Most were large and flattened. The egg was positioned on top of the provision.

We have only two records of flower visiting by females of *M. braunsi*, both for Mesembryanthema.

The only other species of *Meliturgula* for which we have sufficient female flower visiting records to suggest possible oligolecty, is *Meliturgula flavida* (Friese). We collected females principally from Molluginaceae (*Gisekia*, *Limeum* and *Mollugo* species) from eight sites in southern Namibia and in the Nossob River Valley (78 specimens), and Aizoaceae (*Sesuvium sesuvioides* (Fenzl) Verdc.) from one site in southern Namibia (six specimens).

Records for females of *Meliturgula mima* Friese suggest possible oligolecty. We collected females principally from Papilionoideae (*Indigofera* species) from two sites in northwestern Namibia (14 specimens), as well as from Boraginaceae, Caesalpinioideae, Lamiaceae, Molluginaceae and Zygophyllaceae (one or two specimens each).

For other species, flower visiting records for females suggest polylecty, however, it should be noted that no distinction was made between pollen and nectar collection. An example is *Meliturgula haematospila* Cockerell of which we collected females from Malvaceae (*Hermannia* species) from five sites in southern Namibia (20 specimens), Scrophulariaceae (*Aptosimum* and *Peliostomum* species) from 11 sites, mostly in southern Namiba (19 specimens), Zygophyllaceae (*Tribulus* and *Zygophyllum* species) (30 specimens), and Fabaceae (Caesalpinioideae) (*Adenolobus pechuelii* (Kuntze) Torre & Hilc.) at one site in northwestern Namibia (12 specimens). Additionally, females were also collected from Aizoaceae, Asteraceae, Boraginaceae, Fabaceae (Papilionoideae and Mimosoideae), Molluginaceae and Nyctaginaceae (less than five specimens each).

Life history

Meliturgula braunsi is multivoltine and the generations are not synchronised, to the extent that both pupae and freshly provisioned cells were found at the time of excavation. Because of the size of the nest and because old vacated cells were associated with it, the largest nest had obviously existed for a considerable period of time.

Melitturga Latreille

There appear to be no nesting accounts for *Melitturga* in sub-Saharan Africa. Michener (2007) states that nesting by this genus is similar to that of other panurgines. The cells are subhorizontal, the walls are lined with a secreted waterproof coating and the provisions form a flattened spheroid.

Mermiglossa Friese

There appear to be no nesting accounts for the sole species of *Mermiglossa*, *M. rufa* Friese. However, we have obtained some indication of the possible provenance of the provision. As noted above, in northwestern Namibia this bee was found in large numbers in mixed flower patches in arid savanna at two sites where it was visiting only the flowers of two species of Convolvulaceae, *Merremia palmata* Hallier f. and *Ipomoea obscura* (L.) Ker Gawl.

Family Halictidae

The Halictidae, the sweat bees, are species diverse and include some of the commonest bees. All four subfamilies, Halictinae (ten genera and 588 species), Nomiinae (five genera and 232 species), Nomioidinae (21 species representing all three genera, *Cellariella* Strand, *Ceyalictus* Strand and *Nomioides* Schrenk) and Rophitinae (nine species in a single genus *Systropha* Illiger), are represented in Africa south of the Sahara, including southern Africa (Eardley *et al.* 2010; Eardley & Urban 2010).

Flower visiting

Halictidae (example Figure II.4.4) were sampled throughout the study area. The flower visiting records show no clear differences in the range of flower families visited by Nomiinae, Nomioidinae and Halictinae. There is a relatively high incidence of polyphagy in all subfamilies. However, some possible preferences are discernable on closer examination of numbers of records, particularly in the Halictinae. For example: two species of *Seladonia* Robertson appear to visit Asteraceae in preference to other flowers, although females were recorded from eight other families less frequently and less widely. Some species of *Patellapis* (*Patellapis*) (Friese) (formerly as *Lasioglossum*) appear to visit Aizoaceae (Mesembryanthema) by preference, however, one species appears to visit Asteraceae by preference, although this species was recorded visiting Mesembryanthema albeit less frequently and less widely.

Because we had only a few flower visiting records for only one species of Rophitinae, that subfamily was not included in the discussion (Gess & Gess 2004).

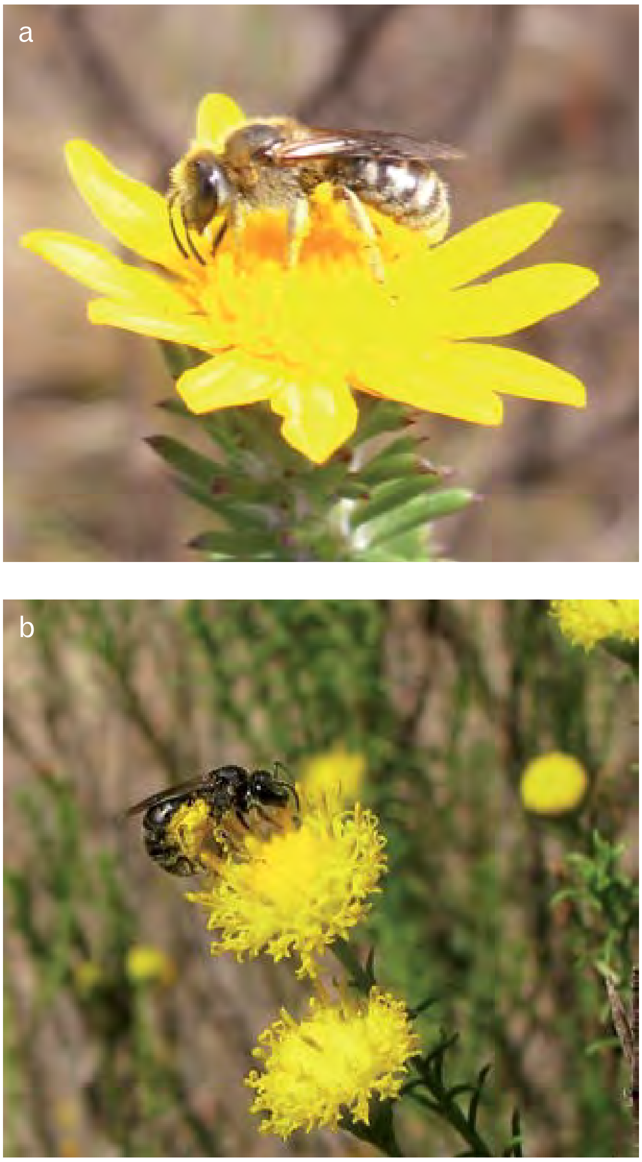


Figure II.4.4.—a. and b. Halictidae: unidentified species visiting flowers of Asteraceae.

Nesting

All the known nests of non-parasitic Halictidae are burrows in soil or rarely in rotten wood. The nesting behaviour of Halictinae ranges from solitary to eusocial with clearly recognisable queen and worker castes. Most parasitic halictids are associated with their close relatives or at least bees of the same tribe, however, some species of *Sphecodes* parasitise unrelated bees such as andrenids and colletids (Michener 2007).

We recorded nesting in sandy soil on the farm Hilton, Grahamstown, by two species of *Seladonia* (as *Halictus*) and a species of *Patellapis* (*Patellapis*) (as *Lasioglossum*) (all Halictinae), a species of Nomioidinae, and a species of *Lipotriches* (*Lipotriches*) (as *Nomia*) (Gess 1981). In the same area, we found *Sphecodes* associated with the nests of *Lipotriches* (*Lipotriches*).

The only detailed study of the nesting of a halictid in southern Africa appears to be that of Kim Timmermann & Michael Kuhlmann (2008) for *Patellapis* (*Patellapis*) *dol-*

eritica Timmermann (as *Patellapis* (*s. str.*) species and *P.* sp. 1; actual identity of species given by Kuhlmann, pers. comm.).

Patellapis (*Patellapis*) *doleritica* Timmermann

Observations relate to seven nests, one of which was investigated. They suggest that *P.* (*P.*) *doleritica* is a communal nester and further suggest that a single female simultaneously provisions more than one brood cell. It was found that females belonging to a single active nest varied from three to seven.

Nest situation

The nests investigated were in a gently sloping sparsely vegetated area in the Nieuwoudtville Wild Flower Reserve. The nest entances were hidden under low growing plants. The soil was a hard mixture of clay, silt and sand.

Nest structure

The nest entrance is not associated with a tumulus or turret. In the nest investigated, the main shaft entered the ground obliquely and then descended more or less vertically. Three secondary shafts left the main shaft at depths of 150 mm, 180 mm and 210 mm. Two of them divided again with some of these tertiary shafts branching again (Figure II.4.5). The brood cells were clustered and were more numerous towards the end of each branch. In total, there were 98 cells, 65 closed and 33 open and being provisioned. They were at depths of from 170 to 230 mm. The cell walls were completely lined with a thin shiny waterproof film. Cell closures consisted of soil material that differed from the surrounding substrate. They were slightly concave on the inside and had no lining.

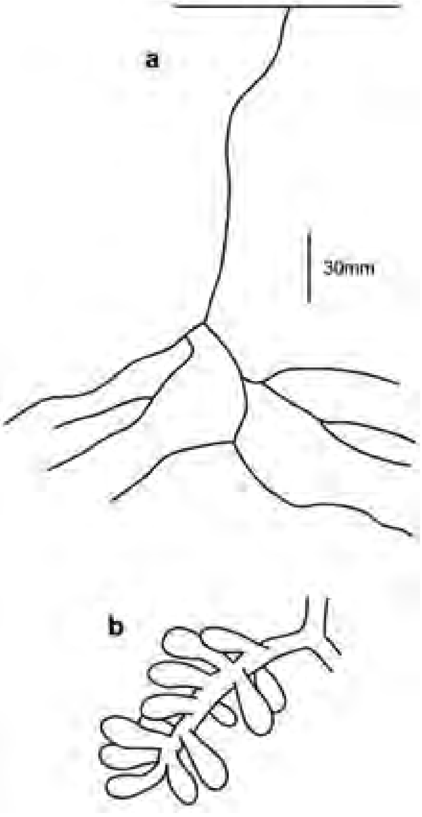


Figure II.4.5.—a. and b. *Patellapis* (*Patellapis*) *doleritica* Timmermann: a. diagrammatic vertical plan of nest; b. cluster of cells at a branch end (actual average maximum width of cells 4.9 mm) (Redrawn from Timmermann & Kuhlmann, 2008).

Provisioning and oviposition

The provision was in the form of a spherical pollen and nectar ball of a pasty consistency positioned at the bottom of the cell near the inner end. The strongly arched egg was attached to the top of the provision with both ends attached to it.

From analyses of pollen from 161 scopal pollen loads and 65 provision balls, it was concluded that pollen had been collected from flowers of seven plant families. It was therefore concluded that *P.* (*P.*) *doleritica* is polylectic with a strong preference for plant species occurring in abundance.

Associates

A cuckoo bee *Sphecodopsis semirufa* (Cockerell) was abundant in the nesting area. It was seen patrolling around nests, inspecting them and perching nearby observing the nest entrance. Several times it was noted that after a pollen laiden *P.* (*P.*) *doleritica* had entered her nest to offload and had then left the nest, a cuckoo bee that had been observing the nest inspected and entered it. Three females were observed entering a nest, staying inside for three to eight minutes and then leaving before the host's return.

Family Melittidae

Melittidae is a small family found primarily in the temperate regions of the northern hemisphere and in Africa. Southern Africa has the greatest diversity of genera and species. All three subfamilies are represented. Subfamily Melittinae is represented by two endemic genera, *Rediviva* Friese and *Redivivoides* Michener and the more widespread *Melitta* Kirby. Subfamily Dasypodainae is represented by the southern African endemics *Afrodasypoda* Engel (the single species *A. plumipes* (Friese), formerly *Promelitta plumipes* (Friese)), *Capicola* Friese (including *Hesperapis* Michener) and *Samba* Friese (including *Haplomelitta* Cockerell). Subfamily Meganomiinae is represented by the Namibian endemic *Ceratomonia* Michener and the more widespread *Meganomia* Cockerell, endemic to Africa and Yemen, but not the more northern African and Madagascan *Pseudophilanthus* Alfken or *Uromonia* Michener (Eardley *et al.* 2010; Eardley & Urban 2010; Michez *et al.* 2010). In Eardley *et al.* (2010), *Samba* Friese and *Haplomelitta* Cockerell were still listed as distinct genera. However, subsequently Michez *et al.* (2010), following a comprehensive phylogenetic analysis, synonymised *Haplomelitta* with *Samba* and divided *Samba* into six subgenera, namely *Atrosamba*, *Haplomelitta*, *Haplosamba*, *Metasamba*, *Prosamba* (known only from western southern Africa) and *Samba* (known only from East Africa).

In melittids, the scopa for pollen carriage is largely restricted to the hind tibia and basitarsus. The genus

Rediviva comprises the largest group of oil-collecting bees in southern Africa. The front tarsus of the female used for oil collection is covered with fine, dense hairs, and the segments are often thickened or elongate with the scope densely plumose for oil carriage (Michener 2007).

Flower visiting

The Melittidae show a high degree of oligophagy and narrow polyphagy and distinct differences in preferences between taxa. There are, however, clear exceptions.

Only within the Dasypodainae were marked preferences for Campanulaceae noted, all records being from the southwest, from the Olifants River Valley north to Springbok in Namaqualand (Gess & Gess 2004). Six of the 12 species of *Capicola* (Dasypodaini), for which we obtained records, were from Campanulaceae. All records were for the genus *Wahlenbergia* (Campanuloideae), mostly species with stellate flowers (including species formerly placed in *Lightfootia*) (examples Figure I.3.23). Three of these species appear to be specialists, having been collected repeatedly solely from these flowers at several sites in several years. Indeed, they appear to be the most important pollinators of *Wahlenbergia* with stellate flowers in the west, south of the Orange River (Gess 1996). By contrast, in the same areas *Wahlenbergia* species with deeply tubular flowers are principally visited by and pollinated by pollen wasps (Gess 1996).

Males were found sleeping in *Wahlenbergia* flowers (Figure II.4.6).

Five species of *Capicola*, four from the Richtersveld, northwestern Namaqualand, were recorded from Mesembryanthema (Aizoaceae). Based on numbers of records and sites, at least one of these species appears to be a specialist. Furthermore, Michael Struck (1994) noted some species of *Capicola* were abundant visitors to some Mesembryanthema, showing a high degree of fidelity at his Namaqualand study site. Another species from the Richtersveld was recorded by us principally from Asteraceae, as, too, was *Afrodasypoda plumipes* (Friese) (as *Promelitta plumipes* (Friese) in Gess & Gess 2003) (Dasypodainae, Promelittini). The twelfth species of *Capicola* was visiting *Indigofera* (Papilionoideae) on the fringe of the Kalahari and *Limeum* (Molluginaceae) on the central Namib fringe. Michez *et al.* (2007) confirm our analysis (Gess & Gess 2004). Michez *et al.* (2007) state that *Capicola* species seem to be oligolectic on a few plant families: Aizoaceae (six species), Asteraceae (one species), Campanulaceae (three species) and Fabaceae (one species).

Figure II.4.6.—*Capicola danforthi* Eardley: male sleeping in flower of *Wahlenbergia annularis* A. DC.

Figure II.4.7.—*Samba* (*Haplomelitta*) *ogilviei* (Cockerell): female in flower of *Monopsis debilis* C.Presl.

We recorded *Samba* (*Haplomelitta*) *ogilviei* (Cockerell) (Sambini) in the same areas as *Capicola* from Campanulaceae. However, though occasionally visiting *Wahlenbergia*, it most often visits *Monopsis debilis* (L.f.) C.Presl (Campanulaceae, Lobelioideae) (Figures I.3.24.d & e; II.4.7) which is apparently its principal forage plant (Rozen 1974 as *M. simplex*) and of which it appears to be the sole visitor and pollinator (Gess & Gess 1994). This statement seems to have been misunderstood by Michez *et al.* (2010) who appear not to have seen all of our specimens because not all are listed, and not to have consulted our catalogue (Gess & Gess 2003). In our catalogue we list 47 female and 21 male *S.* (*H.*) *ogilviei* collected from flowers of *M. debilis* from four sites in five years. Four females and two males from flowers of *Wahlenbergia* spp. at two sites in one of those years, 12 females and two males from flowers of three species of Asteraceae from two sites in three of those years, and two females from flowers of *Galenia sarcophylla* Fenzl (Aizoaceae, non-Mesembryanthema) from one site in one of those years. Connal Eardley's (in Michez *et al.* 2010) two females and 32 males collected from Asteraceae do not add an additional forage plant, but do add to our records. The discussion by Michez *et al.* (2010) based on the examination of pollen loads and their observations support the conclusions of Jerome Rozen (1974) and ourselves (Gess & Gess 1994) that *S. ogilviei* is oligolectic on Campanulaceae, in particular favouring *M. debilis* for pollen collection. We would agree with their conclusion that pollen from Asteraceae found in their examination of pollen loads possibly resulted from contamination during nectar foraging. Connal Eardley's collection of 32 males from Asteraceae (in Michez *et al.* 2010), certainly would suggest that visits to Asteraceae are principally for nectar, as too are probably the visits recorded by us to *Galenia sarcophylla*.

Of the other species of *Samba*, for which flower visiting records are available, three species were collected from flowers of *Indigofera* (Fabaceae, Papilionoideae). Two species, *S.* (*Atrosamba*) *gessorum* Eardley and *S.* (*Metasamba*) *fasciata* Michener, by us in the Richtersveld and the third, *S.* (*Atrosamba*) *atra* (Michener), by Vincent Whitehead in the southwest. *Samba* (*A.*) *gessorum* was additionally collected from *Tylecodon reticulatus* (L.f.) Toelken (as *Crassula dichotoma* L.) (Crassulaceae) in the Kamiesberg by us.

The two species of *S.* (*Prosamba*) were collected from flowers of *T. reticulatus* (as *Crassula dichotoma* L.). The records for *Samba* (*P.*) *griseonigra* (Michener) are those of Bryan Danforth from the Kamiesberg and Vincent Whitehead from Nieuwoudtville (Michez *et al.* 2010). The records for *S.* (*P.*) *spinosa* Eardley are those of Vincent Whitehead from nine sites, from Porterville through the Olifants River Valley to Nieuwoudtville (Michez *et al.* 2010) and of Michael Kuhlmann and Kim Timmermann from its nesting area and a second site near Nieuwoudtville where it was also visiting Asteraceae (Kuhlmann & Timmermann 2011).

We collected the three species of Meganomiinae, *Meganomia gigas* Michener, *Meganomia binghami* (Cockerell) and *Ceratomonia rozenorum* Michener from flowers. All visit Papilionoideae. *Meganomia gigas* was collected at four widely separated sites in northwestern Namibia solely on *Crotalaria*, an association further supported by the records of Rozen (1977a), suggesting that this species may be oligophagous. *Meganomia binghami*, however, although collected from Papilionoideae (three species of *Indigofera* and *Lessertia macrostachya* DC.) at five sites on the Kalahari fringe in southeastern Namibia and across into South Africa, north of Upington, has been recorded, though in smaller numbers, from eight families—seven in our study (six females) and previously from *Gisekia africana* (Lour.) Kuntze (Molluginaceae) (Rozen 1977). The relatively small *C. rozenorum* was recorded from four sites in southeastern Namibia repeatedly from three species of *Indigofera.* This is in line with the records of Rozen (1997a as *Meganomia* species B) for southern Namibia, however, he recorded this bee from *Petalidium* (Acanthaceae) in the northwest.

For the Melittinae we obtained records for three species of *Melitta* (as four undescribed species in Gess & Gess 2004, as three species in Eardley & Kuhlmann 2006), all from Papilionoideae. Insufficient records were obtained for two of the species, *M. barbarae* Eardley and *M. danae* Eardley, to establish a preference. However, the third species, *M. arrogans* (Smith), for which good samples were obtained, is clearly polyphagous having been recorded from another nine plant families (five of these were females).

Flower visiting records for females are given for two additional species in Eardley & Kuhlmann (2006), both records of Vincent Whitehead. They are *M. whiteheadi* Eardley, five females from *Watsonia* (Iridaceae) at Betty's Bay, and *M. schultzei* Friese, one female from *Watsonia* at Nuwerus, both Western Cape.

Vincent Whitehead and Kim Steiner (2001, see also Appendix) list the 15 winter rainfall species of *Rediviva* (Melittinae) together with their known oil, pollen and nectar flowers. For oil collection, all 15 species visit oil-secreting flowers of Hemimerideae (Scrophulariaceae) and five of these species also visit oil-secreting flowers of Orchidaceae additionally. Little specificity is shown, up to

17 species of plants being recorded for any one species of *Rediviva.* The forelegs of the bees are specially modified for oil collection and are variously elongated (Steiner & Whitehead 1990). Clearly, the length of the legs must be sufficient for the bees to reach the oil in the spurs, and therefore the shorter legged species are not able to reach the oil in the long spurs but the longer legged species can collect oil from long and short spurred flowers. Pollen collection by *Rediviva gigas* Whitehead & Steiner is from two localities from two species of *Watsonia* (Iridaceae), and nectar collection by this species by both females and males from *Watsonia* but also from *Wachendorfia* (Haemadoraceae) and *Moraea* (Iridaceae). *Moraea* is represented amongst the nectar flowers of many species, and appears to be preferred by *R. longimanus* Michener, having been recorded repeatedly from *Moraea.* Some species show a possible preference for Asteraceae, and the presence of *Oxalis* (Oxalidaceae) amongst the nectar flowers of several species is of interest. However, most species appear to be relatively polyphagous in their choice of nectar, some being recorded from at least nine plant families.

Although Vincent Whitehead and Kim Steiner made the flower associations of *Rediviva* during their particular study over a period of nearly 20 years and have, in consequence, made the greatest contribution, other contributors should not be overlooked (Vogel 1984 followed by Vogel & Michener 1985 and Manning & Brothers 1986 for KwaZulu-Natal).

Nesting

Where known, the nests of mellitids are single-celled or more usually multi-celled burrows in friable soil. The only published observations on nesting in southern Africa seem to be for *Capicola braunsiana* Friese, *Samba* (*Haplomelitta*) *ogilviei* (Cockerell), *Samba* (*Prosamba*) *spinosa* Eardley and *Meganomia binghami* (Cockerell), to which can be added some scanty observations for *Meganomia gigas* Michener.

Capicola braunsiana Friese

Jerome Rozen (1974) observed *Capicola braunsiana* Friese (as *Hesperapis* (*Capicola*) *braunsiana* (Friese)) nesting 67 km east of Port Nolloth.

Nest situation

Capicola braunsiana was nesting in a sparsely vegetated area in sandy soil in close proximity to mesembs—its pollen plants. The nest entrances were often adjacent to or under small stones on the surface of the ground. In most cases, excavated material was apparently quickly blown away but around some nests it accumulated to form tumuli.

Nest structure

The main shaft descended obliquely with considerable meandering to a depth of about 130–150 mm. The average rate of descent was at somewhat less than 45° to the surface. The wall of the shaft was smooth, without a special lining. The shaft terminated in a linear series of cells. In one of the three nests excavated, a secondary shaft led off above these cells and terminated in a single open cell. The cells were broadly rounded at the inner end and narrower at the outer end. They appeared to be unlined, however, a droplet of water placed on the floor showed that it was waterproofed. A drop on the upper part of the wall was slowly absorbed.

Provisioning and oviposition

Pollen is transported to the nest dry and there formed into a perfect sphere, mealy-moist throughout, pale green in colour and with no detectable odour.

Associates

No parasitic bees were found in association with the nests.

Samba (*Haplomelitta*) *ogilviei* (Cockerell) and *Samba* (*Prosamba*) *spinosa* Eardley

Jerome Rozen (1974) investigated *Samba* (*H.*) *ogilviei* nesting 28 km east of Velddrif, southwest of Clanwilliam in Sandveld, and Michael Kuhlmann & Kim Timmermann (2011) investigated *Samba* (*P.*) *spinosa* nesting 15 km northwest of Nieuwoudtville in fallow land surrounded by Bokkeveld Sandstone Fynbos.

Nest situation

Both *Samba* (*H.*) *ogilviei* and *Samba* (*P.*) *spinosa* were nesting in sparsely vegetated sandy areas in close proximity to flowers. Unlike the nests of *C. braunsiana*, the entrances of *S.* (*H.*) *ogilviei* were not associated with any object.

Nest structure

In the two nests of *S.* (*H.*) *ogilviei* and the single nest of *S.* (*P.*) *spinosa* investigated, the shaft entered the ground obliquely and in the nests of *S.* (*H.*) *ogilviei* ended in a single cell. The single cell of *S.* (*P.*) *spinosa* terminated a short lateral shaft. The cells were comparatively short in relation to their width. There was no visible lining but the cell wall was found to be somewhat waterproof when tested with a droplet of water, and the wall was slightly more rigid than the surrounding soil, an indication that the female had applied some substance that had penetrated the soil.

Provisioning and oviposition

The provision from the cells of both species was a spherical ball. That of *S.* (*H.*) *ogilviei* was described as mealy-moist, pale greyish yellow and was not coated with a waterproof substance. That of *S.* (*P.*) *spinosa* was described as pasty, pale yellowish.

Based on his observations, Rozen (1974) concluded that the provenance of the pollen was *Monopsis debilis* and that visits to Asteraceae were for nectar. Michez *et al.* (2010) examined pollen loads from females and found that most of the pollen was derived from *Monopsis debilis* but that some pollen was from Asteraceae. They suggested that this might have been contamination (see discussion of flower visiting above), however, Michez *et al.* (as reported in Kuhlmann and Timmermann 2011) subsequently state that pollen analyses indicate that it uses pollen of Asteraceae and an unidentified pollen source as well.

Kuhlmann & Timmermann (2011) examined pollen from scopal loads and from the provision of *S.* (*P.*) *spinosa* and found that the pollen was almost entirely derived from *Tylecodon reticulatus* and, consequently, considered this bee to be monolectic. However, there were traces of pollen from Asteraceae in the pollen loads but this was considered to be contamination resulting from nectar collecting visits.

Associates

No parasitic bees were found in association with the nests.

Meganomia binghami (Cockerell)

Jerome Rozen (1977a) observed nesting by *Meganomia binghami* east of Usakos and west of Omaruru in Namibia. Casual observations indicated that most nests were occupied by only one female, but two nests had two females each.

Nest situation

The nests of *M. binghami* were in thorn scrub savanna, situated in sandy areas and near to the pollen plant, *Crotalaria podocarpa* DC. (Papilionoideae), in sandy situations. Where abundant, nests were in large, loose aggregations.

Nest structure

All nest entrances were surrounded by copious tumuli, approximately 100 mm in diameter and 50–80 mm high. The tumulus was loose except that most incorporated a curved entrance turret of consolidated sand. The turret rose from the nest, curved, and then extended horizontally as much as 50 mm so that the entrance was near the edge of the tumulus. Nest entrances appeared open most of the time although several were found plugged, perhaps by females bringing soft soil to the surface. The main shaft descended by a slightly irregular path to depths of up to 1.14 m. Some branches, apparently leading to closed cells, were filled with somewhat coarser soil than that of the substrate. The cells were orientated with the long axis 20 to 45 degrees from the horizontal. No special built-in lining had been constructed and the cell surface was uniformly smooth and dull. A droplet of water placed on the cell surface was absorbed very slowly, indicating that the female had applied a waterproof lining. The cell closure was a deep concave spiral on the inside. It was constructed from finer particles than the surrounding soil.

Provisioning and oviposition

Pollen was collected solely from *Crotalaria* and never from *Indigofera* or other flowers visited, suggesting that *M. binghami* may be oligolectic. Pollen was transported in a moist condition on the hind legs. In the nests, the provisions were shaped into an elongate form, were greenish and homogeneously soft, lightweight, mealy-moist, without any special surface coating, and emitted a slightly sour fermented odour.

Life history

After defecating, larvae were encased in large cocoons. There is apparently a single generation per year.

Male behaviour

Mating takes place close to the pollen plant and the nesting site. Males fly over extremely fast, making a loud buzzing noise, and low over the nesting site and the flowers searching for females. As many as four males were observed pursuing a single female. Pairs normally copulated on the ground but occasionally on vegetation.

Males were never seen entering burrows in the late afternoon.

Meganomia gigas Michener

We observed nesting *Meganomia gigas* at two sites in northwestern Namibia, one 31 km by road west of Kamanjab and the other 5 km by the 'hills' road north of Khorixas Rest Camp (Gess & Gess fieldnotes 1997 and 2004 respectively).

Nest situation

The two nesting areas were in dry Mopane Savanna. The nest aggregations were situated in close proximity to patches of *Crotalaria podocarpa* on which the bees were foraging. The sand at the former site was yellowish and that at the latter red.

Nest structure

Each nest entrance was covered over by a mound of loose sand extracted from the burrow. The burrow entrance was 20 mm in diameter. Most nests investigated were at an early stage of excavation but in one, the main shaft zigzagged downwards to a depth of 1 m after which it branched, both branches continuing downwards to a depth of 1.45 m. No cells were found.

Provision

The fact that flower visiting records for *Meganomia gigas* are all from *Crotalaria* suggests that *M. gigas*, like *M. binghami*, probably provisions with *Crotalaria* pollen and furthermore, unlike *M. binghami*, may be restricted to collecting nectar from *Crotalaria.*

Melitta Kirby

The only note concerning the nesting of *Melitta* in southern Africa seems to be that of Hans Brauns (1930) who noted that nests of *Melitta arrogans* (Smith) (as *Melitta capensis* Friese) situated in the ground at Willowmore were being entered by the parasitic bee, *Nomada gigas* Friese (as *N. gigantea*) (Apidae, Nomadinae).

Family Megachilidae

Megachilidae are worldwide in distribution. All southern African megachilids, except parasitic species, are characterised by the presence of metasomal sternal scopa for pollen carriage. The presently recognised subfamilies are Fideliinae, restricted to the xeric areas of Asia, Africa and South America, and Megachilinae, diversified on every continent. Both are well represented in southern Africa.

Flower visiting

Within the Megachilidae the two subfamilies Fideliinae and Megachilinae, and within the Megachilinae the three tribes Osmiini, Anthidiini and Megachilini, show distinct differences in the percentages of species visiting specific families of plants. As there are only records for one species of Lithurgini (Megachilinae) this tribe is not included in the discussion (Gess & Gess 2004).

Our records for 11 species of Fideliinae show the greatest numbers and percentages of species visiting Aizoaceae, Zygophyllaceae and Neuradaceae—in that order. However, these families do not attract high percentages of species of any of the tribes of Megachilinae. Within the Megachilinae, the highest percentage of species visiting Fabaceae (the family showing the highest percentage for Megachilidae) was 84% Megachilini, followed by 61% Anthidiini and only 14% Osmiini. By contrast, the highest percentage of species visiting Asteraceae (the family showing the second highest percentage for Megachilidae) was 74% Osmiini, followed by 32% Anthidiini and 20% Megachilini. The only other percentages of species above 20% visiting a plant family were as follows: 27% Megachilini visiting Apocynaceae (species previously in the Asclepiadaceae; only 5% Anthidiini and no Osmiini); 23% Megachilini visiting Acanthaceae (only 14% Anthidiini and no Osmiini); and 23% Anthidiini visiting Lamiaceae (17% Osmiini and 14% Megachilini).

As noted above, the Fabaceae visited by bees are predominantly Papilionoideae. In the Megachilinae, 93 species were recorded from Papilionoideae namely, 54 Megachilini; 36 Anthidiini; and three Osmiini. The majority of records were for Crotalarieae and Indigofereae with different ratios of species of Megachilini (41:5) and of Anthidiini (16:16) visiting them. Only 11 species of Megachilinae were recorded from Mimosoideae namely, ten Megachilini; one Osmiini; and no Anthidiini. Of Caesalpinioideae, only *Adenolobus pechuelii* (Kuntze) Torre & Hillc. was visited by Megachilinae namely, two relatively large species of Anthidiini (several records) and one species of Megachilini (one record).

Although varying degrees of polyphagy apply throughout the Megachilidae, some definite preferences are apparent. In the Fideliinae, there are species that show clear preferences for flowers of families visited by a high percentage of species, notably Aizoaceae (Mesembryanthema) and Asteraceae (confirming Whitehead (1984); Whitehead *et al.* (1987)) and others which show preferences for flowers of families that receive visits from few species. For example, *Fidelia* (*Parafidelia*) *freisei* Brauns shows a marked preference for *Sesamum* spp. (Pedaliaceae), having been recorded from flowers of these plants from numerous sites from just north of the Orange River to south of the Kunene in northwestern Namibia. More often than not, this species was the only or the most abundant visitor. This relationship is clearly mutualistic, *Sesamum* being the principal forage plant of this bee and the bee, in not only frequency of visitation, but also in flower fit, the most important pollinator of the flowers.

In the Osmiini, based on records for around 34 species, not only do a high percentage of species visit Asteraceae but many were recorded repeatedly and only from Asteraceae, suggesting a strong preference. Of the Anthidiini visiting Papilionoideae there are species that, though collected on flowers of other taxa, based on numbers of records, show a preference for Papilionoideae and others for Crotalarieae or for Indigofereae. Similarly amongst the species of Megachilini are those that were more frequently and widely taken from Papilionoideae than from other taxa.

Subfamily Fideliinae

The small atypical subfamily Fideliinae is represented in southern Africa by one of its two tribes, Fideliini with a single genus *Fidelia* Friese endemic to Africa. *Fidelia* is represented by 11 species in southern Africa, most of which are endemic to this area (Eardley *et al.* 2010; Eardley & Urban 2010). Nesting by *Fidelia* was observed by Jerome Rozen who investigated *Fidelia villosa* Brauns 50 km southwest of Keetmanshoop, Namibia (Rozen 1970) and *Fidelia pallidula* Cockerell 70 km east of Port Nolloth (Rozen 1977b).

Nest situation

The two nesting areas were in sparsely vegetated, sandy desert. The nests were in aggregations and were excavated in compact sand.

Nest structure

The nests investigated were multicellular. Most of the entrances appeared as small craters at one edge of dry, loose, sandy tumuli, which blew away within a few days. The main shaft descended obliquely in meandering fashion, leading to secondary shafts that, in turn, branched to end in a cell or to end blindly. The cells were arranged singly with the long axis horizontal or nearly so. The cell walls were not impregnated or lined. The cell closure is probably of loose sand, the shaft leading to a completed cell and was found to be filled with sand. The ramified pattern of the nest is established before cell provisioning.

Provisioning and oviposition

The pollen plants of *F. villosa* were mesembs and that of *F. pallidula* was *Sisyndite spartea* E.Mey. ex Sond., a zygophyllous shrub with large yellow flowers.

Females transported dry pollen, carried primarily on the underside of the abdomen by long non-plumose, scopal hairs. Jerome Rozen (1970) observed that the flattened hind tarsus and its very long hairs are not used for transporting pollen, as has sometimes been stated, but is used as a paddle to flip sand from the nest.

The completed provision mass of *F. villosa* was solid, roughly hemispherical, with the flattened surface obliquely upward. The cells of *F. pallidula* were strikingly large and, correlated with this, each cell contained two or three larvae in a huge pollen mass, as is known to be the case in some species of *Megachile* and *Lithurge.* The interior of the provision contained a number of open chambers one in front of the other and each containing a single egg or larva. The provision was mealy-moist except above each egg chamber where it was quite dry.

From our collecting records, it appears that *Fidelia* (*Fidelia*) *paradoxa* Friese on the northwest coast of Namibia may also favour Mesembryanthema.

From our collecting records for females, different origins of provision of other species are indicated:

- *Fidelia* (*Parafidelia*) *friesei* Brauns, principally from Pedaliaceae (*Sesamum* spp.) at seven sites from southern to northern Namibia (44 specimens).
- *Fidelia* (*Parafidelia*) *hessei* (Whitehead & Eardley), principally from Neuradaceae. From *Grielum* spp. at three sites in the sandveld in the southwest (13 specimens) and *Neuradopsis* spp. on the Kalahari fringe in southeastern Namibia (17 specimens).
- *Fidelia* (*Parafidelia*) *ornata* (Cockerell), principally from from Aizoaceae (non-Mesembryanthema). From *Sesuvium* spp. at two sites in southwestern Namibia and *Tribulocarpus* spp. from a site in northwestern Namibia (31 specimens).

Life history

The full-grown larva, apparently after defecating, ingests sand that will later compose the inner layer of the cocoon. The cocoon is composed of two layers. The outer layer was a very thin, opaque, brown, parchment-like silk that adhered closely to the much thicker inner layer. Once the outer parchment-like layer is spun, the larva voids through the anus the mixture of fine sand and the dark shiny material, which must act as cement.

Associates

No parasitic bees were associated with the *Fidelia* nesting sites but meloid larvae were found in provisioned cells of *F. villosa* and *F. pallidula.* Mites were common in cells but none was found attacking immature bees.

Sleeping and sheltering

Vincent Whitehead (1984) found both females and males of *Fidelia pallidula* and *F. friesei* sleeping in flowers. Females of *F. kobrowi* Brauns sleep in their burrows. He noted further that males of *F. paradoxa* Friese, *F. major* Friese and *F. ornata* (Cockerell) have been seen to dig themselves into the soft sand at the end of the day.

Subfamily Megachilinae

Of the large subfamily Megachilinae, all five tribes are represented in southern Africa, Lithurgini, Osmiini, Anthidiini, Dioxyini and Megachilini.

Tribe Lithurgini

Lithurgini are represented in southern Africa by two of the four sub-Saharan species of *Lithurgus* Berthold (Eardley & Urban 2010). There appear to be no nesting accounts for Lithurgini in southern Africa. Michener (2007) summarised the known nesting by the tribe, which gives an indication as to what may be expected. The nests are burrows excavated in dead, dry, often rotten wood or even in dry cow dung. They often branch. Provisions are placed in burrows without cell linings, and often without partitions to demarcate cells. Atypically for bees, eggs are laid before or during provisioning rather than after provisioning, and are thus often within the firm pollen mass rather than on its surface. Cocoons lack the nipples characteristic of other megachilid cocoons.

Our flower visiting records suggest that the provenance of the provision of *Lithurgus spiniferus* Cameron may be Asteraceae from which females were collected in the Eastern Cape, Little Karoo and the Olifants River Valley (24 specimens).

Associates

Bouček (1974) listed two species of *Leucospis*, *L. ornata* Westwood and *L. varicollis* Cameron, as reared from nests of *Lithurge spiniferus* Cameron (as *L. capensis* Friese) from Willowmore, Eastern Cape (vouchers in the Ditsong Museum, Pretoria and Natural History Museum, London).

Tribe Osmiini

In the Afrotropical Region Osmiini are most diverse in southern Africa where they are represented by several genera including one endemic, six Old World and two widespread genera. *Afroheriades* Peters is a southern African endemic with six described species. Six Old World genera include *Othinosmia* Michener (ten species), *Noteriades* Cockerell (six species), *Ochreriades* Mavromoustakis (one species), *Pseudoheriades* Peters (three species), *Stenoheriades* Tkalců (five species), and *Wainia* Tkalců (undecided). The two widespread genera are *Heriades* Spinola (ca. 56 species) and *Hoplitis* (*Anthocopa*) Lepeletier & Serville (undecided) (Eardley & Urban 2010). Michael Kuhlmann (in Kuhlmann *et al.* 2011) recognises seven species of *Wainia* and at least 13 species of *Hoplitis* (*Anthocopa*).

Osmiine bees nest either in burrows, lining their cells with resin or petals, or construct pebble and resin aerial nests on plants or stones. Nesting has been recorded in southern Africa for two species of *Heriades*, three species of *Hoplitis* (*Anthocopa*), three species of *Othinosmia* and four species of *Wainia.*

Heriades (*Heriades*) Spinola and *Pseudoheriades* Peters

Heriades (*Heriades*) and *Pseudoheriades* nest in preexisting burrows in wood or in stems. The nest consists of a series of cells with partitions made of resin. Accounts have been given of the nesting of *Heriades* (*Heriades*) *freygessneri* Schletterer at Port Elizabeth (Taylor 1962c), at Wilderness (Taylor 1965) and at Hilton, KwaZulu-Natal (Taylor 1968), and for *Heriades* (*Heriades*) *spiniscutis* (Cameron) from the southwestern Cape eastwards and northwards through the Eastern Cape and KwaZulu-Natal to Malawi and Kenya (Michener 1968a).

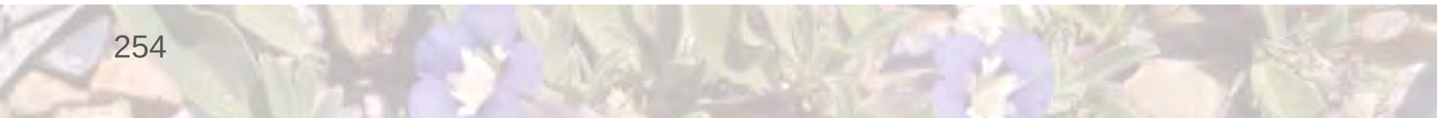
Nest situation

Heriades (*H.*) *freygessneri* at Port Elizabeth was observed investigating holes and crevices in brick outer walls as well as the woodwork of doors. They readily accepted blocks of wood containing the abandoned borings of beetles and termites. At all three of John Taylor’s localities, he used trapnests for his nesting studies (Taylor 1962c, 1965, 1968).

Heriades (*H.*) *spiniscutis* used cavities in a wide range of stems, broken, hollow, dry inflorescence stems of

Table 12.—Numbers and percentages of Megachilidae species, arranged according to tribe, visiting flowers by plant family. Percentages of 20 and more are shown in bold type

Plant taxa	**% out of 123 families**	**Fideliinae**		**Megachilinae**							
		Fideliini (Total: 11 species)		**Lithurgini (Total: 1 species)**		**Osmiini (Total: 35 species)**		**Anthidiini (Total: 44 species)**		**Megachilini (Total: 56 species)**	
		Number of species	**% of species**	**Number of species**	**% of species**	**Number of species**	**% of species**	**Number of species**	**% of species**	**Number of species**	**% of species**
MONOCOTS											
Asparagales											
Asphodelaceae	5.44							1	2.27	7	12.5
Iridaceae	2.04	1	9.09			1	2.86	1	2.27		
CORE EUDICOTS											
Caryophyllales											
Aizoaceae	15.56	6	**54.55**			6	17.14	8	18.18	3	5.36
Amaranthaceae	3.40					2	5.71	3	6.82		
Molluginaceae	0.68					1	2.86				
Nyctaginaceae	0.68									1	1.79
Saxifragales											
Crassulaceae	1.36									2	3.57
ROSIDS											
Zygophyllaceae	9.52	5	**45.45**			2	5.71	6	13.64	2	3.57
Geraniales											
Geraniaceae	1.36					1	2.86			1	1.79
Cucurbitales											
Cucurbitaceae	0.68	1	9.09								
Fabales											
Fabaceae	**55.10**	2	18.18			5	14.29	27	**61.36**	47	**83.93**
Polygalaceae	5.42	1	9.09					2	4.55	5	8.93
Malpighiales											
Euphorbiaceae	0.68	1	9.09								
EUROSIDS II											
Brassicales											
Brassicaceae	6.8	1	9.09					3	6.82	6	10.71
Malvales											
Malvaceae	15.65	2	18.18			3	8.57	12	**27.27**	4	7.14
Neuradaceae	4.08	4	**36.36**			2	5.71				
ASTERIDS											
Cornales											
Loasaceae	0.68							1	2.27		
EUASTERIDS I											
Boraginaceae	8.84					2	5.71	6	13.64	5	8.93
Vahliaceae	1.36					1	2.86	1	2.27		
Gentianales											
Apocynaceae	11.56							2	4.55	15	**26.79**
Lamiales											
Acanthaceae	14.29	2	18.18					6	13.64	13	**23.21**
Lamiaceae	17.00			1		6	17.14	10	**22.73**	8	14.29
Pedaliaceae	2.27	2	18.18							2	3.27
Scrophulariaceae	2.27					1	2.86	1	2.27	2	3.57
EUASTERIDS II											
Apiales											
Apiaceae	2.72							1	2.27	3	5.36
Asterales											
Asteraceae	**36.73**	2	18.18	1		26	**74.29**	14	**31.82**	11	19.64
Campanulaceae	4.76					4	11.43	2	4.55	1	1.79



Iridaceae to woody stems of *Acacia*, bored by beetles (Michener 1968a).

Structure and method of construction of nest

The burrow of the two species is very similar. It is divided transversely to form a series of cells, end to end. The cells are not lined. The partitions between cells are thin discs of translucent, rather soft brownish resin, less than 0.25 mm thick. In some regions, resin discs are omitted by *H. spiniscutis* with only dry pollen loosely filling the spaces between food masses.

The origin of the indigenous resin used is not known for either species. However, Charles Michener (1968a) stated that some *Heriades* are known to collect ‘gum’ from *Euphorbia*. John Taylor (1962c) recorded that at Port Elizabeth *H. freygessneri* collected resin from pine trees and that the nests had a distinct pine odour.

Provisioning and oviposition

The provision of *H. spiniscutis* is cylindrical, of the same diameter as the burrow, bevelled or obliquely concave at the upper end. The mass is firm in consistency. It has a strong yeasty odour. A variable dusting of loose, dry pollen reduces contact with the walls. The egg is laid on the top of the pollen mass. Loose pollen is often placed in some quantity on top of the food mass where it sometimes nearly covers the egg or young larva (Michener 1968a).

The flowers visited by *H. spiniscutis* were mostly Asteraceae. It is likely that the provision was from this source as was the provision of the *H. freygessneri*. Furthermore, we collected females of six species of *Heriades* from flowers, variously in the Eastern Cape, Olifants River Valley and Namaqualand, all of which were visiting mostly Asteraceae.

Interestingly, we collected females of the single species of *Pseudoheriades*, *P. moricei* (Friese) mostly from flowers of Fabaceae (Mimosoideae and Papilionoideae) in the Little Karoo and southern and northern Namibia. In Namibia only one was collected from Asteraceae (*Geigeria pectidea* (DC.) Harv.). Some were in addition collected from Malvaceae (*Hermannia* species).

Life history

The cocoon is cylindrical, of fine fibres in a thin translucent matrix. There is no nipple.

Associates

Various parasitic associates have been reared from nests.

Those recorded for *H. spiniscutis* are *Eurytoma* sp. (Chalcidoidea, Eurytomidae) and two species of Mutillidae, *Mutilla inconspicua* Péringuey from Grahamstown and males of a second species from Cape Point (Michener 1968a).

Those recorded for *H. freygessneri* are *Chrysis laetabilis* du Buysson (Chrysididae) and *Anthrax triatomus* Hesse (Bombyliidae) from Port Elizabeth (Taylor 1962), and *Melittobia* (Eulophidae) and *Afrostelis aethiopica* (Friese) (Megachilinae, Anthidiini) from Wilderness (Taylor 1965).

An additional parasite, *Sapyga* (*Sapygina*) *simillima* Arnold (Sapygidae), was recorded from a species of *Heriades* nesting in a wooden trapnest on the farm Hilton, Grahamstown (Gess 1981).

In addition John Taylor (1965) recorded a scavenging psocid, *Lipocelis* species, from nests of *H. freygessneri* from Wilderness. This scavanger apparently does not harm the bees.

Hoplitis Klug

Nesting by *Hoplitis* (*Anthocopa*) is known for four species. These are as follows:

- *Hoplitis* (*A.*) *conchophila* Kuhlmann (as an undescribed species of *Hoplitis* (*Anthocopa*) by Gess & Gess 1999, 2008; as *Hoplitis* sp. by Koch 2006; Kuhlmann *et al.* 2011), *Hoplitis* (*A.*) *infrapicta* (Cockerell) (Michener 1968b).
- *Hoplitis* (*A.*) *karooensis* (Brauns) (Kuhlmann *et al.* 2011).
- *Hoplitis* (*A.*) *similis* (Friese) (as *Hoplitis* (*Anthocopa*) *anthodemnion* Michener by Michener 1968b, Gess 1981; Gess & Gess 1990b; Kuhlmann *et al.* 2011).
- Nesting of an additional species of *Hoplitis*, not identified to subgenus or species, has been noted (Gess & Gess fieldnotes and voucher specimens).

Hoplitis (*Anthocopa*) *conchophila* Kuhlmann

Nest situation

Hoplitis (*A.*) *conchophila* was found north and south of the Orange River, nesting in empty *Trigonephrus* shells in winter-rainfall desertic sandy areas.

Nest structure

No nest description is given by Koch (2006). We investigated nests from north and south of the Orange River. The walls of the cells positioned within the crown of the shell, are constructed from petals (Gess & Gess 1998, 2008; Kuhlmann *et al.* 2011). Only the petals from a newly constructed nest from the site south of Rosh Pinah were identified (Figure II.4.8). They were cut from the pink petals of *Sarcocaulon* (Geraniaceae) (Figure I.3.32.e & f).

Hoplitis (*Anthocopa*) *infrapicta* (Cockerell)

Nest situation

Hoplitis (*A.*) *infrapicta* (Cockerell) was found by Charles Michener (1968b) nesting on a slope behind Noordhoek on the Cape Peninsula. The nests were in a slightly sloping path of loose gravelly clay.

Structure and method of construction of nest

Two nests containing one cell each were found. As they were only 20 mm apart and one had been completed and closed and the other was being provisioned, Michener (1968b) suggested that they were made by the same bee.

Figure II.4.8.—*Hoplitis* (*Anthocopa*) *conchophila* Kuhlmann: cells constructed from petals of *Sarcocaulon*, succeeded by cells of *Quartinia* sp. (Masarinae) in shell of *Trigonephrus* sp.

The burrow leading to each cell was vertical. The cell itself was curved and slanting. The cell wall was rough, irregular, pebbly, not or scarcely compacted. The lining was of thin purple petals, four or five layers thick. In the cell that was still being provisioned, the petals reached the surface of the soil. Closure of the cell had been achieved by turning the uppermost parts of the petals inward. The inner petals had first been bent over and a little loose soil had been placed on top of them. Then other petals had similarly been turned in and soil added. Finally, the outermost petals had been bent in, with probably one or two additional petal fragments placed on top, and soil added to the level of the ground surface.

Hoplitis (*Anthocopa*) *karooensis* (Brauns)

Nest situation

We found and investigated a nesting aggregation of *H.* (*A.*) *karooensis* at Clanwilliam in the Olifants River Valley, Western Cape (Kuhlmann *et al.* 2011). The nest location was in level sandy ground near the base of a shrub, *Aspalathus spinescens* Thunb. (Fabaceae, Papilionoideae), on the east side of the Clanwilliam Dam.

Nest structure

The nest is a multicellular burrow surmounted by a curved turret constructed from cemented sand (Figure II.4.9.a). In the sample of eight nests investigated, the depth of the burrow including the cells was 50–70 mm. The turret and main shaft were of equal inner diameter, 4.5 mm (average of eight). The flask-like cells, clustered at the base of the shaft, had well cemented walls, such that we were able to remove the cells intact (Figure II.4.9.a & c).

Method of nest construction

The nature of the substance used for the cementing of the walls of the turret, shaft and cell walls was not established but it seems probable that it was plant resin. The cells had been lined with petals.

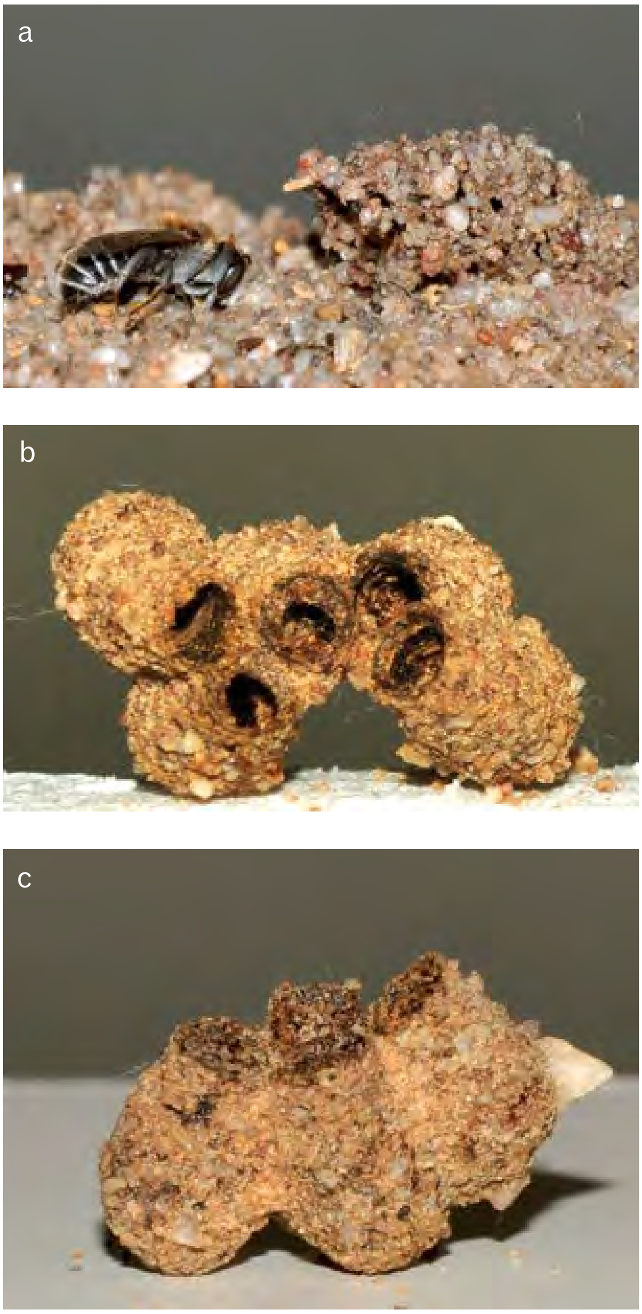


Figure II.4.9.—a.–c. *Hoplitis* (*Anthocopa*) *karooensis* (Brauns) (voucher specimens): a. nest entrance turret and bee; b. and c. cells.

Provision

Pollen from provision was examined and found to be of mixed sizes and sculpturing. The floral origins could not be identified. Females of *H.* (*A.*) *karooensis* were collected variously from flowers of Asteraceae (*Arctotheca calendula* (L.) Levyns) in Namaqualand (1 specimen); Campanulaceae (*Wahlenbergia*, four species) in Namaqualand (10 specimens) and in and west of the Olifants River Valley; Fabaceae (Papilionoideae, *Aspalathus spinescens* Thunb.) in the Olifants River Valley (one specimen); Malvaceae (*Hermannia* species) to the west of the Olifants River Valley (two specimens); and Neuradaceae (*Grielum humifusum* Thunb.) in Namaqualand (one specimen) (Gess & Gess 2003 as *Hoplitis* (*Anthocopa*) sp. C).

Hoplitis (*Anthocopa*) *similis* (Friese)

Nest situation

Hoplitis (*A.*) *similis* nests in vertical banks. Michener's observations (1968b) were made south of Avontuur, Western Cape, where the bees were nesting in a vertical, hard dry clay roadside bank. We investigated nesting by this bee in a vertical, relatively soft sandstone bank of the New Year's River on the farm Hilton, in the eastern Nama-Karoo, northwest of Grahamstown, Eastern Cape (Gess 1981; Gess & Gess 1990b; Kuhlmann *et al.* 2011). The banks in both cases were exposed to the sun. Nests were scattered in large aggregations along the banks.

Structure of and method of construction of nest

Each nest consisted of a single cell and the burrow leading to it. The burrow most commonly sloped down at 20° although some were as steep as 45° (Figure II.4.10.a). The axis of the cell is often steeper than the burrow. The cells were lined with four to six layers of very thin, hairless, pink or purple petals. The petals were too delicate to be separated but it was believed that they were probably whole petals cut off at the base (Michener 1968b). We observed the bees cutting a single disc from the distal end of each of the petals of flowers, for example of *Barleria pungens* L.f. (Acanthaceae) (Figure II.4.10.b). Excavation of the burrows was not observed. Whilst the cell is being provisioned, the petals extend into and line the inner end of the burrow. After oviposition the outer ends of the petals are bent inward to close the cell and mud is pushed in as a plug, which becomes convex on its inner surface. The entrance burrow is completely filled with clay, apparently applied as mud, up to the surface of the bank. As the clay is a different colour from the substrate, it is suggested that it is brought from elsewhere.

Michener (1968b) found old cells being re-used. They were being lined and provisioned. Petal linings of the previous season were blackish. Fresh petals are sometimes applied, after removal of the faeces and cocoon, on such an old lining. Sometimes a petal lining is placed inside an old cocoon. Occasionally a very thin clay lining is added to a cell covering the old, black lining of petals.

Provisioning and oviposition

The cell is filled to a depth of 9–10 mm with firm yellow pollen and the large egg is laid on top, lying on the provisions.

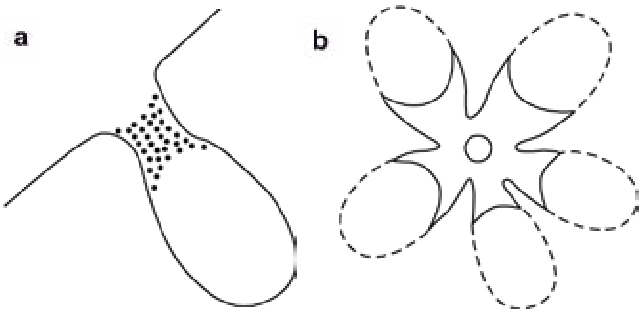


Figure II.4.10.—a. and b. *Hoplitis* (*Anthocopa*) *similis* (Friese): a. vertical plan of nest (actual size); b. diagram of flower of *Barleria pungens* to show discs cut from petals as indicated by dotted lines.

Pollen from the provision was not identified, however, we collected females of *H.* (*A.*) *similis* from flowers of Asteraceae (*Berkheya heterophylla* (Thunb.) O.Hoffm.), Boraginaceae (*Anchusa capensis* Thunb.), and Scrophulariaceae (*Selago* species) in the Hilton nesting area.

Hoplitis sp.

Two nests of *Masarina familiaris* Richards (Vespidae, Masarinae) in a vertical face of clayey soil to the west of Clanwilliam were being attended to by a species of *Hoplitis*, which had usurped the nests (Gess & Gess 1988a). One nest was old, lacking a turret, and the other a newly constructed turreted four-celled nest. The wasp cells utilised by the bee had been widened by the latter prior to the construction of its petal cells. The petals utilised were those of a purple flowered *Cyanella* sp. (Iridaceae) which was growing in the vicinity. After a petal-cell had been sealed with pieces of petal, the excavated cell was sealed with compacted soil.

Pollen from the provision was a mixture of pollen and nectar derived from three or more plant species. Pollen for provision had been collected from plants different from those from which nesting materials had been taken.

Othinosmia Michener

Construction of aerial nests using very small pebbles and resin is known for three species of *Othinosmia*, *O.* (*Megaloheriades*) *globicola* (Stadelmann) (= *Hoplitis globicola* (Stadelmann)), *O.* (*M.*) *jansei* (Brauns) and *O.* (*M.*) *schultzei* (Friese). Nesting in a burrow in the ground, using resin to line the cell is known for *O.* (*Othinosmia*) *filifera* (Cockerell) (= *Hoplitis filifera* (Cockerell)).

Othinosmia (*Megaloheriades*) *globicola* (Stadelmann)

Nests of *Othinosmia* (*M.*) *globicola* (Stadelmann) have been recorded from several sites. The species was originally described in 1892 from individuals taken from nests. Hans Brauns (1892), based in Willowmore in the Eastern Cape, recorded having found the bee to be common in the karoo and stated that he had collected 'dozens' of nests and also one from near Stellenbosch. Charles Michener (1968b) illustrated two nests, which he found in the collection of the South African Museum in Cape Town—one from near Stellenbosch and the other from near Leipoldtville. Since then, in several years, we have found nests at numerous sites in Namaqualand, Klipkoppe and Nieuwoudtville areas, and to the west of the Olifants River Valley (Gess & Gess, fieldnotes and voucher specimens 1980s and 1990s, illustrated in Gess & Gess 1990b as *Hoplitis globicola*). In all instances the nests had been constructed around stems of small shrubs about one metre above ground.

Structure and method of construction of nest

The 17 nests that we examined consisted of eight to 12 cells, all touching, constructed from very small pebbles and resin and arranged in a whorl around the plant stem (Figure II.4.11.a). They are positioned with their long axes

Figure II.4.11.—a. and b. *Othinosmia* (*Megaloheriades*) *globicola* (Stadelmann): a. group of cells before construction of envelope; b. completed nest.

vertical and opening downwards. When cell construction is complete, the cells are enclosed in an envelope similarly constructed from very small pebbles and resin (Figure II.4.11.b).

Associates

The nests are subject to parasitism. Hans Brauns (1892) reared a leucospid, *Leucospis osmiae* Bouček (Leucospidae), and a velvet ant, *Dasylabroides baucis* (Péringuey) (Mutillidae), from nests of *O.* (*M.*) *globicola*. Of the nests examined by Michener (1968b), one was associated with two sapygids.

From nests investigated, we recorded the following: four specimens of a meloid beetle, *Stenoria hessei* Kaszab (Meloidae), from two nests; a clerid beetle, *Trichodes* sp. (Cleridae), from one nest; two females and one male of a velvet ant (Mutillidae) from three nests; and two specimens of a sapygid from one nest (Gess & Gess voucher specimens).

Othinosmia (*Megaloheriades*) *jansei* (Brauns) and *Othinosmia* (*Megaloheriades*) *schultzei* (Friese)

Unlike *Othinosmia* (*M.*) *globicola*, *O.* (*M.*) *jansei* (Brauns) and *O.* (*M.*) *schultzei* (Friese) build their nests on stones or rocks partly embedded in the ground.

Nest situation

The nests of *O.* (*M.*) *jansei* studied by us were on rocks embedded in clayey soil in karroid areas near Grahamstown, Eastern Cape (Gess 1981; Gess & Gess 1990b as *Hoplitis jansei* (Brauns)), and in an area of sandy soil near Sutherland in the west (Gess & Gess fieldnotes 2009 and voucher specimens).

The first record of nesting by *O.* (*M.*) *schultzei* (Friese) is given and illustrated in Friese (1909 as *Osmia schultzei* Friese). We have found the nests of *O.* (*M.*) *schultzei* (Friese) very commonly throughout Klipkoppe, Namaqualand, on rocks, most commonly embedded in the ground (fieldnotes and voucher specimens, various dates 1980s and 1990s; Gess & Gess 1990b as *Hoplitis schultzei*). Michael Kuhlmann and Kim Timmermann (2009) made a detailed study of the nesting of this bee in southeastern Namaqualand to the northwest of Nieuwoudtville in Bokkeveld Sandstone Fynbos.

The advantages of using stones and rocks rooted in the ground is that they are more stable and we have suggested that the ground acts as a heat sink protecting the provision and young from overheating (Gess 1981).

Structure of and method of construction of nest

The nest of the *O.* (*M.*) *jansei* consists of a group of robustly built cells, cemented to the upper surface of the rock (Figure II.4.12.a–e). The long axes of the cells run parallel to the stone surface, which forms part of the wall of the cells attached to it (Figure II.4.12.a). The nature of and the size of the tiny 'pebbles' used to construct the cells is dictated by the nature of the 'pebbles' available in the nesting area. In the western sandy area, the group of cells is lightly covered with a sand and resin coating (Figure II.4.12.a), whereas in the east, the cells are never covered over (Figure II.4.12.e).

The cells of *O.* (*M.*) *schultzei* in Namaqualand are similar to those of *O.* (*M.*) *jansei*, however, the cells are less robustly built and are covered over with a thick domed coating of resin mixed with sand, giving fresh nests a distinctive, markedly yellow colouring (Figure II.4.13.a–e). The cells examined by Kuhlmann & Timmermann (2009) were constructed from 'quartz grains' with their walls coated on the inside with a cellophane-like transparent lining. They suggested that the resin might be derived from Asteraceae, such as *Chrysocoma ciliata* L. known by Kuhlmann to be used as a resin source by *Plesianthidium* (*Spinanthidium*) *trachusiforme* (Friese) (Anthidiini).

Figure II.4.12.—a.–e. *Othinosmia* (*Megaloheriades*) *jansei* (Brauns): a–d. in the west near Sutherland, a. bee constructing cell, b. and c. two cells, b. stone in situ, c. stone removed from ground; d. a completed nest; e. in the east on Hilton Farm, group of cells.

Provision

Provision from a cell of *O.* (*M.*) *jansei*, collected by us from Sutherland, was moist and dark yellow. Pollen from the provision examined microscopically was derived from Asteraceae. Females were all collected from Asteraceae in the Eastern Cape, Sutherland and Namaqualand.

The provision examined by Kuhlmann & Timmermann (2009) was similar in appearance. They microscopically examined pollen from provisions of five nests of *O.* (*M.*) *schultzei* and from pollen loads and concluded that the pollen for provision is derived from Asteraceae. We collected females from Asteraceae (mostly species of *Berkheya*, *Pteronia* and *Arctotheca*) in Namaqualand.

Associates

On Hilton farm, we found an abandoned nest of *O.* (*M.*) *jansei* with open cells which had been used for nesting by a leafcutter bee, *Megachile* (*Eutricharaea*) *gratiosa* (Gerstaecker) (Gess 1981). No other associates have been recorded for *O.* (*M.*) *jansei*.

No re-use of abandoned nests of *O.* (*M.*) *schultzei* has been recorded, however, the active nests are subject to parasitism. A chrysidid, a parasitic wasp, a meloid and a clerid have been recorded.

The first recorded rearing of a ‘parasite’ from a nest of *O.* (*M.*) *schultzei* was by Schultze. This was a chrysidid wasp described by Mocsáry (1910) as *Chrysis schultzei* (now known as *Chrysura schultzei* (Mocsáry)). Since then we have reared *C. schultzei* from a nest of the same bee (Gess & Gess voucher specimens) and on several occasions it has been observed in attendance at nests by Kuhlmann & Timmerann (2009).

Large numbers of a parasitic wasp (Chalcidoidea) were reared from four nests (Gess & Gess voucher specimens).

Figure II.4.13.—a.–e. *Othinosmia* (*Megaloheriades*) *schultzei* (Friese): a. female constructing cell; b. cell under construction; c. partly closed cell; d. cells covered over with a coating of resin mixed with sand; e. two completed nests.

Two adult and two coarctate larvae of a meloid beetle, *Stenoria hessei* Kaszab (Meloidae) were found in three nests (Gess & Gess voucher specimens) and Kuhlmann & Timmermann (2009) noted that they found a dead meloid beetle of the same species in two cells.

A clerid beetle, *Trichodes* sp. (Cleridae) was reared from a nest (Gess & Gess voucher specimens).

Othinosmia (*Othinosmia*) *filifera* (Cockerell)

Nest situation

Nesting by *Othinosmia* (*O.*) *filifera* observed by Charles Michener (1968b) was on a stony dry slope in the Robertson Karoo.

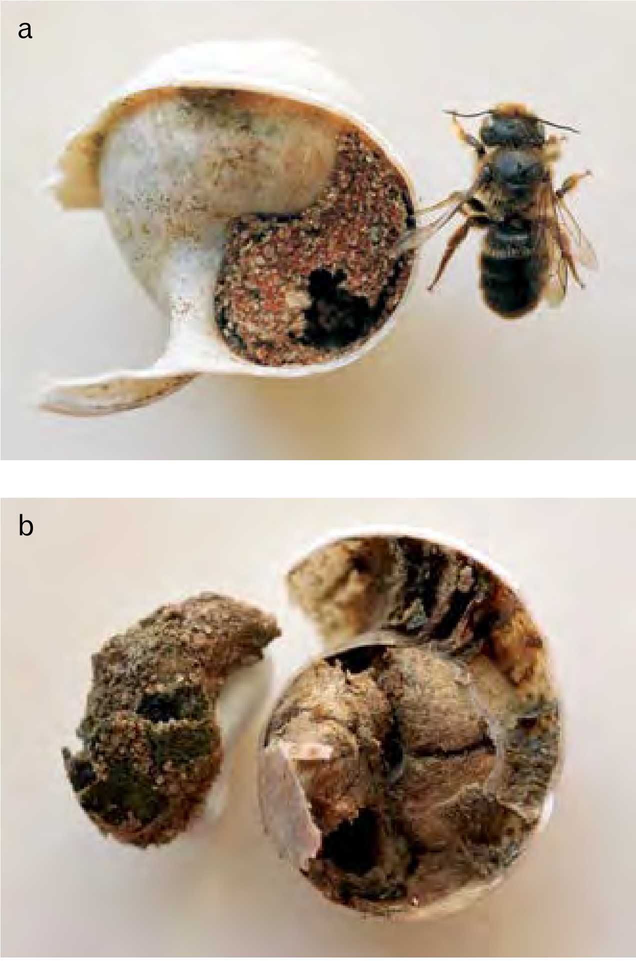


Figure II.4.14.—*Wainia* (*Caposmia*) *afrorufa* (Friese): a. and b. *Trigonephrus* shells broken open to expose nests, a. showing emergence hole and female, b. showing nest structure.

Nest structure

The nest was a rather irregular burrow that sloped downward and ended in a single cell thinly lined with a dark resinous material, which was rather smooth on the inside.

Wainia Tkalců

Nesting by *Wainia* species in southern Africa has been recorded for three species, all of the subgenus *Caposmia*, as follows:

- *W.* (*C.*) *atrorufa* (Friese) (as *W.* (*Wainia*) sp. A by Gess and Gess 1999; *W.* (*Caposmia*) sp. A by Gess & Gess 2008; Kuhlmann *et al.* 2011).
- *W.* (*C.*) *elizabethae* (Friese) (as *Osmia* sp. by Gess & Gess 1988c; as *Hoplitis* sp. by Gess & Gess 1990b, 1998; as *W.* (*C.*) *elizabethae* Brauns by Gess & Gess 2008; Kuhlmann *et al.* 2011).
- *W.* (*C.*) *gessorum* Kuhlmann (as *W.* (*C.*) sp. C by Gess & Gess 2008; Kuhlmann *et al.* 2011).

Nest situation

All three species nest in snail shells. *Wainia* (*C.*) *atrorufa* was found nesting from south of the Orange River southwards at least to Lamberts Bay and *W.* (*C.*) *gessorum* was found nesting only in desertic areas north of the Orange River. Both species were nesting solely in the relatively large shells of *Trigonephrus* Pilsbry (Dorcasiidae), a genus endemic to and restricted to the sandy areas in the west from Cape Town north to Lüderitz (Figure II.4.14). Although *Theba pisana* (Müller) (Helicidae), an invasive exotic snail, has spread from Cape Town north to Port Nolloth, in some areas having become far more abundant than *Trigonephrus*, its shells are not used, the cavity being too small.

The much smaller *Wainia* (*C.*) *elizabethae* was recorded nesting in empty shells of terrestrial snails in sandy coastal areas from Still Bay in the west to Riet River in the east (Figure II.4.15). The shells used were those of an indigenous snail, *Tropidophora ligata* (Müller) (Pomatiidae) and *Theba pisana*, which has spread eastwards at least as far as East London. However, the shells of *T. ligata* for which the highest percentage use was recorded seem to be preferred to those of *T. pisana.* It would appear that the low spiral of *T. pisana* is less suitable for nest construction than the high spiral of *T. ligata.*

Wainia (*C.*) *algoensis*, also a small species, was found in association with shells of *T. ligata* at Kenton-on-Sea to the west of Port Alfred and at Riet River to the east of Port Alfred. No nests were obtained.

Nest structure

Wainia (*C.*) *atrorufa* and *W.* (*C.*) *gessorum* construct linearly arranged cells separated with a thin partition constructed from petal pieces arranged at right angles to the outer wall of the shell. The pollen provision is packed in to fill the entire cell and adheres to the shell. At the outer end of the nest, there is a succession of thick partitions constructed from several layers of petal pieces followed by a layer of cemented sand. The final seal is very robust and is constructed similarly but with the sand layer much thicker and more heavily cemented. The nature of the bonding agent was not established.

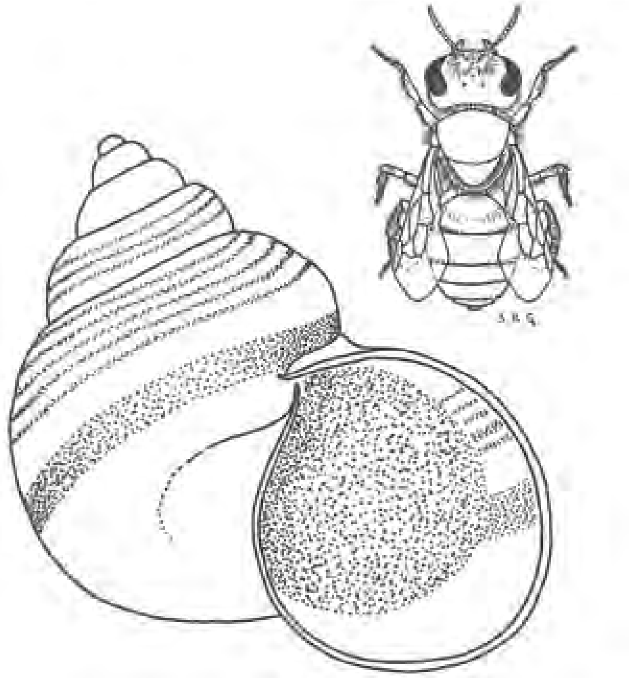


Figure II.4.15.—*Wainia* (*Caposmia*) *elizabethae* (Friese): female and sealed nest in shell of *Tropidophora ligata* (Müller).

The nests of *W.* (*C.*) *elizabethae* consist of one to three cells constructed consecutively in the helix of the shell. Each cell is closed by means of a seal built of sand grains cemented together with an unidentified resinous substance, probably collected by the bee from plants. The final nest seal, of a similar nature to the cell closures but situated not far from the shell aperture, is separated from the outermost provisioned cell by a vestibular cell filled with loose sand.

Provision

Pollen from provision was not identified and only two records of flower visiting by female *Wainia* were recorded—*W.* (*C.*) *atrorufa* from *Hermannia* species (Malvaceae) from Wallekraal in southwestern Namaqualand and *W.* (*Wainiella*) *sakaniensis* (Cockerell) from *Indigofera* (Papilionoideae) from the Gydo Pass, near Ceres, Western Cape.

Associates

Overall, little evidence of parasitism was found, however, numerous Eupelminae (Chalcidoidea, Eupelmidae) emerged from cocoons of *W.* (*C.*) *atrorufa* and *W.* (*C.*) *gessorum*, each from single sites.

Tribe Anthidiini

Anthidiini are represented in southern Africa by 13 nest-building genera and three parasitic genera. The nest-building genera occurring in southern Africa are *Anthidioma* Pasteels and *Aspidosmia* Brauns (western southern African endemics), *Cyphanthidium* Pasteels and *Plesianthidium* Cameron (southern African endemics), *Gnathanthidium* Pasteels (endemic to Africa south of the Sahara), *Serapista* Cockerell (African endemic), *Afranthidium* Michener, *Anthidiellum* Cockerell, *Eoanthidium* Popov, *Pachyanthidium* Friese and *Pseudoanthidium* Friese (Old World distribution), *Anthidium* Fabricius (distribution on all continents except Australia) and *Trachusa* Panzer (widespread) (Eardley & Urban 2010). The parasitic genera are *Afrostelis* Cockerell (African and Madagascan endemic), *Euaspis* Gerstaecker (Old World distribution) and *Stelis* Panzer (widespread) (Eardley & Urban 2010).

Nest constructing Anthidiine bees are generally divisible into two groups on the basis of the materials used for nest construction. One group, commonly known as carder bees, uses solely plant fibres and the other group resin, sometimes mixed with pebbles, soil particles, pieces of leaf or plant fibres.

Nesting in southern Africa

Nests constructed only from plant fibres are known for the following:

- *Afranthidium* (*Afranthidium*) *hamaticauda* Pasteels (as *Afranthidium* (*Oranthidium*) probably *odonturum* (Cockerell) by Gess & Gess 1999; erroneously as *Afranthidium* (*Afranthidium*) *ablusum* (Cockerell) by Gess & Gess 2007; Gess & Gess 2008)).
- *Afranthidium* (*Branthidium*) *braunsi* (Friese) (as *Branthidium braunsi* by Gess 1981).
- *Afranthidium* (*Branthidium*) *micrurum* (Cockerell) (as *Anthidium braunsi micrurum* Cockerell by Michener 1968b).
- *Afranthidium* (*Immanthidium*) *junodi* (Friese) (as *Anthidium junodi* Friese by Skaife 1950, Taylor 1962a & Michener 1968b, and as *Immanthidium junodi* (Friese) in Gess 1981).
- *Afranthidium* (*Immanthidium*) *repetitum* (Schulz) (as *Anthidium repetitum* Schulz by Michener 1968b; Gess & Gess 2007).
- *Afranthidium* (*Nigranthidium*) *concolor* (Friese) (Gess & Gess 2007).
- *Pseudoanthidium* (*Micranthidium*) *truncatum* (Smith) (as *Micranthidium truncatum* Smith in Friese 1902 and Michener 1968b).
- *Serapista denticulata* (Smith) (Stadelmann 1898, quoted by Friese 1905, 1909, 1916 and Michener 1968b).
- *Serapista rufipes* (Friese) (Gess & Gess 2007).

Nests constructed from plant material, pebbles and resin are known for *Aspidosmia arnoldi* (Brauns) (Brauns 1926a).

Nests constructed solely from resin are known for *Plesianthidium* (*Spinanthidiellum*) *volkmanni* (Friese) (Gess & Gess 2007).

The hosts of the nest parasites *Afrostelis*, *Euaspis* and *Stelis* are other Megachilinae.

Afranthidium Michener

The genus *Afranthidium*, divided into 11 subgenera, is principally sub-Saharan with one subgenus in the Palaearctic and at least two other species occurring in this region (Michener 2000, 2007). Eardley and Urban (2010) list 44 species for sub-Saharan Africa, 41 of which have been recorded from southern Africa. For southern Africa, flower visiting records are known for 19 species (Gess & Gess 2007), however, there appear to be nesting records for only six species.

Afranthidium (*Afranthidium*) *hamaticauda* Pasteels

Nest situation and structure

Afranthidium (*A.*) *hamaticauda* has been found by us sheltering and nesting in the empty shells of desert snails, *Trigonephrus* (Mollusca, Gasteropoda, Dorcasiidae), in sparsely vegetated, desertic areas north and south of the Orange River, from the northern Sperrgebiet in southwestern Namibia south to Wallekraal in Namaqualand (Gess & Gess 1999, 2007, 2008). The nests are from white, cotton-wool-like, plant fibres (Figure II.4.16).

Similar anthidiine nests, but no bees, were in addition found in *Trigonephrus* shells from Lutzville further south.

A further species of anthidiine was found nesting in *Trigonephrus* shells at three sites in the Sperrgebiet. The bee is markedly larger than *A.* (*A.*) *hamaticauda*, the papillate cocoon being 13.3 mm × 8.1 mm (average of four) compared with 7.7 mm × 4.3 mm (average of three), and the nests are constructed from golden-brown, not white, fibres (Figure II.4.17).

Figure II.4.16.—*Afranthidium* (*Afranthidium*) *hamaticauda* Pasteels: *Trigonephrus* shell broken open to show nest.

Figure II.4.17.—Unidentified anthidiine with papillate cocoon and *Trigonephrus* shell broken open to show nest.

Provision

No provision was found, however, we collected females of this species from Papilionoideae (*Indigofera* or *Lebeckia*) at all sites in which we found nests (11 specimens).

In addition, we collected females from *Zygophyllum stapffii* Schinz (Zygophyllaceae) from Swakopmund in Namibia (six specimens).

In this connection, it is of interest that we collected two other species, *A.* (*A.*) *karooense* (Brauns) from Papilionoideae (*Indigofera* sp.) near Oranjemund and Aus in the northern winter rainfall area (three specimens) and *A.* (*A.*) *reicherti* (Brauns) from Papilionoideae (*Aspalathus* sp.) near Ceres and Oudtshoorn in the south. In addition, we collected the former from mesembs in the Richtersveld and in the Nieuwoudtville areas (two specimens).

Afranthidium (*Branthidium*) *braunsi* (Friese) and *Afranthidium* (*Branthidium*) *micrurum* (Cockerell)

Nest situation

Afranthidium (*B.*) *braunsi* and *A.* (*B.*) *micrurum* both nest in pre-existing cavities. The former was found in the Eastern Cape on the farm Hilton, Grahamstown, nesting in a vertical 'sandstone' bank (Gess 1981), whereas the latter was found in KwaZulu-Natal near Pietermaritzburg nesting in an erect, dead weed stem, 6 mm in diameter, that was naturally hollow (Michener 1968b).

Nest structure

The cells were constructed from plant fluff. Those of *A.* (*B.*) *micrurum* were arranged in a linear series. There were five cells, however, the nest was not yet complete.

Provision

No provision was found, however, we collected females of *A.* (*B.*) *braunsi* most commonly from Papilionoideae at six sites from the Richtersveld in the north to Ceres in the south (14 specimens). Two females only were collected from Asteraceae at one site in the north.

Females of three other species were collected from Papilionoideae, however, one of these, *A.* (*B.*) *minutulum*, appears to be polyphagous, females having been collected from flowers of five additional families.

Life history

The nests of *A.* (*B.*) *micrurum* were collected in December. The cocoons consisted of a thin, translucent outer layer of fibres and whitish matrix, fixed to the surrounding plant fibres, and a thicker, firm inner layer with a brown matrix. Adults emerged in the following February.

Afranthidium (*Immanthidium*) *junodi* (Friese) and *Afranthidium* (*Immanthidium*) *repetitum* (Schulz)

Nest situation and structure

Afranthidium (*I.*) *junodi* and *A.* (*I.*) *repetitum* nest in pre-existing cavities.

The nests of *A.* (*I.*) *junodi* found by Charles Michener (1968b) were in various holes in a roadside bank near Avontuur, Langkloof, some were abandoned burrows of *Anthophora.* Those found by us on the farm Hilton, Eastern Cape, were in abandoned burrows in the 'sandstone' bank, in abandoned burrows of *Ceratina truncata* Friese, in inflorescence stems of *Aloe ferox*, in abandoned *Ceratina* galleries, in inflorescence stems of *Gasteria*, in stems of *Datura*, *Dasyproctus* in inflorescence stems of *Gasteria* and commonly in trapnests tied to branches of *Acacia karroo* (Gess 1981). The nests studied by Sydney Skaife in Cape Town (1950) and John Taylor in Port Elizabeth (1962b) were in glass tubes inserted into a wooden frame.

All the recorded nests of *A.* (*I.*) *junodi* were constructed in pre-existing tubular cavities (Figure II.4.18), which

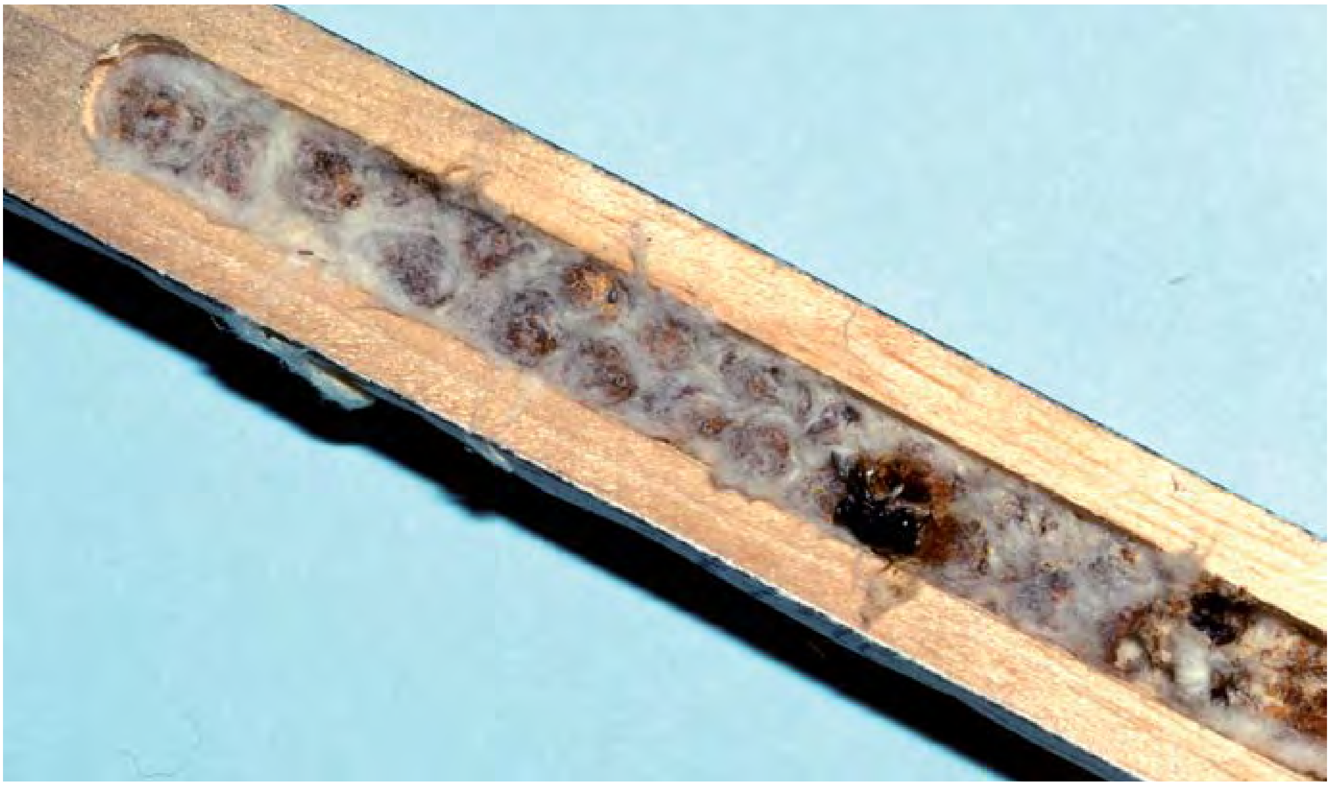


Figure II.4.18.—*Afranthidium* (*Immanthidium*) *junodi* (Friese), nest in trap nest.

necessitated the construction of the cells in a single linear series with one female nest builder per cavity. By contrast, the nests of *A. (I.) repetitum* are constructed in relatively large cavities. The record published by Michener (1968b) is based on part (estimated at one fifth) of a nest removed from an electricity meter box in Estcourt, KwaZulu-Natal and housed in the Natal Museum. This part of the nest, constructed from plant down, contained an estimated 350 cells or cocoons resulting in the estimation of the total number of cells in the nest having been 1 750. He concluded that a considerable group of females had constructed the nest.

The remains of a much smaller nest and an associated adult bee of *A. (I.) repetitum* were submitted to us for identification. They came from a Cape Town householder who had noticed a bee entering a heavy-duty vice on a workbench in his garage. He had later extracted this nest from a cavity in the vice, in which it had been constructed, and a single cell from an electrical double adapter in the same garage. Regrettably, the remains of the nests received were so mangled that no further information could be derived from them. Clearly, the size of the cavity used for nesting will dictate the number of bees that can nest within it and the number of cells that can be constructed.

Subsequently, in June 2000, Josephine Cardale of CSIRO, Canberra, Australia wrote (pers. comm.) that this bee had become established in southern Queensland, Australia. Being a nester in pre-existing cavities, the species is an ideal stowaway candidate, making its accidental transfer with household goods an easy matter.

The origin of the ‘wool’ used by *A.* (*I.*) *repetitum* has not been established, however, Taylor (1962a) recorded that Jacot Guillarmod had seen *A.* (*I.*) *junodi* removing fibres from the stems of *Helichrysum* (Asteraceae) in Lesotho (as Basutoland).

Provision

No provision was found. However, we collected females of *A.* (*I.*) *junodi* from flowers of Papilionoideae, near Clanwilliam and Augrabies (four specimens), Boraginaceae (*Trichodesma*) in the Richtersveld (one specimen), Lamiaceae (*Ballota*) in the Kamiesberg (two specimens) and Asteraceae (*Berkheya*) at Riebeek East in the Eastern Cape (1 specimen).

Associates

Sydney Skaife (1950) obtained a cuckoo wasp, *Chrysis mionii* Guérin (as *Tetrachrysis concinna* Mocsáry), and dead bees swollen with the puparia of a conopid fly, *Physocephala limbata* Kröb. from nests of *A.* (*I.*) *junodi.*

Alan Weaving reared two species of *Leucospis*, one female *L. fallax* Bouček and two females and a male *L. ornata* Westwood, from nests of *A.* (*I.*) *junodi* in trapnests on Hilton (voucher specimens in the Albany Museum).

Afranthidium (*Nigranthidium*) *concolor* (Friese)

Nest situation and method of construction

A nest of *Afranthidium* (*N.*) *concolor* was found in a bare sandy area on a slope at Sors Sors in the Kamiesberg, Namaqualand. It was in an early stage of construction. Projecting from the mouth of a vertical burrow, 6 mm in

Figure II.4.19.—a.–c. *Afranthidium* (*Nigranthidium*) *concolor* (Friese): a. nest entrance lined with plant 'fluff'; b. and c. *Eriocephalus* sp. (Asteraceae), source of plant 'fluff'.

diameter and 41 mm deep, apparently pre-existing, was a short entrance tube constructed from plant fluff (Figure II.4.19.a.). At the base of the burrow was an open, as yet unprovisioned cell, similarly constructed from plant fluff. Examination of the fluff showed it to have been obtained from the seeds of *Eriocephalus* (Asteraceae) growing nearby (Figure II.4.19.b & c).

Provision

No provision was found, nor did we collect this species from flowers at Sors Sors. However, we collected females from flowers at two other sites in Namaqualand, Nababeep and Nieuwoudtville, from Asteraceae (three females), and at the latter site from *Herrea* (Mesembryanthema) (two females).

Afrostelis Cockerell

Eardley and Urban (2010) list six species of *Afrostelis*, four of which have been recorded from southern Africa.

Afrostelis is known to parasitise the nests of other megachilids. The only host record for southern Africa is for *A. aethiopica* (Friese), which has been recorded as parasitic in nests of *Heriades freygessneri* Schletterer (Osmiini) at Wilderness and at Port Elizabeth (Taylor 1965).

Anthidiellum Cockerell

Eardley and Urban (2010) list 17 species of *Anthidiellum*, 13 of which have been recorded from southern Africa. Three subgenera are recognised. There appear to be no records of nesting or for female flower visiting.

Anthidioma Pasteels

Only two species of *Anthidioma* are known, both from southern Africa (Eardley & Urban 2010). Nothing appears to be known of the nesting or flower visiting.

Anthidium Fabricius

Eardley & Urban (2010) list 22 species of *Anthidium* from sub-Saharan Africa, 14 of which have been recorded from southern Africa. Three subgenera are recognised. There appear to be no records of nesting. We have flower visting records for females of two species, *Anthidium* (*Anthidium*) *pontis* (Cockerell) from Acanthaceae (*Blepharis*) from the Eastern Cape (one specimen) and *Anthidium* (*Nivanthidium*) *niveocinctum* Gerstaecker from Asteraceae (*Geigeria*) from northern Namibia (two specimens).

Aspidosmia Brauns

Only two species of *Aspidosmia* are known, both from southern Africa (Eardley & Urban 2010).

Little seems to be known of the nesting of *Aspidosmia*, the only published record of nesting apparently being that of Hans Brauns (1926a). He described nests of *Aspidosmia arnoldi* (Brauns) on stones in the vicinity of Willowmore in the Eastern Cape. In most cases, the nests had been built on the underside of loose stones. They were multicellular, the cells being arranged in rows, and later covered over so that the contour of the cells was obscured. The nests were constructed from macerated plant material, probably from resinous plants. The covering of the cells was impregnated with small stones, which projected irregularly, presenting a knobby surface.

No provision was recorded. However, we collected females of *A. arnoldi* from Papilionoideae (*Lebeckia* and *Wiborgia*) from sites between Clanwilliam in the Olifants River Valley to Springbok in Namaqualand Klipkoppe (three specimens) and from *Stachys* (Lamiaceae) in the Richtersveld (one female).

Nests of the second species, *A. volkmanni* (Friese), have not been recorded, however, we collected females from flowers of Asteraceae (*Berkheya*, *Gorteria* and *Osteospermum*) from sites between the Kamiesberg and north of the Orange River (18 specimens) and *Hermbstaedtia* (Amaranthaceae) in the Richtersveld (two specimens).

Cyphanthidium Pasteels

Only two species of *Cyphanthidium* are known, both from southern Africa (Eardley & Urban 2010).

There appear to be no accounts of nesting by *Cyphanthidium.* However, we collected females of *C. intermedium* Pasteels from Papilionoideae (*Crotalaria*) from northwestern Namibia (one specimen) and of an undetermined species from Acanthaceae (*Blepharis*) in Namaqualand (three specimens).

Eoanthidium Popov

Eoanthidium is widespread in the Old World but is represented in sub-Saharan Africa by only four species, three of which are recorded from southern Africa, two from Zimbabwe and one, *Eoanthidium* (*Clistanthidium*) *tunericum* (Mavromoustakis), from South Africa and Namibia (Eardley & Urban 2010).

There appear to be no nesting accounts for the genus.

The only indication of possible provenance of provision is given by flower visiting for females. We collected females of *Eoanthidium* (*Clistanthidium*) *tunericum* (Mavromoustakis) from flowers of Papilionoideae (one specimen) in the Richtersveld, Boraginaceae (*Codon* formerly Hydrophyllaceae) in the Richtersveld and northwestern Namibia (three specimens), Boraginaceae (*Heliotropium*) in northwestern Namibia (one specimen), and Brassicaceae (*Cleome* formerly Capparaceae) in western-central Namibia (one specimen) (Gess & Gess 2007).

Euaspis Gerstaecker

Euaspis is widespread in Africa, from Nigeria to Kenya and south to South Africa, and in southern and eastern Asia (Michener 2000, 2007). Three (Eardley *et al.* 2010) or four (Eardley & Urban 2010) species have been recorded from southern Africa.

Euaspis has been recorded as parasitising other Megachilidae (*Lithurgus* and chalicodomiform *Megachile*) (Michener 2000, 2007). Iwata (1976) states of *Parevaspis* = *Euaspis* that, 'while it is reported to parasitise *Lithurgus* (Lieftinck 1939), observations show that the Japanese *P. basalis* is a cleptoparasite of *Chalicodoma sculpturalis* only (Iwata 1933). This species does not parasitise any species other than those which make nests with resin. In southeast Asia, it is reported to live in the nest of *Ch. disjuncta* or other allied species and even in Japan, it probably lives on *Ch. disjunctiformis*.' He goes on to give a detailed account of the activities of this bee in converting its host's nest to its own.

Three *Euaspis abdominalis* (Fabricius) were reared from nests of *Megachile* (*Gronoceras*) *felina* Gerstaecker from northern KwaZulu-Natal by Alan Weaving in 1992 (specimens in the Albany Museum collection). Of these, one, a male, is from a nest constructed in an old *Synagris* (Eumeninae) mud nest from Umlalazi Nature Reserve and two, a female and a male, are from a nest constructed within a length of reed put out as a trapnest in the iSimangaliso Wetland Park (formerly Lake St Lucia Game Reserve).

Some further support for a possible predilection for parastising chalicodomiform *Megachile* is given by two observations in the vicinity of Grahamstown. A female *E. abdominalis* was found by Robert Gess sheltering in an aerial mud nest, probably of *Megachile* (*Gronoceras*) *cincta* (Fabricius), built under the windowsill of a brick building (specimen in collection of the Albany Museum). The same species was observed investigating holes in a vertical sandstone bank but it was not established which nests were being parasitised, although circumstantial evidence suggested that it may have been associated with the nests of *Megachile* (*Pseudomegachile*) *schulthessi* Friese (as *Chalicodoma* (*Pseudomegachile*) *schulthessi* (Friese)) (Gess 1981).

Gnathanthidium Pasteels

Gnathanthidium is a monotypic sub-Saharan species which has been recorded from eastern and southern Africa (Eardley *et al.* 2010). There appear to be no records for nesting or flower visiting (Eardley & Urban 2010).

Pachyanthidium Friese

Eardley & Urban (2010) list 16 species from sub-Saharan Africa, six of which have been recorded from southern Africa. Four subgenera are recognised (Eardley *et al.* 2010).

There appear to be no nesting accounts for southern African species, however, two nests of *Pachyanthidium* (*Pachyanthidium*) *bicolor* (Lepeletier) collected in Uganda were seen and described by Michener (1968b). The nests consisted of seven and two cells respectively constructed adjacent to one another on coffee leaves. The cells consisted of resin or gum intermixed with plant hairs.

Michener noted that two females of *Pachyanthidium* (*Pachyanthidium*) *micheneri* Pasteels, a species that occurs in southern Africa, had been seen in Malawi gathering latex from injured tips of *Euphorbia.* In this regard it is of interest that *Pachyanthidium* (*Pachyanthidium*) *cordatum* (Smith) has been recorded from *Dalechampia* sp. (Euphorbiaceae) in northern KwaZulu-Natal (Armbruster & Steiner 1992)

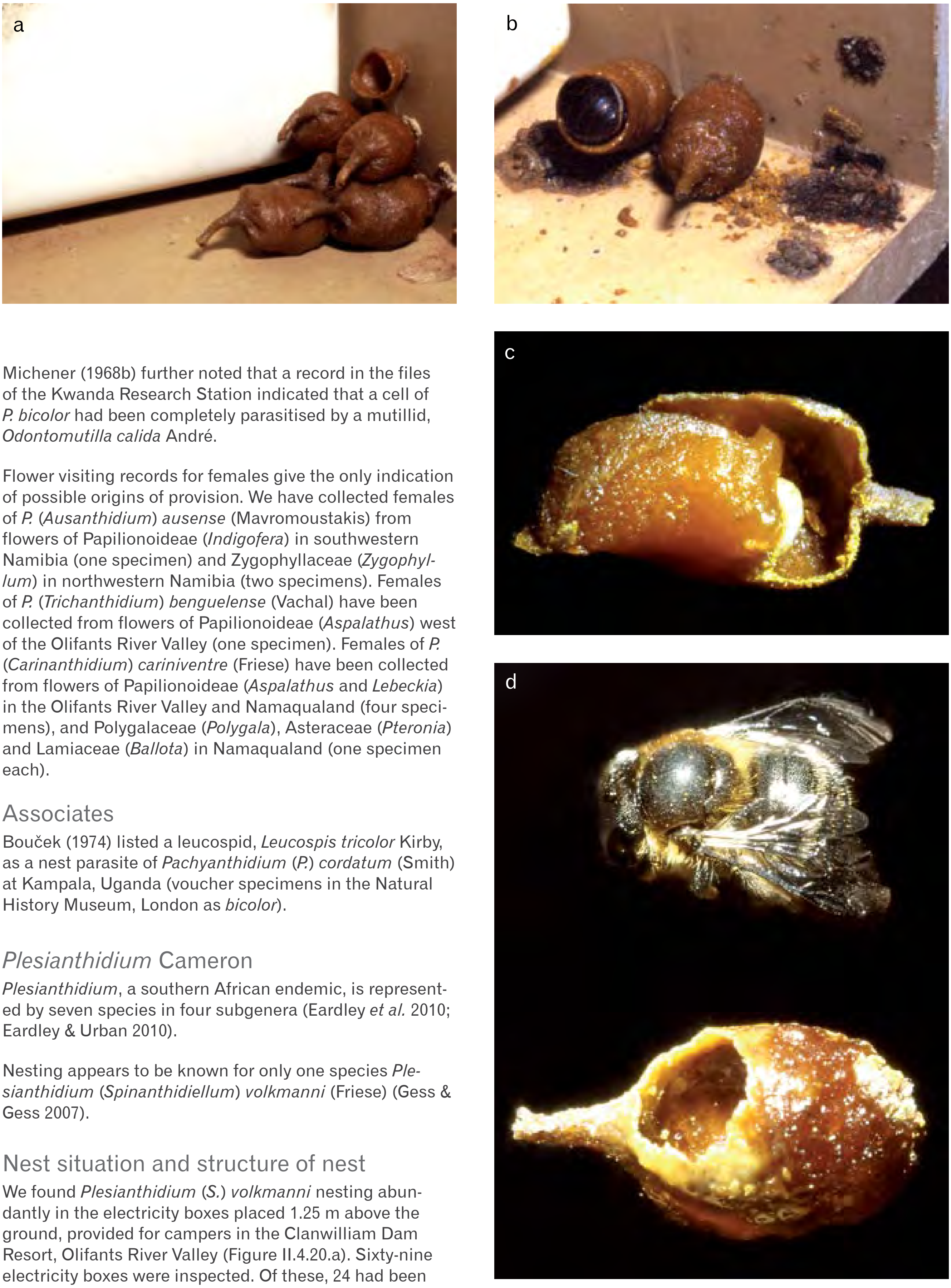


Figure II.4.20.—a.–d. *Plesianthidium* (*Spinanthidiellum*) *volkmanni* (Friese): a. group of cells in electricity box; b. female in partially completed cell; c. cell opened to show provision and larva; d. bee and cell with emergence hole.

Michener (1968b) further noted that a record in the files of the Kwanda Research Station indicated that a cell of *P. bicolor* had been completely parasitised by a mutillid, *Odontomutilla calida* André.

Flower visiting records for females give the only indication of possible origins of provision. We have collected females of *P.* (*Ausanthidium*) *ausense* (Mavromoustakis) from flowers of Papilionoideae (*Indigofera*) in southwestern Namibia (one specimen) and Zygophyllaceae (*Zygophyllum*) in northwestern Namibia (two specimens). Females of *P.* (*Trichanthidium*) *benguelense* (Vachal) have been collected from flowers of Papilionoideae (*Aspalathus*) west of the Olifants River Valley (one specimen). Females of *P.* (*Carinanthidium*) *cariniventre* (Friese) have been collected from flowers of Papilionoideae (*Aspalathus* and *Lebeckia*) in the Olifants River Valley and Namaqualand (four specimens), and Polygalaceae (*Polygala*), Asteraceae (*Pteronia*) and Lamiaceae (*Ballota*) in Namaqualand (one specimen each).

Associates

Bouček (1974) listed a leucospid, *Leucospis tricolor* Kirby, as a nest parasite of *Pachyanthidium* (*P.*) *cordatum* (Smith) at Kampala, Uganda (voucher specimens in the Natural History Museum, London as *bicolor*).

Plesianthidium Cameron

Plesianthidium, a southern African endemic, is represented by seven species in four subgenera (Eardley *et al.* 2010; Eardley & Urban 2010).

Nesting appears to be known for only one species *Plesianthidium* (*Spinanthidiellum*) *volkmanni* (Friese) (Gess & Gess 2007).

Nest situation and structure of nest

We found *Plesianthidium* (*S.*) *volkmanni* nesting abundantly in the electricity boxes placed 1.25 m above the ground, provided for campers in the Clanwilliam Dam Resort, Olifants River Valley (Figure II.4.20.a). Sixty-nine electricity boxes were inspected. Of these, 24 had been used for nesting by *P.* (*S.*) *volkmanni.* Within these, pre-existing cavity clusters of up to seven separate spouted, pot-like cells with, apparently, resin walls had been constructed (Figure II.4.20.a & b). All cells within a cavity were orientated in the same direction but there was no constancy between cavities. In no cases was there more than one cell under construction suggesting that a single female had constructed each cluster.

Provisioning and oviposition

The provision was firm (Figure II.4.20.c). Pollen from the provision examined microscopically appeared to be of mixed provenance and there was an admixture of bright yellow oil. Pollen from the flowers of *Aspalathus spinescens*, the only flowers from which these bees were collected near the nests, was present.

We collected females of this species from Papilionoideae (*Aspalathus* and *Lebeckia*) in the Olifants River Valley and Namaqualand (34 specimens), and only one female each from *Hermannia* (Sterculiaceae) and *Zygophyllum* (Zygophyllaceae) near Nieuwoudtville.

Females of four additional species of *Plesianthidium* were collected from flowers. Females of *P.* (*Carinanthidium*) *cariniventre* (Friese) were collected from Papilionoideae (*Aspalathus* and *Lebeckia*) in the Olifants River Valley and Namaqualand (four specimens), Polygalaceae (*Polygala*), Asteraceae (*Pteronia*) and Lamiaceae (*Ballota*) in Namaqualand (one specimen from each). Females of *P.* (*Spinanthidium*) *bruneipes* (Friese) were collected from Papilionoideae (*Lebeckia*) and Mesembryanthema (*Herrea*) in Namaqualand (two and one specimen respectively). Females of *P.* (*Spinanthidium*) *neli* (Brauns) were collected from Papilionoideae (*Aspalathus*, *Lebeckia* and *Melolobium*) in Namaqualand (five specimens), and Malvaceae (*Hermannia* formerly Sterculiaceae) and Iridaceae (*Homeria*) in Namaqualand (one specimen each). Females of *P.* (*Spinanthidium*) *trachusiforme* (Friese) were collected from Papilionoideae (*Aspalathus*, *Lebeckia*, *Indigofera* and *Wiborgia*) in Namaqualand and west of the Olifants River Valley (six specimens), and Mesembryanthema (*Herrea*), Boraginaceae (*Anchusa*) and Brassicaceae (*Heliophila*) from Namaqualand (two, three and one specimen respectively).

Sleeping and sheltering

If a cell had been only partially constructed at the close of day, the female *P.* (*S.*) *volkmanni* slept head down within the cell with her gaster curved over within the cell so that only the arched terga were exposed.

Associates

There was a high level of success, *P.* (*S.*) *volkmanni* having emerged from most of the *ca*. 20 cells collected. However, a meloid larva emerged from one of the cells and pupated attached to the outside of the cell (Figure II.4.21).

Pseudoanthidium Friese

The Old World genus *Pseudoanthidium* Friese is represented in sub-Saharan Africa by eight species, four of which have been recorded from southern Africa. The only descriptions of the nest seem to be for *P.* (*Micranthidium*) *truncatum* (Smith) from Nigeria (Friese 1902, 1905, 1909, as *Anthidium truncatum* Smith) and from Durban (nest in

Figure II.4.21.—Meloid beetle with remains of pupa attached to outside of cell of *Plesianthidium* (*Spinanthidiellum*) *volkmanni* (Friese) from which the meloid larva emerged.

the Iziko Museum) (Michener 1968b, as *P.* (*Micranthidium*) *truncatum* (Smith)).

Nest situation

The nest *P.* (*M.) truncatum* from Nigeria was situated on a banana leaf. The situation of that from Durban is not given.

Nest structure

Michener records that the two nests were of similar construction but that the one from Nigeria was smaller than the one from Durban. The latter is 20 mm high and 22–40 mm wide. It consists of a mass of dull white plant 'hairs' within which are eight cocoons, variable in orientation and lightly attached to the surrounding plant down.

Provision

There are no records of provision or flower visiting for *P.* (*M.*) *truncatum.*

However, we have collected two species of *Pseudoanthidium* (*Tuberanthidium*) from flowers of Asteraceae, *P.* (*T.*) *damaraensis* (Mavromoustakis) from flowers of *Geigeria* from northern Namibia (one specimen) and *P.* (*T.*) *tuberculiferum* (Brauns) from flowers of *Berkheya* in Namaqualand and *Pteronia* in southwestern Namibia (five specimens).

Associates

Bouček (1974) listed a leucospid, *Leucospis tricolor* Kirby, as a nest parasite of *P.* (*M.) truncatum* (as *Pachyanthidium* (*Pachyanthidium*) *trucatum* (Smith)) at Old Shinyanga, Tanzania (voucher specimens in the Natural History Museum, London).

Serapista Cockerell

The sub-Saharan genus *Serapista* consists of four species, two of which are represented in southern Africa—the widespread *S. denticulata* (Smith) recorded from central, eastern and southern Africa and the more restricted *S. rufipes* (Friese) recorded only from southern Africa (Pasteels 1984; Eardley & Urban 2010).

Serapista construct their nests from plant fibres, sometimes mixed with animal fur or even feathers.

Serapista denticulata (Smith)

Nest situation

All nests recorded for *S. denticulata* were constructed on plants (Stadelmann 1898, quoted by Friese 1905 and 1909; Friese 1916; Michener 1968b, with republication of his Figures 27 & 28 by Roubik 1989; Michener 2000, 2007; Gess & Gess 2007).

Four nests are kept in the Albany Museum. Two were collected by us in the vicinity of Grahamstown, Eastern Cape (Figure II.4.22), identified as *S. denticulata* from the bees reared from them (a female and a male from one, and eight females and three males from the other) and the builder of one, with two in a public display. Others are held in the collection of the South African Museum, Iziko Museum (Margie Cochran pers. comm.).

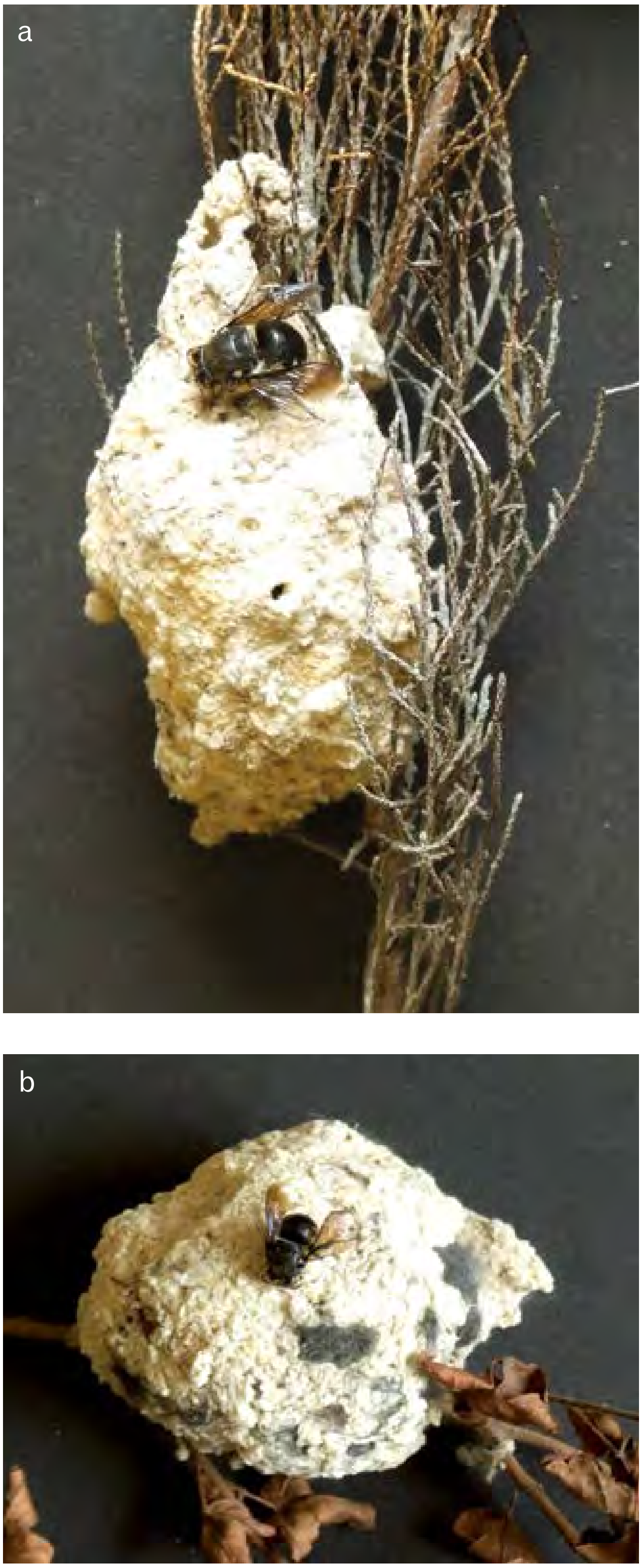


Figure II.4.22.—a. and b. *Serapista denticulata* (Smith): two nests, each with bee, b. showing use of animal fur in addition to plant 'fluff'.

Nest structure

Typical nests are roughly oval in shape with a short entrance tube at the higher end.

The four Grahamstown nests, like those described in literature, are aerial nests built on shrubs, the recorded height above ground of one being around 0.5 m. Two consist entirely of plant down, the other two, in patches, incorporate fine grey mammalian fur. The two nests collected by us are 76 mm and 70 mm in height and 29 mm and 50 mm in diameter respectively. They were constructed on stems of *Elytropappus* (Asteraceae) and *Rhus* (Anacardiaceae).

Provision

There are no records of provision and the only flower visiting record appears to be ours for a single female from *Berkheya heterophylla* (Thunb.) O.Hoffm. (Asteraceae) from near Grahamstown.

Associates

In Bouček (1974) two species of *Leucospis*, *L. tricolor* Kirby from Villiersdorp, Western Cape and Kampala, Uganda, and *L. africana* Cameron from Kuanda, Uganda, are given as reared from nests of *S. denticulata* (vouchers for Villiersdorp in South African Museum, Iziko, Cape Town and for Uganda in the Natural History Museum, London).

Serapista rufipes Friese

Nest situation

Serapista rufipes is remarkable in that it may either construct an aerial nest, or may construct its nest within a pre-existing cavity in the ground (Gess & Gess 2007) (Figure II.4.23). An aerial nest of *S. rufipes*, similar in construction and placement to those of *S. denticulata*, was collected by W.A. Clarke from *Lebeckia* (Fabaceae, Papilionoideae) near Twee Rivieren, Gemsbok National Park in 1966. The identity of the nest builder was based on four female and three male *S. rufipes* emerging from the nest (nest and bees in the collection of the Albany Museum).

Although *S. rufipes* was commonly encountered by us and observed throughout the southwestern areas of South Africa and widely in Namibia, no further aerial nests were found. Nests were also not found in the collections of the South African Museum (Margie Cochran pers. comm.) or in the National Collection, PPRI, Pretoria (Connal Eardley pers. comm.)—both collections with bees as one of their specialisations.

In 2005, when we were sampling flowers on the banks of the lagoon at Lamberts Bay on the southwest coast, we noticed a *Serapista rufipes* disappearing into the sandy ground where it was found to be nesting in what was presumed to be a pre-existing burrow. That this nesting is probably not unusual for this species is supported by the fact that whilst we were sampling bees visiting flowers throughout the semi-arid to arid areas of southern Africa, we frequently observed these bees flying low over the ground.

Nest structure

The aerial nest of *S. rufipes* is similar in size, 72 mm in height and 43 mm in diameter, and structure to those of *S. denticulata* (Figure II.4.23.a).

The nest from the ground had a down-tube projecting from the ground. Within the burrow had been constructed a five-celled, down nest within what was presumed to be a pre-existing burrow in the sandy soil (Figure II.4.23.b & c). The total length of this nest was 90 mm of which 42 mm was an entrance tube, 10 mm in diameter. The lower part of the nest containing the cells was 20 mm across at its widest point, at which two cells had been constructed side by side.

Provisioning

One cell, from which no emergence had taken place, was opened in June 2006. In it was uneaten provision. Some of this, examined microscopically, was found to contain pollen of mixed provenance, two pollen types being present. Most of the pollen in the sample was spherical and thin-smooth-walled. It was possible that it was from *Conicosia* sp. (Aizoaceae, Mesembryanthema), several large plants of which were growing in close proximity to the nest. A small percentage of the pollen grains, also relatively thin-smooth-walled, were about twice the size, elongate-oval and considerably longer than broad.

However, we have collected females of *S. rufipes* from flowers of Papilionoideae (*Crotalaria*, *Indigofera*, *Lebeckia* and *Aspalathus*) from ten sites in the Olifants River Valley and to the west, Namaqualand and southern Namibia (21 specimens), Malvaceae (*Hermannia* formerly Sterculiaceae) in Namibia and Namaqualand (nine specimens), Acanthaceae (*Monechma*) northwestern Namibia (one specimen), Scrophulariaceae (*Jamesbrittenia*) in western central Namibia (one specimen) and Apocynaceae (*Gomphocarpus*) southern Karoo (one specimen).

Figure II.4.23.—a.–c. *Serapista rufipes* Friese: a. nest on plant with bee; b. sand removed to show nest in pre-existing cavity in ground; c. nest showing two emergence holes with bee.

Life history

In late summer, two adults emerged from the nest from Lamberts Bay, each making its way out through the side of its cell (Figure II.4.23.c).

Stelis Panzer

The widespread genus *Stelis* is represented in sub-Saharan Africa by one species, *S. rozeni* Griswold & Parker, which has been recorded from southern Africa (Eardley & Urban 2010).

Stelis parasitises the nests of other Megachilinae. Michener (2000 & 2007, quoting Michener 1955 and others) noted that in most cases, after locating a host's nest, the parasite returns to it repeatedly to place an egg in each of several host cells before they are closed.

It appears that no hosts have been recorded for *S. rozeni*.

Trachusa Panzer

The widespread genus *Trachusa* is represented in sub-Saharan Africa by five species, one of which, *T.* (*Paraanthidium*) *aquiphilum* (Strand) has been recorded from southern Africa in South Africa and Namibia (Eardley *et al.* 2010; Eardley & Urban 2010). In addition, we have collected an undescribed species of *Trachusa* (of the subgenus *Massanthidium* previously known from Ethiopia and Kenya) in northwestern Namibia (Gess & Gess 2007; Eardley *et al.* 2010).

Michener (2000, 2007) notes that, as far as is known, species of *Trachusa* nest in the ground, unlike most anthidiines, making their own burrows. The cells are constructed from pieces of green leaves or resin according to the subgenus.

There appear to be no records for nesting by any sub-Saharan species.

We collected females and males of an undescribed *Trachusa* (*Massanthidium*) from flowers in northwestern Namibia. Our flower visiting records for females are from Papilionoideae (*Crotalaria* and *Indigofera*) and Caesalpinioideae (*Adenolobus*) in northwestern Namibia (two and four specimens respectively), Pedaliaceae (*Sesamum*) south of Swartbooisdrif on the Kunene, northwestern Namibia (six specimens) and Acanthaceae (*Monechma*) northwestern Namibia (five specimens).

Tribe Dioxyini

The Dioxyini have sometimes been included in the Anthidiini, however, they are more likely to be a sister group of the Anthidiini (Michener 2007). Of the seven genera, only

Aglaoapis Cameron is represented in sub-Saharan Africa by one species, *A. alata* (Michener), recorded only from South Africa (Eardley *et al.* 2010; Eardley & Urban 2010).

The Dioxyini are nest parasites of other Megachilinae of the tribes Osmiini, Anthidiini and Megachilini. They are not host specific, various species having been recorded from nests of two of these tribes and one species from all three (Michener 2007). No hosts have been recorded for *A. alata.*

There appear to be no flower visiting records for *A. alata.*

Tribe Megachilini

Two widespread, species-rich genera of Megachilini are represented in sub-Saharan Africa—*Megachile* Latreille by 419 species in 15 subgenera and *Coelioxys* Latreille by 98 species in four subgenera (Eardley *et al.* 2010 following Michener 2007). Eardley & Urban (2010) list the species of *Megachile* omitting subgenera. Of the 15 subgenera, *Callomegachile* Michener, *Chalicodoma* Lepeletier, *Creightonella* Cockerell, *Eutricharaea* Thomson, *Gronoceras* Cockerell, *Maximegachile* Guiglia & Pasteels, *Paracella* Michener and *Pseudomegachile* Friese, at least, are represented in southern Africa.

All *Megachile* construct nests and all *Coelioxys* are parasitic in the nests of other bee species, most usually of other Megachilini (Eardley *et al.* 2010).

Megachile Latreille

The nests of *Megachile* are aerial mud nests or are built in pre-existing cavities, sometimes vacant and sometimes usurped, constructed from mud or from leaf or petal pieces solely or with the addition of soil or resins.

Megachile (*Callomegachile*) Michener

The subgenus *Callomegachile* is largely tropical. It is widespread in the sub-Saharan Africa, with 26 species, eastwards through Asia to China and Japan, and southwards to northern Australia (Michener 2007; Eardley *et al.* 2010).

Those species for which nesting is known construct cells from resin mixed with wood fibres, or together with layers of leaf pieces or mud, in pre-existing cavities (Michener 2000, 2007).

It seems that nesting in southern Africa has been recorded for only two species, *M.* (*C.*) *chrysorrhaea* Gerstaecker, widespread in Africa and known from both west and eastern southern Africa, and *M.* (*C.*) *aridissima* Cockerell, known from Ethiopia and South Africa (Eardley & Urban 2010).

In the course of a trapnesting study, Alan Weaving obtained nests of *M.* (*C.*) *chrysorrhaea* in trapnests set out at St Lucia in KwaZulu-Natal. The nests, which are lodged in the Albany Museum, consist of a series of cells with very thin, almost cellophane-like resin walls (Figure II.4.24).

We found *M.* (*C.*) *aridissima*, nesting in the walls of a ruined building in Bowesdorp, Namaqualand (Gess & Gess fieldnotes 1995 and voucher specimens of the bees). Little of the nests could be extracted but it was clear that they were lined with resin.

Associates

Alan Weaving reared meloid beetles from the nests of *M. (C.) chrysorrhaea* from St Lucia (voucher specimens).

Megachile (*Chalicodoma*) Lepeletier

The subgenus *Chalicodoma* is known from at least 11 Palaearctic and 20 sub-Saharan species (Michener 2000, 2007; Eardley *et al.* 2010). Typically, they construct aerial mud nests on stones, buildings and plant stems.

Megachile (*Chalicodoma*) *murina* Friese

Megachile (*C.*) *murina* is known only from southern Africa (Eardley & Urban 2010).

Figure II.4.24.—*Megachile* (*Callomegachile*) *chrysorrhaea* Gerstaecker, nest in trap nest.

Nest situation

We located nests constructed on stones on the west facing lower slope of the Kamiesberg, Namaqualand, in an area where *Lebeckia sericea* Thunb. (Fabaceae, Papilionoideae) was abundant (Gess and Gess fieldnotes and voucher specimens 1992).

Structure of the nest

The nest, which is multicellular, is constructed from mud (Figure II.4.25.a & b).

Provision

Pollen from the provision was examined microscopically and found to match that of *Lebeckia.* Our flower visiting records for this species suggest a specialisation in Papilionoideae, females (97 specimens), having been collected from species of *Aspalathus* from Riebeek East, Eastern Cape, the Olifants River Valley and Namaqualand including the Kamiesberg, species of *Lebeckia* at various sites in Namaqualand including the Kamiesberg, and of *Lotononis* and *Wiborgia* in the Kamiesberg. We have collected it less commonly but in three years from *Polygala virgata* Thunb. (Polygalaceae) in the Goegap Nature Reserve (four specimens) and only a single specimen from *Stachys aurea* Benth. (Lamiaceae) in the Richtersveld.

Figure II.4.25.—a. and b. *Megachile* (*Chalicodoma*) *murina* Friese: two nests.

Associates

No associates appear to have been recorded for *M.* (*C.*) *murina*, however, Bouček (1974) recorded that John Taylor reared a leucospid *Leucospis ornata* Westwood, 13 females and 11 males, from nests of *M.* (*C.*) *willowmorensis* (Brauns) at Alice, Eastern Cape.

Megachile (*Creightonella*) Cockerell

The subgenus *Creightonella* (example Figure II.4.26) is widespread in the Old World. Michener (2000, 2007) estimates the total number of species at about 50. The greatest diversity is in sub-Saharan Africa with 40 species (Eardley *et al.* 2010).

It seems that nesting has been recorded in southern Africa for only two species, *M.* (*C.*) *cornigera* (Friese) and *M.* (*C.*) *dorsata* Smith, both known only from southern Africa (Eardley & Urban 2010).

Megachile (*Creightonella*) *cornigera* (Friese)

Charles Michener (1968b), who investigated a single nest of *M. (C.) cornigera*, gives a detailed description of it.

Figure II.4.26.—*Megachile* (*Creightonella*) *discolor* Smith, female, visiting flowers (Fabaceae, Papilionoideae).

Nest situation

The nest, found near Pietermaritzburg in KwaZulu-Natal, was in a vertical, roadside bank.

Nest structure

The nest, including the single cell, was 35 mm deep. Beyond the cell, a smaller old burrow continued into the bank, suggesting that the bee had enlarged part of an existing burrow. The bee cell was horizontal, 18.0 × 11.5 mm. The cell lining was constructed of leaf materials. The outer layer, about 1 mm thick, was made of 17 irregular pieces of thick, fuzzy leaves 4–9 mm in diameter. The edges, cut by the bee, were strongly and often irregularly serrate, not smooth as are cuts made by the subgenus *Megachile*. Inside these leaf pieces was a layer up to 0.5 mm thick made of coarsely chewed leaf material. It was noted that, judging by the hairs, the same kind of fuzzy leaves used for the outer layer were used for the inner. The leaf fragments of the inner layer were cemented with black, resinous material, which had dried hard and largely covered both surfaces, cementing this layer to the outer layer and also forming most of the inner surface of the cell.

Megachile (*Creightonella*) *dorsata* Smith

Nest situation

We found *Megachile* (*C.*) *dorsata* commonly on farms near Grahamstown. On the farm Hilton, it was nesting in old or abandoned burrows including those of *Aethiopicodynerus insignis* (Gess & Gess 1976 as *Parachilus insignis*) and on the farm Thursford, a female was found nesting in an old burrow in the ground, probably that of *Dichragenia* sp. (Pompilidae) (Gess field notes 1981 and vouchers).

Nest structure

In the Hilton nest, the cells, arranged in linear succession, were constructed from leaf pieces with incorporated mud and resin. In the Thursford nest, a loose preliminary plug at the bottom of the burrow was constituted of entire leaves of *Grewia occidentalis* (Malvaceae) and a cell above the plug was constructed of the same leaves cemented together with mud and what appears to be resin.

Provision

The provision was not examined. We collected females from flowers of *Blepharis capensis* (L.f.) Pers. (Acanthaceae) (29 specimens), *Bulbine frutescens* (L.) Willd. (Asphodelaceae) (28 specimens), *Cotyledon campanulata* Marl. (Crassulaceae) (seven specimens) and *Acacia karroo* Hayne (Mimosoideae) (six specimens) in the Grahamstown area. We also collected females from flowers of *Gomphocarpus filiformis* (E.Mey.) D.Dietr. (Apocynaceae) (21 specimens) on Tierberg Farm, Prince Albert. No distinction was made between nectar and pollen collection.

Megachile (*Eutricharaea*) Thomson

The subgenus *Megachile* (*Eutricharaea*) is extremely species diverse and widespread, occurring naturally almost throughout the Old World in cool temperate to desertic and moist tropical areas. It has been introduced into the New World and New Zealand (Michener 2000, 2007). It is represented in sub-Saharan Africa by 120 described species (Eardley *et al.* 2010).

They are known as leafcutter bees in allusion to their constructing their cells from pieces cut from leaves or petals. The cells are constructed in almost any suitable pre-existing cavities, including keyholes and holes in fence posts, making them amongst the most familiar bees.

Typically, in the construction of cells by the leaf-cutter bees, long, elliptical leaf portions are used for the sides and round portions for the ends. Green leaves are generally used but sometimes coloured, modified leaves and flower petals are used. When the last cell of a nest has been completed, the entrance is plugged with a thick wad consisting of round sections of leaf. This wad may be up to 20 mm in length. The outermost seal of some species is further strengthened on the outside by the addition of a plug of chewed leaf mixed with grains of sand.

Megachile (*Eutricharaea*) *aliceae* Cockerell

Nest situation

We have recorded *M.* (*E.*) *aliceae* as a usurper of nests of ground nesting masarines and eumenines. Masarine nests included those of *Ceramius nigripennis* de Saussure in the Springbok district, Namaqualand (Gess & Gess 1986) and *Ceramius braunsi* Turner in the Clanwilliam district, Olifants River Valley (Gess & Gess 1990a). Eumenine nests included those of *Aethiopicodynerus insignis* (de Saussure) in the Grahamstown district, Eastern Cape (Gess & Gess 1976) and *Paravespa mima* Giordani Soika in the Prince Albert district, southern Great Karoo (Gess & Gess 1988b) (Figure II.2.46).

Nest structure and method of construction

The bee constructs its flask-shaped petal-cell within the host's cell in such a way that it entirely fills the latter (Gess & Gess 1986, 1990a). The petal-cells from *C. nigripennis* nests were all constructed from lengths cut from the orange 'petals' of the Namaqualand Daisy, *Dimorphotheca sinuata* DC. (Asteraceae), and three of those from *C. braunsi* nests from the pink petals of a species of *Pelargonium* (Geraniaceae) (Figure II.4.27.a). The 'petal' pieces are carried to the nest cut-end first. They are arranged in such a way that a round bottomed 'flask' is constructed with the 'petals' running vertically and tucked under at the bottom. The pollen used for provisioning was derived from two or more plant species. A cell, after provisioning and oviposition, is sealed using shorter pieces of 'petal' laid cross-wise across the mouth of the petal-cell with the ends curved upwards into the mouth of the pollen wasp's mud cell which is then sealed with a mud plug, concave above and with a smooth surface. Sealed mud cells containing bee cells are readily distinguished from sealed cells of *C. nigripennis*, the mud plugs of which are convex above and with the surface left rough (Figure II.4.27.b).

The bee constructs a final closure in the main shaft about 5 mm below the ground surface. This closure consists of a short length of 'petal' laid across the shaft followed by a layer of mud, concave above with the surface smoothed (Figure II.4.27.c).

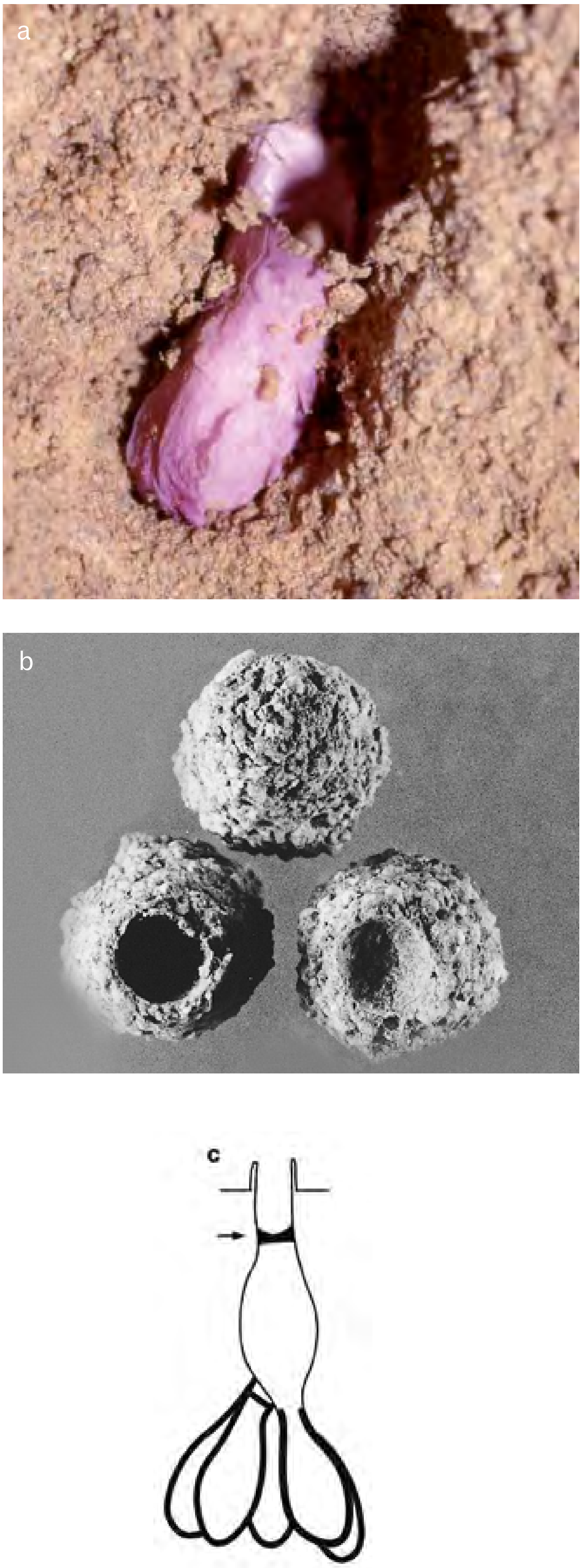


Figure II.4.27.—*Megachile* (*Eutricharaea*) *aliceae* Cockerell: cell constructed of petals within cell of *Ceramius braunsi* Turner (Masarinae); b. three earthen cells of *Ceramius nigripennis* de Saussure (Masarinae), convex seal of *C. nigripennis* (top), concave seal of *M.* (*E.*) *aliceae* (bottom right); c. vertical plan of nest of *C. nigripennis* showing position of *M.* (*E.*) *aliceae* final closure (arrow).

Megachile (*Eutricharaea*) *basalis* Smith

Megachile (*E.*) *basalis* was found south of Omaruru in Namibia constructing its nest cell of entire green leaves in a pre-existing burrow in the ground (Gess & Gess field notes 1997 and voucher material). However, petals must sometimes be used as indicated by a female having been captured flying with a standard petal cut from a flower of *Crotalaria* (Papilionoideae).

No provision was obtained, however, at the same site two females were collected from flowers of *Crotalaria podocarpa* DC.

One female was collected from mauve flowers of Acanthaceae in the Kalahari Gemsbok Park to the south of the Nossob Rest Camp.

It was not established whether the visits were for pollen or nectar.

Megachile (*Eutricharaea*) *frontalis* Smith

Megachile (*E.*) *frontalis* was found by Edward McC. Callan at Grahamstown in association with a cell constructed of green leaves. The situation of the nest was not recorded (voucher material in Albany Museum collection).

Five females were collected from flowers, four from Papilionoideae at sites in the Olifants River Valley, at Karoo Poort and to the northwest of Grahamstown, and one from *Gomphocarpus filiformis* (E.Mey.) D.Dietr. (Apocynaceae). It was not established whether the visits were for nectar or pollen.

Megachile (*Eutricharaea*) *gratiosa* Gerstaecker

Nest situation

John Taylor (1963, 1965, 1968) recorded the nesting of *M.* (*E.*) *gratiosa* in trapnests at Port Elizabeth, Wilderness and Hilton, KwaZulu-Natal, and we found it nesting in trapnests inserted into crevices in a shale krantz and tied to branches of *Acacia karoo* on the farm Hilton, Grahamstown (Gess 1981). In addition, at Hilton we found that it had nested in the open cells of an abandoned nest of *Othinosmia* (*Megaloheriades*) *jansei* (Brauns) (as *Hoplitis jansei* (Brauns)) built on a stone in the clay area.

Nest structure

The nests were mostly constructed from pieces cut from green leaves, however, Taylor recorded petal pieces used on occasion.

Associates

At Port Elizabeth, a few individuals of a megachiline cuckoo bee, *Coelioxys* (*Coelioxys*) *loricula* Smith, were reared from nests.

On the farm Hilton, some nests in trapnests had been parasitised by a meloid beetle, *Zonitoschema eborina* (Fabricius) (Gess 1981), and two species of *Leucospis*, *L. ornata* Westwood (four females) and *L. varicollis* Cameron (one female) (Alan Weaving, voucher specimens 1990/91 in the Albany Museum).

In addition, John Taylor (1963) recorded a miltogramine fly, *Miltogramma* (Sarcophagidae).

Megachile (*Eutricharaea*) *malangensis* Friese

Megachile (*E.*) *malangensis* was found on the farm Vlakwater to the northwest of Grahamstown constructing its nest cells of green leaves in a pre-existing cavity in the ground (Gess & Gess field notes 1981 and voucher material). At the Theronsberg Pass, east of Ceres, a male of this species, together with a male *Coelioxys* sp. were reared from leaf cells built within old cells of an aerial mud nest of an unknown builder (Gess & Gess field notes 1989 and vouchers).

No provision was obtained. A female was collected at Nababeep, Namaqualand from a flower of *Lebeckia sericea* Thunb. (Fabaceae) and a female was collected near Oudtshoorn, Little Karoo, from flowers of *Senecio rosmarinifolius* L.f. (Asteraceae). It was not established whether the visits were for nectar or pollen.

Megachile (*Eutricharaea*) *meadewaldoi* Brauns

Nest situation

Megachile (*E.*) *meadewaldoi* on the farm Hilton nests in old abandoned burrows of clay soil nesting *Bembecinus oxydorcus* Handlirsch (Crabronidae), *Aethiopicodynerus insignis* (de Saussure) (as *Parachilus insignis*) and *Antepipona scutellaris* Giordani Soika (Eumeninae) (Gess & Gess 1975, 1976; Gess 1981).

Nest structure

The cells were constructed from pieces of petal cut from the flowers of low growing plants (*Oxalis* sp. and *Wahlenbergia* sp.).

Megachile (*Eutricharaea*) *semiflava* (Cockerell)

Megachile (*E.*) *semiflava* (Cockerell) was commonly found on the farm Hilton nesting in pre-existing cavities, the old or abandoned burrows of clay soil nesting *Aethiopicodynerus insignis* (de Saussure) (Eumeninae) or the nests of unidentified nesters in the sand pit (Gess & Gess 1976; Gess 1981).

Nest structure

The cells were constructed from leaf pieces.

Provision

The origins of the provision was not established, however, in the Grahamstown area we collected females from *Bulbine frutescens* (L.) Willd. (Asphodelaceae) (seven specimens), *Senecio* sp. (Asteraceae) (four specimens), *Wahlenbergia nodosa* (H.Buek) Lammers (Campanulaceae) (four specimens), and *Aspalathus subtingens* Eckl. & Zeyh. and *Indigofera* sp. (Papilionoideae) (six specimens). Nectar and flower collection were not distinguished.

Megachile (*Eutricharaea*) *stellarum* Cockerell

Nest situation

On Hilton farm, we found *M.* (*E.*) *stellarum* nesting in old or abandoned burrows of clay soil nesting *Dichragenia pulchricoma* (Arnold) (Pompilidae), *Aethiopicodynerus insignis* (de Saussure) (Eumeninae), and *Ceramius lichtensteinii* (Klug) (Masarinae) (Gess & Gess 1974, 1976, 1980; Gess 1981).

Nest structure

The cells constructed from pieces cut from leaves, were of the same outer diameter as the shaft in which they were built and in all cases were built in a single linear succession.

Six *D. pulchricoma* nests, in which the vertical shaft and turret were not yet complete, had clearly been invaded. The most advanced nest of *M.* (*E.*) *stellarum* consisted of five completed cells and one open cell.

Provision

No provision was examined. In the Grahamstown area, we collected females principally from flowers of *Blepharis capensis* (L.f.) Pers. (Acanthaceae) (14 specimens) and species of *Athanasia*, *Berkheya* and *Senecio* (Asteraceae) (19 specimens). Nectar and pollen collection were not distinguished.

Megachile (*Gronoceras*) Cockerell

Megachile (*Gronoceras*) is an endemic sub-Saharan subgenus that is represented throughout the region. There are ten described species (Eardley *et al.* 2010). (example *M.* (*G.*) *cincta* (Fabricius) Figure II.4.28.a & b).

Nest situation

Nests of *M.* (*G.*) *felina* Gerstaecker were constructed in lengths of reed, open at one end and closed at the other used as trapnests by Alan Weaving at Lake St Lucia (voucher specimens in the collection of the Albany Museum 1990, 1991).

Nest structure

The nests consist of a series of linearly arranged cells. The cells are circular in cross section and longer than broad. The walls of the cells are partially those of the cavity and partially of mud and resin used to round off the cavity and to seal the cells.

Associates

From the nests, Alan Weaving reared three *Euaspis abdominalis* (Fabricus), an unidentified mutillid, *Leucospis varicollis* Cameron (Leucospidae) and a meloid beetle *Zonitoschema eborina* Fabricius.

Megachile (*Heriadopsis*) Cockerell

Megachile (*Heriadopsis*) is an endemic, monotypic sub-Saharan subgenus. The single species *M.* (*H.*) *striatula* (Cockerell) is known from the Democratic Republic of the Congo, Malawi and Zimbabwe (Eardley *et al.* 2010). Nothing seems to have been recorded concerning its nesting or flower visiting.

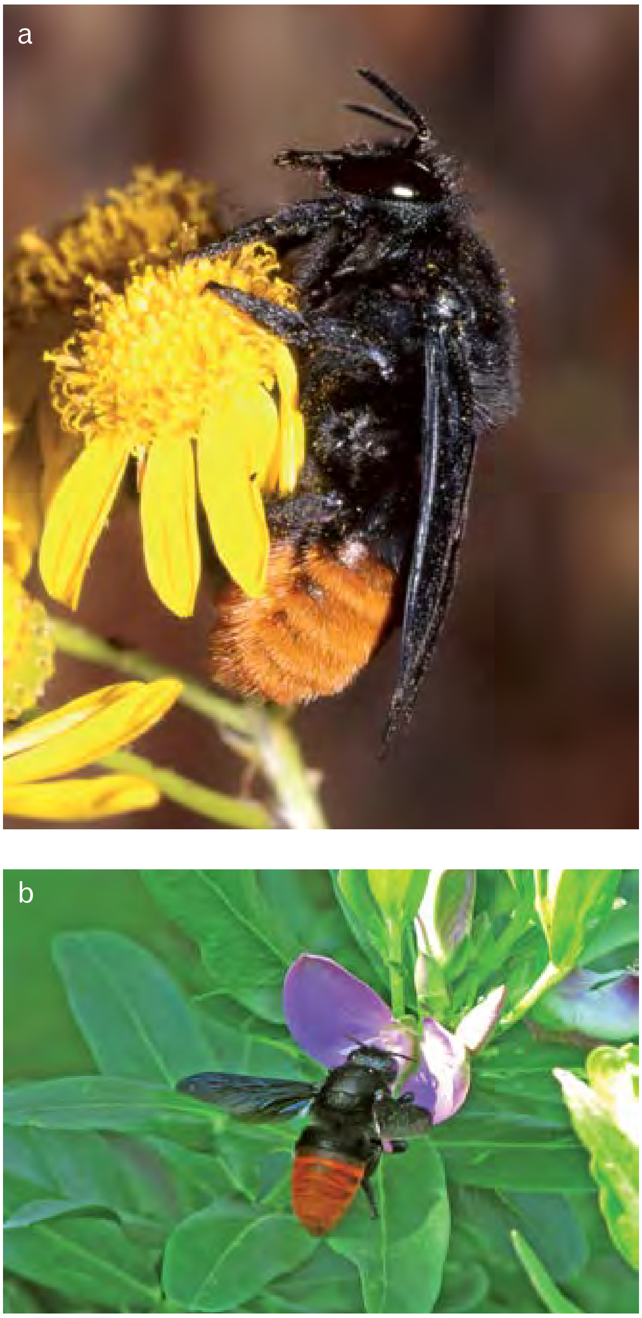


Figure II.4.28.—a.–b. *Megachile* (*Gronoceras*): a. *M*. (*G*.) *cincta* (Fabricius) visiting flowers (Asteraceae); b. *M*. (*G*.) *cincta* (Fabricius), female, visiting flowers of *Polygala myrtifolia* L. (Polygalaceae).

Figure II.4.29.—*Megachile* (*Maximegachile*) *maxillosa* (Guérin) visiting *Crotalaria virgultalis* Burch. ex DC. (Fabaceae).

Megachile (*Maximegachile*) Guiglia & Pasteels

One species only of *Megachile* (*Maximegachile*), *M.* (*M.*) *maxillosa* (Guérin), has been described, however, there are probably more undescribed species. This large black and white bee is widespread in sub-Saharan Africa and in neighbouring parts of the Palaearctic (Eardley *et al.* 2010).

It is a familiar flower visitor throughout the semi-arid to arid areas where we collected it. In Namibia, it is one of the expected visitors to Fabaceae (Papilionoideae), particularly species of *Crotalaria* (Figure II.4.29). In addition, we collected it from Acanthaceae, species of *Blepharis* and *Monechma*, Apocynaceae, *Gomphocarpus filiformis* (E.Mey.) D.Dietr. (formerly as *Asclepias buchenaviana* Schinz), Asteraceae (only one male), Brassicaceae, *Cleome* spp., Pedaliaceae, *Sesamum triphyllum* Welw. ex Aschers and Polygalaceae.

Nothing seems to have been recorded concerning its nesting.

Megachile (*Paracella*) Michener

Megachile (*Paracella*) is found throughout sub-Saharan Africa, and has about 39 species, with around 25 of these species in southern Africa, and is also represented in India and Indonesia. However, the species occurring in India and Indonesia remain to be described (Michener 2007; Eardley *et al.* 2010).

Flower visiting records are available for at least five species of *M.* (*Paracella*) all of which were collected from flowers of Fabaceae (Papilionoideae).

Megachile (*Paracella*) *apiformis* Smith

A female *Megachile* (*P.*) *apiformis* together with a leaf cell was collected from Harare (formerly Salisbury, Zimbabwe; A.D. Caley, voucher material in Albany Museum).

Megachile (*Paracella*) *spinarum* Cockerell

Nest situation

On the farm Hilton we found *M.* (*P.*) *spinarum* nesting in abandoned burrows in the ‘sandstone’ bank, in trapnests

Figure II.4.30.—a. and b. *Megachile* (*Paracella*) *spinarum* Cockerell: a. nest constructed of green leaves within old nest burrow of *Xylocopa sicheli* Vachal (Xylocopinae) in dry inflorescence stem of *Aloe ferox* Mill. (Asphodelaceae); b. *Megachile* (*Paracella*) sp. nest in vacated cell of mud nest of *Sceliphron spirifex* (L.).

inserted into this bank and tied to branches of *Acacia karroo*, in the abandoned burrows of a carpenter bee, *Xylocopa sicheli*, and in dry inflorescence stems of *Aloe ferox* (Gess 1981) (Figure II.4.30).

Nest structure

The cells were constructed from pieces cut from green leaves, those from one nest were identified as having been cut from the leaves of *Maytenus heterophylla*. The cells are constructed in linear series and are of the same diameter as that of the burrow in which the cells are constructed.

Provision

The identity of the provision was not determined. We have collected females most commonly from Papilionoideae (20 specimens) in the Grahamstown area and in southern Namibia.

Associates

From nests in *X. sicheli* burrows, we reared a megachiline cuckoo bee, *Coelioxys* (*Coelioxys*) *penetratrix* Smith, three females of a parasitic wasp, *Leucospis africana* Cameron (Leucospidae), and a species of clerid beetle (possibly *Trichodes aulicus* Klug).

Megachile (*Platysta*) Pasteels

Megachile (*Platysta*) is an endemic sub-Saharan subgenus, with only two described species, one of which is found in southern Africa (Eardley *et al.* 2010; Eardley & Urban 2010). There seem to be no records for flower visiting or nesting.

Megachile (*Pseudomegachile*) Friese

Megachile (*Pseudomegachile*) is widespread in the Old World, with around 30 species known from sub-Saharan Africa and about 21 species occurring in southern Africa (Eardley *et al.* 2010; Eardley & Urban 2010).

Megachile (*Pseudomegachile*) *fulva* Smith

We have found *Megachile* (*P.*) *fulva* nesting in trapnests tied onto branches of *Acacia karroo* on the farm Hilton, and in a horizontally orientated crack between layers of rock in a rock overhang at Tierberg near Prince Albert (Gess 1981, field notes December 1987, and voucher specimens).

Nest structure

In the trapnests, the cells were in linear series; in the crack between layers of rock, the cells were similarly in linear series with several series of two or three cells each parallel and abutting each other. The cells were entirely of mud, the outer surface showing the layers of application of mud and the inner surface smooth.

This bee, at various localities, including Matjiesfontein, Ceres and Springbok, has commonly been seen mining mud at pools and with its mandibles forming a lentil-shaped pellet of mud. The pellet, which is the building material for cell construction, is flown to the nest.

Megachile (*Pseudomegachile*) *laminata* Friese

Megachile (*P.*) *laminata* was found by Alan Weaving (voucher material in the Albany Museum) nesting in a trapnest at Fanies Island, Lake St Lucia. The cells were constructed of resin and of what appear to be pieces of plant matter. In this connection, his record ‘collecting pcs. of bark from fig tree’ on the pin with a female from Hluhluwe Game Reserve is relevant.

Associate

A meloid was reared from one of the cells.

Megachile (*Pseudomegachile*) *schulthessi* (Friese)

Nest situation

We found *Megachile* (*P.*) *schulthessi* nesting in a pre-existing burrow in a bank on the farm Hilton, Grahamstown (Gess 1981).

Nest structure

The nest entrance, 7 mm in diameter, is furnished with a small mud collar. The cells are in linear series, flask-shaped, 9.5 mm in diameter at the widest point and are separated by mud partitions. The final closure is also of mud.

Method of construction

Water is used in the construction of the nest. When sealing the nest, the bee was seen to regurgitate water at a mine site close to the opening of the nest.

Provisioning and oviposition

The provision is moist and sticky and fills half of the cell. The egg is laid on the surface.

The origin of the provision was not determined.

Megachile (*Pseudomegachile*) *sinuata* (Friese)

Nest situation

Megachile (*P.*) *sinuata* was amongst the most common nesters in wooden trapnests hung in shrubs on the farm Hilton and was also found by us nesting in pre-existing cavities in wood and in old burrows of *Xylocopa*, carpenter bees, in pithy aloe inflorescence stems and hollow stems of reeds (Gess 1981 as *Chalicodoma sinuata* (Friese)) (Figure II.4.31.a & b).

Nest structure

The nest consists of a series of cylindrical mud cells equal in diameter to that of the pre-existing burrow. The outer surface of the cells shows the layers of application of mud

Figure II.4.31.—a. and b. *Megachile* (*Pseudomegachile*) *sinuata* (Friese): a and b. nest constructed of mud, a. within old nest burrow of *Xylocopa sicheli* Vachal (Xylocopinae) in dry inflorescence stem of *Aloe ferox* Mill. (Asphodelaceae), b. in trap nest.

and the inner surface is smooth. The outer end of the burrow is sealed with a robust mud plate. In *Xylocopa* borings in *Aloe* inflorescences where the galleries ran both up and down from the entrance hole, the *M.* (*P.*) *sinuata* cells always opened towards the entrance hole so that the upper cells faced downwards and the lower cells upwards.

This bee was found mining mud at various sites in northwestern Namibia, including near Omaruru, west of Kamanjab and north of Palm Wag.

Provisioning and oviposition

The provision examined had the consistency and appearance of dark honey. The origin of the provision was not determined.

Of the records of flower visiting by females, all except one are from flowers of Papilionoideae. They are from the Eastern Cape, Karoo Poort in the Western Cape, the Olifants River Valley, southern and northwestern Namibia (voucher specimens Gess family) and Mamathes in Lesotho (voucher specimens Charles Jacot Guillarmod).

Life history

The cocoon is closely applied to the walls of the cell and the inner surface is dark and shiny as if varnished.

Associates

Coelioxys (*Liothyrapis*) *lativentroides* Brauns (Megachilini) has been reared from cells of *M.* (*P.*) *sinuata* Friese (as *M.* (*P.*) *latitarsis* Friese) (Brauns 1930).

Coelioxys Latreille

Coelioxys species usually use the long, tapering metasomal apex to insert their eggs through the food mass in an open cell, and into the cell wall, between or through leaf pieces in the case of leafcutter bees. In most cases, oviposition occurs while the host is foraging. Oviposition is into cells that have not been closed, however, in some species the eggs are laid after host cell closure, between the leaf pieces that form the closure (Michener 2007).

At the farm Hilton near Grahamstown *Coelioxys* (*Coelioxys*) *penetratrix* Smith was reared from trapnesting *Megachile* (*Paracella*) *spinarum* Cockerell. Circumstantial evidence linked *C.* (*Liothyrapis*) *lativentroides* Brauns and *C.* (*L.*) *bruneipes* Pasteels with nests of other species of *Megachile* nesting in pre-existing burrows in the ground, including nests established in old or abandoned burrows of *Aethiopicodynerus insignis* (de Saussure) (Eumeninae) (Gess 1981).

Hans Brauns (1930) reared *Coelioxys* (*L.*) *lativentroides* Brauns from cells of *M.* (*P.*) *sinuata* Friese (as *M.* (*P.*) *latitarsis* Friese).

In the same publication Hans Brauns (1930) recorded from Willowmore *C.* (*Coelioxys*) *capensis* Smith (as *C. glabra* Friese) as a parasite of *Megachile* (*Paracella*) *nasutula* (Brauns) (as *Amegachile nasutula* Brauns) and *C.* (*Torridapis*) *torrida* Smith (as *C. furcata* Friese) as that of *Megachile* (*Eutricharaea*) *cf. semiflava* (Cockerell) (as *M. venusta* Smith).

At Port Elizabeth, John Taylor (1965, 1968) reared *C.* (*Coelioxys*) *loricula* Smith from trapnesting *Megachile* (*Eutricharaea*) *gratiosa* Gerstaecker.

Whereas all the above associations of *Coelioxys* were with species of *Megachile* (Megachilidae), Jerome Rozen (1969b) at Avontuur recorded an association with *Anthophora* (Apidae). An adult *C.* (*Liothyrapis*) *lativentris* Friese was captured while investigating the burrows of *Anthophora* (*Heliophila*) *rufolanata* Dours (as *Anthophora krebsi* Friese), and a mature *Coelioxys* larva, presumably of this species, was recovered from one of the cells. Rozen believed this to be the first record of a *Coelioxys* parasitising an *Anthophora* cell.

Family Apidae

The Apidae like the Megachilidae are long-tongued bees. They are divided into three subfamilies, Xylocopinae, Nomadinae and Apinae. All are well represented in sub-Saharan Africa including southern Africa. Eardley *et al.* (2010), for sub-Saharan Africa, recognise 314 species in nine genera in the Xylocopinae, 51 species in eight genera in the Nomadinae and 256 species in 17 genera in the Apinae.

The pollen collecting female apids can be distinguished from the pollen collecting megachilids by having a scopa on each hindleg rather than on the ventral surface of the gaster.

Flower visiting

Within the Apidae, the three subfamilies Xylocopinae, Nomadinae and Apinae show distinct differences in the percentages of species visiting specific families of plants (Table 13). For example, Asteraceae, Acanthaceae, Lamiaceae, Boraginaceae and Zygophyllaceae received visits from higher percentages of species of Apinae than Xylocopinae, whereas Aizoaceae and Fabaceae received visits from markedly higher percentages of Xylocopinae than Apinae. The percentages of species of Nomadinae visiting Aizoaceae, Fabaceae and Asteraceae were comparable with those of Apinae but no visits from these bees were recorded for the other four families.

Differences in numbers of species visiting the three subfamilies of Fabaceae, Papilionoideae, Mimosoideae and Caesalpinioideae, are less marked in the Apidae (26, 11, 13 for the respective subfamilies) than in the Megachilidae (93, 11, 13 for the respective subfamilies). The numbers of species recorded for Xylocopinae and Apinae were 19, 5 and 6 and 7, 6 and 7 respectively for the three subfamilies. The greater number of species of Apidae than Megachilidae visiting Caesalpinioideae may be attributed to the fact that Apidae are more successful than Megachilidae at obtaining pollen from anthers with poricidal dehiscence, a common feature of Caesalpinioideae.

The present analysis supports the previous finding for Anthophorini (Gess & Gess 1996) that differences in flower choice between genera and subgenera (despite the lack of distinction between pollen and nectar collection) indicate that the southern African Anthophorini do not, as a rule, practise indiscriminate broad polylecty. As previ-

Table 13.—Numbers and percentages of Apidae species, arranged by subfamily, visiting flowers by plant family. Percentages of 20 and more are shown in bold type

Plant taxa	**% out of 123 families**	**Xylocopinae (Total: 49 species)**		**Nomadinae (Total: 12 species)**		**Apinae (Total: 62 species)**	
		Number of species	**% of species**	**Number of species**	**% of species**	**Number of species**	**% of species**
MONOCOTS							
Asparagales							
Asparagaceae							
Asphodelaceae	1.62	21	2.04			1	1.61
Iridaceae	2.44					3	4.84
EUDICOTS							
Proteaceae	2.44	22	4.08			1	1.61
CORE EUDICOTS							
Caryophyllales							
Aizoaceae	**28.46**	18	**36.73**	3	**25.00**	14	**22.25**
Amaranthaceae	4.07	2	4.08	2	16.67	1	1.61
Molluginaceae	5.69	1	2.04	2	16.67	4	6.45
Plumbaginaceae	0.81					1	1.61
Saxifragales							
Crassulaceae	1.63	2	4.08				
ROSIDS							
Zygophyllaceae	17.89	8	16.33			14	**22.25**
Geraniales							
Geraniaceae	2.44			1	8.33	2	3.25
EUROSIDS I							
Celastraceae	0.81	1	2.04				
Cucurbitales							
Cucurbitaceae	3.25	1	2.04			3	4.84
Fabales							
Fabaceae	**33.33**	21	**42.86**	3	**25.00**	17	**27.41**
Polygalaceae	1.63	2	4.08				
EUROSIDS II							
Brassicales							
Brassicaceae	13.82	6	12.24			11	17.74
Malvales							
Malvaceae	17.89	10	**20.41**	1	8.33	10	16.13
Neuradaceae	1.63	1	2.04	1	8.33		
EUASTERIDS I							
Boraginaceae	**23.58**	9	18.37			20	**32.25**
Vahliaceae	3.25	3	6.12			1	1.61
Gentianales							
Apocynaceae	7.32	4	8.16			5	8.06
Lamiales							
Acanthaceae	**22.76**	10	**20.41**			18	**29.03**
Lamiaceae	**25.20**	10	**20.41**			21	**33.87**
Pedaliaceae	3.25					4	6.45
Scrophulariaceae	9.75	6	12.24	1	8.33	5	8.06
Solanales							
Convolvulaceae	0.81	1	2.04				
Solanaceae	6.50	4	8.61			4	6.45
EUASTERIDS II							
Apiales							
Apiaceae	5.69	6	12.24			1	1.61
Asterales							
Asteraceae	**38.21**	16	**32.65**	5	**41.67**	26	**41.94**
Campanulaceae	6.50	5	10.20			3	4.84

Figure II.4.32.—*Xylocopa flavorufa* (De Geer), female.

ously noted, the greatest polyphagy is exhibited by a few species of *Amegilla* Friese, most notably *Amegilla niveata* (Friese) which was taken from flowers of 18 plant families. This is still well below the degree of polyphagy shown by the honeybee, *Apis mellifera* L., which, in the study area, was recorded from 26 families.

Within the genus *Anthophora* Lateille, the association between the subgenus *Heliophila* Klug and Asteraceae is further supported. Previous flower visiting by *Heliophila* was compared with that of *Pyganthophora* Brooks. It is now possible to add five species of *Paramegilla*, none of which was taken from Asteraceae.

Subfamily Xylocopinae

The Xylocopinae, commonly known as carpenter bees, are divided into four tribes, three of which, Xylocopini, large carpenter bees, and Ceratinini and Allodapini, small carpenter bees, are well represented in sub-Saharan Africa including southern Africa.

Tribe Xylocopini

Within the Xylocopini a single genus, *Xylocopa* Latreille, is currently recognised (Michener 2007). Of this genus, 121 species are recognised for sub-Saharan Africa (Eardley *et al.* 2010) with around 30 species being represented in southern Africa (Eardley & Urban 2010).

Flower visiting

Xylocopa species are polyphagous, with visits of up to 12 families for single species having been recorded.

Nesting

Nest situation

Xylocopa species nest in self-excavated burrows in plant stems, woody, pithy or hollow according to species. Some species such as *X. flavorufa* (De Geer) (Figure II.4.32) and *X. flavicollis* (De Geer) nest in woody stems. The diameter of the stems used is dependent on the size of the bee. For example, burrows of the relatively small *X. flavicollis* can be accommodated in stems of a smaller diameter than those of the large *X. flavorufa*, the carpenter bee frequently found nesting in untreated wood used in buildings. Others such as *X. sicheli* Vachal, *X. hottentota* Smith and *X. caffra* L. (Figure II.4.33) excavate their nests in pithy stems, most often the more robust dry inflorescence stems of aloes. However, we have also found *X. sicheli* nesting in thick dry inflorescence stems of *Berkheya* (Asteraceae) in Nama-

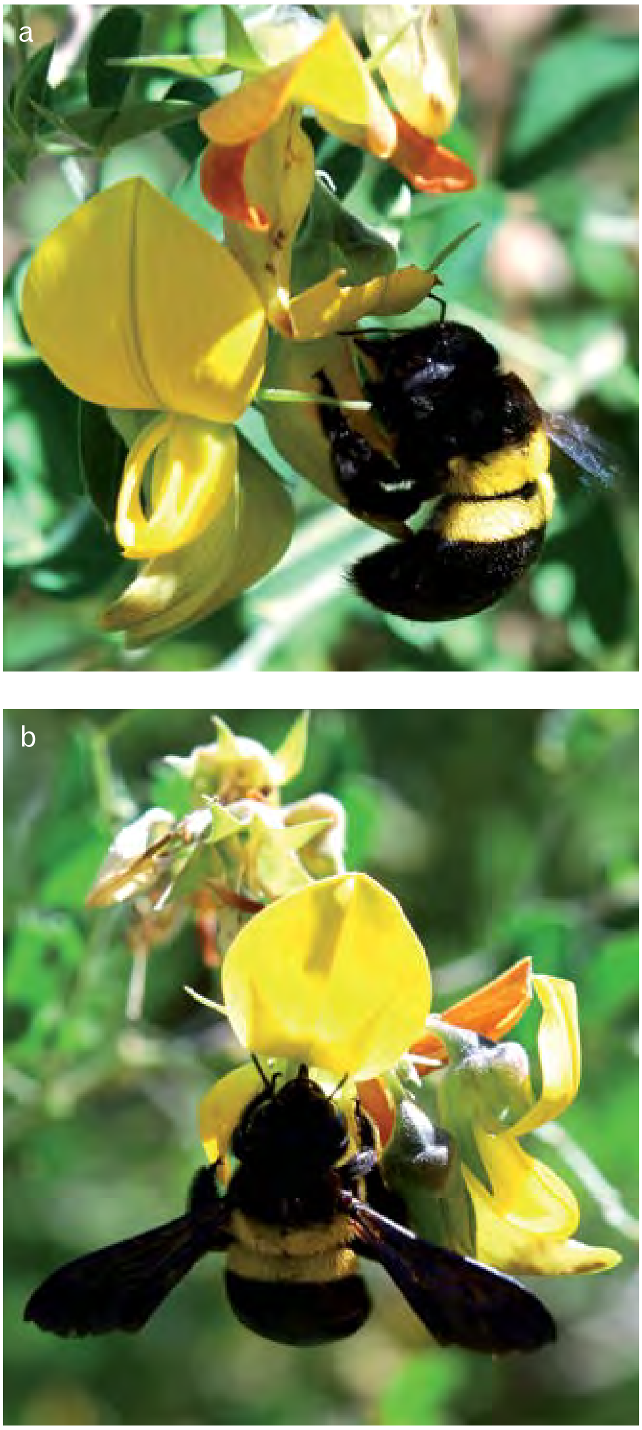
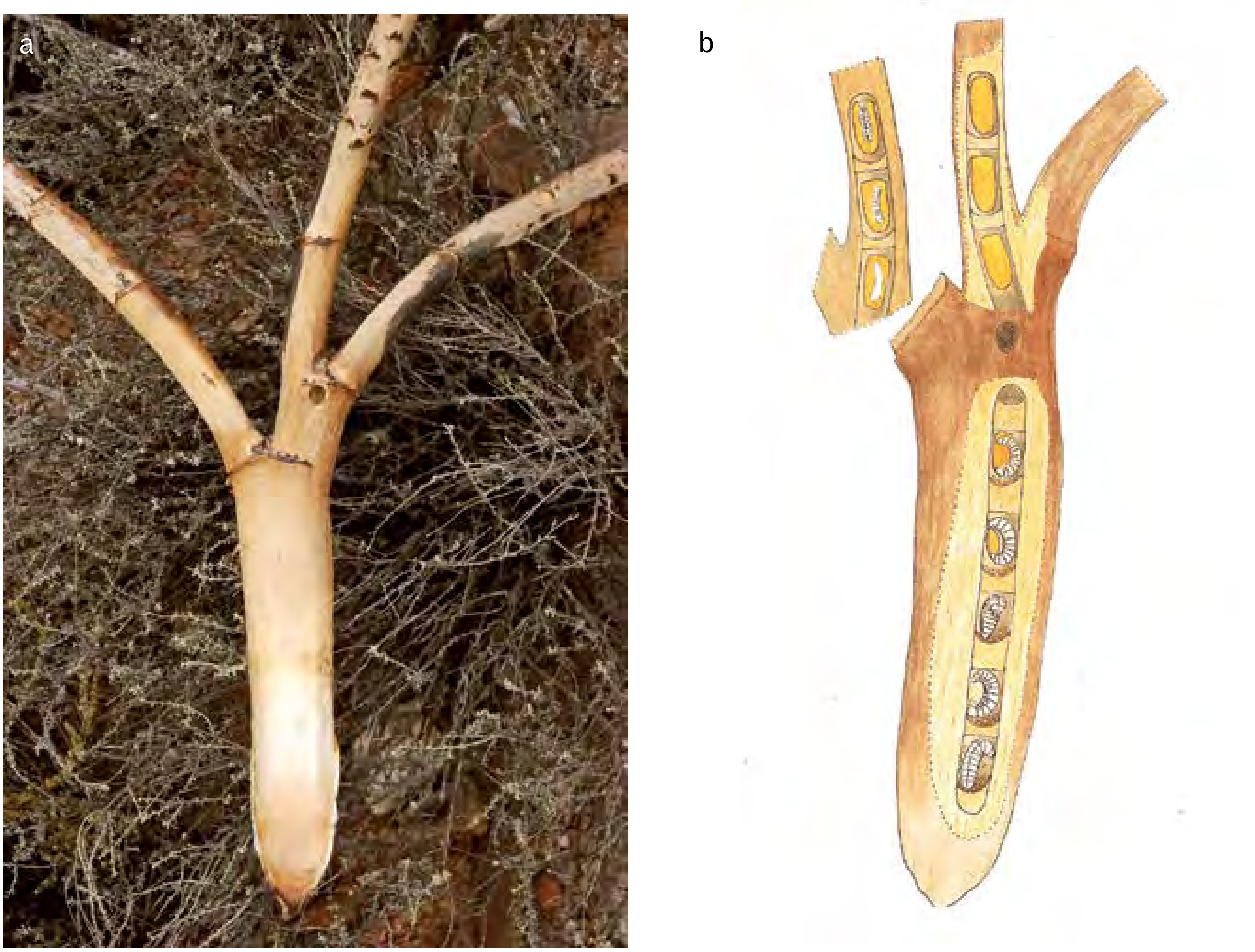


Figure II.4.33.—a. and b. *Xylocopa caffra* (L.), females.



qualand and *X. caffra* on occasion nests in soft wood. *Xylocopa scioensis* Gribodo (formerly *X. caffrariae* Enderlein) nests in hollow stems, such as the culms of reeds.

Nest structure

The burrows of some species such as *X. sicheli* and *X. hottentota* are always unbranched (Figure II.4.34 & 35), whereas those of *X. caffra* nesting in broad aloe inflorescence stems excavate branched burrows with an H-shaped plan. Those, for example *Xylocopa scioensis* Gribodo (formerly *X. caffrariae* Enderlein), nesting in hollow stems, such as reeds, merely cut an entrance hole and clean out the cavity (Figure II.4.36 & 37). Cells are partitioned with material scraped from the burrow walls mixed with 'saliva'.

Oviposition and provisioning

One egg is laid per provisioned cell, the provision being a firm pollen and nectar 'loaf'.

We have collected females of 13 species of *Xylocopa* from flowers from Grahamstown in the southeast, and west and north to the Kunene in the north of Namibia. The impression is that most or all species are polyphagous although some species do show some possible preferences. For example, it seems of note that females of *X. rufitarsis* Lepeletier may show a preference for Papilionoideae. We have collected females from *Aspalathus* and *Lebeckia* species at seven sites in the Olifants River Valley, to the west of the Olifants River Valley, in the Kamiesberg, on the

Figure II.4.34.—a.–c. *Xylocopa sicheli* Vachal nest in dry inflorescence stem of *Aloe ferox* Mill. (Asphodelaceae): a. burrow entrance; b. stem cut longitudinally to show structure of nest, provision and larvae; c. female visiting flower of *Cotyledon campanulata* Marloth.

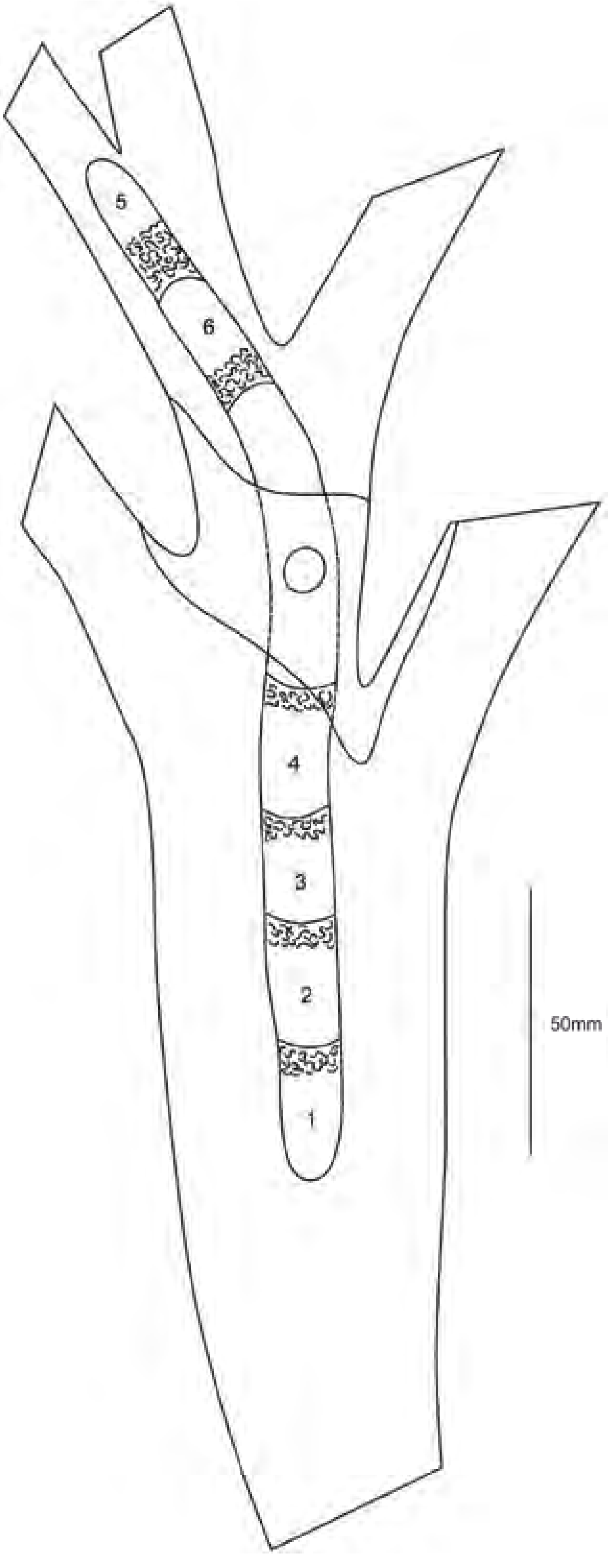


Figure II.4.35.—*Xylocopa sicheli* Vachal nest in dry inflorescence stem of *Aloe ferox* Mill. (Asphodelaceae), diagrammatic plan.

west coast between Port Nolloth and Alexander Bay, and to the east of Alexander Bay in eight years (21 specimens). Charles Jacot Guillarmod collected females from *Calpurnia* species at Mamathes, Lesotho, (seven specimens). Although we also collected females of this species from flowers of Mesembryanthema, Lamiaceae, Malvaceae and Zygophyllaceae, the total number of specimens from these four families was a mere eight.

Figure II.4.36.—a. and b. *Xylocopa scioensis* Gribodo nest in culm of *Phragmites australis* (Cav.) Steud. (Poaceae): a. burrow entrance; b. culm cut longitudinally to show structure of nest, provision and larvae.

Other species seem to find a productive plant at a particular time in a particular summer and show temporary fidelity. For example, on two days at a site near Grahamstown, *Blepharis capensis* (L.f.) Pers. (Acanthaceae) was favoured by females (38 specimens), although we have collected females in small numbers from ten other families.

Life history

Each female makes her own nest and guards her nest until her young emerge.

Unlike most solitary bees and wasps, overwintering is not as fully grown larvae or pupae, but as adults within the natal nest.

Associates

In the Grahamstown area we found that *X. sicheli* was subject to parasitism by *Synhoria hottentota* Péringuey (Meloidae), *Gasteruption robustum* Kieffer (Gasteruptiidae) and *Coelopencyrtus* sp. (Chalcidoidea, Encyrtidae), and *X. scioensis* to parasitism by *G. robustum*.

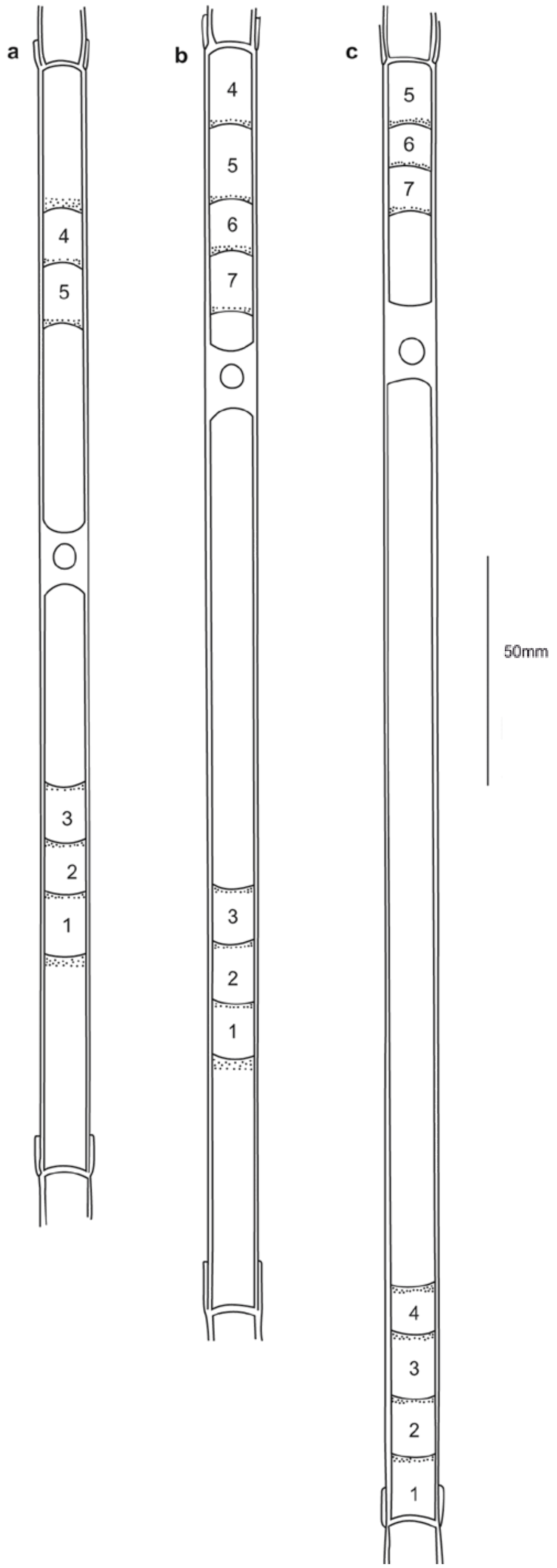


Figure II.4.37.—a.–c. *Xylocopa scioensis* Gribodo three nests in culms of *Phragmites australis* (Cav.) Steud. (Poaceae), diagrammatic plans.

Community of insects associated with *Xylocopa* and *Ceratina* nesting in dry inflorescence stems of *Aloe ferox* Mill. (Asphodelaceae)

Gess (1981) presented a study of insects associated with *Xylocopa* and *Ceratina* nesting in dry inflorescence stems of *Aloe ferox* Mill. (Asphodelaceae). This is summarised in (Figure II.4.38). 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, iv) as in the classification of these insects on the basis of their ethology.

Tribe Ceratinini

Within the Ceratinini, a single genus *Ceratina* Latreille is currently recognised. Of this genus 86 species are listed for sub-Saharan Africa (Eardley *et al.* 2010), with around 40 species being represented in southern Africa (Eardley & Urban 2010).

Flower visiting

Generally, based on our records of flower visits by around 17 species, *Ceratina* species appear to be polyphagous. For example, we collected *C.* (*Ceratina*) *aloes* Cockerell in repeated samples from four plant families, showing no preferences between these families. However, some species appear to exhibit preferences, for example, we collected *C.* (*C.*) *subquadrata* Smith almost exclusively from Asteraceae.

Nesting

Ceratina are plant nesters, excavating burrows in pithy stems.

On the farm Hilton, Eastern Cape, we frequently found two species of *Ceratina*, *C. truncata* Friese and *C. labrosa* Friese, nesting in aloe inflorescence stems together with *Xylocopa*—the former nesting in the narrow branches of the inflorescence and the latter in the broad basal stem and the thicker basal ends of the branches. One male of *C.* (*Pithitis*) *nasalis* Friese was found sheltering in a bored dry stem of *Berkheya decurrens* (Asteraceae) and one female and two males of *C. perpolita* Cockerell were found sheltering in a bored dry inflorescence stem of an unknown *Astroloba* or *Haworthia* species (Asphodelaceae).

An entrance hole is cut and a burrow excavated. The burrows were unbranched.

According to Michener (2007), the cell partitions are made of pith particles, loosely held together without any obvious adhesive. In some species, two or more females sometimes work in the same nest with division of labour.

Associates

Bouček (1974) listed a leucospid, *Micrapion steffani* Bouček, as a nest parasite of *C. truncata* reared by Brauns at Willowmore (voucher specimens in the Ditsong Museum, Pretoria and the Natural History Museum, London).

Tribe Allodapini

The greatest diversity in the Allodapini is in Africa and Madagascar but they do also occur in Asia and Australia.

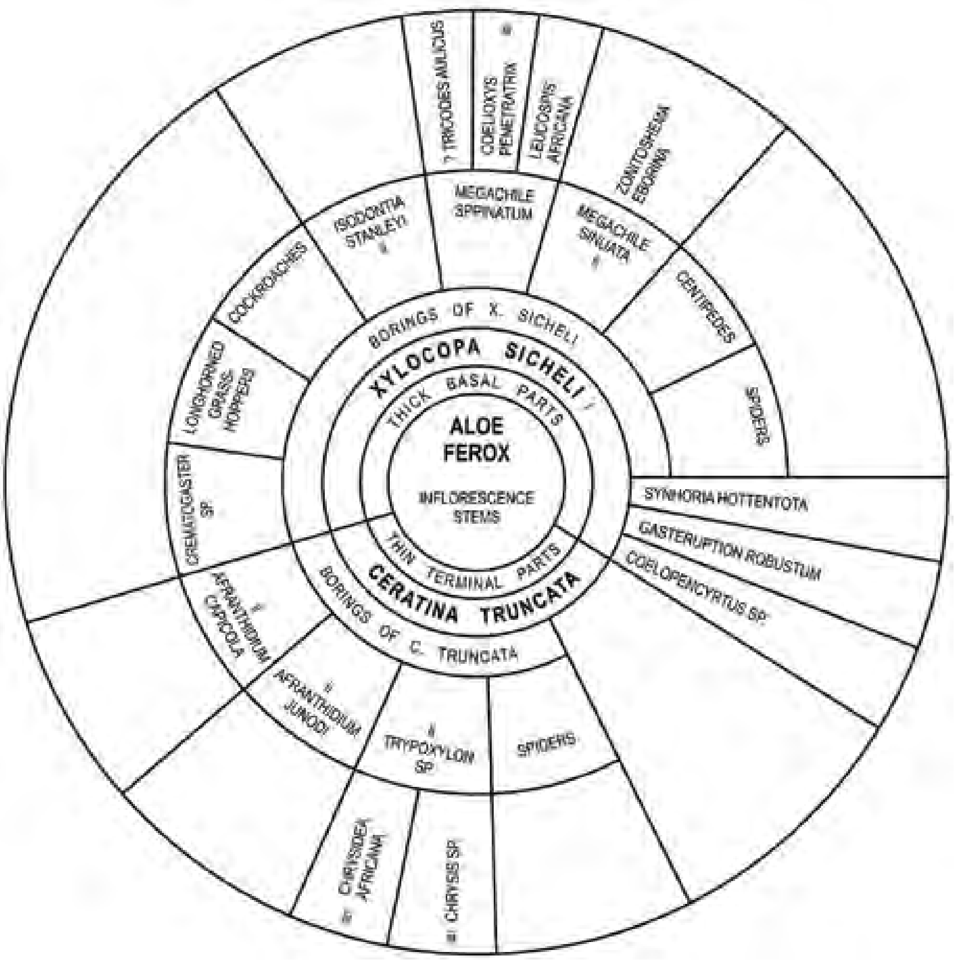


Figure II.4.38.—Diagram showing the community of insects associated with *Xylocopa* and *Ceratina* nesting in dry inflorescence stems of *Aloe ferox* Mill. (Asphodelaceae). With respect to the aculeate wasps and the bees the degree of participation in the construction of their nests is indicated by the numbers (i, ii, iv) as in the classification of these insects on the basis of their ethology.

They are represented in sub-Saharan Africa by seven to nine genera, depending upon the delimitation of the genera (Eardley *et al.* 2010; Eardley & Urban 2010). Most familiar in southern Africa are *Allodape* Lepeletier & Serville (Figure II.4.39) with around 17 of the 35 sub-Saharan species, *Allodapula* Cockerell with all 16 sub-Saharan species, and *Braunsapis* Michener with around 16 of the 40 sub-Saharan species. Three other genera occur within southern Africa namely, *Compsomelissa* Alfken, represented by around five of the nine Afrotropical species, *Macrogalea* Cockerell represented in Namibia by one of the four sub-Saharan species and a southern African endemic, *Nasutapis* Michener, with only one species known.

Figure II.4.39.—*Allodape* sp.

Flower visiting

Allodapini appear to be polyphagous. We recorded flower visits for *Allodape*, *Allodapula*, *Braunsapis* and *Compsomelissa*, about 14 species in all. Two species of *Braunsapis* for which we have numerous records from widely separated sites in the semi-arid to arid areas of Namibia visited flowers of nine and 14 families respectively.

Nesting

Hans Brauns (1926b) and Sydney Skaife (1950, 1953) undertook preliminary studies of nesting by allodapini in southern Africa. Charles Michener of Kansas University, USA, who has made a special study of the tribe, undertook an in-depth investigation of nesting by these bees in southern Africa (Michener 1971). Subsequently Robyn Crewe of the University of the Witwatersrand and his colleagues from Flinders University, Adelaide, Australia, has carried the study forward.

Allodapini nest in pithy or hollow stems or in other cavities such as plant galls or thorns. They are almost unique amongst the bees in having nests without cells. Some species of *Allodape*, *Allodapula* and *Braunsapis* are believed to be parasitic in the nests of other cogeners. The single species of *Nasutapis*, *N. straussorum* Michener, a KwaZulu-Natal endemic, is parasitic in the nests of *Braunsapis facialis* (Gerstaecker).

Allodape Lepeletier & Serville

In a study of 13 African species, nine southern African, Michener (1971) recorded that most nests of *Allodape* contain only one mature adult female although some contain two or more, the supernumerary ones being 'worker-like'.

Eggs are loose, one to several in the bottom of the nest. Each larva receives food individually, and feeding is progressive. Young larvae lie with the eggs at the bottom of the burrow, however, as soon as the larvae are old enough they support themselves, ventral side up, in the burrow by stretching across it, pressing the dorsum of the thorax against one side and the apex of the abdomen against the other. The adult arranges the young from youngest below to oldest above.

In a laboratory study of *Allodape rufogastra* Lepeletier & Serville (Bennett *et al.* 2006), nestmate and nest recognition cues were investigated. Nest owners were found to be able to distinguish between resident and non-resident bees and engaged in significantly more antagonistic interactions with non-residents. Analysis of head extracts suggested that secretions from the head may partially serve as a nestmate recognition cue. Extracts taken from nest collars revealed nest-specific blends of compounds that would facilitate nest identification and discrimination.

A species of *Allodape* described from Uganda, *A. greatheadi* Michener, with a reduced scopa, is presumed to be parasitic in the nests of other species of *Allodape* (Michener 1975, 2007).

Allodapula Cockerell

In a study of nine species of the southern African genus *Allodapula* in southern Africa, Michener (1971) noted that in nests worker-like or supernumerary individuals vary from scarcer than in *Allodape* to present in a fifth of the nests. This is less abundant than in *Braunsapis.*

The eggs are firmly attached by their posterior ends to the walls of the nest burrow, in patterns, often regular and characteristic of species or species groups. At first, the larvae remain in the egg chorion, supported by it.

The larvae in a nest are usually more or less of the same age and are fed progressively from a single, common food mass. When the larvae leave the chorions, they form a group around the food mass. In some species they form a ring around the food mass and support themselves and the food mass by pressing against the nest wall.

When feeding is complete, the larvae arrange themselves longitudinally in the nest burrow with the age sequence noted for *Allodape* and *Braunsapis* lacking.

Allodapula guillarmodi Michener, which has a reduced scopa, is presumed to be a social parasite in the nests of other species (Michener 1975, 2007).

Braunsapis Michener

In a study of 13 African species, nine southern African, Michener (1971) recorded that most species of *Braunsapis* have one or more workers in 35–45% of the nests that contain eggs and/or young.

He noted that the comments on eggs and larvae of *Allodape* are applicable to *Braunsapis* except that in some species the eggs, or some of the eggs, are stuck to the bottom of the nest or the nest wall near the bottom of the nest. As far as he could establish the larva makes no use of this attachment.

Braunsapis vitrea (Vachal) has been found nesting in thorns of *Acacia karroo* in Limpopo (Schwarz *et al.* 2006). This species showed female biased sex allocation in the absence of worker-like behavioural castes.

Some extraterritorial species of *Braunsapis* are known or thought to be social parasites of other species of *Braunsapis* (Michener 2007).

Compsomelissa Alfken

Michener's findings (1971) on the nesting of *Compsomelissa* were based on his studies of one species, *C. stigmoides* (Michener) (as *Exoneurella stigmoides* Michener), in Kenya and as *Halterapis* for two further species, namely *C. angustula* (Cockerell) (as *H. angustula* (Cockerell)) in East Africa and *C. nigrinervis* (Cameron) (as *H. nigrinervis* (Cameron)) in southern and eastern South Africa.

He found no evidence of a worker caste.

He recorded that the eggs are attached by their posterior ends to the nest wall and that the young larvae retain this position by not completely leaving the chorion. Older larvae of *C. stigmoides* seemed to support themselves by pressing against the burrow walls, somewhat as do those of *Allodape* and *Braunsapis.*

He found that food is provided individually and progressively to young larvae of *C. stigmoides* but that a larger larva may get all the food needed for its future development in one mass. However, he found that *C. nigrinervis* practises mass provisioning. After one egg is laid and provision provided, another is laid above it and provisioned.

The sequence of immature stages in the nest burrow of *C. stigmoides* was irregular whereas in nests of *C. nigrinervis* there was a regular sequence from oldest below to youngest above, the reverse of the sequence in other allodapines but the same as that of *Ceratina* and other bees that provision young in series.

Macrogalea Cockerell

Michener's comments (1971) on the nesting of *Macrogalea* are based on the study in East Africa of 35 nests of one species, *Macrogalea candida* (Smith), the distribution of which includes Namibia.

He found inconclusive evidence of supernumerary, probably worker-like, individuals in some nests.

Eggs are attached to the nest walls by their posterior ends. Young larvae remain in the chorion projecting from it. Older larvae support themselves by curling in the burrow in such a way that the hooked dorsal hairs cling to the rough burrow walls.

As no larvae were found with food, it was concluded that they must be fed progressively.

The arrangement of the immature stages in the burrow was irregular.

The nesting of two other of the four African species of *Macrogalea* have been studied, *M. zanzibarica* Michener, which demonstrates social organisation (Tierney *et al.* 2002) and one other species which is a social parasite (Michener 2007; Eardley *et al.* 2010).

Nasutapis Michener

The single species of *Nasutapis*, *N. straussorum* Michener, is a labour parasite. It has greatly reduced mouthparts and lacks a pollen collecting scopa (Michener 1971, 2007).

Michener found *N. straussorum* in 36 nests of *Braunsapis facialis* (Gerstaecker) near Umhali, KwaZulu-Natal.

The age distribution of young suggested that a female enters a host nest and stays there, replacing the host as an egg layer although one or more host females remain and serve as foragers. *Braunsapis facialis* larvae are not destroyed but continue to be reared along with the *N. straussorum* larvae, however, no further *B. facialis* are produced. The mechanism for preventing production of further host young was unclear.

Subfamily Nomadinae

The subfamily is represented in southern Africa by the tribes Nomadini, Epeolini, Ammobatodini and Ammobatini. Nomadini is represented by three of the ten sub-Saharan species of its single widespread genus, *Nomada* Scopoli. Epeolini is represented by ten of the *ca.* 13 sub-Saharan species of the widespread genus *Epeolus* Latreille. Ammobatodini is represented by the single sub-Saharan species *Ammobatoides braunsi* Bischoff, known only from the holotype from Willowmore, Eastern Cape. Ammobatini is represented by the single species of the Old World genus *Ammobates* Latreille, *A. auster* Eardley, in Namibia; ten of the *ca.* 20 sub-Saharan species of the Old World genus *Pasites* Jurine; and the 14 species of the southern African endemic genus *Sphecodopsis* Bischoff (Eardley *et al.* 2010; Eardley & Urban 2010).

The Nomadinae are parasitic in the nests of other bees of several families. Rozen (1991) recorded that the parasitic female enters the open cell of the host whilst its owner is away from the nest. The parasite inserts its egg, unusually small for a bee, into the wall or lining of the cell. The first stage parasite larva emerges after the host has provisioned and closed the cell, when it kills the host larva or egg before feeding on the provision.

Tribe Nomadini

Nomada gigas Friese (as *N. gigantean*) was observed by Hans Brauns (1930) at Willowmore where it was entering nests, situated in the ground, of *Melitta arrogans* (Smith) (as *M. capensis* Friese) (Melittidae).

Tribe Epeolini

Hans Brauns (1903) found two species of *Epeolus*, *E. caffer* Lepeletier (as *E. militaris* Gerstaecker) at Port Elizabeth and *E. friesei* Brauns at Willowmore, both in association with species of *Colletes* (Colletidae) which he believed to be their hosts. These appear to be the only observations for southern Africa. However, his observations are supported by the fact that, as far as is known, all *Epeolus* are nest parasites of *Colletes* species (Michener 2007).

Tribe Ammobatini

In southern Africa, *Pasites histrio* (Gerstaecker) (as *Morgania histrio transvaalensis* Bischoff) is parasitic in the nests of *Tetraloniella minuta* (Friese) (as*Tetraloniella minuta* Friese) (Rozen 1969a).

Sphecodopsis capensis (Friese) (as *Pseudodichroa capensis*) is parasitic in the nests of *Scrapter niger* Lepeletier & Serville (as *Scrapter longula* (Friese)) (Rozen & Michener 1968).

Sphecodopsis fumipes (Bischoff) (as *Pseudodichroa capensis*) is parasitic in the nests of *Scrapter erubescens* (Friese) (as *Scrapter crassula* Cockerell) (Rozen & Michener 1968).

Circumstantial evidence suggests that *Sphecodopsis vespericena* Eardley may be parasitic in the nests of *Scrapter bicolor* Lepeletier & Serville (Eardley & Brothers 1997).

Subfamily Apinae

The Apinae are presently (Michener 2007) understood to include the taxa previously grouped as Apidae together with all but the parasitic genera of what was formerly the family Anthophoridae. The parasitic genera, which previously were included in the Anthophoridae, are now considered to belong in the subfamily Nomadinae.

In southern Africa they are represented by the tribes Ctenoplectrini, Eucerini, Anthophorini, Melectini, Meliponini and Apini with its single genus, *Apis* L., originally restricted to the Old World but now spread worldwide. Nesting by the non-parasitic Apinae ranges from solitary to social, the most developed sociality being demonstrated by the honeybee, *Apis mellifera* L., best known because they are used for commercial honey production and often referred to simply as 'bees'. Honeybees, followed by some species of anthophorines, are the most polylectic of bees and are amongst the important, though not dependable, pollinators. *Thyreus* Panzer represents the parasitic tribe, Melectini, in southern Africa.

Tribe Ctenoplectrini

Ctenoplectrini is a small tribe, Old World in distribution, with two genera, both of which are represented in southern Africa; *Ctenoplectra* Kirby by around four of the seven sub-Saharan species and *Ctenoplectrina* Cockerell by one of the three sub-Saharan species (Michener 2007; Eardley *et al.* 2010; Eardley & Urban 2010).

Ctenoplectra is known to nest in beetle holes in wood and in abandoned mud-and-resin megachilid nests (Rozen 1978). It has been suggested that *Ctenoplectrina* is cleptoparasitic (Eardley *et al.* 2010).

Tribe Eucerini

Eucerini is a relatively large and diverse tribe, mainly New World in distribution. Two genera, *Tetralonia* Spinola with about eight of the 14 sub-Saharan species and *Tetraloniella* Ashmead with about 22 of the *ca.* 33 sub-Saharan species are represented in southern Africa (Eardley *et al.* 2010; Eardley & Urban 2010).

Flower visiting

We collected about 14 species of *Tetraloniella* visiting flowers. Thirteen plant families were represented, with up to six families per species.

Nesting

Nest situation

Jerome Rozen (1969a) gave an account of nesting by *Tetraloniella minuta* (Friese) (as *Tetralonia minuta* Friese) in the Grahamstown area, Eastern Cape, in an area of hard, dry clayey soil, but did not establish the mode of excavation of the nests, noting that turrets were not present and that most lacked a tumulus. Although not suggested by Rozen, it seems likely that the bees were using pre-existing cavities.

In the Eastern Cape, we have found *T. minuta* nesting in old or abandoned burrows of *Bembecinus cinguliger* (Crabronidae, Bembicinae) and *Aethiopicodynerus insignis* (formerly *Parachilus insignis*) (Vespidae, Eumeninae) in non-friable clayey soils (Gess & Gess 1975,1976; Gess 1981).

In addition, we found *Tetraloniella nanula* (Cockerell) nesting in bare soil in Paradise Kloof in the Richtersveld National Park (Figure II.4.40).

Nest structure

In the burrows of *T. minuta* investigated by Rozen, there were numerous cells from both the current generation and previous generations. The cells are lined with a thin, waterproof coating of wax-like material. The wall is probably impregnated with some secretion because it is harder than the surrounding soil. Some cells are arranged in a linear series of two, whereas others are single.

Figure II.4.40.—*Tetraloniella nanula* (Cockerell): nest entrances, one open.

Provisioning and oviposition

The provisions are placed at the bottom end of the cell to a depth of somewhat less than half the cell length. They are of orange-coloured pollen and nectar. In several cells containing eggs, the upper half of the provisions were moist, with the lower part nearly dry.

Life history

The entire cocoon is semi-transparent, brown and parchment-like. The top of the cocoon has a central nipple-like projection.

Associates

Jerome Rozen (1969a) found larvae of an ammobatine bee, *Pasites histrio* (Gerstaecker) (as *Morgania histrio transvaalensis* Bischoff), and meloid and mutillid cocoons in cells.

Tribe Anthophorini

Anthophorini are widespread. They are well represented in southern Africa by the Old World genera *Amegilla* Friese with *ca.* 32 of *ca.* 71 sub-Saharan species and *Anthophora* Latreille with *ca.* 31 of the 55 sub-Saharan species, and also by *Pachymelus* Smith with *ca.* four of the seven species known only from Africa and Madagascar (Eardley *et al.* 2010; Eardley & Urban 2010).

Most *Amegilla* and *Anthophora* excavate burrows in soil either in the ground or in vertical banks, depending on the species. Nesting in aggregations is common. Nest construction differs between species. The cells are furnished with a wax-like lining produced by the combination of liquid triglyceride-rich material secreted by Dufour's gland, situated at the base of the sting, and saliva. The provision is a viscous or liquid mixture of pollen and nectar. There is no cocoon.

Amegilla Friese

Nesting by *Amegilla* in southern Africa is known from three species, *A.* (*Micramegilla*) *atrocincta* (Lepeletier), *A.* (*Micramegilla*) *niveata* (Friese) and *A.* (*Zebramegilla*) *punctifrons* (Walker).

Amegilla (*Ackmonopsis*) *mimadvena* (Cockerell)

Flower visiting

Nothing is known of the nesting of *A.* (*A.*) *mimadvena* (Cockerell) despite the fact that this is a showy bee seen visiting flowers (Figure II.4.41).

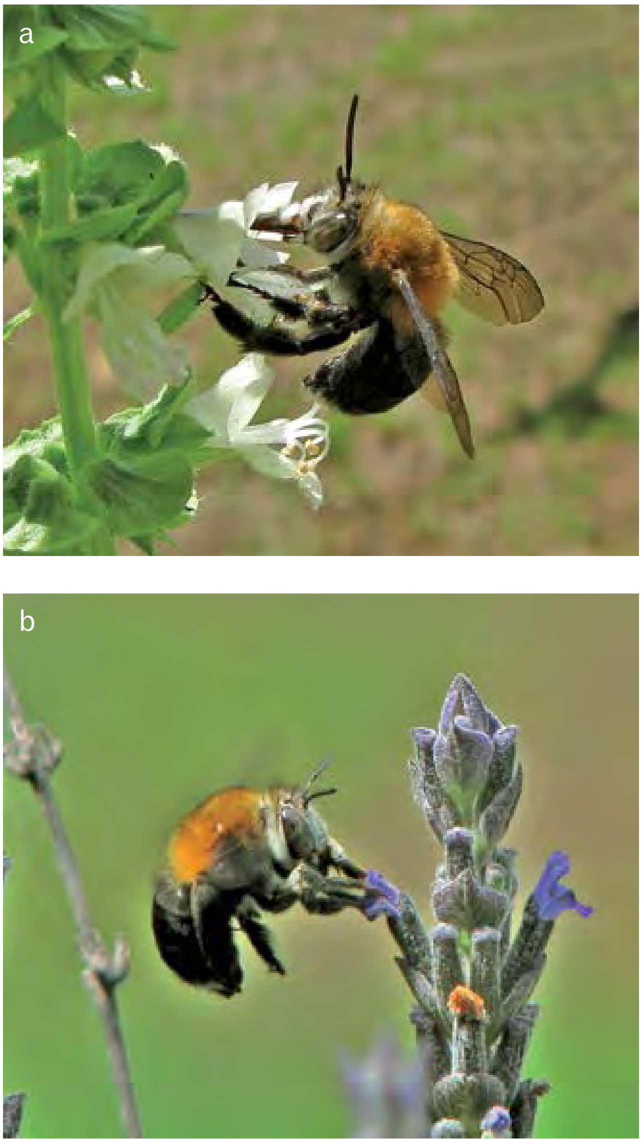


Figure II.4.41.—*Amegilla* (*Ackmonopsis*) *mimadvena* (Cockerell) a. and b. visiting flowers (Lamiaceae).

Amegilla (*Micramegilla*) *atrocincta* (Lepeletier)

Nest situation

Several nesting areas were located, on the farms Hilton and Clifton, west northwest of Grahamstown in the south-eastern extension of the Nama-Karoo (Gess & Gess 1990b, 1996). The nesting sites were in bare areas of clayey soil in low scrub, all in close proximity to water. The surface of the ground was horizontal to sub-horizontal.

Brauns (1913) commented that at Willowmore he found *A. atrocincta* (as *Anthophora plumipes*) nesting in hard level ground, the nest entrance beneath a stone. We have found no nests of this description.

Nest structure

The nests investigated by us consisted of a subterranean burrow surmounted by a cylindrical erect or inclined turret constructed from mud and having an inner diameter of 9 mm and reaching lengths of up to 80 mm. Individual applications of mud are visible on the outside of the turret but the inside is smoothed (Figure II.4.42.b).

Nests investigated were single or two-celled but it is possible that more cells are constructed. The burrow of the two-celled nest bifurcated just below the surface of the ground. The main shaft led directly downwards whereas the second, at first sloped gently, before continuing downwards, parallel to the first shaft. Cells were constructed at a depth of 130–208 mm ($n = 5$). The sides of the cells were parallel and the base rounded. The cells were of the same diameter or marginally greater than that of the shafts (Figure II.4.43). The walls were smooth and lined with white wax. Each cell was closed with a mud and wax plug, somewhat smoothed and concave above. Above each cell plug was a capping of mud, above which a portion of shaft formed a chamber, slightly shorter than a cell. The chamber was filled with mud pellets and was sealed with a mud plate. The shaft above was filled with loose earth and there was an additional mud plate at a variable height along its length. In one nest, a mud plate sealed the shaft at ground level within the turret.

Method of construction of nest

Water is used in the excavation of the burrow, construction of the turret, smoothing of the cell walls and in the construction of the seals. The female, whilst standing on the mud at the edge of the water (Figure II.4.42.a), imbibes water.

Whilst excavating the shaft the female passes the extracted mud back beneath her and, in constructing the turret, positions it using the tip of her gaster.

The wax lining of the cells forms a distinct layer that can readily be separated from the earthen walls. The mud plug is laid down spirally with each load of mud not matching but overlapping. The central aperture is crudely plugged. The lower surface of the plug, including the final closure has a visible coating of wax, probably added with the mud. The upper surface is given a light wax coating. An additional mud capping is added above the stopper and this is bonded with the walls of the shaft above the cell, the plug

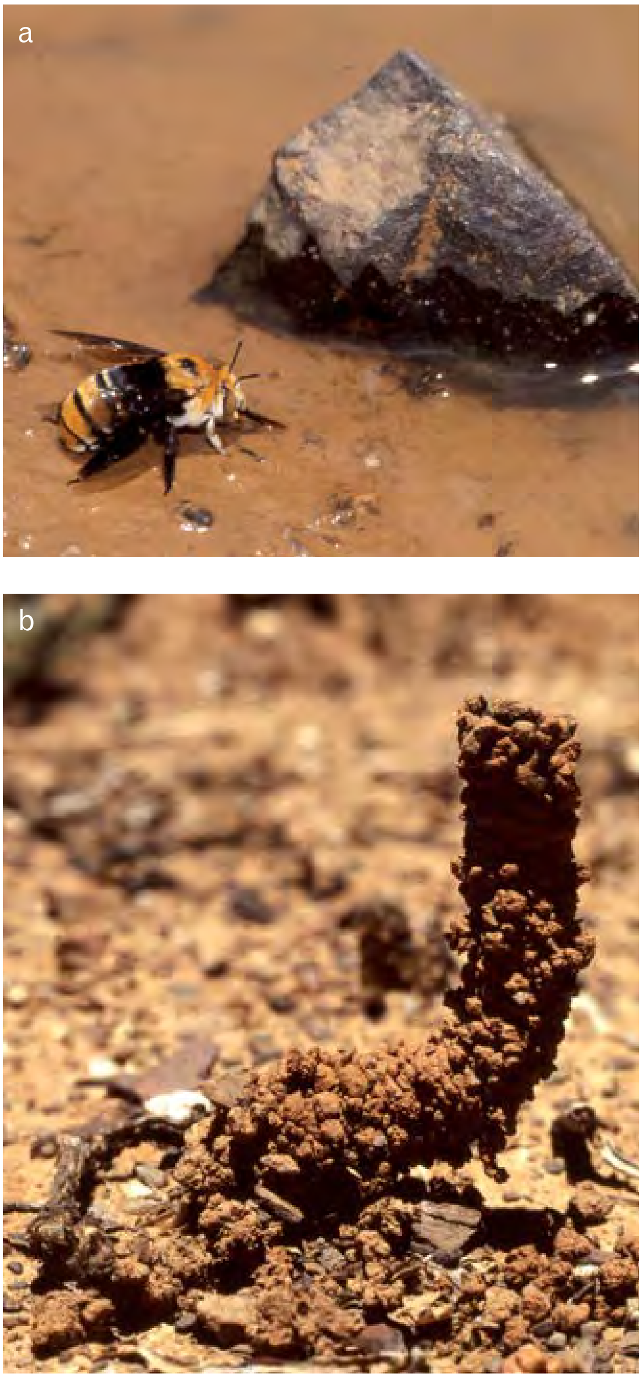


Figure II.4.42—a. and b. *Amegilla* (*Micramegilla*) *atrocincta* (Lepeletier): a. female imbibing water; b. nest entrance turret.

being separated from the shaft walls by the wax lining of the cell.

Provisioning and oviposition

The provision is in the form of a syrup on which the egg or larva floats. Pollen from the cells of two nests on Clifton was examined microscopically. Though mixed, the bulk of the pollen matched that of *Cotyledon campanulata* Marloth (Crassulaceae) whilst this plant was in full flower. However, later in the season, when the flowering of this plant was almost over, an appreciable amount of pollen of *Blepharis capensis* (L.f.) Pers. and *Peristrophe cernua* Nees (both Acanthaceae) was present in the provision.

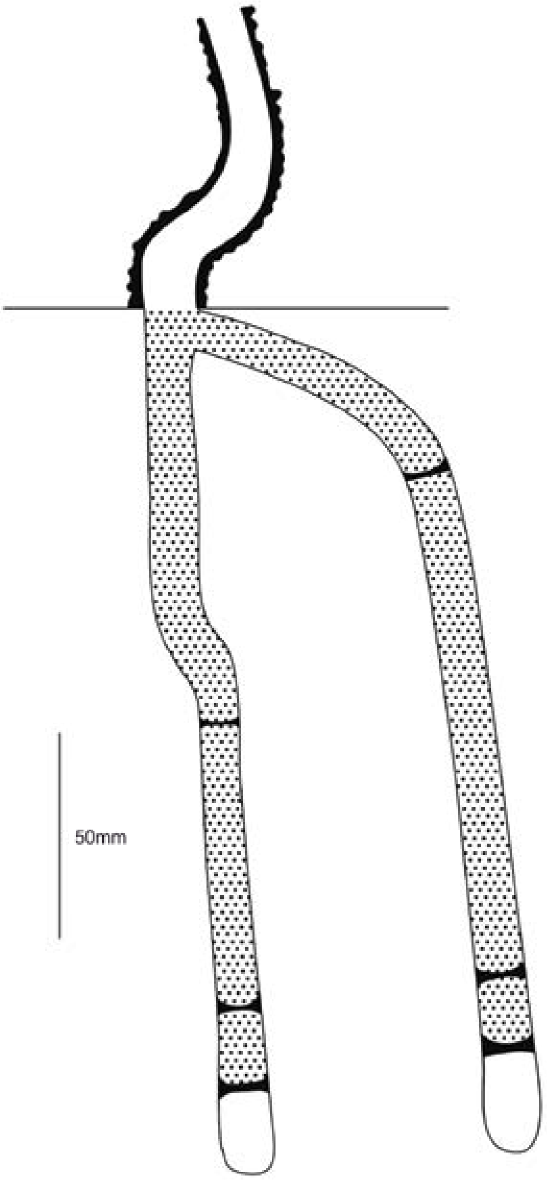


Figure II.4.43.—*Amegilla* (*Micramegilla*) *atrocincta* (Lepeletier): diagrammatic vertical plan of nest.

The cells, when freshly opened, had a marked odour, which could be described as ‘meady’ or ‘cheesy’, probably a combination of odours from the provision and from the ‘wax’.

Sheltering and sleeping

We observed one female sheltering head downwards in her nest. Males and unmated (therefore nestless) females were observed by Brauns (1913) spending the night on low plants, up to 10 bees in a row on a single twig, holding on firmly with their mandibles, and in smaller numbers under stones.

Associates

One nest had been usurped by a megachilid. This nest contained one *A. (M.) atrocincta* cell which had been lined with wax and partly provisioned. The cell and shaft above it had been filled with gravel to a height of 30 mm above the cell. The megachilid had then constructed a petal cell.

In another nest, eight non-phoretic triungulin larvae of a meloid beetle were found in the single sealed cell.

Amegilla (*Micramegilla*) *niveata* (Friese)

Hans Brauns (1913) found *Amegilla* (*Micramegilla*) *niveata* (as *Anthophora niveata* Friese) nesting at Willowmore.

Nest situation

The nests of *A.* (*M.*) *niveata* were excavated by preference in more or less steep slopes rather than in level ground.

Provision

No provision was obtained.

As noted by Hans Brauns (1913), *Amegilla* (*M.*) *niveata* visits all flowering plants. We have collected females of this species widely from the Eastern Cape, west through the Little Karoo and the southern Karoo, and north through the Olifants River Valley, Namaqualand to northern Namibia from flowers of a wide range of plants belonging to 17 families, making it highly polyphagous.

Amegilla (*Zebramegilla*) *punctifrons* (Walker)

Amegilla (*Z.*) *punctifrons* is widespread in sub-Saharan Africa, and apparently occurs throughout the subcontinent, except that it is noticeably absent from the Western and Northern Cape and the southern half of Namibia (Eardley 1994).

Nest situation

Brauns (1913) noted that *A.* (*Z.*) *punctifrons* nests in extensive aggregations in bare level ground in the vicinity of Willowmore. We located two further nesting areas, one in the eastern Nama-Karoo on Clifton and the neighbouring farm Thursford, and the other in the southern Great Karoo at the interface between the Succulent and Nama-Karoo, on the farm Tierberg, near Prince Albert (Gess & Gess 1996). The sites of the nesting aggregations in these areas are bare patches or horizontal to gently sloping clayey ground in karroid scrub with a strong succulent element. In all instances, although there was an abundance of similar bare areas and although the bare areas selected were extensive, the nests were crowded together, new nests being added around the fringes of the aggregations.

Nest structure

Access to all nests was direct. In no instance was there any form of entrance turret. Three nests on Tierberg were investigated. The shaft, 6–6.5 mm in diameter, in all three nests initially sloped gently downwards before continuing sub-vertically at a constant diameter to a depth of 95–105 mm below which it ended in one to three sub-vertical to sloping cells in linear series. In two nests, there were secondary shafts in addition to the main shaft, in one a single secondary shaft and in the other two. The secondary shafts in turn end in a linear series of cells (Figure II.4.44). Between the last cell in a series and the opening to the next excavated shaft, the shaft had been filled with earth and sealed off with a mud plate. The walls of the cells were cemented and smoothed, and coated with wax. Each was 10 mm long and 7–7.5 mm in diameter at mid-length.

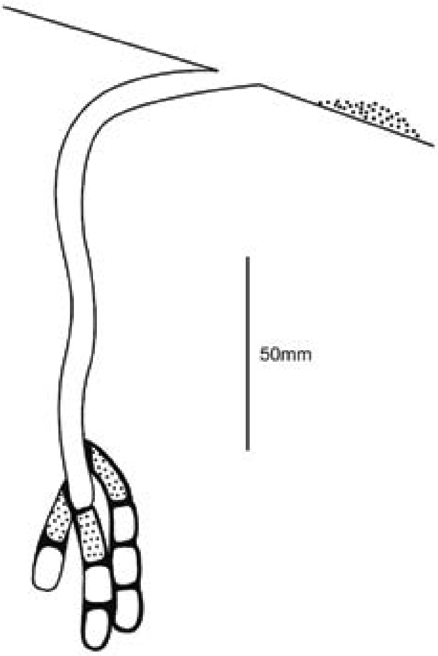


Figure II.4.44.—*Amegilla* (*Zebramegilla*) *punctifrons* (Walker): diagrammatic vertical plan of nest.

Method of construction of nest

Water is not used in the excavation of nests. Soil is extracted using the mandibles, the bee continuously turning on its long axis. The spoils of excavation are raked out of the nest and accumulate to one side of the nest entrance. The entrance to a well-established nest is concealed with loose earth through which the bee digs when entering. In densely populated aggregations, there are no distinct tumuli, the entire surface of the compacted clayey soil becoming covered with destructured soil.

Provisioning and oviposition

The provision from the cells of the nests investigated was a very wet mixture of pollen and nectar. Pollen examined microscopically was of two types.

In the vicinity of the nesting area on the farm Clifton, females were collected from flowers of *Blepharis capensis* (L.f.) Pers. (Acanthaceae) during two summers (16 specimens). Interestingly, a female was collected from *Blepharis obmitrata* C.B.Clarke in northwestern Namibia. It is unknown whether the flowers were being visited for nectar only or for both nectar and pollen.

Sheltering and sleeping

Brauns (1913) noted that he found sleeping clusters of up to 30 males and females mixed on low bushes, the bees being firmly clamped on by means of their mandibles. More rarely, males were found sheltering together with males of *Amegilla* (*Micramegilla*) *niveata* (Friese) (as *Anthophora niveata*) in hollow stems lying on the ground and in dry, open seed capsules of *Datura*. Actively nesting females appeared to retire to their nests at night.

Associates

During the nesting season, we repeatedly observed female *Thyreus* in attendance at and digging through nest closures of *A. (Z.) punctifrons* on Thursford and Clifton suggesting a parasitic association. A sample of eight consisted of seven *Thyreus alfkeni* (Brauns) and one *Thyreus delumbatus* (Vachal). Brauns (1913, 1930) recorded that *Thyreus delumbatus* (as *Crocisa braunsiana* Friese) was present in large numbers in association with nesting aggregations of *A. (Z.) punctifrons* (Walker) (as *Anthophora circulata*) at Willowmore.

A single female mutillid was observed digging through the loose earth closure of a nest on Thursford suggesting a parasitic association.

Amegilla (*Zebramegilla*) *obscuriceps* (Friese)

Amegilla (*Zebramegilla*) *obscuriceps* is apparently endemic to southern Africa. It is widespread in South Africa and has been recorded from the eastern Highlands of Zimbabwe (Eardley 1994).

A female *A.* (*Z.*) *obscuriceps* was found nesting in the vertical wall of a ruined building in Bowesdorp, near Kamieskroon, Namaqualand (Gess & Gess fieldnotes 1997 and voucher specimens), suggesting that not all species of the subgenus *Zebramegilla* nest in horizontal to sloping ground.

Anthophora Latreille

Nesting by *Anthophora* in southern Africa is known from three species of *Anthophora* (*Heliophila*), *A.* (*H.*) *praecox* Friese, *A.* (*H.*) *rufolanata* Dours and *A.* (*H.*) *vestita* Smith, one species of *Anthophora* (*Paramegilla*), *A.* (*P.*) *epichariformis* Gribodo, and three species of *Anthophora* (*Pyganthophora*), *A.* (*P.*) *braunsiana* Friese, *A.* (*P.*) *diversipes* Friese and *A.* (*P.*) *krugeri* Eardley.

Anthophora (*Heliophila*) *praecox* Friese

Anthophora (*Heliophila*) *praecox* has been recorded from the Western and Eastern Cape, the Orange Free State and Lesotho (Eardley & Brooks 1989). Hans Brauns (1913) found nests of this species at Willowmore and we have found nests on Hilton, on Tierberg and at Bowesdorp (Gess & Gess 1996; Gess & Gess field notes and voucher specimens, Hilton 1977, 1978, Tierberg 1987 and Bowesdorp 1998).

Nest situation

The nests on Hilton were in a water-cut vertical bank, those on Tierberg in a water-cut vertical bank and the mud wall of a building, and those at Bowesdorp and at Willowmore in the walls of buildings. Nests are crowded together in aggregations.

Nest structure

The nest is a single to multicellular burrow, in some cases with at least two cells in linear series. Access to the burrow is by a simple entrance hole without any form of entrance turret. The cells are smoothed on the inside, lined with a varnish-like substance, and closed with a mud seal coated on both surfaces with the same substance.

Method of nest construction

It was not clear whether the burrows were self-excavated or pre-existing. Those on Hilton were in reddish ‘sandstone’ and the cells had been lined with mud, clearly introduced into the nest, suggesting that the burrows might have been pre-existing. In those on Tierberg, no such difference in the substrate and the cell lining was apparent.

The burrows in an erosion gulley on Tierberg were crowded together and apparently interlinked, sharing more than one entrance and a single entrance being used by more than one female, suggesting nest sharing.

Oviposition and provisioning

Pollen from provision taken from a nest cell from Tierberg was examined microscopically and found to be from Asteraceae. Comparison with pollen from the nesting area suggested that the pollen was derived from *Pteronia incana* (Thunb.) Kuntze (Asteraceae).

We collected females of this species from Asteraceae, *Berkheya* species at two sites in the Eastern Cape and in the Western Cape to the east of Ceres and in the Olifants River Valley.

An egg, curved, white and 3.5 mm long from tip to tip, in a nest on Hilton had been laid onto the vertical surface of the provision. It was attached at the upper end, the rest of the egg hanging free from the provision.

Associates

Thyreus calceatus (Vachal) was commonly in attendance at nests on Hilton.

Remains of a mutillid and a chrysidid were obtained from nests on Tierberg.

Anthophora (*Heliophila*) *rufolanata* Dours

Nest situation

Jerome Rozen (1969b) found and investigated several nests of *A.* (*H.*) *rufolanata* (as *Anthophora krebsi* Friese) in a hard earth roadside bank near Avontuur in the Langkloof, Western Cape. We found nests in the ‘sandstone’ bank on Hilton, and in a vertical sandbank at Klein Alexandershoek, to the west of Clanwilliam (Gess & Gess field notes and voucher specimens of females from nests, Hilton 1977 and Klein Alexandershoek 1987).

Nest structure

The nest burrows entered the banks at right angles to the vertical surface and then immediately descended until they changed angle to run horizontal and end in cells. The cells are lined, the lining about 1 mm thick and, when hardened, permitting the cells to be removed intact. The cells are then furnished with an inner wax lining. The cell closure apparently lacked a wax lining.

Provisioning and oviposition

The provision was moist and yellow, in one cell being nearly liquid and smelling of sour milk.

Associates

Jerome Rozen (1969b), captured an adult cuckoo bee, *Coelioxys* (*Liothyrapis*) *lativentris* Friese (Megachilinae) that was inspecting burrows of *A.* (*H.*) *rufolanata*.

Anthophora (*Heliophila*) *vestita* Smith

Anthophora (*Heliophila*) *vestita* was found nesting at Willowmore by Hans Brauns (1913).

Nest situation

The nests of *A.* (*H.*) *vestita* at Willowmore were in the mud brick walls of houses and outbuildings.

Associates

Hans Brauns (1913) observed and recorded a melectine bee, *Thyreus albomaculatus* (De Geer) (as *Crocisa valvata* Brauns), as a nest parasite of *A.* (*H.*) *vestita*.

Anthophora (*Paramegilla*) *epichariformis* Gribodo

Anthophora (*Paramegilla*) *epichariformis* has been recorded from the southwestern Western Cape (Eardley & Brooks 1989) and somewhat to the east on Tierberg where it was nesting in the riverbank (Gess & Gess 1996).

Nest situation

One nest was located on Tierberg. It was situated near the base of a high, sub-vertical, south-facing bank of the Tierberg River beneath an overhang. The riverbank is of a grey, poorly sorted, modern alluvium.

Nest structure

The nest consisted of a burrow, which had been excavated into the riverbank. There was no entrance turret. The shaft penetrated horizontally for 20 mm and then turned at right angles to run sub-vertically downwards, more or less parallel to the surface of the bank, to a depth of 100 mm, terminating in three cells in linear series, each sealed with mud. The walls of the cells were cemented and sealed with a waxy coating.

Method of construction

Water did not appear to have been used for the excavation of the burrow. The nature of the bonding agent used for cementing the walls and seals of the cells was not identified.

Provisioning and oviposition

The provision is moist and has a strong odour. The pollen, examined microscopically, was found to be from Asteraceae. It was compared with pollen from plants in the nesting area and was found to match that from a species of *Pteronia.*

The egg, laid onto the surface of the provision, is curved, yellow and 4.5 mm from tip to tip.

Anthophora (*Pyganthophora*) *braunsiana* Friese

Nest situation

Two nesting aggregations of *A.* (*P.*) *braunsiana* have been recorded. Jerome Rozen (1969b) found an aggregation of 30 nests on a termite mound in the vicinity of Avontuur, in the Langkloof, Western Cape and Alan Weaving found an aggregation in a road in the Mountain Zebra Park in the Eastern Cape (voucher specimens 1988, two females from nests, in the Albany Museum) (Figure II.4.45). Nests were investigated by Jerome Rozen.

Nest structure

All active burrows were open and had neither tumuli nor turrets. In constructing burrows, females had used existing cavities where they occurred, had walled off passage-

ways to active termite galleries and had excavated holes between galleries.

Typically, the cells were clustered at the end of the burrow in several linear series as many as four cells in a row. Cells in a series were sometimes arranged at an angle, one against another.

Method of construction

The female excavates a cavity for a cell, and then by cementing together fine pieces of termite carton, it constructs a hard cell wall approximately 1–2 mm thick. If the cavity is too large for the cell, the excess space is first filled with fine uncemented carton, which is then cemented over.

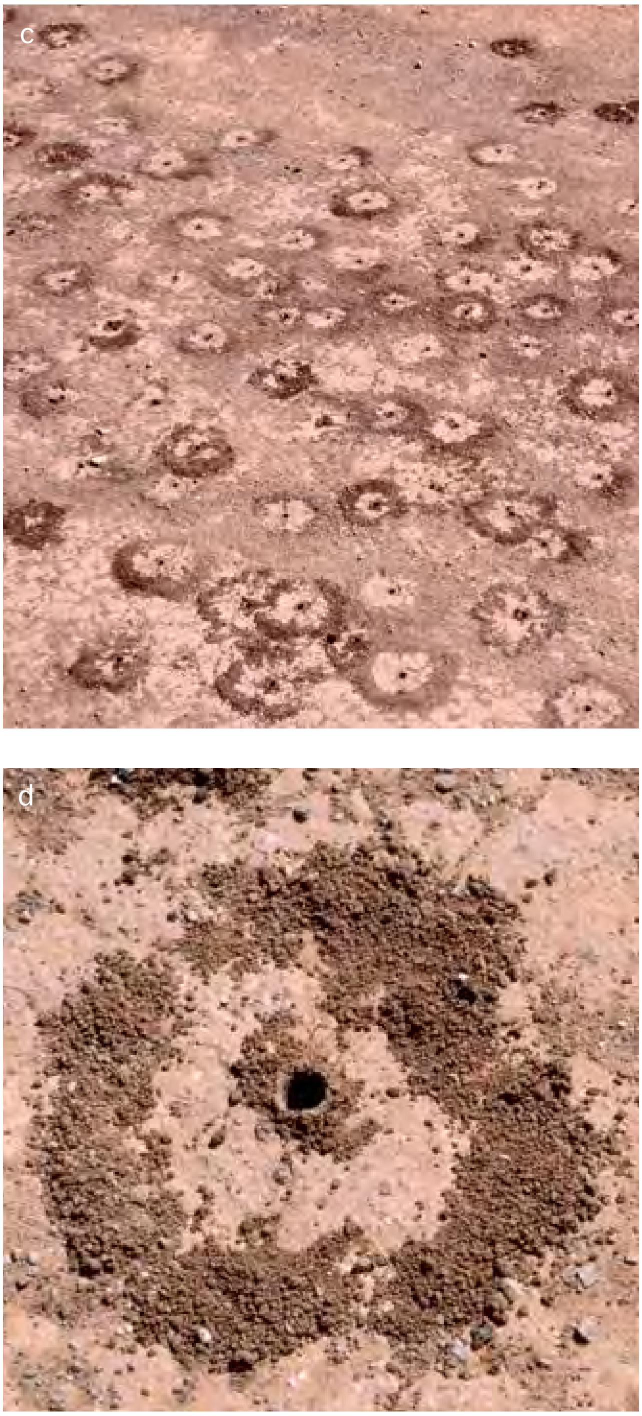


Figure II.4.45.—a.–d. *Anthophora* (*Pyganthophora*) *braunsiana* Friese: a. female at rest; b. female at nest entrance; c. nest aggregation; d. nest entrance.

The wall is lined all over with a thick, waterproof coating of wax. The inside of the cell cap is concave, lined with wax, and smooth except for a central dimple. The outer surface is nearly flat and smooth.

Provisioning and oviposition

The provision is a moist, homogeneous paste, deposited near the rear of the cell. Even incomplete provision masses have a sour milk smell.

The egg is deposited on top of the food mass.

Life history

The larva does not begin to defecate until sometime after it has consumed the provisions. Faeces are applied over the entire cell wall. No cocoon is spun.

Associates

Larvae and eggs of *Thyreus lieftincki* Rozen (Melectini) were the most common nest associates encountered.

A meloid larva and a mutillid cocoon were also discovered, and mites occurred in many cells.

Anthophora (*Pyganthophora*) *diversipes* Friese

Nest situation

We found a nesting aggregation of *A.* (*P.*) *diversipes* near Leliefontein, Kamiesberg, in a clearing in Renosterveld (Gess & Gess field notes 1992 and voucher specimens, one female, one male and four turrets). The bees were busy constructing and provisioning nests in an active termite nest (Figure II.4.46) that had been invaded by ants.

Nest structure

The nest is a multicellular burrow surmounted by a short, slightly flared, mud turret, showing no smoothing of the applied mud (Figure II.4.46.b). The burrow is tortuous and the cells lined with white 'wax', the lining 0.2 mm thick.

Method of construction

It is clear that water is required for the excavation of the nests and that the turrets are constructed from mud extracted from the burrow, the pygidium being used for positioning the mud.

Provision

The cells, when freshly opened, had a marked odour similar to that of the provision of *Amegilla atrocincta*, which we described as 'meady' or 'cheesy', probably a combination of odours from the provision and from the 'wax'.

Pollen from the provision was examined microscopically and was found to be of at least two types, both smooth walled.

Figure II.4.46.—a. and b. *Anthophora* (*Pyganthophora*) *diversipes* Friese: a. nest aggregation on termite heap; b. three nest entrance turrets.

The origin of the pollen was not established. However, in the nesting area at the time that nests were investigated, females were collected from flowers. Four females were collected from flowers of *Herrea* sp. (Mesembryanthema) and two from flowers of *Zygophyllum divaricatum* Eckl. & Zeyh. (Zygophyllaceae), both with smooth walled pollen.

In subsequent years, three females were collected from flowers of *Hermannia disermifolia* Jacq. (Malvaceae, including Sterculiaceae) at a lower level in the Kamiesberg; three from flowers of *Tetragonia* sp. (non-Mesembryanthema) and one from flowers of *Lobostemon* sp. (Boraginaceae) at Clanwilliam; and one from flowers of *Lobostemon trichotomus* DC. (Boraginaceae) to the west of Clanwilliam.

Anthophora (*Pyganthophora*) *krugeri* Eardley

Nest situation

We found *Anthophora* (*P.*) *krugeri* nesting in a vertical water-cut earth bank in Goegap Nature Reserve, near Springbok (Gess & Gess field notes 1994 and voucher specimens, two females from nests) and in the wall of a ruined building near Leliefontein, Kamiesberg (Gess & Gess field notes 1995 and voucher specimens, four females from nests).

Provison

No provision was obtained from nests from either site.

On the same day we observed the nests in Goegap, we collected four females from flowers of *Herrea* sp. (Mesembryanthema) and four females from flowers of *Hermannia disermifolia* Jacq. (Malvaceae, including Sterculiaceae). At the same site in following years, we collected four females from flowers of *Herrea* and two from *Hermannia disermifolia*. Further females were collected from flowers of *Hermannia* spp. west of Clanwilliam and near Ladismith, Little Karoo. It is not known whether the visits were for nectar or pollen.

On the same day we observed the nest in the Leliefontein nesting area, we collected three females from flowers of *Anchusa capensis* Thunb. (Boraginaceae). In a previous year in the same area, we collected two females from flowers of *Herrea* sp. and one female from flowers of *Zygophyllum divaricatum* Eckl. & Zeyh. (Zygophyllaceae). It is not known whether the visits were for nectar or pollen.

Tribe Melectini

All Melectini are nest parasites of other Anthophorini. In southern Africa, the tribe is represented by about 22 species of around 39 sub-Saharan species of *Thyreus* Panzer (Eardley *et al.* 2010; Eardley & Urban 2010).

Females of Melectini break into closed cells of their hosts, oviposit on the cell closure or upper cell wall and reclose the cells with moistened earth (Michener 2007).

Jerome Rozen (1969b) described *Thyreus lieftincki* Rozen from near Avontuur in the Langkloof, where he found it parasitising nests of *Anthophora* (*Pyganthophora*) *braunsiana* Friese. *Thyreus lieftincki* was found to insert her eggs through a small hole in the cell cap. As many as five eggs were found in a cell. On hatching, the larva kills its sibling and the host eggs or possibly the host's larva. It then feeds on the provision. The mature larva does not spin a cocoon.

Near Grahamstown, we observed both *Thyreus alfkeni* (Brauns) and *T. delumbatus* (Vachal) digging through nest closures of *Amegilla* (*Zebramegilla*) *punctifrons* (Walker), and *T. calceatus* (Vachal) in attendance at nests of *Anthophora* (*Heliophila*) *praecox* Friese.

At Willowmore Hans Brauns (1913, 1930) similarly recorded *T. delumbatus* (as *Crocisa braunsiana* Friese) (Figure II.4.47) associated with *A. (Z.) punctifrons* (as *Anthophora circulata* (Fabricius)).

Hans Brauns (1913) observed and recorded *Thyreus albomaculatus* (De Geer) (as *Crocisa valvata* Brauns) as a nest parasite of *Anthophora* (*Heliophila*) *vestita* Smith, nesting in mud walls at Willowmore.

Tribe Meliponini

The Meliponini are the stingless honeybees. They are found in tropical and sub-tropical areas throughout the world. In southern Africa, they are therefore restricted to the more northerly areas where they are represented by the four essentially African genera. These genera are *Cleptotrigona* Moure with a single species, *Hypotrigona* Cockerell with two of the four species, *Liotrigona* Moure with both species, *Meliponula* Cockerell with two of the 12 species and *Plebeina* Moure with a single species (Eardley *et al.* 2010; Eardley & Urban 2010).

Flower visiting

In their flower visiting Meliponini are highly polyphagous. *Meliponula* (*Meliplebeia*) *beccarii* Friese is a common visitor to *Tribulus* (Zygophyllaceae), a pioneer plant on overgrazed land in northwestern Namibia (Figure II.4.48).

Nesting

Meliponini are the only highly social bees other than the true honeybees, Apini. They form colonies of a few dozen to 100 000 workers or more. The nests of most species are in pre-existing cavities. They are made from wax secreted from the metasomal terga mixed with resins and gums collected by the bees (Figure II.4.49). Some species add other materials such as mud or faeces.

The brood cells are either clustered or arranged in combs that are usually horizontal, the cells opening upwards. The egg is positioned standing up on the semi-liquid provision. The cells are surrounded by food storage pots, quite different from and larger than the cells (Michener 2007).

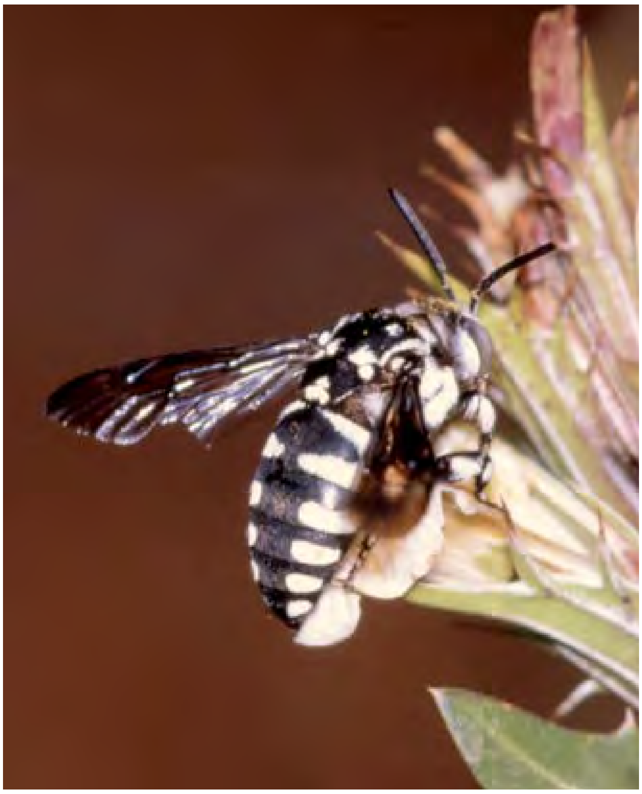


Figure II.4.47.—*Thyreus delumbatus* (Vachal), female.

Figure II.4.48.—*Meliponula* (*Meliplebeia*) *beccarii* Friese visiting flower of *Tribulus* sp. (Zygophyllaceae).

Figure II.4.49.—Wax nest entrance of meliponine with workers.

Meliponiculture is uncommon in Africa where the honey harvesting is mostly destructive whereas in South America meliponiculture is extensively practised (Eardley 2004).

Tribe Apini

The Apini, with a single Old World genus *Apis*, are the true honeybees. Of the two African species only *Apis mellifera* L. occurs in southern Africa (Eardley *et al.* 2010) (Figure II.4.50). *Apis* has been spread throughout the world for honey production and for rendering pollination services, however, in the southern hemisphere it is only in Africa that its original range extended into the south temperate zone.

Flower visiting

In its flower visiting, *Apis mellifera* is highly polyphagous.

Nesting

The familiar wax combs of honeybees are constructed either in exposed situations, for example, on trees or vertical banks, or in pre-existing cavities, for example in rock crevices, in trees and less commonly in the ground. The cells are variously used as brood cells or for storage of honey or pollen. Brood cells for the production of workers and males form part of the comb but queen-producing cells are constructed separately and are not hexagonal in shape.

Figure II.4.50.—a. and b. *Apis mellifera* L.: a. with empty corbiculum; b. with loaded corbiculum.

Randall Hepburn and Sarah Radloff (Hepburn & Radloff 1998) give a review of the knowledge of honeybees in Africa.

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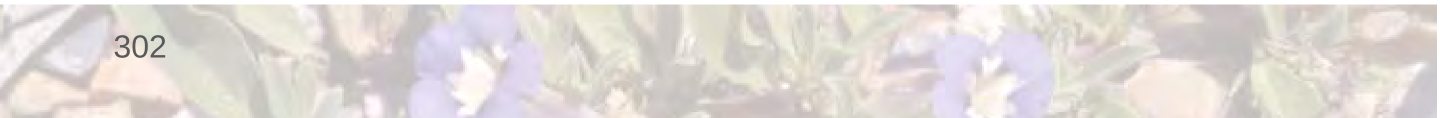

APPENDIX:

Some references to literature useful for identifying southern African aculeate wasps and bees.

CHRYSIDOIDEA

Chrysididae

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VESPOIDEA

Vespidae: Masarinae

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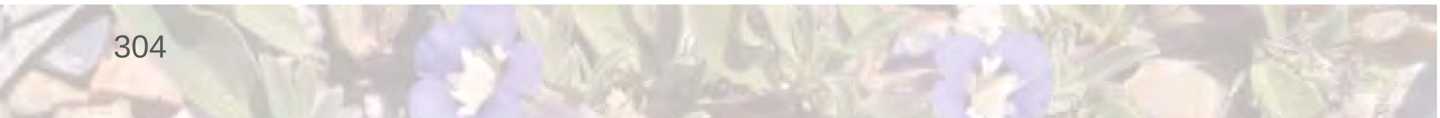

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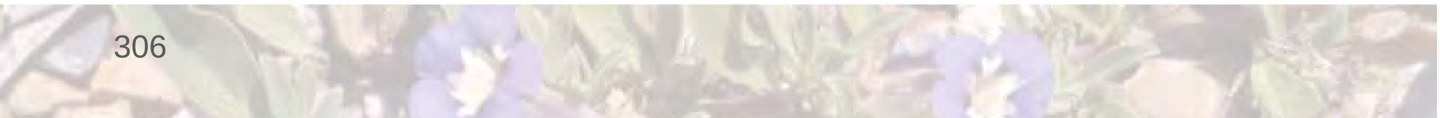

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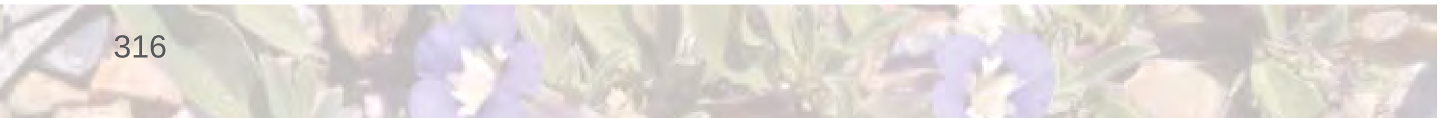

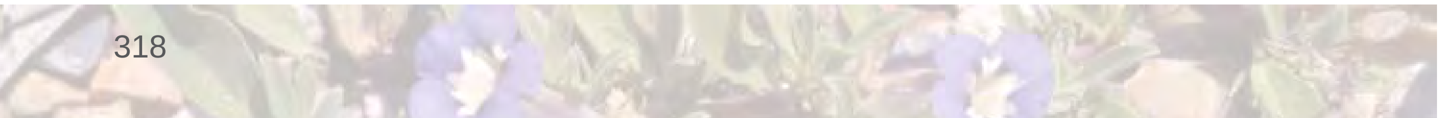

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In order to maintain essential populations of organisms, be they plant or animal, it is necessary to have an understanding of their requirements. In this work, the authors have compiled all that is known for southern Africa of the biology of wasps and bees, important pollinators and predators, and have shown how agricultural land use and coastal development impact on the diversity of wasps and bees. The principal focus is the semi-arid to arid areas—the authors' main study areas over the past 40 years. The work is intended for all who are interested in natural history, conservation and farming, and as a starting point for further observations and research.

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United States of America
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